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Faculty of Environmental and Life Sciences

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Enhancing Wild-Felid Conservation by Resolving Biases in Population-Density Estimation and Evaluating Human Perceptions of Felids

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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Big cat populations are threatened worldwide by poaching for illegal trade of their body parts, habitat loss and degradation, and negative interactions with humans. Ensuring healthy populations in the wild and peaceful coexistence with humans has become a cornerstone of wild felid conservation. Towards this end, knowledge of population abundances is a prerequisite for the judicious implementation of management strategies. Camera trapping is now the standard and globally ubiquitous method of population estimation of big cats. However, estimates from camera-trap studies are often biased by opportunistic sampling that deploys traps where they are most easily placed and will catch most animals, often on trails. This non-random sampling with respect to habitat tends to produce a male bias in captures, due to male-avoidance behaviours by the smaller females and their cubs. Resulting biases in population estimation often undermine the resources, time and effort involved in the camera-trap studies. This thesis aims to resolve biases in density estimates of big cats derived from camera trap studies by evaluation of alternative deployment protocols for unbiased camera trapping, and to evaluate social perceptions of wild felids in Bhutan as a first step towards enhancing positive interactions of human with wild felids.

Chapter 2 evaluates bias in conventional camera trapping by comparing density estimates of individually identifiable big cats between trail-based and random deployments across 400 km^2 of montane forest in Bhutan. Three camera traps were deployed in each of 100 2x2-km grid cells: one pair on a trail, and one in the exact centre of the cell (making it random with respect to habitat). Each deployment caught some individuals not caught in the other, with the trail deployment catching males of most species much more frequently than females. The random deployment tended to catch fewer total individuals but more females, leading to higher total density estimates and wider confidence intervals. Given the potential for the trail-based deployment to produce precisely wrong estimates from its larger sample and male bias,

and the logistical difficulties inherent to random deployment combined with its risk of catching too few individuals for estimation, the overall recommendation is for a mixed deployment.

Chapter 3 compares population density estimates between Spatially Explicit Capture-Recapture (SECR) models and Random Encounter Models (REM) for individually identifiable spotted cats, and assesses the density of Asiatic golden cats, which are not individually identifiable, with REM for different combination of random and trail-based deployments. It applies REM field protocols and analytical methods and compares them with the most robust density estimates derived from SECR in chapter 2. The chapter evaluates the sensitivity of REM density estimates to the accuracy of REM input parameter measurements. It compares the precision in density estimates from REM and SECR by computing their coefficients of variation. The chapter further evaluates the influence on REM density estimates of adding in trail cameras, comparing outcomes with the density estimates from the random-only deployment of camera traps. It includes the first assessment of the density estimates for the region of one unmarked felid (Asiatic golden cat), six unmarked prey species and two unmarked sympatric carnivores using REM.

Chapter 4 evaluates the movement paths taken by common leopard, Asiatic golden cat, dhole, and leopard cat, obtained by GPS tracking, with reference to their use of habitat within the camera-trapping grid. The chapter computes separate home ranges for all the individuals to enumerate differences in home ranges between sexes and different geographical locations. It further quantifies the resource selection functions of all the carnivores. The analyses reveal a contrast in home range and resource selection by carnivores between the Southern and Northern habitats of Bhutan. Larger felids tend to select resources nearer to human settlement compared to the smaller felids.

Chapter 5 evaluates the knowledge, attitudes, and practices of local communities in our study area with respect to conservation of wild felids and dhole. The chapter quantifies knowledge of wild felids, and the perceived importance of wild-felid conservation, for four communities at the edges of two national parks in Bhutan. It explores social factors contributing to positive or negative human-felid interactions, and human behaviours influencing the social acceptance of wild felids. The chapter adds to knowledge of human-felid interaction by the key informants (local leaders, government officials, and NGO personnel) in our study area and their recommendation for felid conservation. It finds that government incentives influence the social acceptance of wild carnivores by local communities, without improving positive attitudes towards them.

Chapter 6 synthesizes the key conclusions drawn from each preceding chapters, emphasizing the significance of employing camera traps at both trail and random locations for robust density estimation. We found out that the unmarked method for density estimation can serve as a viable alternative in scenarios where identifying individuals within a population is challenging. Additionally, our findings indicate varying movement patterns among montane wild carnivores in Bhutan across different habitat types, impacting their resource selection behaviours. Furthermore, we observed social acceptance of communities for the conservation of wild carnivores is positively affected by government initiatives and incentives.

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Chapter 1 General Introduction

Populations of wild fields have declined globally over recent centuries, from ever-expanding anthropogenic activities that threaten every fragile ecosystem on earth (Gray & Prum, 2012; Loveridge et al., 2010). Amongst all mammals, the carnivores and particularly the wild felids are at high risk of extinction in the current era of human land-use change and exploitation of natural resources (Anile et al., 2019; Cardillo et al., 2008). For example, over the past 150 years, global tiger populations have declined by 93% from habitat degradation, poaching and hunting of the prey population, and persecution (Mondol et al., 2009; Sanderson et al., 2010). The tiger currently occupies only 7% of its historical geographic range, and despite some conservation successes, notably in Bhutan, its populations are still declining and fragmenting (Gilbert et al., 2023). Historically wild felids have existed wherever placental mammals have been found, for at least the last 30 million years, from Asia through Europe to the Americas (Hunter, 2015; Sunquist & Sunquist, 2017). However, recent, and rapid declines in their populations and habitats have reduced and fragmented the geographic ranges of most wild felid species (Goodrich et al., 2008). Approximately 60% of the 39 species of extant wild felids are confined to Asia, where they are frequently threatened by illegal trade in wildlife parts, negative interactions with humans and loss of habitat from developmental activities (IUCN, 2023; Loveridge et al., 2010). For example, big cats are often involved in conflicts with humans triggered by their depredations on domestic animals, and small wild felids are traded for their skin and fur (Cavalcanti et al., 2010; Jackson et al., 2010; Michalski et al., 2006).

1.1 Role of wild felids in ecosystem function

Wild felids form the apex predators in most of the global ecosystems that have rich faunal and floral diversities (Sunquist & Sunquist, 2017). They are often referred to as keystone species for their ecosystems, providing important ecosystem services, maintaining the biodiversity and functioning of the ecosystem (Dalerum et al., 2008; Owen-Smith & Mills, 2008; Sinclair et al., 2003). Of all the wild felids larger-sized cats (often referred to as big cats) have the largest home range requirements amongst the terrestrial mammals, thereby fulfilling one of the criteria for an umbrella species (Carbone & Gittleman, 2002; Noss et al., 1996). Although big cats make poor biodiversity indicators, being relatively tolerant of human-disturbed ecosystems, their sensitivity to habitat fragmentation makes them good indicators of unfragmented landscape (Crooks, 2002; KE, 2003; Linnell et al., 2000). Smaller felids play important roles in ecosystem dynamics by influencing prey behaviour and demography,

consequently modifying plant abundance, composition, succession, and diversity (Estes et al., 2011; Terborgh et al., 2001). As a result, the loss of this group of wild felids can cause regime shifts in ecosystem structure, and even loss of ecosystem services (Nagy-Reis et al., 2017; Terborgh et al., 2001).

Wild felids occupy multiple trophic levels determining various aspects of ecosystem balance and function (Qi, et al., 2020; Ripple et al., 2014; Dickman et al., 2014; Macdonald, et al., 2010). As apex predators, wild felids regulate or limit prey populations the food chain, reducing overgrazing and thereby maintaining a balance of plant species in the ecosystem (Dickman et al., 2014; Ray et al., 2013). Wild felids may prevent dominance by any one species in a landscape, facilitating coexistence of multiple species (Loveridge et al., 2010; Foster, 2008). For instance, in Bhutan, the presence of tiger in the forests surrounding villages reduces losses of crops and livestock; in contrast, incidences of livestock predation by common leopard and wild dog increase when tigers are absent from the vicinity of a village (Thinley et al., 2018). Despite their low density, wild felids can exert cascading ecological effects on other species, as mediated by their controlling effects on mesocarnivores (Ripple et al., 2014). This not only helps in controlling the herbivore population through predation but also in structuring ecosystems along multiple food-wed pathways (Ripple et al., 2014). Wild felids have cascading effect on ecosystems where their presence may change behaviours of prey species to avoid predation, leading to changes in vegetation and the entire geomorphology of the landscape (Ripple et al., 2014; Karanth et al., 2004).

Considering the importance of wild felids generally to ecosystem processes and their sensitivity to environmental changes, the health of their populations depends on sustaining relatively intact food chains (Noss et al., 1996). Consequently, conserving wild fields can be a valuable strategy in designing protected areas and planning conservation efforts for ecosystem health (Andreasen et al., 2001; Dalerum et al., 2008). Many studies emphasise the importance of monitoring wild felid population for maintaining protected areas, and establishing successful conservation measures (Dul'a et al., 2021; Nagy-Reis et al., 2017).

This thesis concerns the effective conservation management of wild felids in Bhutan. Given that we can only manage what we monitor, it focuses firstly on addressing current challenges to unbiased and representative monitoring of felids with camera trap deployments, which have become the most ubiquitous method of estimating population sizes over the last 40 years. The thesis goes on to consider how rural people in Bhutan can best coexist with large felids. My study area straddling two of Bhutan's national parks offers the possibility to explore

monitoring and management strategies for four species of individually identifiable spotted cats and one species of unmarked cat, and their unmarked prey. In this general introduction, I will introduce the current state of knowledge on felid monitoring with camera traps, leading to the specific aim of my thesis to improve monitoring protocols.

1.2 Current monitoring protocol and need for evaluation

Population monitoring is one of the fundamental pre-requisites of wildlife management and conservation (Nichols & Williams, 2006; Rowcliffe & Carbone, 2008; Witmer, 2005). Monitoring is important for informing management efforts to conserve ecological processes and population dynamics, and for enabling socially justifiable management strategies (Bai et al., 2018; Rovero & Marshall, 2009). Inaccurate population monitoring undermines the evidence-base for managing threatened species, potentially leading to erroneous prioritisation of species and locations, and ensuing conservation actions (Bai et al., 2018; Bischof et al., 2016). Wild felids including big cats are monitored frequently for population trends, ranging behaviour, and impacts of anthropogenic interventions on felid habitat, to inform conservation management and policy interventions (O'Brien & Johnson, 2005; Bai et al., 2018). This information benefits conservation managers, the scientific community and stakeholder government agencies, to meet conservation commitments for big cats (Majumder et al., 2017; Schaub et al., 2006). Many species of carnivores are solitary, shy and wide ranging in their behaviour, with naturally low densities, raising concerns about their status and population trends (Balme et al., 2009). Robust and frequent monitoring is required for threatened species, to assess their status and to evaluate potential conservation interventions (Karanth K.U., 2017). Monitoring of wild cats and other terrestrial carnivores requires large effort and incurs huge cost (Alibhai et al., 2017), prompting a need to weigh the cost of monitoring against the improvement that it makes to decision making (Hauser et al., 2006).

Counting of wild cats for management purposes dates back to the 1970s in Southeast Asian countries, when abundances of tigers were based on densities derived from pugmark counts (Karanth, 1995). This technique was considered prone to failure, as its estimates are neither total counts nor sample statistics, bearing no logical or consistent relationship to the true size of the tiger population (Karanth & Sunquist, 1992). The use of passive detectors such as camera traps became popular in counting wildlife including large felids such as tiger during the 1980s, with the development of computer-based statistical packages and analytic methods (Karanth & Nichols, 1998). Thereafter, camera trapping has proven to be a cost-effective, non-invasive and a relatively low-effort tools for gathering a wide range of ecological data on

terrestrial wildlife (Gregory et al., 2014). The use of camera traps in wildlife research has drastically increased over the past two decades (Cordier et al., 2022; Gilbert et al., 2021; Mugerwa et al., 2023). Camera traps are now a ubiquitous tool in conservation and ecology, being more effective than live traps and other methods in detecting animal presences (Wearn & Glover-Kapfer, 2019). Camera traps are an increasingly accessible tool, with continuous improvements in camera quality, cost-efficiency, and utility for addressing fundamental ecological questions (Burton et al., 2015; Caravaggi et al., 2017; Smith et al., 2020). The utilitarian value of camera trap in wildlife studies, particularly of predator-prey ecology, has skyrocketed in recent years, largely due to advances in statistical techniques including occupancy modelling and spatial capture-recapture analysis (Augustine et al., 2018; MacKenzie et al., 2017; Royle et al., 2013; Smith et al., 2020).

Capture-recapture (CR) modelling of camera-trap data has become the gold standard method for monitoring the populations of individually identifiable big cats (Green et al., 2020). Within the last 10 years, this method has been combined with the spatially explicit capture-recapture (SECR) framework to become the most widely used technique for wild felid density estimation (Dupont et al., 2019; Royle et al., 2013). SECR was independently developed by Borchers and Efford (2008) and Royle and Young (2008), to model the latent locations of individuals defined by their home range or activity centre, in addition to the individual latent states modelled in conventional non-spatial capture-recapture models (Efford et al., 2009; Efford et al., 2004; Gimenez et al., 2007; Royle, 2011). Unlike conventional capture-recapture models, SECR's ability to yield spatially explicit estimates of abundance provides an important metric for conservation and management (Bischof et al., 2016; Dupont et al., 2019). The basic assumption of SECR is that the detection probability of each individual animal varies in space according to individual space-use with respect to the spatial locations of detectors (Efford, 2014). The additional spatial parameters required for estimating density make SECR more data intensive than non-spatial counterparts (Royle & Converse, 2014). The ability of SECR to accommodate both individual locations and states makes it particularly fit for analysing data collected from non-invasive camera trap monitoring, and it is the most used method for studying elusive rare species such as wild felids (Blanc et al., 2013; Dupont et al., 2019; Royle, 2011).

The fundamental assumptions inherent to CR and SECR methods for estimating wild felid population densities remain poorly tested and, worse, may be being widely violated (Harmsen et al., 2010). Inaccurate density estimates result, and become magnified when extrapolated to regional scales (Hearn et al., 2017). A key assumption underlying all capture-recapture

models is equal capture probability for all individuals (Pollock et al., 1990; Royle et al., 2009). This was identified as key source of bias by authors of the original analytical tools (Otis et al., 1978; Pledger & Efford, 1998). Since then, simulations by (Harmsen et al., 2011) have shown the potential for frequent and substantial bias in capture-recapture density estimates in conditions of unequal capture probabilities. Their study concluded that published abundance estimates of low- density populations based on capture-recapture analysis of camera-trap data rarely present sufficient information on heterogeneity to adequately judge the reliability of the estimates. Camera traps are usually placed on man-made trails and ridgelines that are easily accessible to researchers (Karanth, 1995; Karanth & Sunquist, 1995; Singh et al., 2014). These trails are frequently used by male felids for ambushing prey and reducing energy costs of movement through inhomogeneous habitat (Montalvo et al., 2023; Singh et al., 2014). Female felids tend to avoid trails while they are nursing cub, to protect against infanticide of cubs by male felids or by other large carnivores (Singh et al., 2014). Various cat species have been documented to have sex-specific trail attraction/repulsion, which invalidates the assumption of a fixed activity centre (Singh et al., 2014). The conventional deployment of cameras along trails for the purposes of maximising encounters, results in a non-random placement with respect to the animals' movements. This non-random placement can interact with various other differences between the sexes in habitat use in response to sex-specific life-history trade-offs (Wearn et al., 2013).

The resultant non-random sampling from trail-based camera deployments introduces biases into subsequent estimates of population densities from by CR and SECR (Montalvo et al., 2023; Singh et al., 2014; Wearn et al., 2013) and may further lead to misguiding estimates of population health extrapolated to regional levels (Hearn et al., 2017). For example, in 2016 the WWF reported an increase in the global wild tiger population, for the first time in recorded history (WWF, 2016). Even though this claim was based on an immense monitoring effort across its range, using a wide diversity of field methods, it was rebutted on the basis that tiger monitoring is not currently fit-for purpose (Karanth et al., 2017). Broadly, inaccurate, or uncertain estimates of population size represent a reputational risk for institutions producing estimates, and for the role of conservation science in evidence-based policymaking (Karanth et al., 2017).

1.3 Density estimation of unmarked wild animals

Camera traps studies were initially focused on density estimation of naturally marked species, such as individually identifiable spotted cats. Advancement in sensor technologies have now

led to widespread adoption of camera traps to survey distributions, abundances and behaviours of much more diverse wildlife (Burton et al., 2015). Density estimates derived from camera trap surveys have nevertheless remained constrained to capture-recapture analysis based on uniquely identifiable body marks (Rowcliffe et al., 2008). However, the majority of mammals of conservation interest lack natural markings for individual identification, which then demands physical capture and marking of animals, which is generally invasive, and financially and logistically challenging (Chandler & Royle, 2013). Recently several attempts have been made to quantify population sizes of unmarked species using new statistical approaches to camera-trap data, with sufficient reliability for managerial purposes (Gilbert et al., 2021; Moeller & Lukacs, 2021). Density estimation methods from unmarked animals include Random Encounter and Staying Time (REST) model (Nakashima et al., 2018), the Spatial Count (SC) model (Chandler & Royle, 2013), the Random Encounter Model (REM) (Rowcliffe et al., 2008), distance sampling (DS) model (Howe et al., 2017), Time To Event (TTE) model, Space To Event (STE) model and Instantaneous Sampling (IS) estimators (Moeller et al., 2018). Estimating density from unmarked animal populations is now a major focus of camera-trap research, and reviews of the research literature have observed compositional changes in camera-trap studies with a recent decline in capture-recapture studies in favour of these new methods (Delisle et al., 2021; Moeller et al., 2018).

The Random Encounter Model (REM) developed by Rowcliffe et al., (2008) uses movement behaviour and intrinsic properties of camera traps to estimate animal densities. It has become a widely applied method, as it does not require species-specific design (Palencia et al., 2022). REM is based on conventional gas theory where individual animals are treated like ideal gas particles, and resultant density estimate are from the collective detection viewshed of a camera array. It assumes that detectors are randomly placed with respect to animal movement, and density is estimated from encounter rates (number of photographs recorded per unit time), animal movement speed, and camera's detection zone (Rowcliffe et al., 2008). The REM has been developed over the past decade, with incremental improvements over the years to protocols for measuring parameters required for the model (Garrote et al., 2021; Palencia et al., 2021; Rowcliffe, 2021). The REM method has seldom been tested and cross validated against densities derived from other methods. However, few papers are published on the comparative density estimates between other density estimation methods and REM (Cusack, et al., 2015; Swanson, et al., 2015; Rovero & Marshall, 2009; Zero et al., 2013), Palencia et al., (2022) found that the accuracy of REM density estimates is sensitive to the input parameter values required for the model. For instance, poor estimation of speed and encounter

rate underestimates the density (Palencia et al., 2022). We focused exclusively on REM for comparative density estimate between marked and unmarked methods because REM uses encounter data from a random placement of camera traps that is more efficient and cost-effective than other unmarked methods, and is particularly advantageous when working in remote or challenging environment as in Bhutan (Palencia et al., 2022; Kavčić et al., 2021). REM explicitly models the detection probability of individuals, which is essential for accuracy of density estimates and reliability, unlike other unmarked methods for density estimation that ignore or assume perfect detection (Loonam et al., 2021; Nakashima et al., 2018).

1.4 Movement ecology of wild carnivores

Information on the spatial distribution and home range size of animals is crucial for understanding their spatial dynamics, particularly for large carnivores in fragmented landscape (Farhadinia et al., 2020). Spatial information on animal movement can contribute to diverse knowledge on wildlife populations, including abundance, distribution, geneflow, and disease spread (Calabrese et al., 2016; Nathan et al., 2008). Recent technological developments in telemetry equipment and GPS telemetry enabling real-time locations of wildlife have given researchers the ability to collect substantially larger datasets of spatial locations, with greater precision (Fieberg & Kochanny, 2005; Nathan et al., 2008).

The home range is typically defined as an area that animals use to secure resources for reproduction and survival and it reflects animals' interactions with surrounding environment and energetic constraints (Börger et al., 2008; Burt, 1943). Home range measures space use by animals and provides information on ecology that is useful for conservation application (Broekman et al., 2023). Home-range size provides ecological information on resource use, population distribution and social interactions (Butler et al., 2020; Messinger et al., 2019; Ofstad et al., 2019; Wang & Grimm, 2007). Home-range size and the extent of movement by an animal is closely related to its body size and resource requirement (Harestad & Bunnel, 1979). For felids and other carnivores, home-range sizes vary significantly between populations within the same species, in response to prey population density and productivity of surrounding environment (Harestad & Bunnel, 1979; Kelt & Vuren, 2001; Nilsen et al., 2005).

The spatial distribution of a species is usually determined by the availability of food, water, cover and mates, constituting the key resources limiting reproductive success (Aryal et al., 2015; Dickie et al., 2022). Food or other resource preferences or aversions can be revealed in

disproportionate use with respect to availability (Manly et al., 2002). Differences between species in resource selection underpin the niche differentiation that permits species coexistence (Rosenzweig, 1981). It is assumed that species will select the highest available quality of resources that satisfy their life requirements (Manly et al., 2002). Resource availability relates to resource density and quality, and the consumer's ability to exploit the resources through movement (Pyke et al., 1977).

Resource selection by an animal can be analysed statistically with a resource selection function (RSF), defined as a statistical model used to analyse and understand the habitat preferences of an animal (Boyce, 2006; Morris et al., 2016; Street et al., 2021). RSFs are generally a class of exponential models of space use that estimate the probability distribution of animal locations with respect to different resources or environmental conditions in an area, taking account the availability of each resource and thereby providing a measure of the behavioural selection for or against each resource (Manly et al., 2002; Street et al., 2021). The models are fitted using logistic or conditional logistic regression applied to data on animal locations and resource distributions in the landscape (Elith & Leathwick, 2009; Fieberg et al., 2021; Manly et al., 2002). They can be used to characterise the distribution and abundance of organisms and more broadly can be used to predict species diversity and interactions in a resource landscape (Boyce, 2006; Manly et al., 2002; Nilsen et al., 2005). The resource selection function is estimated from animal locations, nowadays usually collected through radio or GPS telemetry as the method depends on obtaining sufficient locations of animals to ascertain the distribution of animal across landscapes (Hebblewhite & Haydon, 2010; Street et al., 2021).

1.5 Societal factors influencing the conservation of wild felids

Wild felids and many wild carnivores generally are susceptible to polarising opinions on their value, with stakeholders often set against carnivore conservation programmes (Dickman, 2009; Lewis et al., 2017; Treves & Karanth, 2003). Throughout human evolution and cultural development, people have lived amongst large carnivores, competing with them for meat and respecting them as symbols of power and prestige (Russo et al., 2023). Human-wildlife conflict is defined by the International Union for Conservation of Nature (IUCN) as the conflict that occurs when the requirement of wildlife and human beings overlap, either having negative effects of wildlife on humans, or negative effects of humans over wildlife (Distefano, 2005). Predation on livestock is the most common form of negative human-carnivore interaction cited globally (Dickman, 2009; Sillero-Zubiri, 2001), and in retaliation carnivores

are persecuted by local communities (Danish et al., 2023). There are numerous reasons for human-carnivore conflicts and most prominently the large dietary requirement and home range that draws carnivores near to human settlement (Inskip & Zimmermann, 2009; Treves & Karanth, 2003). Larger carnivore species require larger home ranges and are specialized for ungulate predation, making domestic ungulates particularly vulnerable to opportunistic attacks (Meriggi & Lovari, 1996; Seidensticker et al., 1999). Effective mitigation measures for human carnivore conflict now involve a multidisciplinary approach connecting across the natural and social sciences (Lozano et al., 2019; Pooley et al., 2014; Tallis & Lubchenco, 2014). The application of socio-ecological approaches to studies of human-carnivore relations requires consideration of many ecological and social components, including the different actors' perceptions and values regarding carnivore species and their ecosystems (Lischka et al., 2018; Lozano et al., 2019). This kind of complex knowledge is still lacking in many rural areas where conflicts human-carnivore conflicts can result in most damage to human and carnivore well-being. For example, in Bhutan until my study addressed the issue, there had been no assessment of social interactions amongst rural people capable of influencing acceptance of carnivores in their communities. The effective conservation of wild felids and carnivores in landscapes with human land use ultimately requires unbiased knowledge of carnivore population sizes, movement ecology and the diversity of ways that humans and carnivores can and do relate to each other.

1.6 Closing the gap: study design and contribution

In order to fill current gaps in knowledge of wild felid population health for conservation monitoring, and social influences on felid acceptance for conservation management, this thesis aims to test the accuracy and precision of alternative felid monitoring protocols in montane forests of Bhutan, to study spatiotemporal site use by felids in these forests, and to investigate factors influencing human attitudes to wild felids amongst forest-dwelling communities. The specific objectives are to (i) test and mitigate bias in density estimates derived from camera-trapping through comparative analysis of results from traditional trail-based camera and randomized camera placement; (ii) evaluate difference in density estimates of wild felids from marked and unmarked density estimation techniques; (iii) study the home range size, movement behaviour and resource use pattern of montane carnivores of Bhutan; and (iv) evaluate social factors responsible for co-existence of wild felids and other carnivores with humans. Figure 1.1 summarises the thesis aim and objectives, outlining methods underpinning each objective.

Chapter 2 of this thesis field tested detection heterogeneity between the different sexes of two species of naturally marked big cats: clouded leopard (*Neofelis nebulosa*), and common leopard (*Panthera pardus*), and two of naturally marked small cats: leopard cat (*Prionailurus bengalensis*), and marbled cat (*Pardofelis marmorata*). We compared the density estimates of these felids with unique individual body markings between a camera-trap deployment on trails and a deployment at random location with respect to habitat. Population densities were estimated using the Spatially Explicit Capture Recapture (SECR) model. We used data from a total of 298 camera traps at 199 stations across 400 km^2 of montane forest in southern Bhutan, with paired camera traps at 99 trail stations and single cameras at 100 random stations. In this chapter we developed the SECR density models based on an influence of sex on detection probability, and an interaction effect of sex and camera placement (trail or random) on detection probability, compared with the null model of homogeneous captures. The overlapping deployments allowed us to analyse the proportion of individuals of each sex present but missed by each of the trail and random deployments (the 'ghost' individuals). We further modelled detection heterogeneity and bias in density estimates from trail-based deployment of camera traps. We also estimated single-sex population densities as a potential alternative method of density estimation when detection is male or female biased, assuming an equal sex ratio in the population. Finally, we compared the density estimates from different combinations of trail and random camera traps for marked felid species.

Chapter 3 evaluates the differences between density estimates derived from SECR and from Random Encounter Modelling (REM). We estimated densities of four marked wild felids (clouded leopard, common leopard, leopard cat, and marbled cat) applying REM field protocols and analytical methods and compared them with the most robust density estimates derived from SECR in chapter 2. We modelled the sensitivity of REM density estimates to the accuracy of REM input parameter measurements. We compared the precision in density estimates from REM and SECR by computing their coefficient of variation. We further evaluated the influence on REM density estimates of adding in trail cameras, comparing outcomes with the density estimates from the random-only deployment of camera traps. Finally, we calculated the density estimates of one unmarked felid (Asiatic golden cat), six unmarked prey species and two unmarked sympatric carnivores recorded by the survey.

Chapter 4 explores movement ecology and behaviour of montane carnivores of Bhutan. We used data from GPS collars on one female and two male common leopards, two female dholes (Asian wild dogs), one female Asiatic golden cat and one male leopard cat. We modelled the home ranges of these carnivores using an area-corrected and weighted autocorrelated kernel

density method of home range estimation. We computed separate home ranges for all the individuals to evaluate the differences in home ranges between sexes and different geographical locations. We further quantified the resource selection functions of all the carnivores. We modelled resource selection functions using habitat covariates (elevation, tree cover, distance to river, distance to settlement, and distance to human wildlife conflict sites), and a species interaction model for sex-based and prey-species influences on resource selection for each species.

Chapter 5 evaluates the knowledge, attitudes, and practices of local communities in our study area related to conservation of wild felids and dhole. For four communities at the edges of two national parks in Bhutan, we quantified knowledge of wild felids and perceived importance of wild-felid conservation. We then modelled social factors contributing to positive or negative human-felid interactions, and human behaviours influencing the social acceptance of wild felids. We explored influences on the social acceptance of carnivores by communities using structural equation modelling. Finally, we interviewed key informants in our study area to explore their knowledge of human-felid interactions and their recommendation for felid conservation. We recommend the initiation of a sustainable financing system for livestock loss, and technological advancements to strengthen human-felid co-habitation.

This study makes several unique contributions to the field of camera trapping for wildlife studies, spatial ecology, and human-felid coexistence. Firstly, it provides a comprehensive analysis of random and conventional sampling in wildlife studies and particularly in camera trapping studies. We also explored how random study design in a mountainous landscape provides opportunities for cost-effective wildlife study design. Uniquely we explored density differences between random placement and opportunistic placement of camera traps in wildlife studies. The study specifically focused on wild felids, which often serve as indicators of ecosystem health, providing valuable insights into broader ecological processes. They are also keystone species, and studying them helps understanding of how changes in their populations can have cascading effects on other species and ecosystem process. We further explored movement patterns and habitat use by felids and other carnivores in mountainous landscapes of Bhutan for the first time. Finally, we explored influences of social-ecological factors on coexistence of wild felids and human communities residing in the wild felid habitat.

Our analysis of the differences between random and conventional sampling for camera-trap deployment revealed a need for a comprehensive analysis encompassing different landscapes

and species. Current knowledge on the application of random study design in mountainous landscape needs improving to understand how random study design can present a cost-effective opportunity for wildlife studies in landscapes with difficult access such as those in Bhutan. Our study on the movement ecology of wild felids and wild dogs was the first of its kind in Bhutan, albeit with small sample size. There remains a lack of comprehensive studies on field movement and habitat use by carnivores in regions like Bhutan. The human component is often neglected in wildlife conservation strategies, and there is a need for more research on the social factors that influence human-wildlife coexistence, especially in communities residing in wild felid habitats.

Figure 1.1. Schematic illustration of the overall study design, summarizing aim, objectives, activities to achieve the objective and the project outputs from the PhD study.



Chapter 2 A comparison of felid population density estimates from camera traps placed randomly versus on trails

Contributions

The concept of this chapter was initially developed by Dr Paul Glover-Kapfer from World Wildlife Fund UK and Dr Oliver Richard Wearn who worked as postdoctoral researcher at Zoological Society of London. Dr Wearn and Professor C. Patrick Doncaster visited the field sites with me for a feasibility study before the start of project that led to development of this chapter. Later, I developed the initial ideas, along with Professor Doncaster, by designing the full field study in Bhutan's Jigme Singye Wangchuck National Park and Royal Manas National Park. Dr. Wai Ming Wong of Panthera International visited the field site and trained field rangers on operation of Panthera V7 camera traps. All fieldwork was approved by the University of Southampton Ethics and Research Governance panel (ERGO 53715).

I conducted all of the camera-trapping fieldwork, along with Mr. Dechen Norbu and Mr. Sither Dorji from Wangchuck Centennial National Park, and Mr. Sangay Tshering from Jigme Singye Wangchuck, from February 2020 until May 2021. The field survey was supported by local forest rangers and Mr. Kuenly Tenzin from World Wildlife Fund Bhutan program office. Fieldwork was partially impacted by COVID-19 related travel restrictions and summer monsoon. However, with support from the Royal Government of Bhutan (which administered two rounds of free quarantine facilities for field assistants) and the Department of Forests and Park Services of Bhutan, there were no major disruptions to the fieldwork.

I managed the camera trap photographs and analysis of data, with guidance from Dr. Wearn. I wrote the chapter, and drafts were reviewed by Professor Doncaster, Dr. Wearn, Dr. Ming and Dr. Rinjan Shrestha who works at World Wildlife Fund Canada office.

The camera traps and batteries were donated in kind by Panthera International and cost for the fieldwork was supported by funding support from World Wildlife Fund's innovation grant, Zoological Society of London, and Panthera's Kaplan Graduate fellowship.

Abstract

Density estimation is one of the fundamental prerequisites of wildlife management and conservation. This study aims to characterise and resolve biases associated with the current "gold-standard" methods for big-cat density estimation, which involves capture-recapture modelling of data from camera traps placed on trails. Our study tested bias across all the big cats (clouded leopard, common leopard, and tiger), and small spotted felids (leopard cat and marbled cat) in the study area of southern Bhutan montane forest. We deployed 300 camera traps over an area of 400 km^2, placing 100 pairs on trails as for a trail design (trail deployment, '100T' stations), and 100 singly at grid-cell centre points as for a random design with respect to the animal habitat (random deployment, '100R' stations). The comparative density estimates from these two different placements of cameras were analysed using a spatially explicit capture-recapture (SECR) model for the spotted cats. We observed that trail deployment favoured male detections. In contrast, random deployment favoured female detections. Combining random and trail deployment reduced the sex bias in detections for all the cat species. We tested for influences of deployment (random, trail), sex (male, female), and their interaction (deployment * sex) on population density. Likelihood Ratio Test (LRT) and Akaike's Information Criterion (AIC) confirmed that population density does depend on the interaction of deployment with sex for all felids except the common leopard, when applied to the full 100T + 100R deployment. The interaction reflects the predominance of males on trails and females in the random deployment. The density estimates from random-only or from trail-only deployments each miss some individuals that are capture by the other deployment, except for the leopard cat. The consequence of disregarding sex-specific detection heterogeneity is underestimation of density from the trail deployment, which can be mitigated by including sex-dependent detection in the density model. Prediction of male-only density in the trail deployment can be used as an alternative way to estimate population density that avoids bias from unmodelled heterogeneity, assuming a 1:1 sex ratio, although it aligns only loosely with reference densities obtained from the full 100T + 100R deployment.

We estimated density with and without accounting for an influence of sex on the baseline individual detection probability ('sex-based' and 'no-sex' models respectively), and the scale parameter (sigma). We explored hypothetical mixed-deployment scenarios in which a different proportion of random and trail deployment were combined to assess the best density estimates. The result from these combinations reveals that an allocation of ~50% of camera stations to random cameras will likely give a reasonable compromise between accuracy and precision.

2.1 Introduction

Big cats are globally threatened with extinction due to anthropogenic habitat loss and demand for their body parts in the illegal wildlife trade markets (Macdonald & Loveridge, 2010). The effective management of their populations, conservation prioritization, and assessment of their conservation status, require accurate information about population sizes (Shi et al., 2023). Camera traps have emerged as the standard tool for assessing populations of individually identifiable spotted cats (Karanth & Nichols, 1998; Karanth et al., 2006). In particular, the use of Capture-Recapture (CR) and later consideration of spatial points in Spatially Explicit Capture Recapture (SECR) have become gold-standard method for density estimation of big cats and other spotted cats (Green et al., 2020). However, density estimates from capture-recapture studies are often biased by the naïve assumption of equal probability of detection over the sampled area, ignoring individual detection heterogeneity (Mohamed et al., 2021; J. Royle et al., 2009; Stevenson et al., 2022). For many big cat species, females tend to avoid trail habitat to prevent harassment and infanticide of cubs by males, and male-biased detection is often observed in camera traps deployed on regular trails (Balme et al., 2013; Srbek-Araujo, 2018). This bias tends to result in underestimation of occupancy and density if site-specific heterogeneity of detection is not accounted for in models (Royle & Dorazio, 2006, 2008). In effect, the population is not representatively sampled by trail-based deployments. A potential solution to this problem might be random deployment of camera traps with respect to the animal's habitat or combining random deployment with a trail-based deployment of camera traps. This would reinstate representative sampling (if entirely random) or allow testing for differences in habitat use (if random + trail representatively samples the principal cat habitats). For studies with limited availability of cameras, the potential risk is that random placements of cameras may have many fewer detections than trail placements, resulting in less data capture. This chapter aims to examines the capture heterogeneity by sex for 5 species of cats in Bhutan, with the aim of resolving bias in density estimates from camera trap studies and guiding best practice in camera-trap deployments.

The use of camera traps as a wildlife monitoring tool dates back over 100 years and it has become an essential tools of wildlife monitoring over recent years with the advancement of sensor and imaging technologies (Wearn & Glover-Kapfer, 2017). Camera trapping is now a ubiquitous tool for monitoring wildlife, providing a higher sampling rate than other monitoring and study techniques for many sampling scenarios (Cordier et al., 2022; Wearn & Glover-Kapfer, 2019). The availability of mass-produced and cost-effective commercial

camera traps (Rovero et al., 2013), and the advancement of the methodology of analysis of camera trap data, have led to an increase in the number of publications on camera trap studies over the years (Kelly, 2008; Rowcliffe & Carbone, 2008). Camera traps are used for various purposes in wildlife studies, including discovering new species, population studies, site occupancy, and studying the movement ecology of wildlife (Burton et al., 2015; Pollock, 1982; Rowcliffe & Carbone, 2008).

The use of camera traps to monitor individually-identifiable big cat populations started in the early 1990s (Dheer et al., 2022; Karanth, 1995). It has now become the standard tool for estimating the population densities of big cats (Karanth & Nichols, 1998; Karanth et al., 2006) as it provides more reliable evidence on animal presence (Sunarto et al., 2013). The method of mark-capture-recapture or capture-recapture has become the standard technique for estimating population densities of marked or spotted big cats (Anderson et al., 1982; Boudreau et al., 2020; Karanth & Nichols, 1998). Most of the capture-recapture studies do not account for spatial dependence of detection probability on location of traps relative to animals (Borchers, 2012). The critical information on home range and movement is then not meaningfully exploited in conventional capture-recapture studies while estimating abundance and density (Gopalaswamy et al., 2012). Any inability to sample the entire population creates ‘holes’ in the study area, and surveying in blocks leads to inclusion of areas not used by the target species, which weakens estimates from conventional capture-recapture studies (Gopalaswamy et al., 2012; Karanth & Nichols, 1998).

The recent incorporation of spatial data capture-recapture analysis led to development of a method called Spatially Explicit Capture-Recapture (SECR), which considers the spatial relationship between the detectors and the animal and yields robust density estimates (Kristensen & Kovach, 2018). This has demonstrable advantages over conventional capture-recapture analysis and has become the most used method for big-cat density estimation (Efford & Fewster, 2013; Foster & Harmsen, 2012; Royle et al., 2013). Density is estimated from the known points of an animal in a defined space, and it helps to reduce bias from edge effects, which is usually observed in non-spatial capture-recapture studies (Efford & Boulanger, 2019). The effective sampling area is not definable in non-spatial capture-recapture studies, which are consequently able to estimate only population size and not density. In contrast, SECR can estimate population density from the estimated population size in the effective sampling area (Iijima, 2020). The early use of camera traps focused on individually identifiable animals with natural markings. Now there are a growing number of methods for the survey of unmarked animals (Burton et al., 2015; Gilbert et al., 2021). For

unmarked big cats such as puma (*Puma concolor)* and lion (*Panthera leo)*, camera trap data can yield density estimates from methods such as the N-mixture model (Royle, 2004), Random Encounter Model (REM: (Swanson, et al., 2015), Space To Event (STE) and Instantaneous Sampling (IS) models (Moeller et al., 2018). These methods will be evaluated in Chapter 3.

The estimates obtained for animal density, movement, and site use are based on presence-absence information from the images captured by the cameras, and depend on the locations of camera traps in the survey area (Kolowski & Forrester, 2017). The current methods divide the survey area into a grid of regular squares or circles, or points, based on the species home range, assuming that the animals in the survey area have equal opportunity for capture (Anderson et al., 1982; Kays et al., 2020; Lancia et al., 2005). The camera traps are often placed on the paths that are more frequently visited by the animals to ensure multiple detection of animal at multiple locations over the time (Karanth, 1995; Karanth & Sunquist, 1995; Singh et al., 2014). Researchers develop individual detection histories from the animal captures at different locations to estimate densities (Karanth & Nichols, 1998). However, fundamental assumptions inherent to these methods remain poorly tested and, worse, may be being widely violated, biasing the density estimates, and becoming magnified when extrapolated to regional scales (Hearn et al., 2017).

A key assumption underlying all capture-recapture models is equal capture probability for all individuals within the sample plot (Pollock, 1982). This was identified as a key source of bias by authors of the original analytical tools (Otis et al., 1978; Pledger & Efford, 1998). Since, then simulations have shown the potential for frequent and substantial bias in capture-recapture density estimates in the presence of unequal capture probabilities (Edwards et al., 2018; Efford, 2014; Harmsen et al., 2011). (Edwards et al., 2018; Efford, 2014; Harmsen et al., 2011) concluded from simulations that currently published abundance estimates of low-density populations based on capture-recapture analysis of camera trap data do not present sufficient information on heterogeneity to adequately judge the reliability of the estimates. High heterogeneity level in individual capture probability between males and females are observed in the big cats including tigers and jaguars (Piña-Covarrubias et al., 2022; Singh et al., 2014).

The national estimate of tiger density in 2014 for India is thought to be misleading and overestimated due to unexplained heterogeneity in detection probabilities (Gopalaswamy et al., 2019). It was observed that the current density estimation techniques, closed population

model (capture-recapture) and spatial model (SECR) either overestimates or underestimates the population of wild cats depending on the distribution of cameras with respect to subject habitat use (Obbard et al., 2010; Sollmann et al., 2011).

Attempts have been made to characterize the heterogeneity in detection probability of individuals over the habitats for different species, but the majority of studies have used opportunistic sampling without reporting details of sampling design and the camera deployment or have used computer-based simulations (Burton et al., 2015; Stevenson et al., 2022). In this study of spotted cats in Bhutan, we anticipate fundamental differences between the sexes in habitat use in response to different life-history trade-offs, and that these sex differences interact with non-random placement of camera traps – a characteristic of almost all sampling studies of large mammals. For example, males may prefer to travel along linear habitat features such as trails, rivers, or ridges (Harmsen et al., 2017; Wearn et al., 2013), perhaps to minimise energetic costs and maximise prey encounters. These habitat features are also those typically favoured by researchers when deploying their camera traps. Females, being the smaller of the sexes in all big cats, may deliberately avoid such features to minimise non-breeding interactions with males, especially whilst supporting cubs (Singh et al., 2014). A small portion of males are recorded at the off-trail locations compared to the trail location and more females are recorded in off-trail locations compared to the males (Montalvo et al., 2023). Cameras placed off-trail in past studies have recorded individuals that are missed by the trail cameras, and tend to improve the overall density estimates, as shown in the case of bay cats (*Catopuma badia*) in Borneo (Wearn et al., 2013). Among partially arboreal big cats, such as clouded leopards, females may also avoid males by spending more time in the canopy where the larger-bodied males find it difficult to follow(Law & Tatner, 1998).

This chapter aims to calibrate the camera trapping biases in five species of cats in Bhutan. We compared captures in simultaneous and superimposed trail-based and random deployments of camera traps, in order to test the following hypothesis. $\boldsymbol{H_1}$: Trail-only designs can provide unbiased estimates, only so long as sex related capture heterogeneity is modelled, and both sexes have some possibility of capture on trails (but precision might be improved by including off-trail cameras if female capture probability on trials is low); $\boldsymbol{H_2}$: Females will show more localised patterns of detection and smaller apparent home-ranges than the larger-bodied males; $\boldsymbol{H_3}$: Failing to account for sex-dependent use of trail or off-trail habitats will underestimate density estimates, due to unmodelled heterogeneity in detection probabilities; $\boldsymbol{H_4}$: Reduced-effort survey designs (either fewer camera traps or fewer sampling sites) will result in reduced precision of density estimation, but designs including some randomly placed

cameras will result in more accurate density estimation than those only containing trail-based cameras (i.e., approximately right, rather than precisely wrong estimation).

We further hypothesised that it may be possible to estimate male-only population density from a trail-only deployment of camera traps, on the assumption that males use trails more frequently than off-trail locations, from which further to estimate whole population density on the assumption of a 1:1 sex-ratio. We can test the first assumption by comparing sex-biases in captures between trail and random deployments; we cannot test the second assumption, but can tentatively assume a 1:1 sex-ratio for the more abundant species on the basis of Fisher's sex ratio theory (Fisher, 1999; Hamilton, 1967).

2.2 Materials and methodology

2.2.1 Study area

The fieldwork was carried in Jigme Singye Wangchuck National Park and Royal Manas National Park which are in the south-central part of Bhutan. These two protected areas have an unusually rich wild cat diversity, with seven wild cat species including tiger (*Panthera tigris*) and common leopard (*Panthera pardus*) (Tempa et al., 2013). In 2019 they were accredited by Conservation Assured Tiger Standards (CA|TS) for the highest global standards in tiger conservation (WWF, 2019). This subtropical region is sparsely populated, mountainous, and densely forested. The altitude ranges between 200 and 2,000 m and forest habitats consist of mixed broadleaf and coniferous old-growth trees growing on steeply inclined ridges between stream channels and river valleys. It also acts as an important climatic corridor of forests connecting subtropical lowland habitat with higher-elevation temperate forests (JSWNP, 2022). The main sources of income for communities are agriculture, livestock rearing, and forestry (JSWNP, 2022; Wang & Macdonald, 2006). The study area has relatively high density of wild tiger, common leopard and clouded leopard compared to typically-reported densities (Penjor et al., 2018).

2.2.2 Sampling design

We defined a 400 km^2 area straddling the two national parks as the study site. This area was then divided into 100 contiguous spatial grid-cells each of 2 x 2 km in Arc.Map.10.8.2 (ESRI, 2021) as shown in Figure 2.1. We adopted a 2 x 2 km grid size, which was a balance between ensuring sufficient spatial recaptures (necessary for SECR) and covering a sufficiently large area to encompass the home-ranges of sufficient individual cats (Tobler & Powell, 2013).

Two modes of camera deployment protocols are adopted in this methodology: random deployment and trail deployment (Figure 2.1).

Trail deployment of camera traps

The trail deployment comprised 100 stations with paired cameras (to capture both flanks of each individual), at a density of one station per 4 km^2 (Figure 2.1). Each of these stations was located along a human/animal trail, riverbed, or ridgeline, in line with current conventional protocols. Camera traps were equipped with white flash to aid individual identification from imagery. This sampling design conforms to currently-used methods for capture-recapture of a low-density species, such as the clouded leopard (Wearn & Glover-Kapfer, 2017).

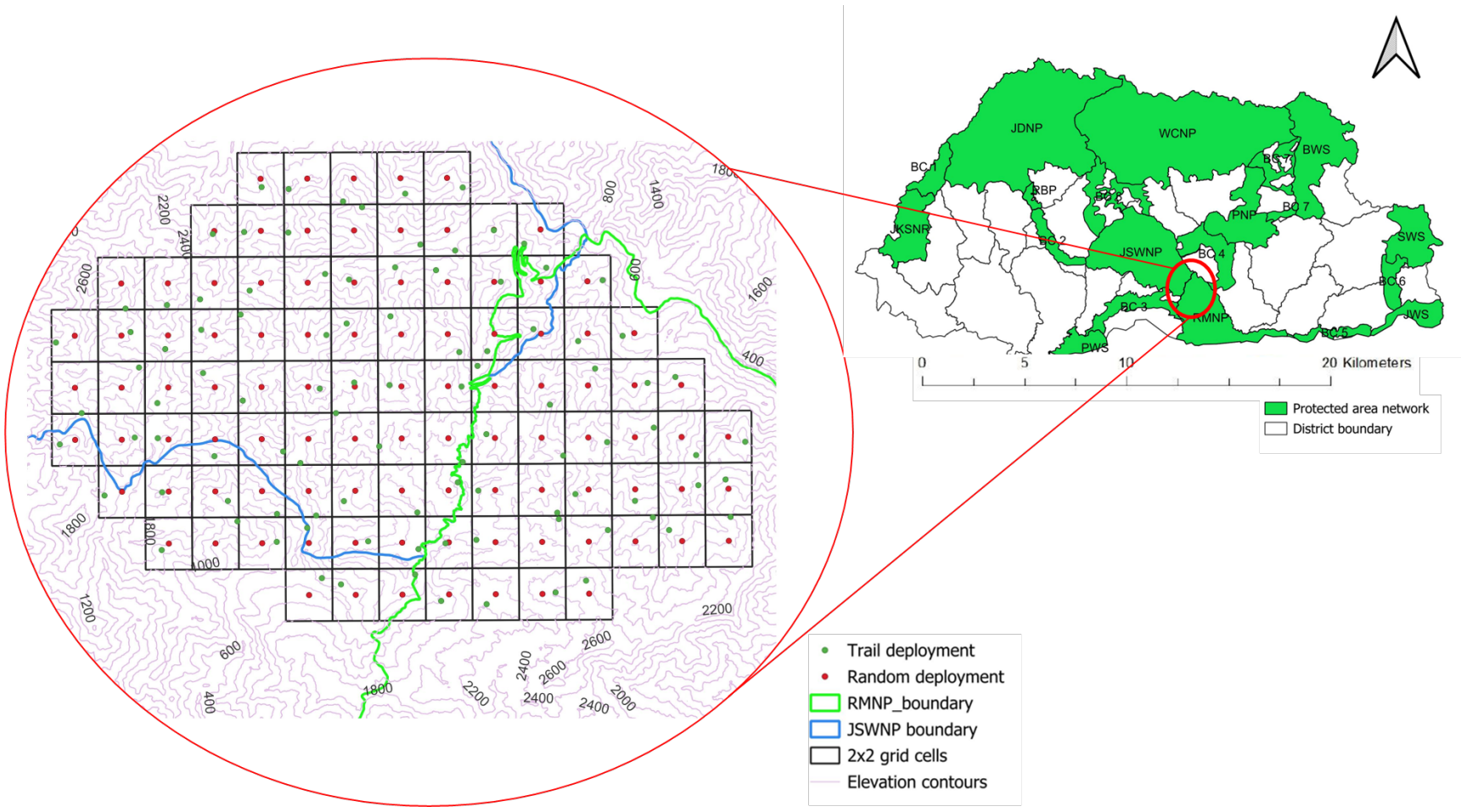

Figure 2.1. Study area with overlay of 2x2 km grid cells with trail deployment (green dot) and the random deployment (red dot). The study area falls in Jigme Singye Wangchuck National Park (JSWNP) and Royal Manas National Park (RMNP) and their buffers. The number on the contours shows the elevation in meters above sea level. The map on the right shows the protected area network of Bhutan (BWS: Bumdeling Wildlife Sanctuary, JDNP: Jigme Dorji National Park, JKSNR: Jigme Khesar Strict Nature Reserve, JWS: Jomotsangkha Wildlife Sanctuary, PNP: Phrumsengla National Park, SWS: Sakteng Wildlife Sanctuary, WCNP: Wangchuck Centennial National Park) including biological corridors (BCs numbered 1-7).

Random deployment of camera traps

The random deployment comprised 100 single-camera stations at the same density as trail-based locations but deployed at the exact mid-point of each 4-km^2 grid square (±50 m to avoid major obstructions such as rocks or trees or cliffs, an error covering no more than 0.06% of the 2x2 km grid cell) according to the decision tree shown in Figure 2.2. A very small proportion of random cameras (4 camera stations) were positioned on animal trails and ridgelines, reflecting the rarity of these habitat features in the study area. The spatial regularity of the random design ensured that cameras sampled randomly with respect to the heterogenous habitat. This design conforms to best practice for broad-spectrum wildlife monitoring, yielding robust data also on prey species (some of which may avoid locations targeted during trail sampling). Past work (Wearn et al., 2013) has suggested that the random grid may give lower overall capture probabilities than trail grid, but crucially may capture certain individuals in the population, such as females, that are missed by the trail grid, which reduces bias in the resulting density estimates.

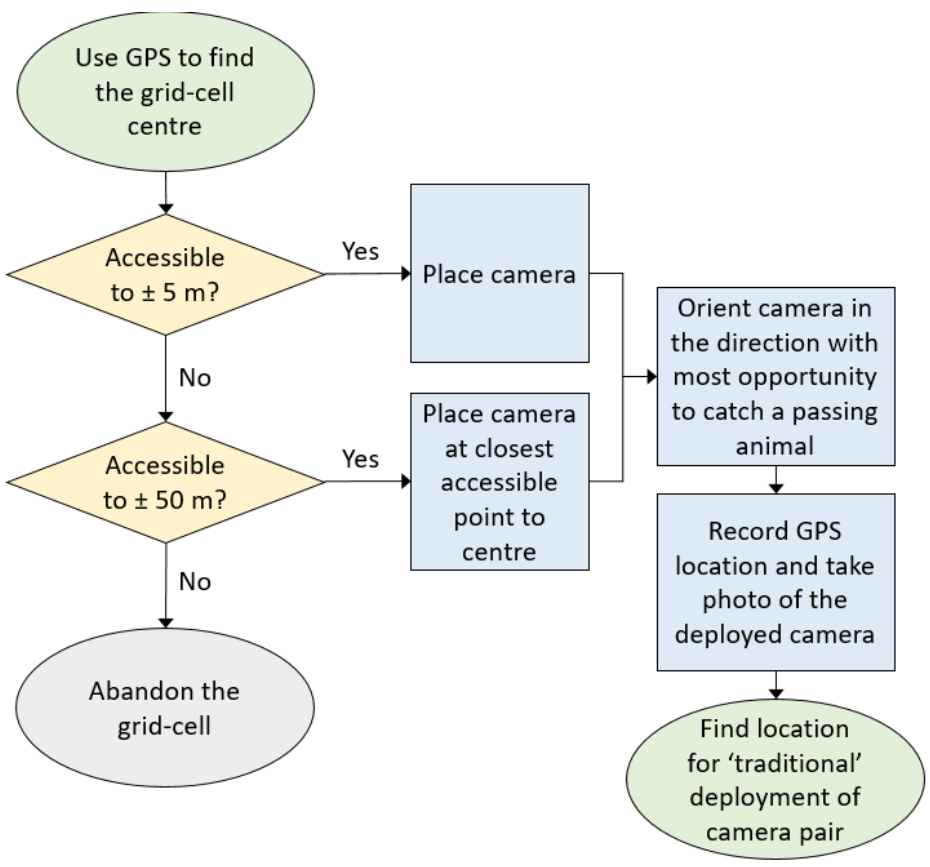

Figure 2.2. Decision tree from camera trap deployment at the random deployment site. The flow chart shows the decision made in the field, if researcher can reach within ± 5m, we deploy the camera trap, when the random deployment site is on the cliff or inaccessible, deploy the camera trap within ±50m from the exact random point.

2.2.3 Camera traps and timing for the camera trap session

We used Panthera V7 Xenon white flash camera traps with lithium-ions batteries for this survey. The camera houses 3 pairs of 5.4V AA batteries which last for more than 90 days in low traffic areas, and more than 60 days in high traffic areas. We configured the cameras to take 3 photos per trigger. Photos within a trigger were separated by 1 second in daylight and 15-30 seconds when using the flash. The cameras were placed 30 cm above the ground to enable capture of large to smaller sized wild cats. The camera traps were set to operate for 24 hrs/day for 3 to 5 months with one battery revision after 60 days. We deployed 300 camera traps in 200 camera stations, comprising 100 trail stations each taking a pair of cameras, and 100 random stations each taking a single camera (Figure 2.2). From 13th October 2020 to 5th May 2021, a total of 23,592 trap nights was achieved in this survey.

2.2.4 Camera-trap data preparation

The survey generated more than 250,000 photographs from 298 cameras at 99 stations (two cameras had a firmware malfunction leading to rapid battery drain). The raw data from the camera traps were downloaded using a USB flash drive module that generates unique numbered folders for individual cameras. The corresponding image folders were manually placed into nested directories of folders (PhD\field-works\camera trapping\camera trap images\camera station (grid number)\mode of deployment (trail and random)) as some software requires specific path and folder name to process further analysis (Young et al., 2018). The raw data were all backed up in cloud storage of the University of Southampton for data security.

We used image-management software Digikam.7.6 to process the camera trap images for the classification of images based on species types and the station. The hierarchical subjects or a list designating different animal species was prepared in the DigiKam software and tagged to the image metadata according to the species captured. We used camtrapR package (Niedballa et al., 2016) to sort images by species to different folders. The getSpeciesImages function of camtrapR package enables tagged images to be stored in different file directories. The details of the image management protocol for this study are shown in Figure S1 of appendix 1.

2.2.5 Statistical background

We used Spatially Explicit Capture-Recapture (SECR) methods for estimation of population density of spotted wild felids. SECR is any individual encounter model which includes

auxiliary spatial information and may include capture-recapture data (Royle et al., 2013). SECR input data generally take the form of a collection of encounter histories for ***i*** unique individuals encountered across ***j*** traps on ***k*** sampling occasions (Maronde et al., 2020). SECR models involve a collection of random variables ***s,*** ***u*****,** and ***y***, where ***s*** is the activity centre/home range centre, ***u*** is the location of the individuals at the time of sampling, and ***y*** is a response variable that typically takes values of 1 for detected or 0 for not detected (Royle et al., 2013). The Spatially Explicit Capture Recapture model is unique in that it considers the spatial organization of individual animals and the detectors (camera traps) (Borchers & Efford, 2008; Efford et al., 2004). The general assumption of SECR is that the individuals in the population have a fixed home range with a fixed activity centre $\boldsymbol{s_i}$ around which individual ***i*** moves and concentrates its activity in that area. There are *N* independent activity centres distributed uniformly over the region or area ***S***.

$$\mathbf{s}_i \sim \boldsymbol{Uniform\ (S)}$$

S can be a polygon that contains a trapping array and can be a sub-set of some larger area or polygon. Therefore, the activity centres are the outcome of the point process of the state-event ***S***, and can be homogenous if the density is constant throughout ***S*** or inhomogeneous if density varies through ***S.*** The number of individuals ***i*** (1, 2, 3,…*N*) in a population of size *N* exposed to sampling is estimated as the sum of the activity centres $\boldsymbol{s_i}$. The population density (***D****,* sometimes represented by ***μ)*** is the ***N*** number of activity centres $\boldsymbol{s_i}$ per unit area of ***S.***

$$\boldsymbol{D = N/S}$$

Where ***N*** is the parameter value of the model, and ***S*** is the known area of the prescribed state-space, which can be subset into protected areas-(i.e. $\boldsymbol{P \subseteq S}$, where ***P*** can be a park or tiger reserve or study area) (Royle et al., 2009). The point process can also be a model of number of individuals in a population of size ***N***. We write a model (***S|μ***) where ***μ*** is the number of points per unit area (population density). Hence, we can model population size in both Poisson and Binominal process: ***N*** ~ Poisson (***μ***||***S***||), or ***N*** ~ Binomial (***M***, ***Ψ***), with ***Ψ*** = ***(μ***||***S***||)/***M***, where || represents the magnitude of the area vector and ***M*** is a convenience measure, which is a large integer used when conducting Bayesian analysis (Royle et al., 2013). We model capture histories with an encounter model that uses two parameters: ***g0*** describing the probability of capture at the activity centre of an individual, and ***σ*** the scale parameter determining how rapidly capture probability declines with distance from the

activity centre (Gardner et al., 2010; Royle et al., 2013). The basic model is called the half-normal model, typically referred to as the Gaussian model:

$$g_{ij} = g_0 \, exp\,(-d^2/(2\,\sigma^2))$$

where $g0$ is the baseline detection probability given a camera trap located exactly at the activity centre and σ is the scale parameter. The capture probability declines with increase in the distance from the activity centre according to the function, with d representing distance between camera trap and Home Range Centre. The equation below represents the data-generating process (i.e., detection and non-detection). Data g_{ij} occurs as a Bernoulli process with probability g_{ij}

$$g_{ij}|s_i = Bernoulli\,(g_{ij})$$

These simple hierarchical models describe the basic assumptions of SECR: the population size N is Poisson distributed, the activity centres are uniformly distributed in two-dimensional state-space, and the capture probability is a function of distance between activity centre and the trap:

$$N \sim Poisson\,(\mu||S||)$$

$$s_i \sim Uniform\,(S)$$

$$y_{ij} \sim Bernoulli\,(p(||x_j - s_i||))$$

The density estimate can be based on a null model, also referred to as a default model, where no covariates influence the detection function $\lambda_0/g_0 \sim 1$, or it can be based on models with covariates influencing the detection function (for example, a sex-dependent model where $g_0 \sim sex$ (Efford & Efford, 2022; Tobler & Powell, 2013).

$$log\,(g_{0,jk}) = g_0 + \beta_{sex}$$

Where, g is the detection probability, j is the number of detectors (camera traps), and k is the sampling occasion. The SECR model can estimate density with both the Maximum Likelihood Estimator (MLE) (Efford & Efford, 2022) and a Bayesian estimator (Gopalaswamy et al., 2012). Applying both frameworks for estimation of density helps to cross-validate the estimates (Gopalaswamy et al., 2012).

2.2.6 Preparing Input data for density estimation

Identifying unique individuals is one of the important prerequisites of population estimation from capture-recapture analysis (Amstrup et al., 2005; Foster & Harmsen, 2012; Pollock, 1982). For all the spotted cats, unique individuals were identified by comparing the left and right flanks of individual animals captured on the cameras. We used both right and left flanks of individuals captured in trail deployment to identify the unique individuals captured in the single-camera stations of the random deployment. We identified 25 different individuals of clouded leopard by comparing left and right flanks from the photographs. As the study had a single camera at the random station, the individuals that had no corresponding match with either right or left flank pictures in the trail-based camera stations were further identified to individual where they displayed unique patterns on the back, tail and head. .

Each unique individual was assigned an individual identification tag in the DigiKam software, and its sex was identified based on presence or absence of external testicles (Petersen et al., 2020). We tagged F for female, M for male and NA for those individuals with no clear photograph of the inguinal region.

One of the closure assumptions of SECR for density estimation is that individuals are recaptured at least once over the study period (Gerber et al., 2012). We tabulated the individual records in different camera stations using the recordTableIndividual function of camtrapR. The spatial detection histories for individuals were generated from the individual record spatialDetectionHistory function of camtrapR.

For data analysis with the SECR framework, we recorded the capture histories over 60 consecutive sampling days to avoid violating the closure assumption for a resident population (Karanth & Sunquist, 1995; Pollock, 1982). Estimating densities for a closed (resident) population requires a minimum of 30 days to capture sufficient individuals present in a study site and a maximum of 90 days to minimize the chance of summing the size of a supposedly closed population from an actual flux of individuals through the study site (Efford et al., 2009; Karanth & Sunquist, 1995; Pina Covarrubias, 2019; Zimmermann & Foresti, 2016). The detail of framework for SECR is shown in Figure 2.3.

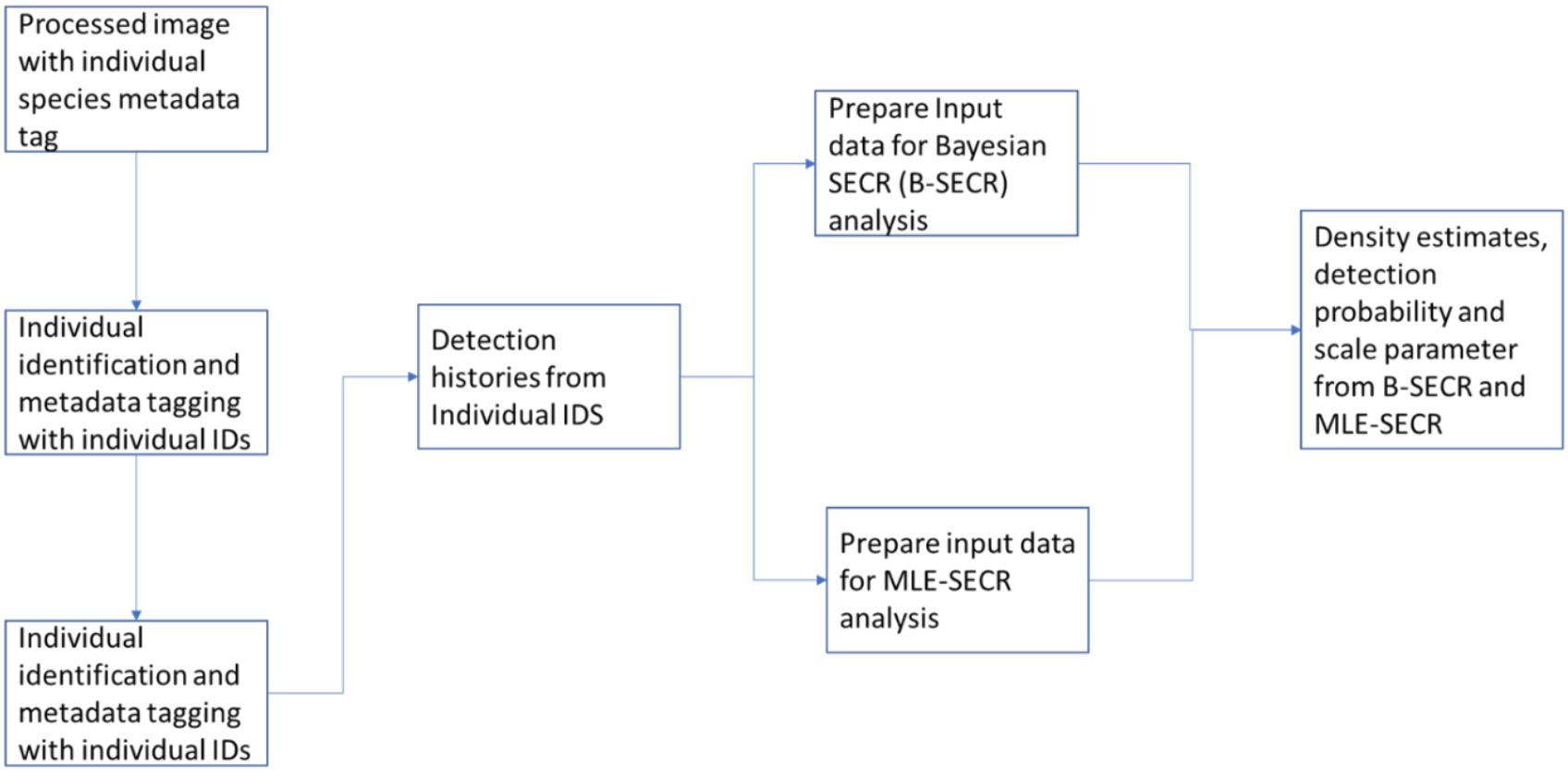

Figure 2.3. Illustration of data preparation and steps for SECR analysis

2.2.7 General SECR frameworks

We applied both maximum-likelihood and Bayesian frameworks for the density estimation of spotted wild cats. Both Bayesian and maximum-likelihood based SECR provides flexibility in modelling depending on the type of statistical packages in use. The maximum-likelihood approach has more flexibility for modelling with different covariates compared to the Bayesian approach using SPACECAP package (Efford et al., 2009; Gopalaswamy et al., 2012; Zimmermann & Foresti, 2016) but the Bayesian framework with BUGS or JAGS model code is more flexible than the MLE (Royle & Converse, 2014). We used the spatial detection histories prepared using camtrapR for model fitting based on maximum-likelihood estimation. For the buffer distance around the cameras (an input parameter for SECR), beyond which the detection probability of species becomes near zero (Efford, 2019; Piña-Covarrubias et al., 2022), we followed the recommendation of using around four times the initial estimate of sigma (Efford, 2022). This resulted in a buffer distance of 25 km around the outermost trail and random camera stations. The mesh spacing comprises equidistant points corresponding to the centre point of the home range. We chose a mesh spacing of 0.25 km, which equals the mean distance moved per day by adult male clouded leopards and common leopards reported in studies from Thailand (Grassman et al., 2005; Penjor et al., 2018) and tigers from a study in Bhutan (Tempa et al., 2019). We used the same buffer dimensions for the common leopard, leopard cat and the marbled cat.

We applied half normal detection function for all the models, which comprises two detection

parameters ***g0*** the detection probability and sigma that describes decline of the encounter rate from the home range centres (Royle, 2011; Tobler & Powell, 2013). Sex of an individual and the site-specific covariates were modelled as a determinant of the detection probability and the scale factor sigma. We constructed models to test two broader objectives: one to check for evidence of bias in the density estimates from the trail-based deployment of camera traps and the other to check the accuracy of density estimates from different combinations of trail and the random cameras.

2.2.8 Calibrating biases in trail based SECR design

To check the different propensity of males and females in using trails, we compared the density estimates from camera deployments at 100 trail stations ('100T') and at 100 random stations ('100R'), given by four different models: 'deployment' (***D ~ 1, g0 ~ deployment, σ ~ sex***), 'sex' (***D ~ 1, g0 ~ sex, σ ~ sex***), 'interaction' modelling the interaction between sex and deployment (***D ~ 1, g0 ~ deployment * sex, σ ~ sex***) and the null model (***D ~ 1, g0 ~ 1, σ ~ sex***). Here 'deployment' refers to mode of camera trap deployment in the field, which is either trail or random, while 'sex' is either male or female or unknown. We compared each of these models for their AIC, and the Likelihood Ratio Test (LRT) was performed between nested models (i.e., between interaction model versus deployment model, interaction model versus sex dependent model, interaction versus null model, deployment versus null model and sex dependent versus null model). Compatibility of model comparisons was performed prior to the LRT and AIC comparison using function AICcompatible, an inbuilt model function of secr package. This model comparison is used to compare the density biases in SECR caused by the differences in detectability of males and females on the trail. All the models were constructed on maximum likelihood-based hybrid mixture model, keeping sigma dependent on sex constant as we have prior information regarding differences in the home range of males and females in case of felids.

We evaluated how the use of a trail-only deployment biases the overall density estimates of felids from SECR. For this we compared the density estimate from trail deployment (100T) with the reference full deployment of 100T + 100R stations. The density was estimated from the null model for both trail deployment and the combined deployment ***(D ~ 1, g0 ~ 1, σ ~ 1).*** This helps us to test the hypothesis that trail-only surveys are negatively biased because they miss some individuals in the population (referred to as 'ghost individuals') that never, or very rarely, use trails, in particular females. Our hypothesis was supported if the density estimate from combined deployment is greater than the density estimates from trail deployment (100T

+ 100R > 100T) and rejected if it is otherwise (100T ≥ 100T + 100R).

For evaluating the sex-dependent density bias from the trail deployment of camera traps, we compared the density estimates from the trail deployment between the null model ***(D ~ 1, g0 ~ 1, σ ~ 1)*** and the sex-dependent model ***(D ~ 1, g0 ~ sex, σ ~ sex)***. We accepted our hypothesis if the density estimate of sex model was greater than the null model (100Tsex > 100Tnull) and rejected if it is otherwise (100Tnull > 100Tsex). For testing density estimates from a single sex, we ran the secr null model twice, firstly using males only from the trail deployment, and secondly using females only from the random deployment, and each time doubling the resultant estimate (based on prior findings that most males in our study are caught on trails and most females off trails, and assuming a 1:1 sex ratio). We calculated the activity range (in km^2) of male and female captures from trail and random deployments using formula $\boldsymbol{\pi (\sigma \sqrt{5.99})^2}$ (Royle et al., 2013), where $\boldsymbol{\sigma}$ is the scale parameter interpreted as radius of bivariate normal model of space use, and the product ($\boldsymbol{\sigma \sqrt{5.99}}$) gives the 95% of space used by individuals from the home range centre. The value under the root corresponds to the square of distance between home range centre and the trap location in a Gaussian encounter probability model having chi-square distribution with 2 degree of freedom (i.e., for $\alpha = 0.05$ corresponds to $\sqrt{5.99}$) (Oberosler et al., 2022).

2.2.9 Effect on accuracy of density estimates from random and trail deployment of camera traps

We constructed a total of 14 models for each species, to compare density estimates obtained by sampling different combinations of trail and random deployments. The first eleven models were the standard models provided in the secr package (Efford & Efford, 2022; Zimmermann & Foresti, 2016). The remaining three models included the *sex* of individuals as a covariate. The standard secr models were: 1) ***M0***— basic null model which assumes the detection probability is constant throughout the study area; 2) ***MK***— the detection probability is specific for specific site (site learned responses); 3) ***Mk***— the detection probability is specific for the specific site (site transient response); 4) ***Mb***— the detection of individuals is affected by a learned response from first detection: trap happy or trap shy; 5) ***MB***— individuals becomes trap happy or trap shy due to a transient response to a preceding detection (influenced by last independent capture); 6) ***Mt*** — all the individuals have equal detection probability for particular detection occasions but the probability of detection differs for every occasion; 7) ***MT***— there is linear trend in baseline detection probabilities over occasions; 8) ***Mbk***— the individual detection is affected by the learned response from first detection and

detection probability is specific for the specific site; 9) ***MBk***—as ***"MB"*** but the effect is limited to specific sites; 10) ***Mbt***— a change in behaviour follows after the animal is caught once, resulting in a different detection probability for each occasion; 11) ***Mh2*** — the finite mixture model in which individuals have heterogenous detection probabilities.

The models with individual covariates (in this case 'sex') recorded from the survey were fitted with the hybrid mixture model, which enables accounting for missing information on sex for some individuals (Efford & Efford, 2022; Zimmermann & Foresti, 2016). The sex-dependent models were: 12) ***g0sex_sigma***— the detection probability varies for males and females; 13) ***g0sex_sigmasex***— sex affects the baseline detection probability and the scale parameter; 14) ***g0_sigmasex***—sex affects the scale parameter, and 15) a null model. The prefix of all model specifications represents the species: CL for clouded leopard, L for leopard, LC for leopard cat and MC for the marbled cat (for example CL_M0 represents the null model for clouded leopard). The sex ratio is derived from the sex-based model, which used sex ratio ('pmix') as a function of detection.

We selected maximum-likelihood models for density estimation using Akaike's Information Criterion (AIC) (Zimmermann & Foresti, 2016). The models were compared by calculating the delta AIC (Δ_i) and models with $\Delta_i < 2$ was selected for density estimation (Bumham & Anderson, 2002). The models with $\Delta_i > 2$ were dismissed even though models with Δ_i of 2-7 is described as considerably less support -(Burnham et al., 2011). For more than two models with $\Delta_i < 2$, We performed model averaging to estimate the density (Zimmermann & Foresti, 2016). We present the top models amongst the 11 standard models in secr, and the top models including the sex of individuals, given that this was a focus of our hypotheses in this study.

We estimated densities of clouded leopard with Bayesian SECR using SPACECAP package version 1.1.0 in R (Gopalaswamy et al., 2012). We prepared the animal detection file containing individual IDs, location and capture occasion from the spatial detection history file created by camtrapR package. The trap deployment file containing trap IDs, location and deployment record was prepared from the camera deployment, monitoring and retrieval records maintained during fieldwork. We prepared the buffer containing mesh spacing which represents the potential activity centres of the clouded leopard (Penjor et al., 2018). The distance between these equidistant points was set to 0.25 km to enable fine-scale modelling of their actual home ranges from camera trap data (Gopalaswamy et al., 2014). We executed 60,000 Markov chain Monte Carlo (MCMC) iterations with the first 10,000 discarded as burn-in and no thinning. The data augmentation value was set to 240, which was ten times the

number of identified individuals (Penjor et al., 2018; Petersen et al., 2020). We used a half-normal detection function and a Bernoulli process for the encounter rate (Noss et al., 2012; Piña-Covarrubias et al., 2022).

2.2.10 Effect of detector randomization on accuracy of density estimates

To evaluate the effect of camera trap placement on the population density estimates, we estimated density from two scenarios representing common alternative constraints on camera-trap deployments – limited availability of traps or limited availability of stations, which enforce different combinations of camera traps and camera stations. The reduced sample size scenarios for these simulations were chosen using the random number generator function of Microsoft Excel. We generated three consecutive random numbers corresponding to sampling grid cell's number, and the average of the three was taken as the sample for the density estimation following different combinations of random and trail stations.

The first scenario was based on a total availability of 100 camera traps (a constraint of equipment), with density estimates from the 100 camera traps placed at trail and random deployment in the following alternative combinations: paired cameras at 50 trail deployment; paired cameras at 33 trail plus single cameras at 34 random deployments (totalling 67 deployment stations); paired cameras at 25 trail plus single cameras at 50 random deployments (totalling 75 deployment stations); paired cameras at 12 trail plus single cameras at 76 random deployments (totalling 88 deployment stations); full random deployment (100 random deployment stations).

The second scenario was based on a total available sampling effort of 100 grid-cells (a constraint of time/human resources) for trail and random deployment of camera traps. We estimated density from deployments with the following alternative combinations of camera traps in 100 grid-cells: paired cameras at 100 trail stations plus single cameras at 100 random stations (full deployment, totalling 300 cameras at 200 stations, two stations per gid cell); paired cameras at 100 trail stations (full trail deployment, totalling 200 cameras, one per grid-cell); paired cameras at 75 trail stations plus single cameras at 25 random stations (totalling 175 cameras at 100 stations, one station per grid-cell); paired cameras at 50 trail stations plus single cameras at 50 random stations (totalling 150 cameras at 100 stations, one station per grid-cell); paired cameras at 25 trail stations plus single cameras at 75 random stations (totalling 125 cameras at 100 stations, one station per grid-cell). Comparison of the density estimates from these alternative combinations will inform future deployments on the influence

of camera trap placements on sex-based detectability and the trade-offs between precision and accuracy of estimation.

2.3 Results

Seven different species of wild felids were recorded in the study area. These comprised the three big cats: clouded leopard (*Neofelis nebulosa*), common leopard (*Panthera pardus*) and tiger (*Panthera tigris*), and four smaller cats: Asiatic golden cat (*Cattopuma temmeckki*), leopard cat (*Prionailurus bengalensis*), marbled cat (*Pardofelis marmorata*) and jungle cat (*Felis chaus*). Of these seven, one of the stations recorded six (Asiatic golden cat, clouded leopard, common leopard, jungle cat, leopard cat, marbled cat and tiger). We could not proceed with further analysis of jungle cat data due to limited captures from the study site. The camera traps detected two morphs of common leopard: common spotted morph and melanistic (Eizirik et al., 2003), and six morphs of Asiatic golden cat: cinnamon, golden, grey, melanistic, ocelet and rosette (Nijhawan et al., 2019).

The survey recorded 25 unique individuals of clouded leopard, 18 common leopards, 105 leopard cats, 47 marbled cats and 5 tigers from the study area. Except for clouded leopard and tiger, we observed male biased captures in the trail-only deployment, which reduced when random and trail stations were combined as shown in Figure 2.4. Moreover, the trail deployment captured most of the males present in the study area leaving few individuals to be captured in the random-only deployment. Male felids were captured with the following frequencies on trail vs random-only deployments: clouded leopard 10:1, common leopard 7:0, leopard cat 43:5, marbled cat 22:0, tiger 2:1. These figures raise the expectation of a good estimate of male population density from the trail deployment (Figure 2.4). In contrast, the individuals captured at the random deployment were mostly females even though this deployment recorded less animals compared to the trail deployment except for tiger (female captures on trail-only vs random deployments: clouded leopard 4:5, common leopard 2:6, leopard cat 15:18, marbled cat 7:10, and tiger 1:1) as shown in Figure 2.4. These figures suggest that females use both trail and off-trail habitats, in contrast to males avoiding off-trail habitat. For all species, trail-only and random-only deployments both miss some individuals, but the trail-only misses particularly females even though it captures more total individuals as shown in Figure 2.4.

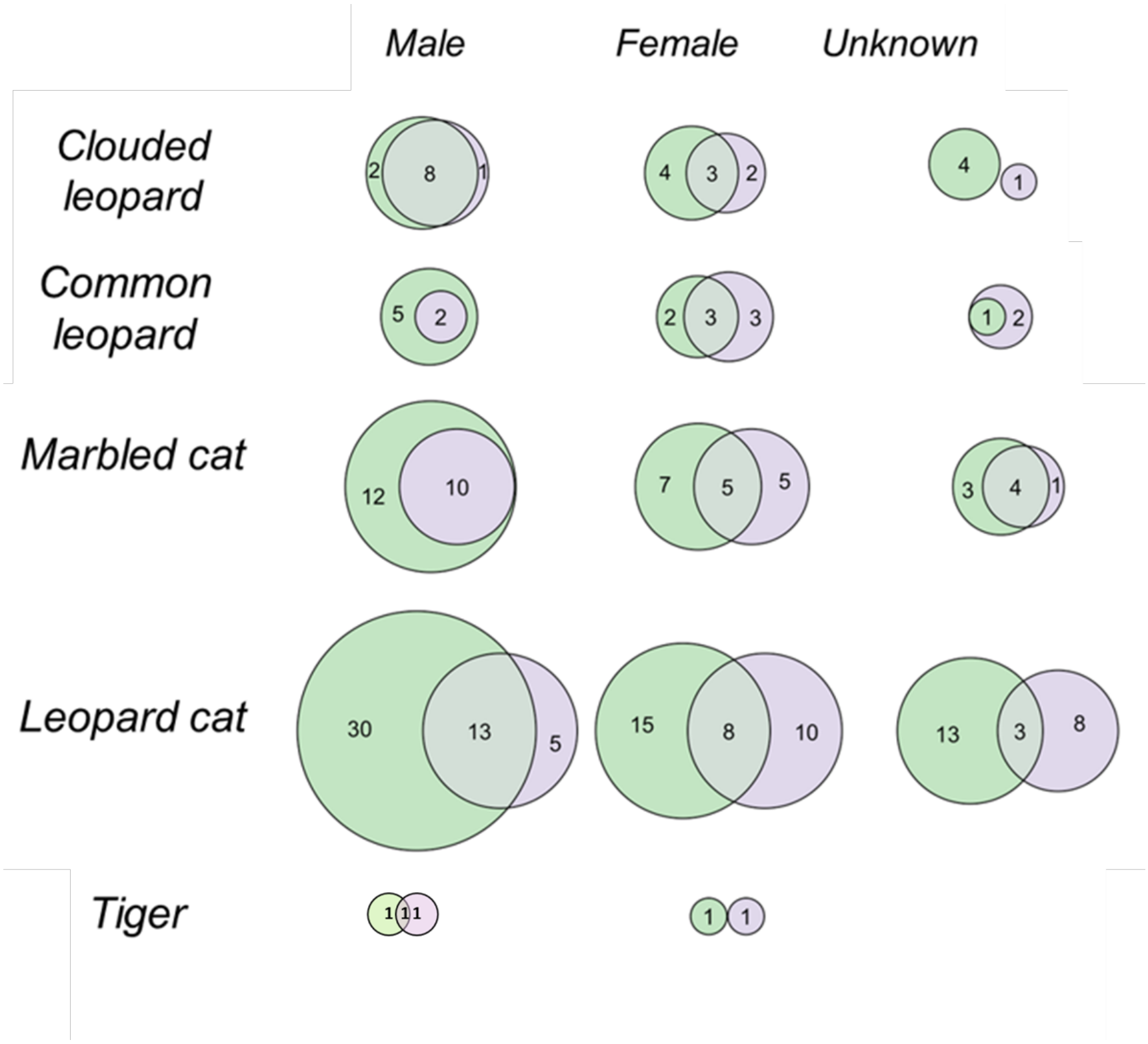

Figure 2.4. Euler's plots showing individuals of different species of wild felid detected in only trail (green), only random (purple) and in both the trail and random (overlap) deployments. Different sexes of individuals detected are shown for each combination of camera stations. Unknown represents individuals whose sex could not be identified. E.g., for common leopard the M:F ratio in trail cameras is (5+2) :(2+3) and in random cameras is (0+2):(3+3).

There were higher numbers of male than female detections (number of times an animal came into contact with the detector camera traps) in the trail deployment for common leopard (8 male and 4 female detections), leopard cat (121 males and 52 females) and marbled cat (56 males and 16 females) (Figure 2.4). More female-biased detection was observed from random deployment for clouded leopard (2 females and 1 male), common leopard (20 females and 0 males), leopard cat (36 females and 15 males), and marbled cat (9 females and 0 male) (Figure 2.4). This further corroborates the finding that the males of these felid species favour trail habitat and the females favours the random habitat. The study design where the trail

deployment is supplemented with the random deployment improves the sex biases in detection as seen in random plus trail deployment in Figure 2.5 for all the cat species except tiger.

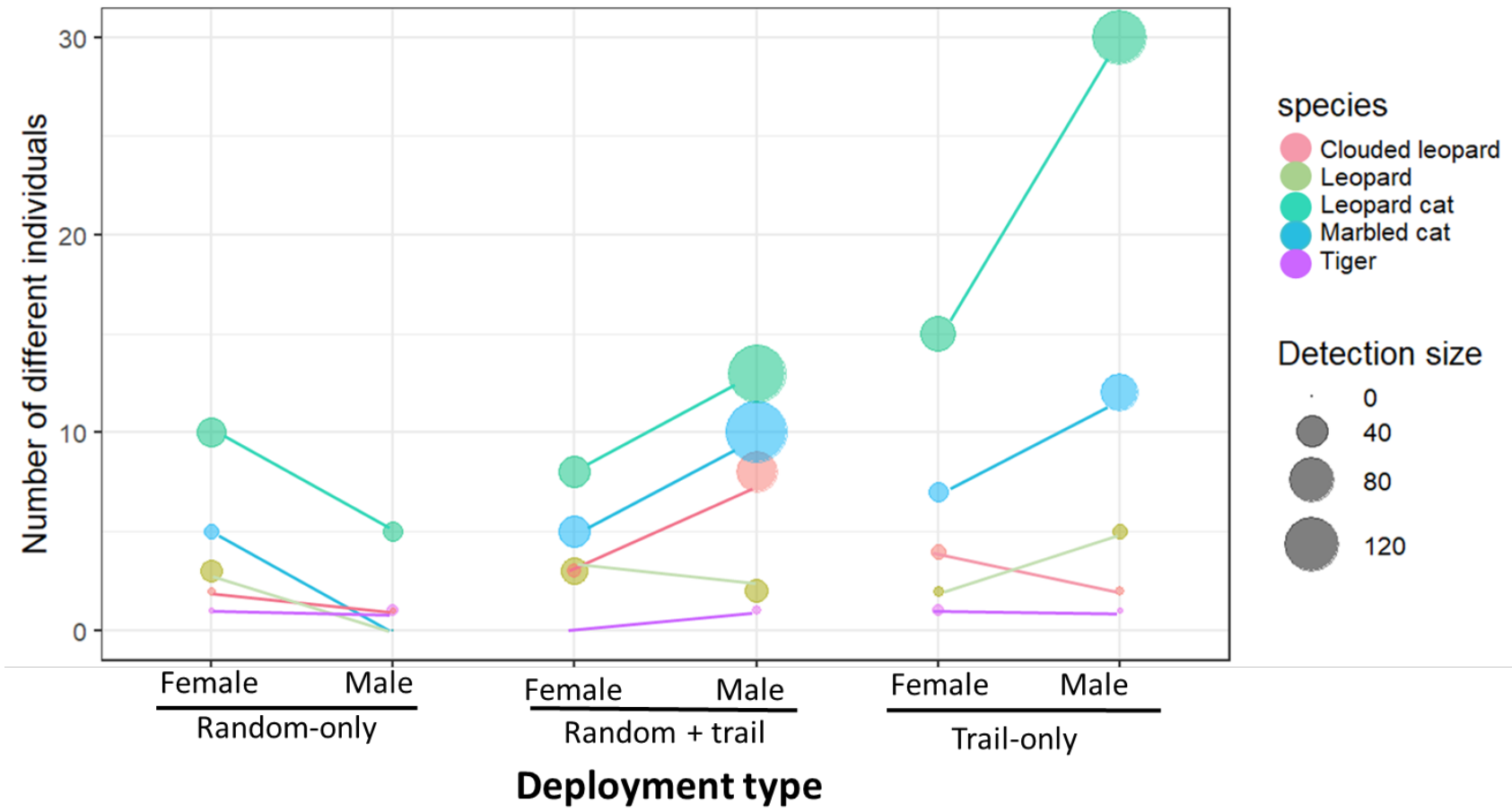

Figure 2.5. Numbers of individuals of each sex of felids recorded in the random-only, trail-only, and random plus trail deployments. The different colours represent different species of felids, and the size of the bubbles corresponds with the total number of detections (number of times an animal came in contact with the camera).

2.3.1 Propensity for trail use by male and female felids

The LRT between deployment (trail, random), sex (male, female), their interaction, and null model reveals that the interaction between deployment and sex is influential in explaining population density for all species except the common leopard (Table 2.1). This interaction signals the presence of heterogeneity in detection of males and females in the trail and random locations as indicated in Figs 2.4-5 above. This detectable interaction corroborates the findings from the frequency analysis of males favouring trails and females favouring off-trail habitats. We observed differences in the density estimates from these models, albeit small. For the clouded leopard the density estimate for the null model is 6% lower than the interaction model (Table 2.1, Figure 2.6), slightly underestimating density, which is expected whenever there is unexplained heterogeneity in capture probability in a capture-recapture model. The density estimate of common leopard from the null model is 5% lower than the

interaction model. Similarly, the density estimates of tiger from the null model is 4% lower than the interaction model (Table 2.1, Figure 2.6). The smaller density difference for large cats and the null model giving higher estimates for smaller cats (leopard cat and marbled cat, Table 2.1, Figure 2.6) may be due to the inclusion of random cameras in the full deployment.

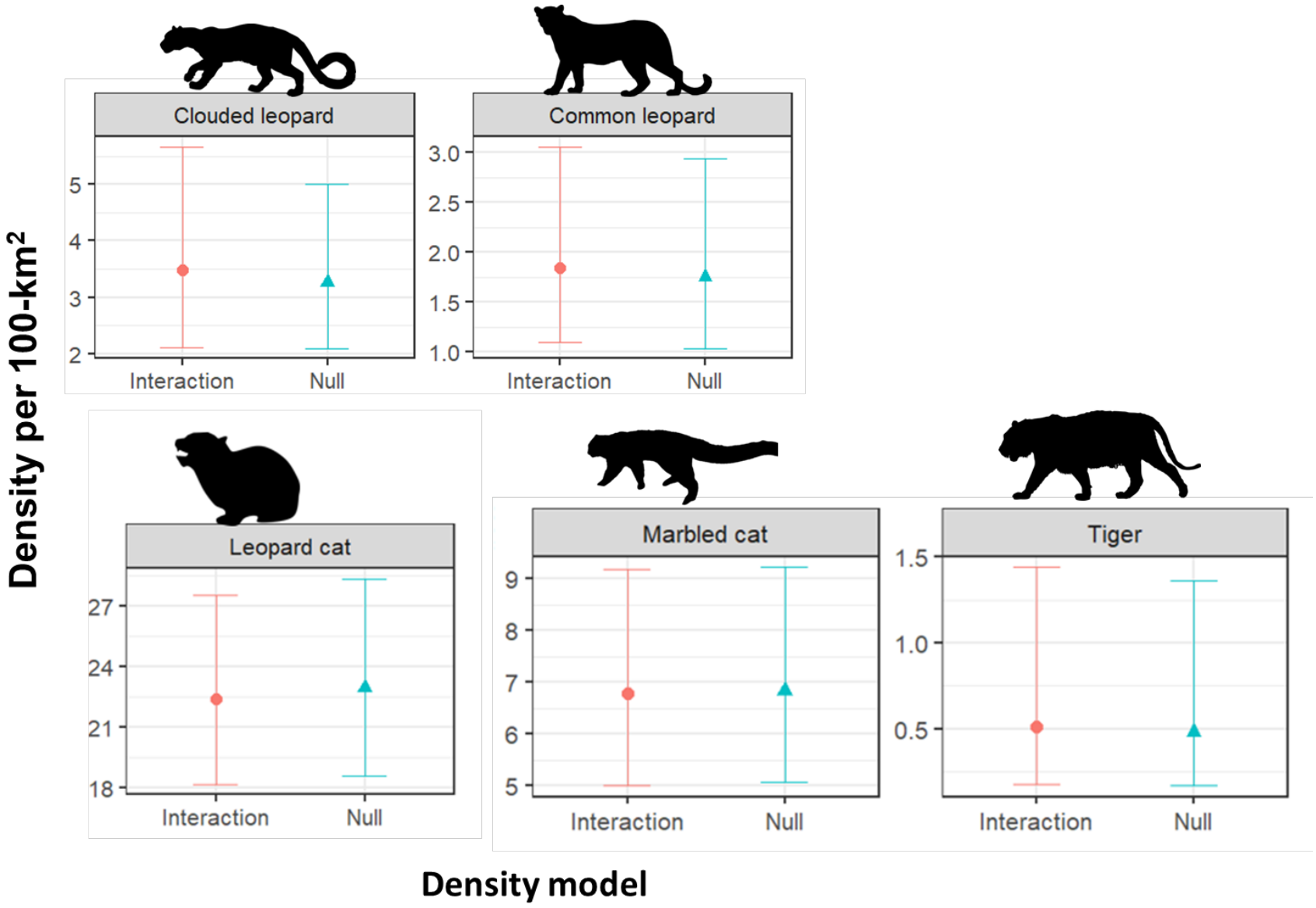

Figure 2.6. Density estimates of felids from interaction (sex * deployment) and the null secr model from the full deployment (100T + 100R). The red dot represents interaction model, and the cyan triangle represents the null model. The error bar represents the 95% confidence interval.

Inclusion of the random deployment might have helped to balance out the heterogeneity due to more capture of females from the random deployment. We tested for this effect by comparing interaction estimates from the full (100T + 100R) deployment with null estimates from the trail-only deployment (100T). Figure 2.7 shows a relative underestimation of population density from trail-only deployments that don't account for sex, for clouded leopard, common leopard and marbled cat, but not for leopard cat. The density estimate of clouded leopard from 100T is 28% lower (2.5 individuals per 100-km^2) than the interaction model (3.48 individuals per 100-km^2) as shown in Figure 2.7. For the clouded leopard, it can be recommended from this study that a deployment that combines random and trail cameras is less prone to underestimate population density than a trail-only deployment, even from null-

model estimates (estimates 6% lower than the full model with interaction, Table 2.1, Table 2.2). Alternatively, modelling sex-dependent detection for a 100T deployment (estimates 8% lower than full deployment with interaction model, Table 2.1, Table 2.2) can present an acceptable trade-off when there are adequate female captures in the sample. However, the best approach (as indicated by the LRT tests in Table and AIC in Table S1 appendix 1) is to use both random and trail cameras and model the interaction between sex and camera placement. For leopard there was weak evidence that trail-based surveys are inherently biased, as the LRTs do not give strong support to either the sex or the interaction model (Table 2.1) and AIC (Table S1 appendix 1).

The leopard cat showed no evidence of density underestimation our two simple tests for ghost individuals and unmodelled heterogeneity (Figs 2.6 and 2.7), despite the interaction model fitting better than either the sex or the deployment models (Table 2.1) and AIC (Table S1 appendix 1). We might risk overestimating leopard cat density without accounting for sex or placement dependency. The marbled cat showed weak evidence of density underestimation in the trail-based deployment, which was 11% lower than the estimate from the interaction model on the full deployment (Figure 2.7). The combination of trail plus random cameras and a null model can be recommended, producing a 1% density overestimation compared to the interaction model on the full deployment, Table 2.1). As for the clouded leopard, we can estimate density with the sex model using a trail-only study design but, as for clouded leopard, the trail-only deployment risks under-sampling females.

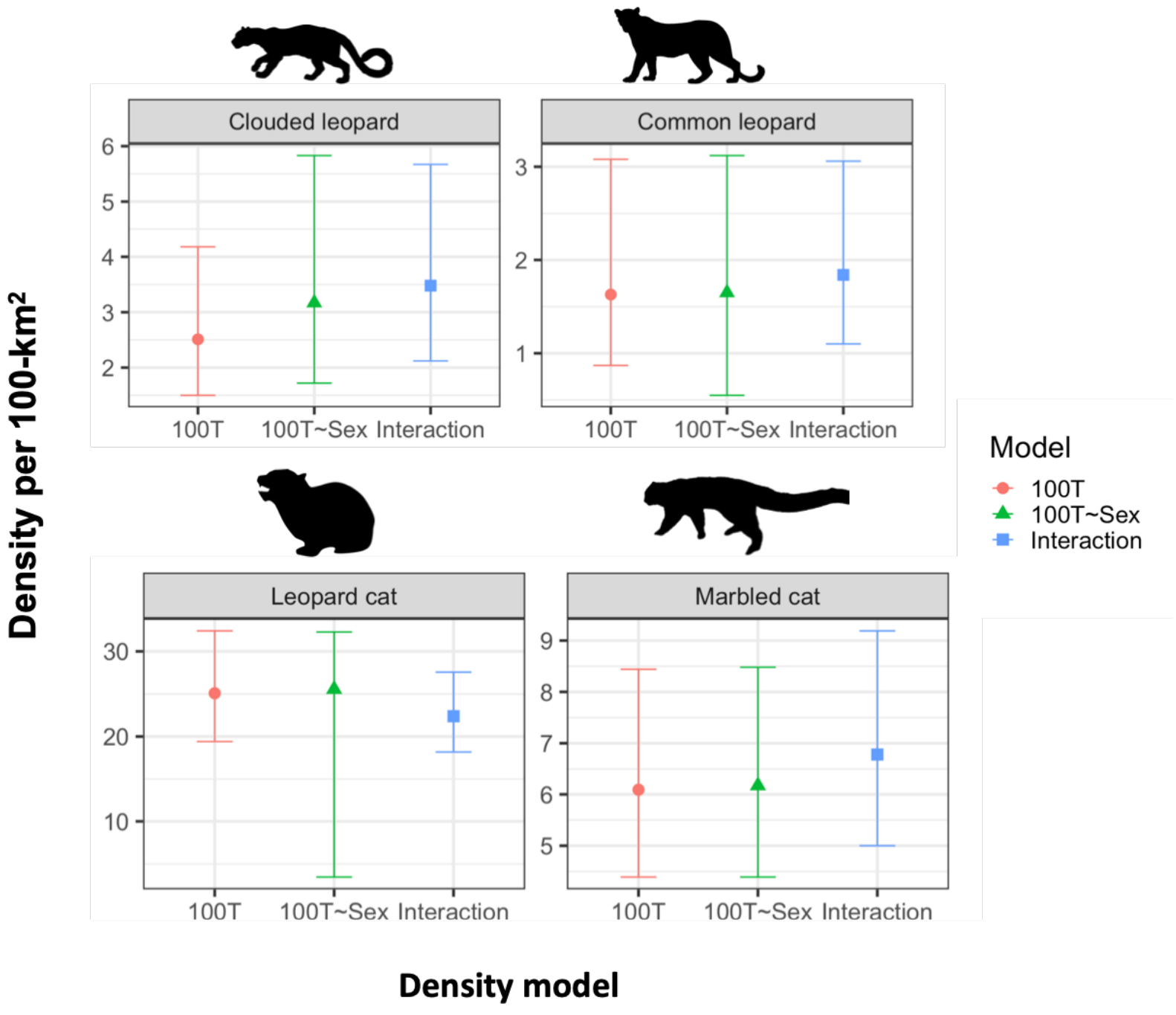

Figure 2.7. Density estimates and 95% CI of felids from the null model of 100 trail stations (100T, red dot), sex dependent model (100T~Sex, green triangle), and the interaction model (deployment*sex, blue square) from the full deployment (100T + 100R).

Table 2.1. *P*-values from Likelihood Ratio Test (LRT) for density estimates of felids from four models: deployment (random, trail), sex (male, female), interaction and null applied to the full 100T+100R deployment. For example, the LRT of clouded leopard with interaction versus (Vs) deployment model has *p*-vale = 0.017, indicating that the interaction model fits better than the deployment model. Grey areas encompass models that are not comparable with each other. $\widehat{D}$ is the density of felids per 100-km^2, UCL and LCL are lower and upper 95% confidence limits. In the model specification, we kept the scale parameter ***sigma ~ sex*** constant for all the models with prior information about difference in the home range of male and female felids.

Vs	Deployment	Sex	Null	$\widehat{D}$ **(LCI– UCI)**
		Clouded leopard		
Deployment			0.004	3.26 (2.11 – 5.03)

Sex			0.006	3.48 (2.12 – 5.69)
Interaction	0.017	0.012	0.001	3.48 (2.12 – 5.67)
Null				3.27 (2.12 – 5.03)
Common leopard				
Deployment			0.34	1.76 (1.04 – 2.96)
Sex			0.30	1.84 (1.11 – 3.07)
Interaction	0.03	0.31	0.33	1.84 (1.1 – 3.06)
Null				1.75 (1.04 – 2.95)
Leopard cat				
Deployment			0.00	22.94 (18.55 - 28.36)
Sex			0.00	22.40 (18.20 - 27.58)
Interaction	0.00	0.00	0.33	22.38 (18.18 - 27.56)
Null				22.96 (18.57 - 28.39)
Marbled cat				
Deployment			0.00	6.83 (5.06 – 9.21)
Sex			0.03	6.79 (5.01 – 9.21)
Interaction	0.02	0.00	0.00	6.78 (5.0 – 9.19)
Null				6.84 (5.07 – 9.23)
Tiger				
Deployment			0.00	0.48 (0.69 – 1.37)
Sex			0.47	0.49 (0.17 – 1.42)
Interaction	0.73	0.14	0.22	0.50 (0.17 – 1.43)
Null				0.48 (0.17 – 1.36)

2.3.2 Ghost individuals and density bias from trail-only deployment

We observed difference in density estimates from trail and random deployment when modelled without accounting sex specific detection. The density estimate of clouded leopard from random deployment was slightly higher compared to that from trail deployment. Whereas for the common leopard, the density estimate from random deployment was 23% higher than the trail deployment. The density estimates for the leopard cat and the marbled cat from trail deployment were higher than those from random deployment (56% higher for the leopard cat and a 24% higher for the marbled cat). The difference in the density estimates from trail-only and random-only deployments shows that some 'ghost' individuals are missed from the trail cameras (mostly females) while others are missed from the random cameras (mostly males) leading to differences in density estimates (Figure 2.8). This also supports our overall hypothesis *H4: Reduced-effort survey designs (either fewer camera traps used or fewer sampling sites) would show reduced precision but designs including some randomly placed cameras would be more accurate than those only containing trail-based cameras* for felid species except for the leopard cat. For tiger we could not compute the density difference between random-only and trail-only deployment due to the smaller sample size.

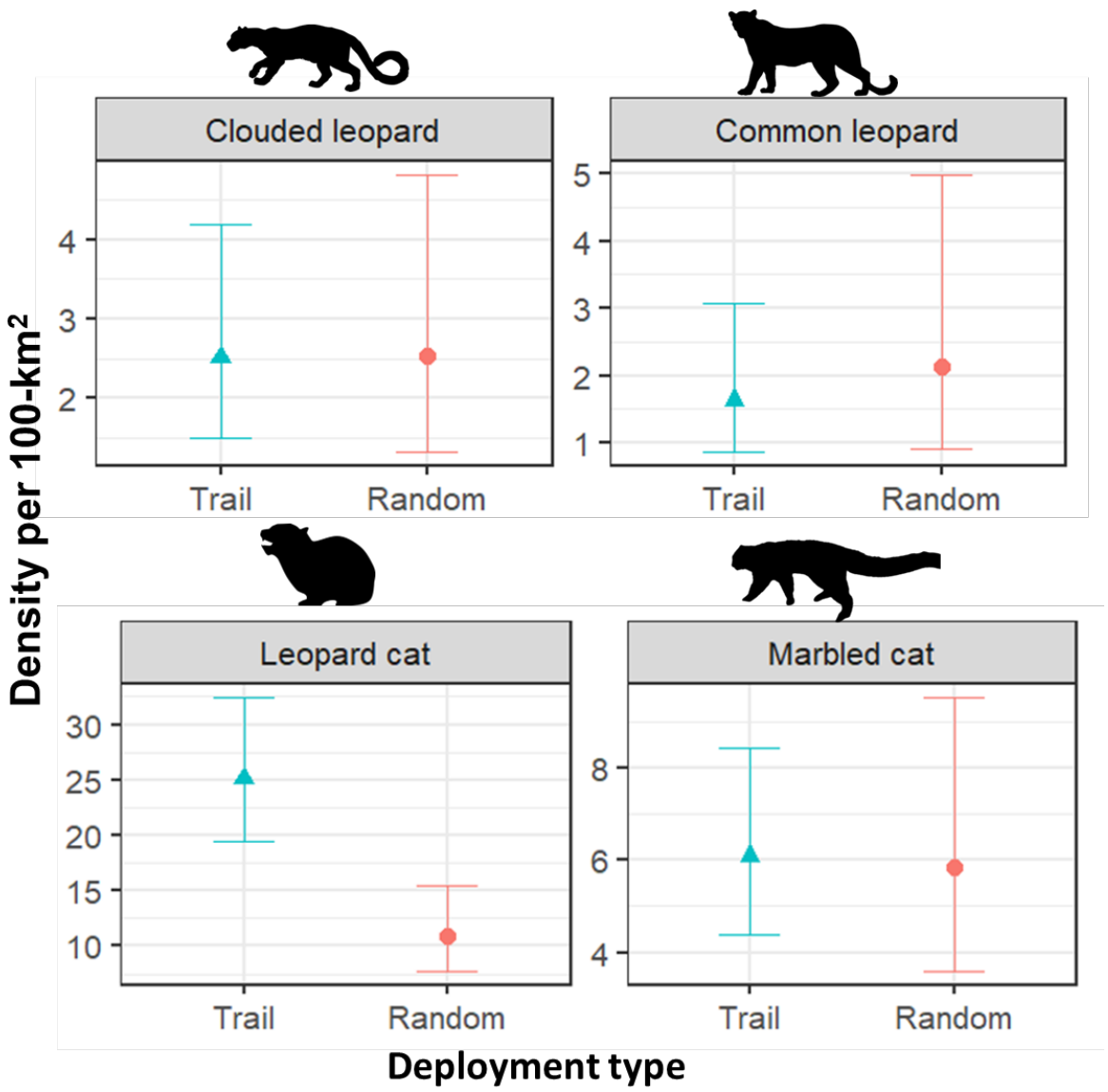

Figure 2.8. Density estimates and 95% CI of felids from the null model for trail-only deployment (100T), represented by cyan triangle, compared to the random-only deployment (100R), represented by red dot.

2.3.3 Unmodelled heterogeneity and bias in density estimates

We observed that ignoring sex-dependent detection leads to under estimation of density from the trail (100T) deployment. The density estimates of clouded leopard from the null model applied to the trail deployment is 22% lower than the sex-dependent model (Table 2.2). Similarly, the density estimates of common leopard from the null model applied to the trail deployment is 12% lower than the model sex (Table 2.2). For smaller cats, the density from the sex model performs better but the difference is smaller than the big cats (Table 2.2). It was observed in the previous section that inclusion of random deployments raises density estimates. The density estimates of felids from the combined deployment (100T +100R) is higher than the trail-only deployment for clouded leopard, common leopard, and marbled cat, supporting the hypothesis that trail-based surveys are negatively biased because they miss some individuals in the population that never, or very rarely, use trails (Table 2.3). This supports our hypothesis *H3: Failing to account for sex-dependent use of trail or off-trail would underestimate density estimates, due to unaccounted for heterogeneity in detection*

probability. For leopard and marbled cat, there are small density differences (Table 2.2), which weakly supports the hypothesis (Table 2.4).

Table 2.2. Comparative density estimates of cats from trail-based (100T) null and sex-dependent model of full trail deployment (100T), and the null model from the full deployment (100T + 100R).

Species	Dataset	Model	Density
Clouded leopard	100T	Null	2.51 (1.5 – 4.18)
Clouded leopard	100T + 100R	Null	2.73 (1.77 – 4.21)
Clouded leopard	100T	Sex-dependent	3.48 (2.12 – 5.69)
Leopard	100T	Null	1.63 (0.87 – 3.08)
Leopard	100T + 100R	Null	1.83 (1.1 – 3.06)
Leopard	100T	Sex-dependent	1.84 (1.11 – 3.07)
Leopard cat	100T	Null	25.08 (19.41 – 32.42)
Leopard cat	100T + 100R	Null	21.8 (17.72 – 26.83)
Leopard cat	100T	Sex-dependent	25.58 (19.61 – 32.97)
Marbled cat	100T	Null	6.08 (4.39 – 9.52)
Marbled cat	100T + 100R	Null	6.7 (4.96 – 9.06)
Marbled cat	100T	Sex-dependent	6.79 (5.01 – 9.21)

The detection probability of males was higher compared to females from both the random and trail deployments except for common leopard and marbled cat (Figure 2.9). More detection of males can be due to territorial behaviour of male compared to the females. The higher probability of detection of females over males for common leopard is an unexpected result (as observed in Figure 2.9).

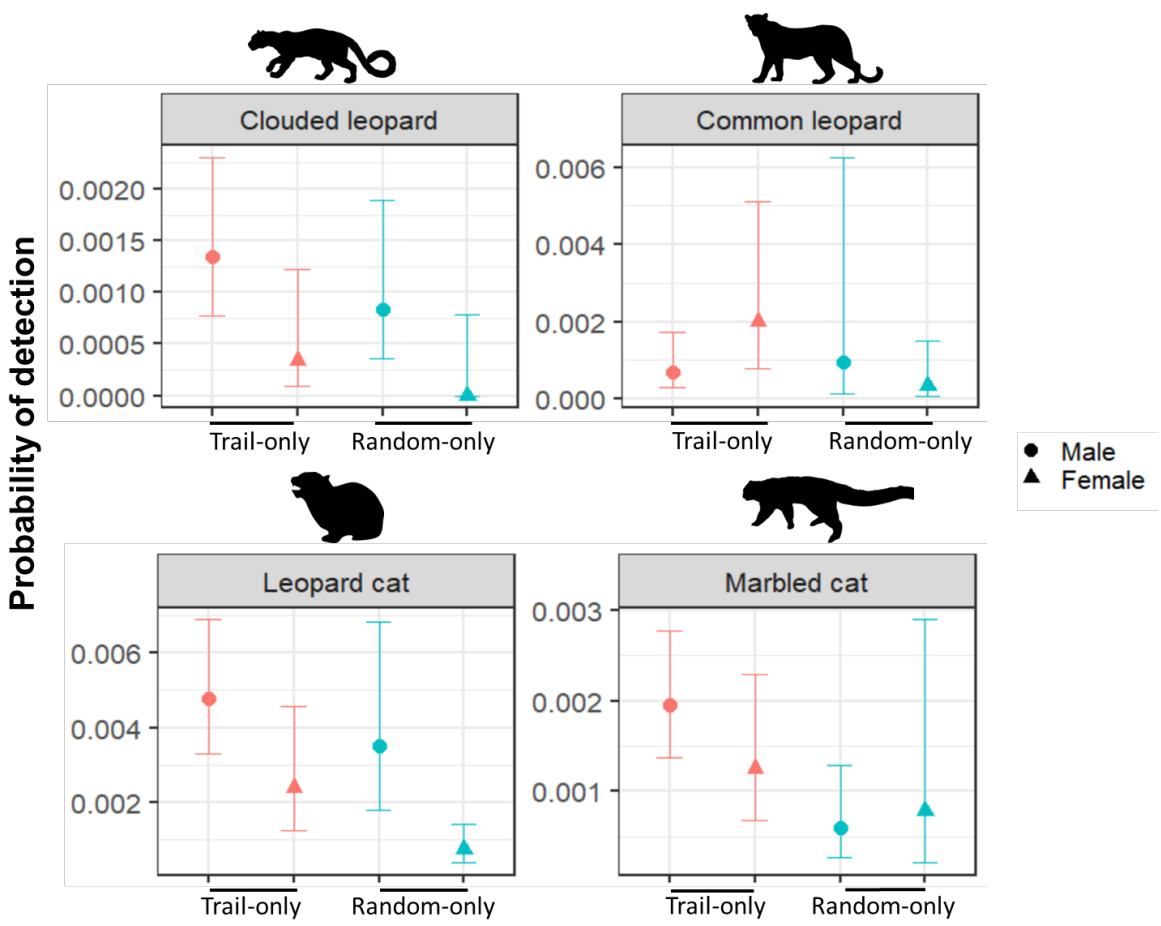

Figure 2.9. Detection probabilities and 95% CI of male and female felids from trail only (100R) and random only deployment (100T). Red colour represents trail deployment and the cyan represents the random deployment. Similarly, dot represents male and the traingle represents the female.

Table 2.3. Summary of hypotheses testing comparative density estimates from combined deployment (100T + 100R) and trail-only deployment (100T) for felids.

Species	Hypothesis	Expected result	Actual result	Conclusion
Clouded leopard	Trail-based surveys are negatively biased because they miss some individuals in the population that never, or very rarely, use trails	Density estimates from a design including random cameras are higher than a trail-only design (i.e., $D_{100T+100R} > D_{100T}$)	$D_{100T+100R} > D_{100T}$	**Hypothesis supported**
Leopard			$D_{100T+100R} > D_{100T}$	**Hypothesis supported**
Leopard cat			$D_{100T+100R} < D_{100T}$	Hypothesis not supported
Marbled cat			$D_{100T+100R} > D_{100T}$	**Hypothesis supported**

Table 2.4. Summary of hypotheses testing comparative density estimates from null model and sex-dependent model of trail-based deployment (100T) for felids. Where D~sex corresponds to the influence of sex (male, female) on detection probability and the sigma. D~null represent the null model.

Species	Hypothesis	Expected result	Actual result	Conclusion
Clouded leopard	Sex-dependent heterogeneity in detection leads to negative bias in density estimates from trail-based surveys when it is not accounted for.	Models that neglect sex-dependent detection yield lower density estimates than those that do account for it (i.e., $D_{sex\text{-}dependent} > D_{null}$)	$D_{sex\text{-}dependent} > D_{null}$	**Hypothesis strongly supported**
Leopard			$D_{sex\text{-}dependent} > D_{null}$	Hypothesis weakly supported
Leopard cat			$D_{sex\text{-}dependent} > D_{null}$	Hypothesis weakly supported
Marbled cat			$D_{sex\text{-}dependent} > D_{null}$	Hypothesis weakly supported

2.3.4 Estimating population density from a single sex

Population density estimation using data from a single sex generally yields more reasonable results for males from the trail deployment than for females from the random deployment (Table 2.5). This is to be expected given the paucity of ghost males not caught in the trail deployment. The method provides an option for density estimation where captures are heavily male biased and random deployment is not possible. However, male-only estimation tends to underestimate population density, being 28% lower for clouded leopard, and 16% lower for common leopard, compared to the reference full deployment (Table 2.5), although very similar for the marbled cat. For the common leopard, the density is overestimated by 11% compared to the reference density, which may be due to the larger number of males in the trail deployment.

Table 2.5. Single-sex population density (individuals per 100-km^2) estimation, using males from the trail-only deployment (100T), and females from the random-only deployment (100R). Density x 2 represents the population estimate after doubling the single-sex density on the assumption of a 1:1 sex ratio; reference density is the estimate from the full deployment using the interaction model (100T + 100R). All density estimates (and 95% CL) are from the null model. For female clouded leopard, the model did not converge.

Species	Sex	Density estimate	Density x 2	Reference density
Clouded leopard	Male	0.86 (0.38 – 1.91)	1.72	2.73 (1.77 – 4.21)
Common leopard	Male	0.77 (0.38 – 1.9)	1.54	1.83 (1.1 – 3.06)
Leopard cat	Male	12.22 (8.87 – 17.02)	24.44	21.8 (17.72 – 26.83)
Marbled cat	Male	3.32 (2.13 – 5.14)	6.64	6.7 (4.96 – 9.06)
Clouded leopard	Female	-	-	2.73 (1.77 – 4.21)
Common leopard	Female	1.12 (0.35 – 3.55)	2.24	1.83 (1.1 – 3.06)
Leopard cat	Female	3.43 (2.02 – 5.82)	6.86	21.8 (17.72 – 26.83)
Marbled cat	Female	1.79 (0.96 – 3.36)	3.58	6.7 (4.96 – 9.06)

2.3.5 Sex-differences in home ranges of felids

As hypothesized, female tend to show smaller home range sizes compared to males, in both trail and random deployments, except for leopard cat and marbled cat from the trail deployment (Figure 2.10). This likely reflects the localized activity pattern of female felids for nursing cubs and avoiding infanticide from males, and also the reduced need to maintain a large territory to ensure mating success. The female activity range of clouded leopard is 38% lower than the male ranges from the random deployment and 6% lower from trail deployment (Figure 2.10). For common leopard, the home range of female is 39% lower than male from random and 64% lower from trail deployment. This reflects male leopards being trail users,

with their larger home ranges attributable to greater dietary needs and ranging in search of mates. The activity range of male marble cats is 63% higher than the females. The change in the sigma, which determines the activity range of individual species for different combination of trail and random deployments are shown in Figure S2-S5 appendix 1 of the supplementary information. Overall, this supports our hypothesis, *H2: Females show more localized patterns of detection than males and a smaller apparent home-range than males*.

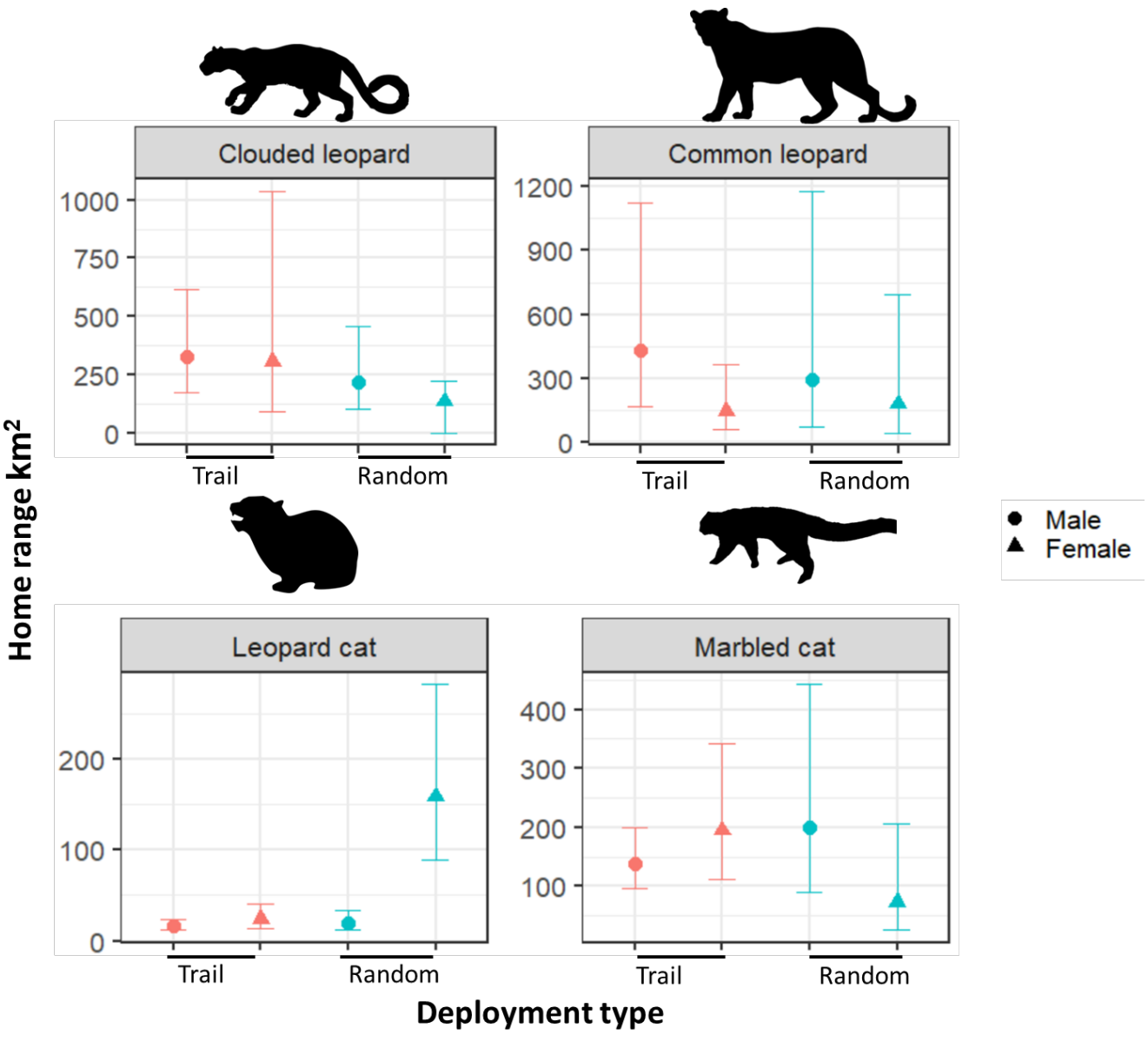

Figure 2.10. Sex-specific home ranges of felids from trail only (100T) and random only deployments (100R). The dot represents (activity range) in km^2 of male and triangle represents the activity range of female from trail only and random only deployment. Red colour represents trail only deployment and the cyan represents random only deployment. The error bar represents the lower and upper 95% confidence interval.

2.3.6 Density of felids in the study area

We used the full deployment (100T + 100R) for comparing density estimates of felids in the study area by Bayesian and MLE approaches. The density estimates of clouded leopards by the Bayesian approach, which does not account for effect of sex on detection probability and

sigma, was 3.14 ± SE 0.59 individuals /100-km^2. From the density estimates of clouded leopards by the maximum-likelihood approach, the finite mixture model ***CL_Mh2*** (heterogenous detection probabilities) has the lowest delta AIC (Δ_i) and therefore best explains the data, as shown in Table 2.6. The density estimates of clouded leopards from all camera stations (trail plus random stations) was 3.50 ± SE 0.96 individuals /100-km^2. Of the models accounting for sex-based differences in capture probability, **CL_g0sex_sigma** (effect of sex on baseline detection probability), and **CL_g0sex_sigmasex** (effect of sex on baseline detection probability and scale factor) best describe the data. As both models have delta AIC (Δ_i) < 2, the density estimate from model averaging was 3.50 ± SE 0.91 individuals /100-km^2. This estimate does not differ detectably from those of models that do not account for sex (Table 2.6), or from the Bayesian estimates, with confidence intervals (CI) of each mean encompassing the other mean, where each confidence limit (CL) extends to ~1.96 SE either side of the mean.

Comparison of the maximum-likelihood density estimates across the four cat species (Table 2.6) shows them increasing in inverse proportion to their body sizes. From all cat species, density estimate is highest for leopard cat, which might have been favoured by small body size and availability of easy prey. Each species had density estimates that did not differ detectably between no-sex and sex-based models but did differ detectably between the species. The lack of influence of sex indicates that the inclusion of random stations may suppress a sex-bias otherwise present in the trail stations. This possibility is fully explored in the next section.

Table 2.6. Density estimates of clouded leopard, common leopard, leopard cat and marbled cat based on maximum likelihood models incorporating latent covariates and the sex covariates. The camera trap combination 100 T +100 R identifies the full deployment of paired cameras at 100 Trail stations and single cameras at 100 Random stations (totalling 300 cameras at 200 stations in 100 contiguous grid-cells each of 2x2 km). The models presented are the best-fitting models for the species, as determined by smallest delta AIC (dAIC). The no-sex model does not account sex-based effect on detection probability and sigma, whereas the sex-based models assume an effect of sex on detection probability and sigma. *K* is the number of estimated parameters; density is the number of individuals per 100 km^2, with SE in brackets.

Station Combination	Species	Model	model specification	*K*	logLik	AICc	AICwt	Density
100 T + 100 R	Clouded leopard	No sex	CL_Mh2	5	-279.31	571.78	0.93	3.5 (0.96)
		Sex	CL_g0sex_sigma	5	-292.12	597.4	0.71	3.5(0.91)
	Common leopard	No sex	L_M0	3	-237.20	482.24	0.67	1.8(0.48)
		Sex	L_g0_sigmasex	5	-243.94	503.34	0.59	1.7(0.47)
	Leopard cat	No sex	LC_Mh2	5	-648.57	1307.7	1.00	26.4(2.6)
		Sex	LC_g0sex_sigmasex	6	-701.82	1416.5	1.00	24.4(2.3)
	Marbled cat	No sex	MC_Mh2	5	535.57	1082.6	1	7.7(1.2)
		Sex	MC_g0sex_sigma	5	-581.14	1173.7	0.64	6.8(1.06)

2.3.7 Effect of detector randomization on density estimates

Modelling total availability of 100 camera traps

Full random deployments yielded the highest density estimates for clouded leopards from model Mh2 model no sex (without consideration of influence of sex on the baseline detection probability and sigma). The highest density from sex model was combination of 12 trail and 76 random deployments (Table 2.7, Table S2 appendix 1). Sex model from full random deployment estimated unrealistically high density for clouded leopard (Table S2 appendix 1). The unrealistically high density estimates from the sex-based model may result from an estimated 93% ± 12% of detections being female in this deployment. Higher detections of females at random locations indicates a preference for off-trail movement by females, which contributes to their underrepresentation in the trail-only deployment. The paired cameras at 100 trail deployment obtained slightly lower density estimates from no-sex and much lower from sex-based models (Table 2.8). Similar to random-only deployment, the sex ratio is skewed towards females in the trail-only deployment with 62% ± SE 13% female detection

compared to males 38 ± SE 13%. Accuracy of the density estimates improves with more randomization of the stations as shown in Table 2.7 for the combination of 25 trails and 50 random stations even without accounting the sex as a detection covariate.

Table 2.7. Density estimates of clouded leopard, common leopard, leopard cat and marbled cat from different combinations of trail (T) and random (R) deployment, given a total availability of 100 camera traps. The T + R combination identifies the number of trail stations with paired cameras and random deployments with single cameras. The models presented are the best-fitting models for the deployment, as determined by the lowest AIC (Table S2 appendix 1). Parameters are as for Table 2.6.

Deployment combination	**Model**	**Species**	Model specification	**Density**
50 T + 0 R	No sex	Clouded leopard	CL_M0	3(1.09)
		Common leopard	L_M0	1.2(0.75)
		Leopard cat	LC_M0	16.1(3.3)
		Marbled cat	MC_M0	6.01(1.1)
	Sex	Clouded leopard	CL_g0sex_sigma	3.4(1.46)
		Common leopard	L_g0_sigmasex	1.3(0.82)
		Leopard cat	LC_g0_sigmasex	17.4(4.1)
		Marbled cat	MC_g0_sigmasex	5.98(1.1)
33T + 34R	No sex	Clouded leopard	CL_M0	1.3(0.52)
		Common leopard	L_Mk	4.49(5.6)
		Leopard cat	LC_M0	22.7(3.8)
		Marbled cat	MC_MBk	6.9(2.2)
	Sex	Clouded leopard	CL_g0sex_sigmasex	1.2(0.51)
		Common leopard	L_g0sex_sigmasex	6.12(5.8)
		Leopard cat	LC_g0sex_sigmasex	23.0(4.5)
		Marbled cat	MC_g0_sigmasex	6.18(1.4)
25T + 50R	No sex	Clouded leopard	CL_M0	3.6(0.98)
		Common leopard	L_M0	0.85(0.4)
		Leopard cat	LC_M0	10.1(2.0)
		Marbled cat	MC_Mh2	8.86(1.9)
	Sex	Clouded leopard	CL_g0_sigmasex	5.28(2.5)
		Common leopard	L_g0sex_sigma	0.85(0.4)
		Leopard cat	LC_g0sex_sigmasex	12.0(2.6)
		Marbled cat	MC_g0_sigmasex	9.31(2.0)
12T + 76R	No sex	Clouded leopard	CL_M0	2.93(0.9)
		Common leopard	L_M0	2.40(1.0)
		Leopard cat	LC_Mh2	15.27(2.96)
		Marbled cat	MC_Mh2	7.97(1.6)
	Sex	Clouded leopard	CL_g0_sigmasex	9.92(9.4)
		Common leopard	L_g0_sigmasex	5.68(4.0)
		Leopard cat	LC_g0_sigmasex	13.8(2.3)
		Marbled cat	MC_g0sex_sigma	6.82(1.2)
0T + 100R	No sex	Clouded leopard	MC_Mh2	4.0(1.99)

	Common leopard	L_M0	2.11(0.9)
	Leopard cat	LC_Mbk	18.7(6.4)
	Marbled cat	MC_M0	17.6(5.6)
Sex	Clouded leopard	CL_g0sex_sigmasex	3.8(9.33)
	Common leopard	L_g0sex_sigma	2.43(1.3)
	Leopard cat	LC_g0sex_sigmasex	11.7(2.1)
	Marbled cat	MC_g0_sigmasex	6.48(1.80)

For density estimates of common leopards from full trail deployment, the no-sex model obtained highest estimates from 12 trail plus 76 random stations, whereas the sex-based model obtained highest estimates from 33 trail plus 34 random stations (Table 2.7). The full random deployment obtained higher estimates than were obtained from 50% trail deployment (Table 2.7). In this respect and as for the clouded leopard, the no-sex model from the full random deployment appeared to outperform the sex-based model from the full trail deployment (Table 2.7, Table 2.8). Like clouded leopard, there are more detection of females than males in full random deployment, of all individuals detected at full random deployment 88% ± SE 11% and 12% ± SE 11% are males. The ratio is reversed for deploying a paired camera at full trail deployment, with 52% ± SE 17% males and 48% ± SE 17% females. Putting camera traps at trail-only location might produce male-biased density estimates. As shown in Table 2.7, deploying a paired camera at 25 trail station and a single camera at 50 station estimates precisely wrong density compared to the other combinations.

Similarly for density estimates of leopard cats from 100 cameras, both the no-sex and the sex-based models obtained highest estimates from 33 trail plus 34 random deployment (Table 2.7), and closest to the estimates from full deployment (Table 2.6). Full random deployment of 100 cameras obtained a higher no-sex estimate than the sex-based estimate obtained from 50 trail deployment, even though the sex-based estimate from the full trail deployment exceeded the no-sex estimate (Table 2.8). In effect, if we assume that the full random deployment was unbiased, it out-performed a full trail deployment that attempts to account for known bias with a sex-based model. Unlike for clouded leopard and common leopard, the sex dependent model output revealed higher proportion of male's detections than females for full random and full trail deployments. Of all the detections at full random locations, 62% ± SE 0.09% were males and 38 ± SE 0.09% were female detections Likewise, there were more detections of males at 59% ± SE 0.08% than females at 41% ± SE 0.08% for a full trail deployment (Section 3.7.2). The higher detection frequencies of males in the case of the leopard cat can be attributed to its smaller size and home range. The grid size was specifically designed for clouded leopard having larger home range.

The density estimates for marbled cat were higher for a full random deployment (Table 2.7) than for 50 trail deployments (Table 2.7). However, the full random deployment yields very much higher SE and correspondingly wider CI, leading to less precise and unrealistically high estimates compared to the trail-only deployment (and compared to full deployment in Table 2.6). As with the clouded leopard and common leopard, the full random deployment yielded more detections of females than males, with 59% females ± SE 0.13% and 41% ± SE 0.13% males. In contrast, the full trail deployment yielded more males than females, with 64% ± SE 0.13% males and 36% ± SE 0.08% females (Section 3.7.2). Similar to clouded leopard and the common leopard, the accuracy of the density estimates of marbled cat in relation to the full deployments improve with randomization of camera deployment as shown in Table 2.7. The detailed simulation for different combination of trail and random camera traps are shown in Table S2-S10 in appendix 1.

Modelling total availability of 100 grid cells

We further compared four different combinations of trail and random stations examining the effect on the density estimates of clouded leopard, common leopard, leopard cat and marbled cat, given a total availability of 100 grid cells (Tables 2.8).

With availability of 100 grid cells, full trail-based deployment yielded the highest density for clouded leopard from a model that does not account for sex-based detection (Table 2.8). While considering sex-based detection, the 75 trail plus 25 random deployments yielded the highest density estimates as shown in the bottom row of Table 2.8. The limit of 100 grid cells provides an opportunity to deploy camera traps across a larger area compared to that available for a limit of 100 cameras (except for the random-only deployment). The density estimates were slightly higher for most of the station combinations with the 100-cell limit than the estimates from the 100-trap limit, unsurprisingly since more stations allow more individual detections (Table 2.8).

For the common leopard, density estimates slightly increased with more randomization of camera stations. The highest density estimates for both no-sex and sex-based models were obtained from 50 % random and trail deployments. Even with a 100-camera limit, deploying more cameras at random stations yielded higher density estimates than deploying camera traps over a larger area of 100 grid cells. Distributing 100 cameras 12 trail and 76 random deployments yielded 2-fold higher density estimates compared to distributing 150 cameras across 75 trail 25 random deployments, as shown in Table 2.8.

The density estimates of leopard cats were highest from a full trail deployment for both

without sex and sex-based models (Table 2. 8), higher than for all estimates with the 100-camera limit (Table 2.7) and close to the estimate for full deployment (100T +100R). Deploying more cameras over a wider portion of the study area allowed detection of more individuals, resulting in higher density estimates, for this smaller cat species, in contrast to the larger cats.

As with the larger-sized cats, for the marbled cat the density estimates from the 100-cell limit (Table 2.8) showed little difference to those from the 100-camera limit (Table 2.7), with all reasonably close to estimates from the full deployment (Table 2.6). The highest density estimates were obtained from 75 trail plus 25 random deployments, with both the no-sex and sex-based models. The estimates from the100-cell limit tended to have smaller SEs than those from the 100-camera limit, reflecting the larger sampling area. The detailed simulation for different combination of trail and random camera traps are shown in Table S2-S10 in appendix 1.

Table 2.8. Density estimates of clouded leopard, common leopard, leopard cat and marbled cat from different combination of trail (T) and random (R) cameras, given a total availability of 100 grid cells. The T + R combination identifies numbers of trail deployments with paired cameras and random deployments with single cameras. Parameters as for Table 2.6. The density for 0T + 100R is same as for Table 2.7.

Deployment combination	**Model**	**Species**	Model specification	**Density**
100T + 0R	No sex	Clouded leopard	CL_Mh2	5.7(1.47)
		Common leopard	L_M0	1.63(0.5)
		Leopard cat	LC_M0	25.0(3.2)
		Marbled cat	MC_Mh2	6.15(1.1)
	Sex	Clouded leopard	CL_g0sex_sigma	3.1(0.97)
		Common leopard	L_g0sex_sigmasex	1.64(0.5)
		Leopard cat	LC_g0sex_sigma	25.5(3.4)
		Marbled cat	MC_g0sex_sigma	6.11(1.0)
75 T + 25 R	No sex	Clouded leopard	CL_Mh2	4.56(2.3)
		Common leopard	L_M0	1.6(0.5)
		Leopard cat	LC_Mh2	22.2(3.1)
		Marbled cat	MC_Mh2	8.01(1.6)
	Sex	Clouded leopard	CL_g0_sigmasex	9.61(1.2)
		Common leopard	L_g0sex_sigmasex	1.6(0.52)
		Leopard cat	LC_g0_sigmasex	21.8(3.0)
		Marbled cat	MC_g0sex_sigmasex	6.68(1.1)
25T + 75R	No sex	Clouded leopard	CL_M0	2.83(0.9)
		Common leopard	L_M0	1.41(0.5)
		Leopard cat	LC_Mbk	14.0(4.8)

		Marbled cat	MC_Mh2	6.25(1.1)
	Sex	Clouded leopard	CL_g0sex_sigmasex	2.50(1.6)
		Common leopard	L_g0sex_sigmasex	2.36(1.1)
		Leopard cat	LC_g0_sigmasex	11.9(2.3)
		Marbled cat	MC_g0_sigmasex	5.9(1.05)
50T + 50R	No sex	Clouded leopard	CL_M0	2.57(0.7)
		Common leopard	L_M0	2.9(0.96)
		Leopard cat	LC_Mh2	23.6(2.6)
		Marbled cat	MC_Mh2	7.27(1.6)
	Sex	Clouded leopard	CL_g0sex_sigmasex	3.30(0.9)
		Common leopard	L_g0sex_sigmasex	2.90(0.9)
		Leopard cat	LC_g0sex_sigmasex	22.40(2.3)
		Marbled cat	MC_g0sex_sigma	6.08(1.1)
0T + 100R	No sex	Clouded leopard	MC_Mh2	4.00(1.99)
		Common leopard	L_M0	2.11(0.9)
		Leopard cat	LC_Mbk	18.7(6.4)
		Marbled cat	MC_M0	17.6(5.6)
	Sex	Clouded leopard	CL_g0sex_sigmasex	3.80(9.33)
		Common leopard	L_g0sex_sigma	2.43(1.3)
		Leopard cat	LC_g0sex_sigmasex	11.70(2.1)
		Marbled cat	MC_g0_sigmasex	6.48(1.80)

2.4 Discussion

We assessed the presence of detection heterogeneity between sexes of wild felids and its influence on density estimates. We found differences in detectability of males and females between trail and random deployments of camera traps. The difference in the density estimates from random and trail deployments was analysed for all big cats (clouded leopard, common leopard, and tiger) and small cats (leopard cat and marbled cat) in the study area. These differences in density estimates suggest a widespread presence of heterogeneity in the detection probability of animals within the sampled area. This is problematic for felid monitoring generally, which often assumes that all individuals have an equal chance of detection by camera traps or other detectors (Foster & Harmsen, 2012). Heterogeneity in detection probability generally lowers the reliability of abundance estimates (Harmsen et al., 2010; Piña-Covarrubias et al., 2022). The current methods do allow for variation in detectability through covariates or finite mixture models, but the question remains as to whether these statistical fixes deliver sufficient accuracy (Madsen & Royle, 2023). Our comparison of random to trail-based deployments allowed us to test the equal-capture assumption, and thereby to explore the causes of bias in abundance estimates. Our interpretations are inevitably constrained by not knowing the actual composition of felids in

the area any better than could be surmised from the full deployment of both trail based and random cameras. It would be informative in future work to run simulation models of captures in different deployments for populations of known compositions.

Male skewed detection in trail deployment was observed for all the cat species except for clouded leopard and tiger (albeit the latter had a very small sample size). This propensity for males to be captured on trails leaves few male individuals to be detected only at random stations. In contrast, several females were detected only at random stations, and fewer were detected only at trail stations. Male preferences for trails and females for off-trail habitat are observed in other cat species, including the jaguar (Harmsen et al., 2020; Montalvo et al., 2023). Males tend to minimize their energetic costs by using linear features such as natural trails, mountain ridges and rivers, which may also maximize probability of prey encounters (Harmsen et al., 2010; Wearn et al., 2013). Females on the other hand tend to avoid such features to avoid conflicts with larger males and other females whilst raising their cubs (Singh et al., 2014). A study of the European wildcat (*Felis silvestris silvestris*) revealed that females tend to select better habitat, avoiding human-disturbed and linear features such as paved roads, water sources and areas with higher tree canopy cover (Oliveira et al., 2018). Although studies have noted preferences of big cats for walking on trails instead of dense forest that are presumed as traditional route of big cats later modified into roads or trails (Di Bitetti et al., 2006; Penjor et al., 2019), and trail behaviour is observed even in captivity (Smith et al., 2023), little empirical evidence exists on sex-based preferences for linear features. Our study supports sex-specific use of trail and off-trail location by wild cats.

Our analyses of the simultaneous trail-based and random deployments revealed the presence of an interaction between sex and deployment type. Failing to include the sex-specific detection in a density model leads to underestimation of densities. The assumption of equal capture probabilities of all animals within the study area (Pollock, 1982) is the main source of bias in density estimates from trail deployment of camera traps (Otis et al., 1978; Pledger & Efford, 1998). We observed improvement of density estimates from models of sex-specific detection combined with inclusion of random (off-trail) camera traps that reduced detection heterogeneity by capturing more females. Others have previously reported that most studies on density estimates of big cats lack proper descriptions of study design and quality of data, and also lack information on numbers of individuals, different sexes and numbers of recaptures from which to estimate heterogeneity in the capture histories (Efford, 2014; Foster & Harmsen, 2012). Presence of features such as game trails, and linear features not only bias the estimates of wild felids, but also smaller animals including rodents (Kolowski &

Forrester, 2017). We recommend a mixed approach of camera trap study design which includes both trail cameras to accommodate trail dwellers and random camera traps to accommodate those animals preferring or using off-trail habitat. It is likely that the standard trail-based approach can be used for study design considering sex-based detection heterogeneity in the density estimation model but there is always risk that bias may become large.

Inadequate survey design in camera trap studies leads to variation in individual detectability and zero probability of capture of some individuals at their home range centre (ghost individuals) resulting in biased density estimates. In our study we observed that trail cameras missed capture of some individuals, mostly females, and random cameras missed males. A gridded survey design deploys camera traps inside grid cells of size based on extent of the animal's home range (O'Connell & Bailey, 2011). However, camera trap placement is not always consistent with the effective distance required for animal detection, failing to account for some individuals that are not trail users (Kolowski et al., 2021). We observed increase in density estimates for clouded leopard, common leopard, and marbled cat when combining capture histories from both trail and random deployment of camera traps, ascertaining presence of unrecorded individuals which we termed here as 'ghost' individuals. Differences in trail preferences were not only observed between sexes of the same species, but it also between species. Neotropical wild felids including jaguars and pumas occupying relatively similar niches likewise had different preferences for trails, with puma having a higher propensity to use trails and jaguars a higher propensity for off-trail movement (Harmsen et al., 2010).

Although a fully randomized design of surveys is the recommended ideal for biological field studies (Quinn & Keough, 2002), camera trapping is laborious and resource intensive, often requiring compromise in this assumption (Dickman, et al., 2015; Montalvo et al., 2023). Off-trail cameras moreover have reduced capture probabilities for some species, to the extent that density estimation from our random-only deployment was either not calculable or extremely imprecise for several cat species. Full randomization may miss more total individuals than are missed by the trail deployment of camera traps. We observed higher density estimates from full random deployment of camera traps compared to trail deployment for common leopard and marbled cat, with female biased captures. To mitigate over representation of one specific gender in the density estimate, we recommend coupling of random deployment along with the trail deployment. One way to balance the gender-specific bias in density estimates is to estimate male-only density from the trail deployment, or female-only density from the random

deployment, and double the density on the tentative assumption of a 1:1 sex-ratio based on Fisher's sex ration theory (Fisher, 1999). Our analyses suggested that this could work well in cases where there are more records of one sex, depending upon survey design.

We relied on sex-based models to improve the density estimates from trail-only stations, and these did improve the estimates for clouded leopard, common leopard, and leopard for both types of trail-only deployment (camera-limited 50T + 0R and cell-limited 100T + 0R), and for marbled cat for the cell-limited 100T +0R deployment. Our results parallel other studies where inclusion of sex as a covariate has improved density estimates compared to the density estimates derived from null models (Sollmann et al., 2011). The accuracy of the density estimates was further improved with the addition of a random deployment but using only a random deployment yielded too few captures for reliable density estimation. Using the full deployment of 300 cameras over 100 trails plus 100 random stations as a reference, density estimates from random-only deployments tended to be more accurate (i.e., closer to estimates from the full deployment) but less precise (i.e., larger 95% CI) compared to the estimates from trail-only deployments. To improve both the precision and the accuracy of density estimates, we recommend deployments that combine trail with random stations, and running simulations before proceeding with the field survey. Researchers can run simulations to explore the best combination of trail and random stations by providing dummy data of Density (D), detection probability (g0), and sigma. Such simulations can be run before conducting fieldwork, using freely available R packages including 'secr.design' (Efford & Efford, 2023) and 'oSCR' (Sutherland et al., 2019).

Extensive camera trapping fieldwork incurs huge costs in equipment, time, and human resource (Dickman, et al., 2015). Cost increases with the number of sampling units (Tarugara et al., 2019), and surveys involving estimation of animal abundance are mostly focused on trade-offs between number of sampling units and number of sampling occasions, without accounting for the influences on estimation accuracy caused by placement of the sampling units (Gálvez et al., 2016). For research areas of the size of our study area, availability of 100 camera traps can provide powerful density estimates if the survey design takes into consideration detection heterogeneity and proper simulation before conducting fieldworks. Our simulations with actual data from different combinations of trail and random camera deployment revealed that deployment of 100 camera traps across 50 trail stations and estimating SECR density with sex-dependent model yielded density estimates close to those from the combined deployment of 100 trails and 100 randoms (our reference density). This simulation also revealed that more randomization of camera traps, leaving few paired cameras

on trails, can yield density estimates similar to the reference density. The accuracy of the estimates was species specific with respect to the combination of trail and random camera deployments.

2.5 Conclusion

The density estimates derived from trail-based deployment produces substantial bias in estimating population density unless it considers the sex -specific heterogenous behaviour of wild cats. We determined species-specific tendencies for trail and off trail movement, which represent individual life history trade-offs and can influence the optimal design of camera trapping studies. We found strong evidence of male bias in trail-based density estimates, and female bias in random-based density estimates. We urge field researchers and conservation mangers to consider species-specific and sex-specific detection heterogeneity when estimating animal abundance and specifically when estimating wild cat densities with SECR. Advances in the sophistication of statistical packages for density estimation have enabled more flexibility for incorporating survey specific and site-specific covariates such as sex, randomness of deployment, which in our experience enhance the density estimates. We further recommend that inclusion of even a few randomly deployed trail cameras will likely enhance density estimates.

Chapter 3 Comparative density estimates of big cats and prey between methods for marked and unmarked individuals

Contributions

This chapter was initiated under guidance of my principal supervisor Professor C. Patrick Doncaster in collaboration with external supervisors Dr Oliver Wearn who worked as Senior Technical Specialist at Fauna & Flora International. I developed the aim and objectives of this chapter on prior recommendations by Dr Wearn and Dr Wai Ming Wong of Panthera International. I developed the fieldwork protocols, along with Dr Wearn, and with reviews from Professor Doncaster and Dr Wong. The fieldwork was supported by rangers from Jigme Singye Wangchuck National Park, Royal Manas National Park, and Wangchuck Centennial National Park under the Department of Forest and Park Services of Bhutan. Mr Kuenly Tenzin from World Wildlife Fund Bhutan project provided support by monitoring the fieldwork and providing field gears to the rangers. I managed the raw camera trap and camera calibration data with guidance from Dr Wearn, assisted by Miss Sonam Wangmo and Mr Kinley Dorji of Wangchuck Centennial National Park. I conducted analysis of data and results with help from Dr Wearn who was instrumental in debugging R codes and enhancing the results of the analysis. This chapter has led to the development of a nationwide protocol for surveying the prey of snow leopards, in collaboration with the Nature Conservation Division of Department of Forests and Park Services of Bhutan. I wrote the chapter, and Professor Doncaster and Dr Wean reviewed the draft versions.

Abstract

Capture-recapture estimation of animal abundance from camera trap photos of individuals with identifying marks favours only the few species that possess body markings revealing individual identities. However, the majority of wild animals are free from individually variable natural markings, requiring either capture for tagging, or an alternative approach for density estimation to conventional capture-recapture methods. Random Encounter Modelling (REM), Distance Sampling on Camera Traps (CTDS), Random Encounter and Staying Time (REST), space and time to event models (STE and TTE) and the instantaneous sampling estimator (IS) have recently become widely used methods of population-density estimation without individual identification. These methods can also address the issue that density estimates of wild cats from individual identification are often biased by rejection of a high proportion of photographs that lack sufficient clarity to identify individuals.

In this chapter, we estimated population densities of clouded leopard, common leopard, leopard cat, and marbled cat from REM applied to photo-captures from a deployment of 100 single camera traps across a 400-km^2 grid, positioned at the exact centre of each 2×2 km grid-cell to ensure random placement with respect to habitat. We compared the REM estimates with the most robust SECR estimates reported in Chapter 2, given by 100 paired trail-based cameras plus 100 randomly placed cameras with respect to habitat. In addition, we estimated the population density of the Asiatic golden cat with the REM protocol only, as golden cats lack the unique coat markings necessary for SECR estimates. We ran linear mixed-effect models (LLM) to assess the effect of REM parameters and species on the accuracy of REM estimates with reference to SECR. We further estimated population densities of six prey species and two sympatric carnivores found in the study area by implementing the REM protocol, to obtain comparative estimates from random and trail deployment of camera traps.

We observed overestimation of densities from REM for clouded leopard (3.6 times higher than SECR), common leopard (8 times the SECR estimate) and marbled cat (1.2 times the SECR estimate) compared to SECR estimates. For marbled cat REM estimates lay within SECR 95%-CI. Underestimation of density by REM was observed for leopard cat (1.5 times lower than SECR) compared to SECR ($p < 0.05$). LLMs revealed that conservative estimation of REM parameters can either increase or decrease the accuracy of REM estimates compared the estimates from SECR. Careful measurement of movement speed was found to be the most important determinant of REM accuracy for our survey, compared to detection zone and angle of detection. The REM density estimate for the Asiatic golden cat yielded 7.62.1± SE 3.6

individuals/100-km^2. Density bias for golden cat increased as the trail deployment expanded, in comparison to the estimate from the random-only deployment. Amongst prey species, muntjac was the most abundant, and gaur the least abundant in the study area. Dhole was the most abundant sympatric carnivore in the study area. This density comparison will help to validate the reliability of REM estimates and decisions regarding choice of techniques for studying populations of unmarked animals.

3.1 Introduction

Population estimation is fundamental to understanding the ecological processes and population dynamics of species in need of conservation and management (Engen & Saether, 2003; Schaub & Abadi, 2011). Individual identification is a prerequisite for most of the methods of population-density estimation using camera traps (Moeller et al., 2018). Estimation of the size of population using capture-recapture has been used since the 1980s, by constructing detection probabilities using-recapture and re-sighting of marked individuals in the population (Royle, 2004; Seber, 1982). The recent addition of spatially explicit capture-recapture methodologies has improved the conventional capture-recapture models (Moeller et al., 2018; Sollmann et al., 2011). These methods are restricted to tagged individuals, and to the few species with natural individually identifiable markings. Artificial tagging of individuals is ethically sensitive, requires high technical capacity, and defeats the non-invasive advantage of camera trapping (Palencia et al., 2022). Other methods involving genetic material are expensive and time consuming (Moeller et al., 2018; Palencia et al., 2022; Royle, 2004). To address these constraints, several alternative protocols for density estimation have been developed for unmarked animals without individually identifiable coat patterns (hereon referred to as unmarked animals). These include the N-mixture model by Royle et.al (2004), Random Encounter Model (REM, (Rowcliffe et. al., 2008), and more recently space to event (STE), time to event (TTE), and instantaneous sampling (IS) models (Moeller et al., 2018). To date there are nine different protocols including the capture-recapture studies for the estimation of abundance (Gilbert et al., 2021; Wearn et al., 2022). Comparative studies of these methods on different species have revealed inherent drawbacks to each (Twining et al., 2022). Genetic finger printing produces most precise density estimates compared to capture-recapture studies involving camera traps, but it is comparatively most expensive (Twining et al., 2022). The cross comparison of density estimates from other methods have produced ambiguous results (Balestrieri et al., 2016; Twining et al., 2022). We chose REM for our study as it is an increasingly widely used method for estimating density

for unmarked species, and it has been found that REM estimates produce useful information for species management (Cusack , et al., 2015b). REM was specifically developed for density estimation from camera-trap data (Rowcliffe et al., 2008; Wearn et al., 2022). In this chapter, we compare REM density estimates of four wild felids and their prey in Bhutan to the density estimates from Spatially Explicit Capture-Recapture (SECR) models obtained in Chapter 2.

For free-ranging Felidae, the detectability of individuals is usually low, due to low population densities, cryptic-elusive behaviours, avoidance of males by females while raising cubs, avoidance of humans, and habitat complexity, making it difficult to gather sufficient data for population estimation (Palencia et al., 2022; Wearn et al., 2022). The rising prevalence of camera trapping for monitoring wildlife reflects the promise of camera traps as a cost-effective sampling tool when compared to alternative monitoring tools for medium-to-large sized mammals and birds (Palencia et al., 2022; Wearn et al., 2022). Early remotely triggered camera traps were expensive items of equipment, but with advancements in sensor technologies they have become a relatively low-cost technology for capturing information on multiple species, making it possible to obtain information on highly cryptic species (Wearn & Glover-Kapfer, 2017).

Camera traps are used for diverse analytical purposes, encompassing studies of distribution, occupancy, animal behaviour and species richness (Burton et al., 2015; Gilbert et al., 2021). Publications on camera trap studies have shown an 81-fold increase since 1994, although the growth has slowed since 2017 (Delisle et al., 2021). Camera-traps studies of absolute abundance are most frequently focused on capture-recapture estimates, rather than unmarked approaches (Gilbert et al., 2021). Nevertheless, there has been a significant decline in studies centred on capture-recapture, and a recent decrease in spatial capture-recapture studies has also been observed (Delisle et al., 2021). In contrast, camera-trap studies are increasingly focusing on occupancy, interspecific interactions, and automated image classification (Burton et al., 2015; Delisle et al., 2021). Non-invasive capture-recapture studies are restricted to only species that have individually unique natural markings to allow recapture, such as spotted or striped coat patterns (Royle, 2004). To overcome this limitation, an increasing number of methodologies have been developed for abundance estimation without requirement for individual identity (Twining et al., 2022). Modelling site occupancy of species has become a reliable tool, which does not require individual identity, but occupancy models are merely studies of the distribution of animals, which do not account for population abundance (Twining et al., 2022). The Random Encounter Model was the first method for density estimation of unmarked animals from camera trapping, based on the animal's speed, its

proximity to the camera trap, and the camera detection zone (Rowcliffe et al., 2008; Wearn et al., 2022). REM uptake has remained low over the years, because of its requirements for randomly deployed cameras with respect to habitat, and a protocol for determining detection zone at each camera. Most camera-trap studies involve non-random placement of camera traps along animal trails, to maximise detection rates. REM also lacks capacity to incorporate site- and survey-specific covariates into estimates of animal densities (Wearn et al., 2022). However, multi-species applications of REM, combined with improvements in abilities to estimate the values of input parameters, have demonstrated that REM has high potential to yield information of value for species management (Swanson, et al., 2015; Palencia et al., 2022).

In this chapter, we used REM to compute density estimates of five wild cat species: Asiatic golden cat, clouded leopard, common leopard, leopard cat and marbled cat), two sympatric carnivores: Asiatic black bear (*Ursus thibetanus*) and dhole (*Cuon alpinus*), and six prey species: gaur (*Bos gaurus*), Himalayan goral (*Naemorhedus goral*), Himalayan serow (*Capricornis sumatraensis thar*), muntjac (*Muntiacus muntjak*), sambar deer (*Rusa unicolor*) and wild boar (*Sus scrofa*). This is the first-time density estimates using REM have been made for Asiatic golden cat, Asiatic black bear, mainland clouded leopard, common leopard, dhole and prey species including Himalayan goral, Himalayan serow, and gaur.

We compared our REM density estimates on individually marked felids with the densities estimated by Spatially Explicit Capture-Recapture (SECR) in chapter 2, to evaluate relative biases in density estimation from REM. Our first hypothesis ($\boldsymbol{H_1}$) is that the density estimates from REM can be biased when input parameters required for REM estimation (hereafter referred to as REM parameters) are compromised by variation in species-specific behaviours or by limitations in the capacity of field survey equipment to accurately measure REM parameters. Secondly, we investigated how density changes when an increasing number of trail-based cameras are introduced into the REM analysis. We hypothesized ($\boldsymbol{H_2}$) that inclusion of more trail-based cameras will positively bias the REM density estimates, since we expect that camera placement on trails is not random with respect to felid movement (typically, felids preferentially use trails). Additionally, we hypothesized that the density estimates from REM will be less precise compared to the density estimates from SECR for wild felids ($\boldsymbol{H_3}$) due to the uncertainty associated with each of the input parameters.

3.2 Methodology

3.2.1 Study areas and camera-trap sampling

We sampled 400 km^2 of Royal Manas National Park and Jigme Singye Wangchuck National Park in central-south Bhutan. The 400 km^2 was partitioned into 100 grid-cells each of 2 x 2 km, corresponding to the mean daily distance moved by clouded leopard and common leopard (Grassman, 2000) as detailed in the methodology section of chapter 2 (Figure 2.1). In each grid cell, a pair of camera traps were installed on an animal trail, at a location where there were signs of animal presence, and a single camera trap was installed at the exact centre of the grid cell, representing a random location with respect to the animal's habitat as followed in the section 2.2 of the chapter 2. Of all the 100 grid-cell centres, only 4 were located on an animal trail. We used Panthera V7 Xenon white-flash camera traps equipped with motion detection sensors. Panthera V7 camera traps can take up to 10 photos per second in burst mode during daylight, with a delay between each trigger that can be set from 0.3 to 10 seconds. We configured the cameras to take 3 photos per trigger during daylight, with a 1-second delay between every trigger. During hours of darkness, the cameras were configured to take a single photo per trigger, with a delay of 15-30 seconds to recharge the flash for the next capture. These widely dispersed nocturnal photographs are not suitable for the calculation of REM parameters, specifically the calculation of movement speed and activity level across the 24-hour period. The cameras were placed 30 cm above the ground to enable capture of all felid species, as well as their prey.

The camera traps were set to operate for 24 hrs/day for 3 to 5 months, with one battery revision after 60 days. This deployment of 300 cameras in 100 grid cells was active for 23,592 trap nights from 13th October 2020 to 5th May 2021.

3.2.2 Comparative density estimation with Random Encounter Modelling (REM)

We compared differences in REM density estimates between three types of camera deployment: trail-only (100T + 0R), random-only (0T + 100R) and a combination of trail and random (100T + 100R, hereon referred to as 'full deployment'), for five felid species (Asiatic golden cat, clouded leopard, common leopard, leopard cat and marbled cat) and six different prey species: gaur , Himalayan goral, Himalayan serow, muntjac, sambar deer and wild boar. Furthermore, we compared the density estimates between trail and random deployment for

two sympatric carnivores: Asiatic black bear and dhole. We ran the REM analysis for trail deployment even though REM assumes random deployment. We did this to understand biases introduced by non-random deployments, and the potential for REM to be used with the non-ideal study designs that are commonly used in camera-trap studies.

REM estimates the densities of unmarked animals based on random encounters between moving animals and the static passive detectors (camera traps), taking into consideration key variables that affect the animal encounter rate (Palencia et al., 2022; Rowcliffe et al., 2008). The key variables are the camera detection zone, determined from the radius and angle of detection by the camera trap, and the day range, measured as the daily distance travelled by the animal (Rowcliffe et al., 2008). With these key parameters, the density estimate is computed from the REM equation:

$$\boldsymbol{D = \frac{y}{t} \cdot \frac{\pi}{v \,.\, r.(2+\theta)}} \qquad \textbf{eqn 1}$$

Where $\boldsymbol{y}$ is the number of encounters, $\boldsymbol{t}$ is the total survey effort (measured by the total active time of the animal in front of detectors), v is the day range of the animal, and $\boldsymbol{r}$ and $\boldsymbol{\theta}$ are respectively the radius and angle of the camera detection zone (Palencia et al., 2021; Rowcliffe et al., 2008), referred to as 'REM parameters'. The structure of REM formula shows that $\boldsymbol{D}$ is equally sensitive to all three input parameters: $\boldsymbol{y/t}$, $\boldsymbol{v}$, r (i.e., changing any of these parameters by the same proportion will have the same proportionate effect on D, which is relevant to simulations shown in Table S1, appendix 2). Typically, the day range parameter is dissolved into two components – movement speed and activity level (the proportion of the diel period when a species is active and available for detection) – which are multiplied together in order to yield day range.

3.2.3 REM parametrization

We managed the raw camera-trap images using XnViewMp photo editor (https://www.xnview.com/en/xnviewmp/) by tagging each image with basic information including: species name, station number, deployment type, number of individuals in the photograph, and animal coming in first contact with camera trap (1 for first contact and NA for subsequent sequence of images that are tiggered by the animal coming in contact with the camera trap). We calibrated the Panthera V.7 camera traps as shown in Figure S1, Appendix 2 to define the intrinsic properties of the camera trap, which allowed us to calculate the position of objects of known size and the radial distance of the captured animals from the camera

(Palencia et al., 2021; Rowcliffe, 2021; Wearn et al., 2022). We calibrated each camera's field of view using a 1-m pole, graduated with a 10 cm section of two contrasting colours to measure the detection height of individual cameras. The details of the deployment calibration are provided in Appendix 2a.

We used an online image digitization tool (https://lauravzarco.github.io/animaltracker/) to digitize the animals captured by the camera traps and the pole positions for later measurement of the animal's position and speed, as shown in Appendix 2b. For each camera-trap photo sequence, the movement sequence of the animal was measured with the CTtracking set of functions in R (Rowcliffe, 2021). This tool was also used to measure detection distances, speed, and angle of detection. The position of the animal was standardized on ground level at the midway point between the forelimbs (as shown in Appendix 2b) (Wearn et al., 2022). The encounter rate of an animal was estimated considering every entry to the camera detection zone as a new encounter (Palencia et al., 2021). For animals that moved in groups (wild boar, dhole and occasionally bear), we counted the total number of individuals in each trigger and assigned one contact to each individual, since it was difficult to identify exactly which animals triggered the cameras and how many times (Wearn et al., 2022).

Day range

The day range is typically calculated as the product of the activity level (proportion of time spent active) and the average speed of movement (Rowcliffe et al. 2016).

$$\boldsymbol{V = \mu \times p} \qquad \text{eqn 2}$$

Where $\boldsymbol{\mu}$ is the average speed of movement while active, and $\boldsymbol{p}$ is the proportion of time spent in front of the camera trap. We estimated activity level using the 'activity' R package v.1.3.1 (Rowcliffe et al., 2014), and the speed $\boldsymbol{s}$ was measured on each encounter $\boldsymbol{i}$ ($\boldsymbol{i}$ = 1,2,…..n) by dividing the distance travelled ($\boldsymbol{d}$) by the duration of encounter ($\boldsymbol{t}$) (Palencia et al., 2021; Rowcliffe et al., 2016). Hence the average speed $\boldsymbol{s_i}$ for $\boldsymbol{i^{th}}$ encounter is given by:

$$\boldsymbol{s_i = \frac{d_i}{t_i}} \qquad \text{eqn 3}$$

Faster speeds are more likely to be encountered than slower speeds, so we estimated a bias-corrected speed by fitting a size-biased distribution (Rowcliffe et al. 2016). We fitted average

speed to the size-based lognormal distribution (eqn4) for all the species except for leopard cat (we lacked sufficient data in the latter case). The log-normal was found to be better fitting to the data than the gamma and Weibull distributions, as also found in previous studies (Rowcliffe et al., 2016; Wearn et al., :

$$\boldsymbol{f_{lognormal}(s_i|\mu\theta) = \frac{1}{s_i\theta\sqrt{2\pi}}\, exp\left(-\frac{(\log(s_i)-\varepsilon)^2}{2\theta^2}\right)} \quad \text{eqn 4}$$

Where, $\boldsymbol{f()}$ is the true probability density function of speed in the absence of sampling bias, and the $\boldsymbol{\theta}$ is the logarithmic standard deviation. $\boldsymbol{\varepsilon}$ is mean of logarithm given by $\boldsymbol{\varepsilon = \log(\mu) - \frac{\theta^2}{2}}$ (Rowcliffe et al., 2016). For the leopard cat, most detections occurred at night, when the Xenon flash setup (with a long delay between successive images) precluded us from estimating movement speed. Instead, the day range was derived from previous telemetry studies in Thailand . Telemetry-based estimates would be expected to underestimate movement speed due to the low temporal resolution of the data (Rowcliffe et al., 2016). We corrected the estimate from Grassman et al. (2005) following the approach in .

Detection zone

The detection zone was estimated by applying distance sampling analysis to the animal positions (radius and angle) in the camera trap image sequences (Palencia et al., 2021; Rowcliffe et al., 2014; Wearn et al., 2022). We only used the positions upon first detection, since we knew definitely that the camera had triggered in these cases. We assumed that camera sensitivity decreases in relation to the field of view, such that the probability of the camera reacting to an animal's presence declines monotonically with both distance and angle (Rowcliffe et al., 2011). The pattern of declining detectability was modelled using standard distance sampling theory, which states that the detection probability is a function of distance (point transect) and angle (line transect) (Buckland et al., 2004; Rowcliffe et al., 2011). For the distance sampling, we ran both half-normal (eqn5) and hazard (eqn6) models for detection probability as a function of distance and angle:

$$\boldsymbol{a(y) = exp\left(\frac{-y^2}{2\alpha^2}\right)} \quad \text{eqn 5}$$

$$\boldsymbol{a(y) = 1 - \exp\left(-\left(\frac{\alpha}{y}\right)^{\gamma}\right)} \quad \text{eqn 6}$$

Where ***a(y)*** is the detection probability at distance or angle ***y***, ***α*** represents the width of the function and ***γ*** in the hazard model represents the shape of the model. We calculated the detection radius (m) and angle (in radians) from the model with the lowest AIC (hazard model for all) for all the felines and for Asiatic black bear, Himalayan serow, Himalayan goral, sambar deer, serow and wild boar. For dhole and muntjac, we ran the half-normal model only, as the hazard model failed to converge. The estimated angles from distance sampling were doubled to obtain the angle across both the left and right fields of the camera trap.

3.2.4 REM density estimation

With availability of information on daily contact rate, speed, detection radius and angle, we estimated population density using the 'bootTRD' function of the 'camtools' R package (https://github.com/MarcusRowcliffe/camtools). Parameters were initially estimated in conventional units for interpretation (camera time in days, speed in meters per second and radius in meters) and later harmonized across parameters for the REM density estimation (camera time in hours, speed in meters per hour, radius in meters). The Panthera camera traps we used were not suitable for speed estimation at night, due to the long recovery times of cameras (approximately 15-30 seconds) when using the Xenon flash. We therefore calculated average speed and activity level for the 10 hours of daylight only (08:00 to 18:00 in our study site). The product of these two estimates provided the day range in metres per hour, which we multiplied by 10 to obtain day range during one daylight period. For the number of encounters (y in eqn 1), we only counted those detections occurring in daylight hours. For the estimation of the detection zone, we assumed that the radius and angle of detections was similar with and without the flash and used all animal position data to estimate these parameters. The density estimates were in individuals per km^2, which was multiplied by 100 to convert to individuals per 100 km^2. All the analyses were performed in R 4.3.0 (R Core Team, 2023).

3.2.5 Evaluation of bias in REM models

We evaluated bias in the REM density estimates obtained from this study by reference to the best SECR density estimates obtained in Chapter 2 (hereon referred to as reference density). For REM, we estimated density from the random deployment (0T + 100R), on the basis that REM requires randomly deployed camera traps. For the SECR reference densities, we used the full trail plus random deployment (100T + 100R) with a null model. Further, we ran linear mixed-effect models with REM bias as response variable for different combinations of random and trail stations to estimate the influence of non-random deployment on REM

estimation. Bias was calculated for each density estimate by subtracting the reference SECR density estimate from the REM density estimate and then dividing by the reference SECR density estimate (Palencia et al., 2022). A positive value indicates overestimation of density, negative shows underestimation of density and a zero indicates no bias in the REM estimate. We considered species, and quality of REM parameters (how accurately the detection zone and day range were calculated) as fixed factors in the models. The quality of REM parameters was based on the proportion of day and night photographs of the species. We categorized the REM parameter values derived from camera trap photographs as 'large sample' for species with more than 50% of their photos taken during daylight hours in the entire survey, and as 'small sample' for species with less than 50% of their photos taken during daylight hours. REM parameter values derived from larger sample sizes were treated as more accurately estimated than those from smaller sample sizes. The number of different simulations of station combinations (trail and random) were treated as random effects (Palencia et al., 2022). Considering a random intercept model, our full LMM model was:

$$\boldsymbol{Bias}\left(\frac{\boldsymbol{REM-SECR}}{\boldsymbol{SECR}}\right)_{\boldsymbol{ij}} = \boldsymbol{\alpha} + \boldsymbol{\beta_1} \times \boldsymbol{Spp_{ij}} + \boldsymbol{\beta_2} \times \frac{\boldsymbol{y}}{\boldsymbol{t_{ij}}} + \boldsymbol{\beta_3} \times \boldsymbol{r(m)_{ij}} + \boldsymbol{\beta_2} \times \theta(\boldsymbol{rad})_{\boldsymbol{ij}} + \boldsymbol{a_i} + \boldsymbol{\varepsilon_{ij}} \quad \text{eqn7}$$

Where bias is modelled as an intercept (**α**), plus species type (Common leopard, clouded leopard, marbled cat, and leopard cat), quality (small sample or large sample) of REM parameters (***y/t***= encounter rate, ***r (m)***= detection radius in meters, and ***ɵ(rad)***= angle of detection in radius), the random intercept $\boldsymbol{a_i}$ that is assumed to be normally distributed with mean 0 and variance $\boldsymbol{\sigma_a^2}$, and the error ($\boldsymbol{\varepsilon_{ij}}$) term. Details of the explanatory variables are provided in Table S3, Appendix 2. The index ***i*** refers to station combination and ***j*** to observed density bias for each station combination. We followed Zuur et al. (2010) in assessing residuals for homogeneity, normality ($\boldsymbol{\varepsilon \sim Normal(0, \sigma)}$, $\boldsymbol{a \sim Normal(0, \sigma)}$, and independence.

We calculated the precision of estimates from the coefficient of variation of the mean that allow us to present SE as a percentage of mean (Lyet et al., 2023; Twining et al., 2022). We compared the precision of REM from 100R with the reference SECR estimate from 100T + 100R. The CV was calculated with following formula:

$$\boldsymbol{CV_{mean}} = \left(\frac{\boldsymbol{SE}}{\boldsymbol{Y}}\right) \boldsymbol{x\ 100} \quad \text{eqn8}$$

Where SE is the standard error (standard error of REM or SECR estimates), and Y is the point estimate. Additionally, we estimated the REM-based density of Asiatic golden cat under

different combinations of trail and random stations, as for the marked felid species in chapter 2.

3.3 Results

3.3.1 Population-density estimation by REM evaluated against reference SECR

We observed significant differences (ranging between ~0.6 to 8 times the SECR estimates) in the density estimates from REM with 100 random-only deployments compared to the reference densities derived from the 100-trail plus 100 random deployment for all the felid species as shown in Figure 3.1. The largest differences between REM and SECR density estimates were for common leopard and clouded leopard (Figure 3.1). The density estimate of clouded leopard from REM was 3.6-times higher than that from SECR. Similarly, the density estimate of common leopard from REM was 8 times higher than the estimate from SECR. The density estimate of leopard cat from REM was almost 1.5 times lower than the density estimates from SECR (Figure 3.1). Estimates for marbled cats varied as well (1.2 times higher than the SECR estimate), although the confidence interval of the estimate overlapped the other estimate (Figure 3.1). For clouded leopard, simulating an increase in the speed parameter (or any REM parameter value except angle of detection) by around 3.3 folds reduces the density difference towards near zero (i.e., the density estimate after speed manipulation comes to $\widehat{D}$= 2.69 ± 1.08). For common leopard, we noted that a seven-fold increase in speed reduced the differences in the estimates to almost zero (density after increasing speed 7-fold was $\widehat{D}$= 1.89 ± 1.24). In contrast to the larger felines, the REM-derived density estimate for the leopard cat demonstrates a discernible negative difference in comparison to the density estimate obtained from the reference SECR method (Figure 3.1). Reducing the speed estimate by 1.8 folds increases a density estimate closer to that derived from SECR (i.e., the density after speed reduction was $\widehat{D}$= 26.65 ± 8.23). For marbled cat, increase in speed by 1.3 times reduces the density estimate equal to that from SECR (density after increasing speed was $\widehat{D}$= 6.26 ± 2.80). This evidence supports our first hypothesis **H_1:** "the density estimates from REM can be biased when parameters required for REM estimation are compromised due to species specific behaviour behaviours or by limitations in field survey equipment's ability to accurately measure REM parameters". It is also consistent with other hypothesis regarding biased reference density and inadequate randomized camera deployment.

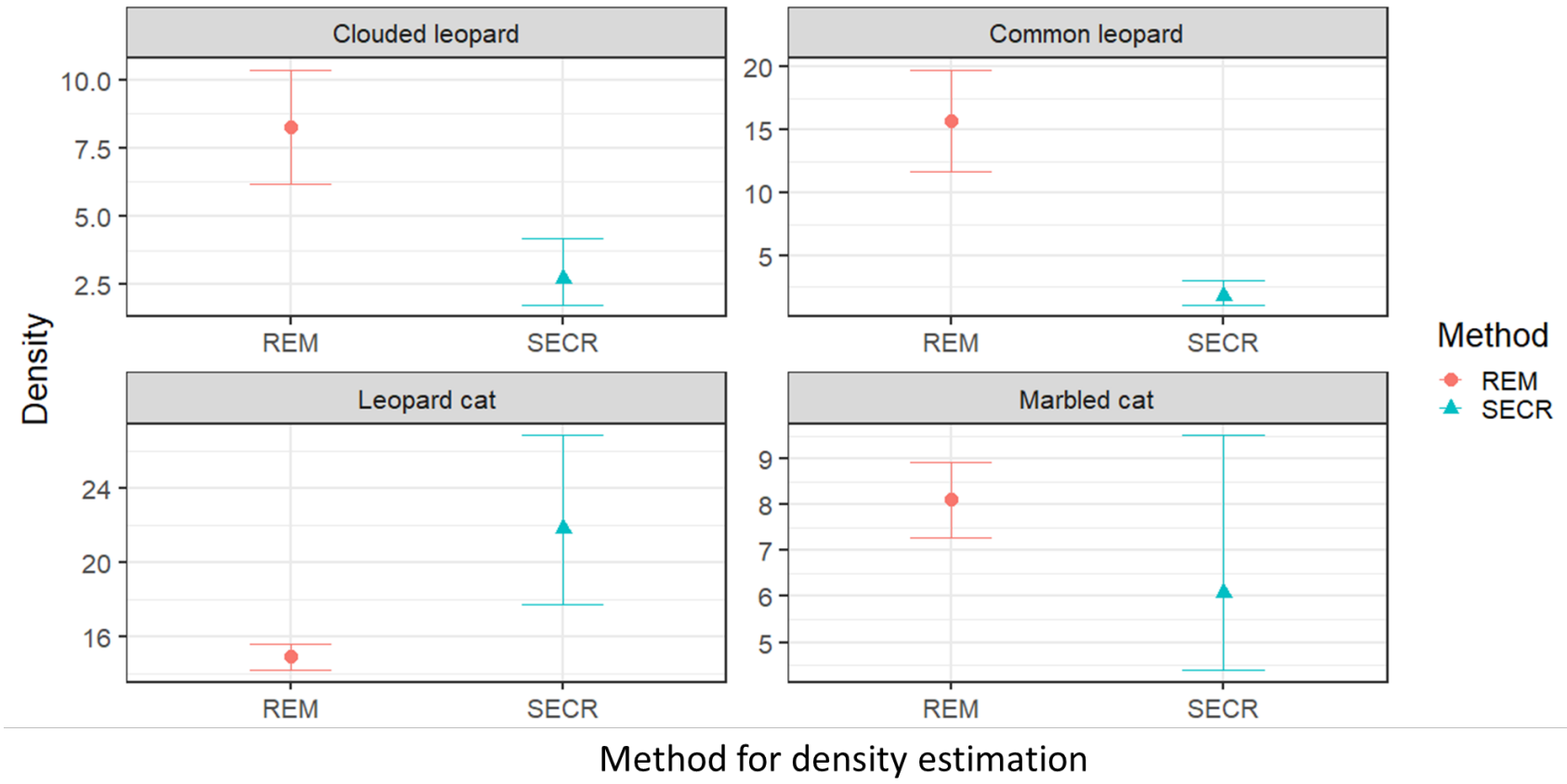

Figure 3.1: Density estimates of wild felids from REM (red dot), using the deployment of 100 random stations (0T + 100R), compared to estimates from SECR (cyan triangle) using full deployment (100T + 100R). The error bar represents the 95% confidence interval.

3.3.2 REM density bias from trail deployment

The density estimates for each felid species increased with an increasing number of trail stations (100T +0R, 100T + 100R) compared to the estimate from 100R. The lower day range for clouded leopard from the random deployment results from a conservative measurement of speed (which was measured from daylight photographs), as clouded leopards have more nocturnal behaviour than all other felids except the leopard cat (Figure 3.2, Figure S2 -S3 appendix 2). The day-range of clouded leopard from the full deployment (100T + 100R) was slightly higher than the day-range for the random-only deployment. Trail deployments had more captures of clouded leopard during daytime (8.7% and 23.3% of captures for random and trail-based cameras, respectively), favouring a representative (more samples) speed estimate. However, the density estimate was 2.4 times higher than estimate from random only stations (Table 3.1) indicating bias from the addition of trail-based camera traps. In the case of common leopard, the density estimates from the trail-only deployment is higher than that from the random-only deployment (Table 3.1). Typically, the REM density estimate for leopard cat and marbled cat is more biased by the addition of trail deployments compared to the larger sized felines. The density estimates from trail and trail plus random is almost 5-fold higher than the random only deployment for leopard cat (Table 3.1). Similarly, for marbled cat the density estimates from trail and trail plus random is approximately 4 times higher than

the density estimates from random only deployment. Higher bias in density from inclusion of more trail for the smaller-sized cat may be due to it having temporarily localized activity centres, which cause a greater number of encounters with the camera traps (Figure 3.2, Table 3.1). The marbled cat and to a lesser extent the leopard cat have two distinct activity centres at dawn and dusk as seen in Figure 3.2 (Figure S2-3, Appendix 2). Additionally, we noted that including trail-based cameras reduces the angle of detection for clouded leopard (by 60% for both 100T + 0R and 100T +100R) and marbled cat (by 52% for 100T +0R and 44% for 100T + 100R) leading to smaller detection zone (Figure S4, Appendix 2). Whereas for the leopard cat, the angle of detection increases by 6% for the trail deployment and remained the same for the full deployment (Table 3.1). The detection angle for common leopard and leopard cat remained the same for all deployments. Unlike detection angle, we observed an increase in the detection radius for all cat species by including trail cameras except for clouded leopard in full deployment. These results supported hypothesis 2, "*inclusion of more trail-based cameras will positively bias the REM density estimates, since we expect that the camera placement on trails is not random with respect to felid movement*".

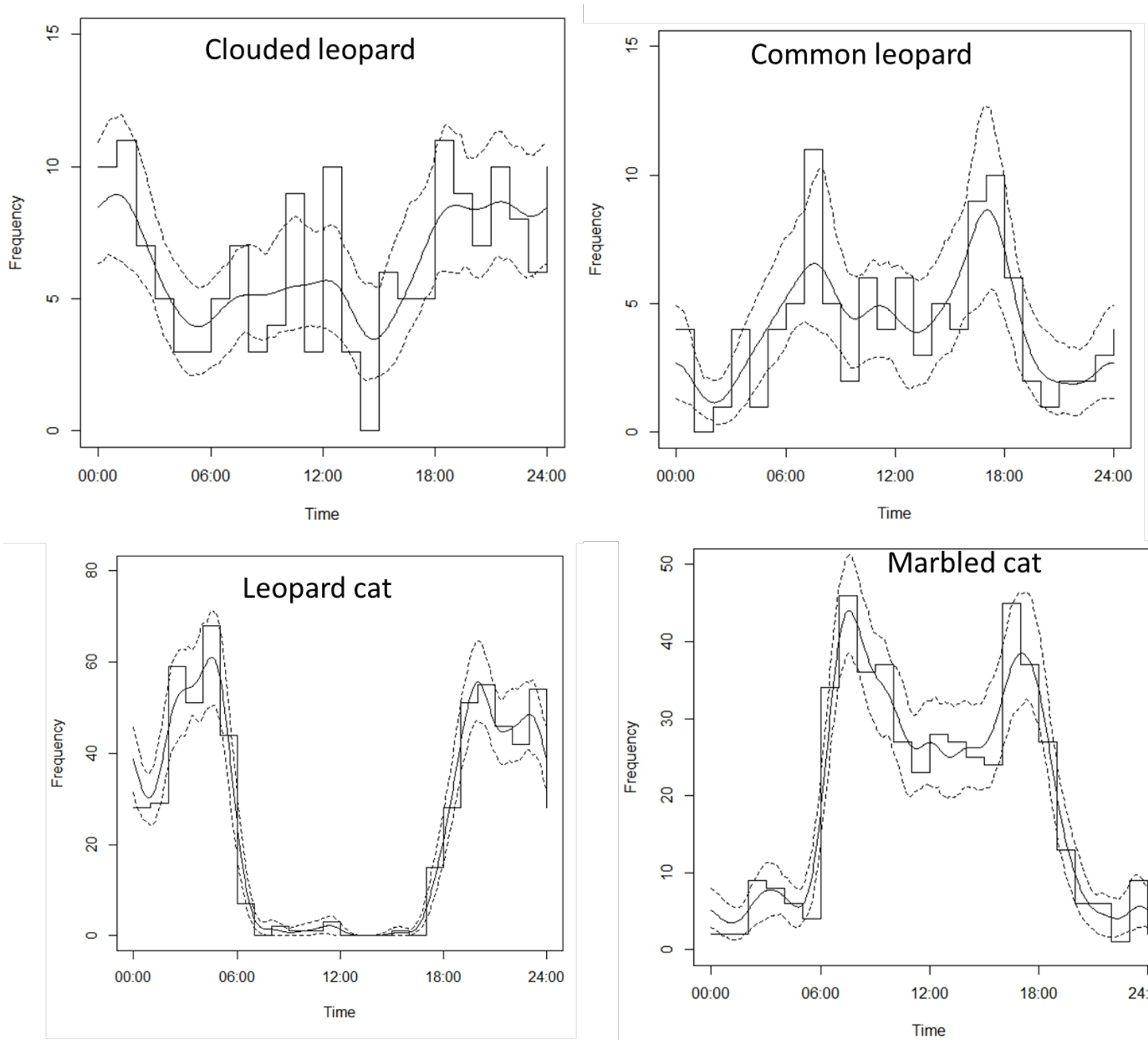

Figure 3.2. Activity pattern four different wild felids computed based on rate and time of encounter with the camera traps. The x-axis presents 24-hour time, and the y-axis represents the number of times the animal came in contact with the camera traps. The straight lines show the data distribution, continuous smooth line shows fitted circular kernel model, and dashed line shows lower and upper confidence limits of 95% confidence interval. The number of contacts is calculated from the first contact of the animal with the camera traps.

Table 3.1. Density estimates of clouded leopard from different combinations of the trail (T) and random cameras (R). Paired cameras at trail and a single camera at random. REM parameters (y/t = encounter rate; V= the average speed (day range); r=radius of detection; and θ= angle of detection) and n contacts shows the number of encounters of the animal at the camera traps. The speed was calculated from daylight hour. Density estimates are given in number of individuals per 100 km^2 and the number in brackets depicts standard error. The species are presented alphabetically.

Species	**Station combination**	**REM Parameters**					**REM $\hat{D}$**	**SECR $\hat{D}$**
		y/t	***V*(km/day)**	***r*(m)**	***θ*(radians)**	**n(contacts)**		
Clouded leopard	100T + 100R	0.002	12.88(1.18)	3.56 (0.23)	0.14 (0.03)	150	**15.84(4.60)**	**2.7 (0.60)**
	100T + 0R	0.003	13.61(1.53)	4.20(0.53)	0.14(0.01)	120	**19.67(6.91)**	**5.70(1.47)**
	0T + 100R	0.001	12.88(1.18)	3.75(0.37)	0.35(0.05)	13	**8.27 (3.43)**	**4.00(1.99)**
Common leopard	100T & 100R	0.002	17.52 (1.72)	5.25 (0.31)	0.19 (0.01)	100	**10.08 (3.75)**	**1.80(0.48)**
	100T & 0R	0.003	17.52(1.72)	5.25(0.24)	0.19(0.01)	71	**15.6 (5.78)**	**1.63(0.50)**
	0T & 100R	0.002	17.52(1.72)	5.25(0.24)	0.19(0.01)	29	**14.32(8.71)**	**2.11(0.90)**
Leopard cat	100T + 100R	0.006	12.06 (1.26)	4.05 (0.10)	0.19 (0.01)	585	**40.28(11.12)**	**21.8(2.30)**
	100T + 0R	0.018	9.12(0.95)	4.13(0.14)	0.19(0.04)	435	**61.24(22.88)**	**25.00(3.20)**
	0T + 100R	0.006	13.67(1.91)	3.96(0.11)	0.18(0.04)	147	**14.88(4.39)**	**18.70(6.40)**
Marbled cat	100T + 100R	0.008	29.84(1.50).	5.35 (0.27)	0.14 (0.01)	482	**28.79(9.08)**	**6.7(1.03)**
	100T + 0R	0.011	30.52(1.71)	5.45(0.34)	0.12(0.04)	408	**27.09(9.66)**	**6.15(1.10)**
	0T + 100R	0.002	37.01 (2.96)	4.41(0.88)	0.25(0.04)	74	**8.11(3.71)**	**6.48(1.80)**

3.3.3 Precision of marked and unmarked methods

Density estimates from REM using random only deployment was less precise (i.e., higher CV) compared to density estimates from SECR (100T + 100R) (Table 3.2). Considering the overestimation of density from REM for clouded leopard (i.e., 3 times higher than reference SECR estimate, Table 3.1), REM density estimates for clouded leopard are both less accurate and less precise than the density estimates from SECR. Similarly, for common leopard the REM density estimate is many times less accurate in overestimation and many times less precise compared to the reference SECR density (Table 3.2)

For marbled and leopard cats, the more precise density estimates from SECR correspond to the more accurate and least biased estimates (Table 3.2, Table S2, Appendix 2). Hence, density estimates from SECR combine precision and accuracy for wild felids compared to REM, supporting the hypothesis ***H_3*** *"the density estimate from REM will be less precise compared to the density estimates from SECR for wild felids".*

Table 3.2. Coefficient of variance of mean density estimates from REM (0T + 100R) and SECR (100T +100R). The table further shows summary of hypothesis testing of H_3 regarding the precision of density estimates from REM and SECR.

Species	$CV_{meanREM}$(%)	$CV_{meanSECR}$(%)	Expected results	Actual results	Conclusion
Clouded leopard	41.47	22.22	$CV_{REM} > CV_{SECR}$	$CV_{REM} > CV_{SECR}$	Strongly supported
Common leopard	60.57	26.67	$CV_{REM} > CV_{SECR}$	$CV_{REM} > CV_{SECR}$	Strongly supported
Leopard cat	29.50	10.55	$CV_{REM} > CV_{SECR}$	$CV_{REM} > CV_{SECR}$	Strongly supported
Marbled cat	45.57	15.37	$CV_{REM} > CV_{SECR}$	$CV_{REM} > CV_{SECR}$	Strongly supported

3.3.4 Causes of REM inaccuracy with respect to SECR

We ran a linear mixed-effect model (LLM) as described in section 2.3 to assess the cause of REM bias with respect to SECR. Residuals plots showed the model fitting adequately to the data (Figure 3.3).

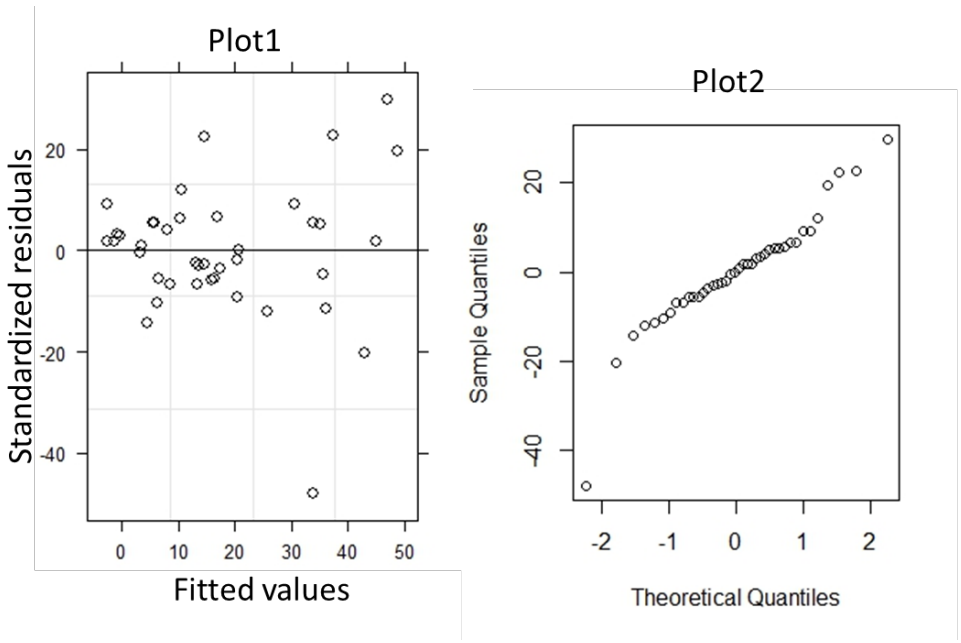

Figure 3.3. Residual plots for the LLM model of bias described in section 2.3. Plot 1 shows independence in sequential residuals, and homogeneity of variance. Plot 2 shows little evidence of deviation from a normal distribution of residuals (slight kurtosis).

LLM predictions did not shows any significant association between bias and REM density estimates for common leopard (Figure 3.3). The REM density estimates of clouded leopard, and leopard cat are significantly overestimated compared to that of marbled cat (Figure 3.3). We saw effect on REM accuracy by small sample REM values for detection zone, encounter rate and day range (Figure 3.3) for leopard cat and clouded leopard.

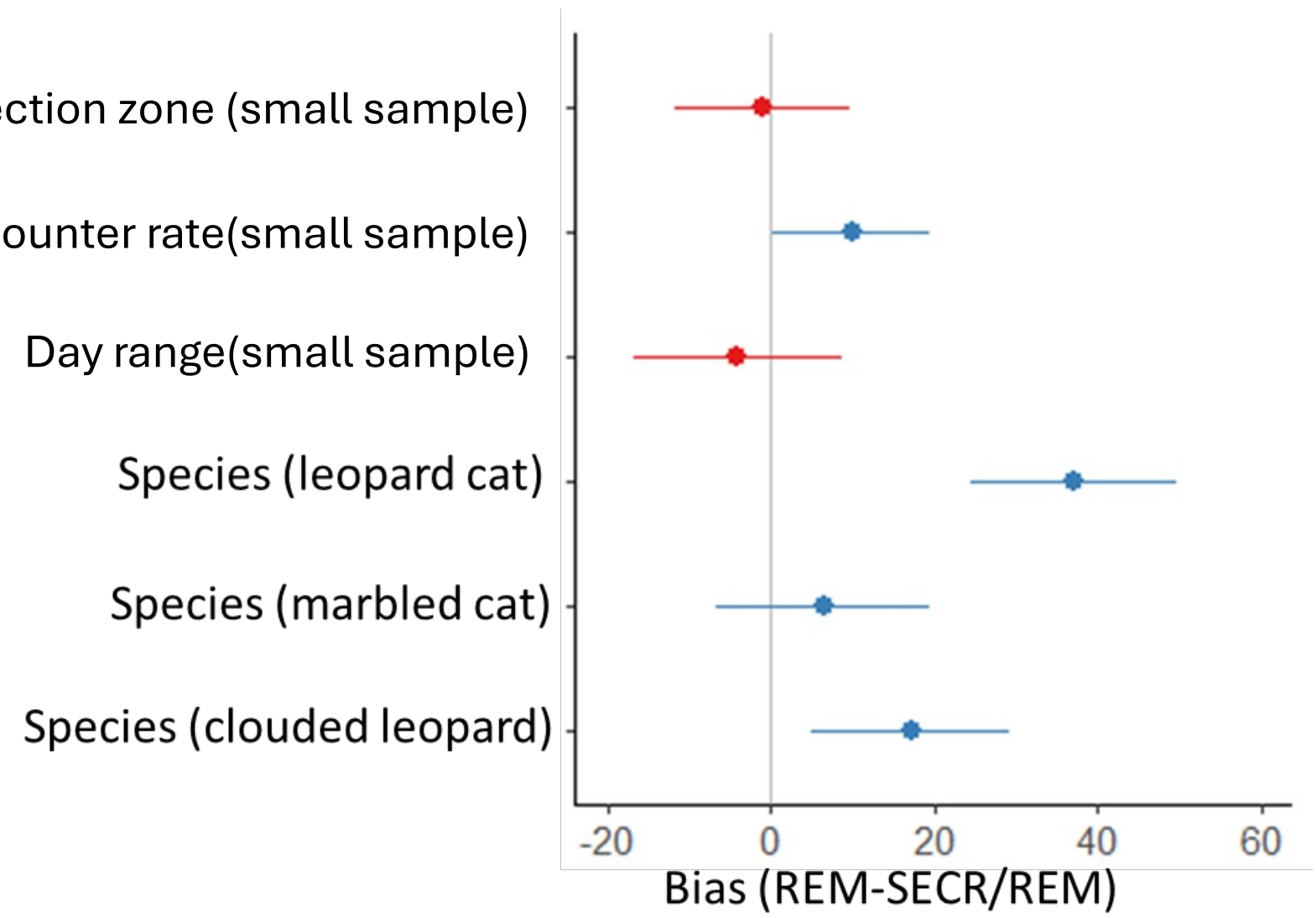

Figure 3.3. Effect of predictors included in the LLM model on REM bias calculated from reference SECR estimates for marked felids. Negative biases in red, positive in blue, showing estimated size of influence and 95% CI.

We found that small sample REM parameter values of day range and detection zone underestimated the density, and small sample encounter rates overestimated the density, when applying REM as shown in Figure 3.4. The model has marginal R^2 of 0.50 indicating there is substantial effect from the fixed variables (REM parameters and species) on the bias as shown in Table S4, Appendix 2. The conditional R^2 associated with the random effect (station combination) was 0.53. This further supports hypothesis 1, that density estimates from REM can be biased when input parameters required for REM estimation are compromised by variation in species-specific behaviours or by limitations in field survey equipment's ability to accurately measure REM parameters.

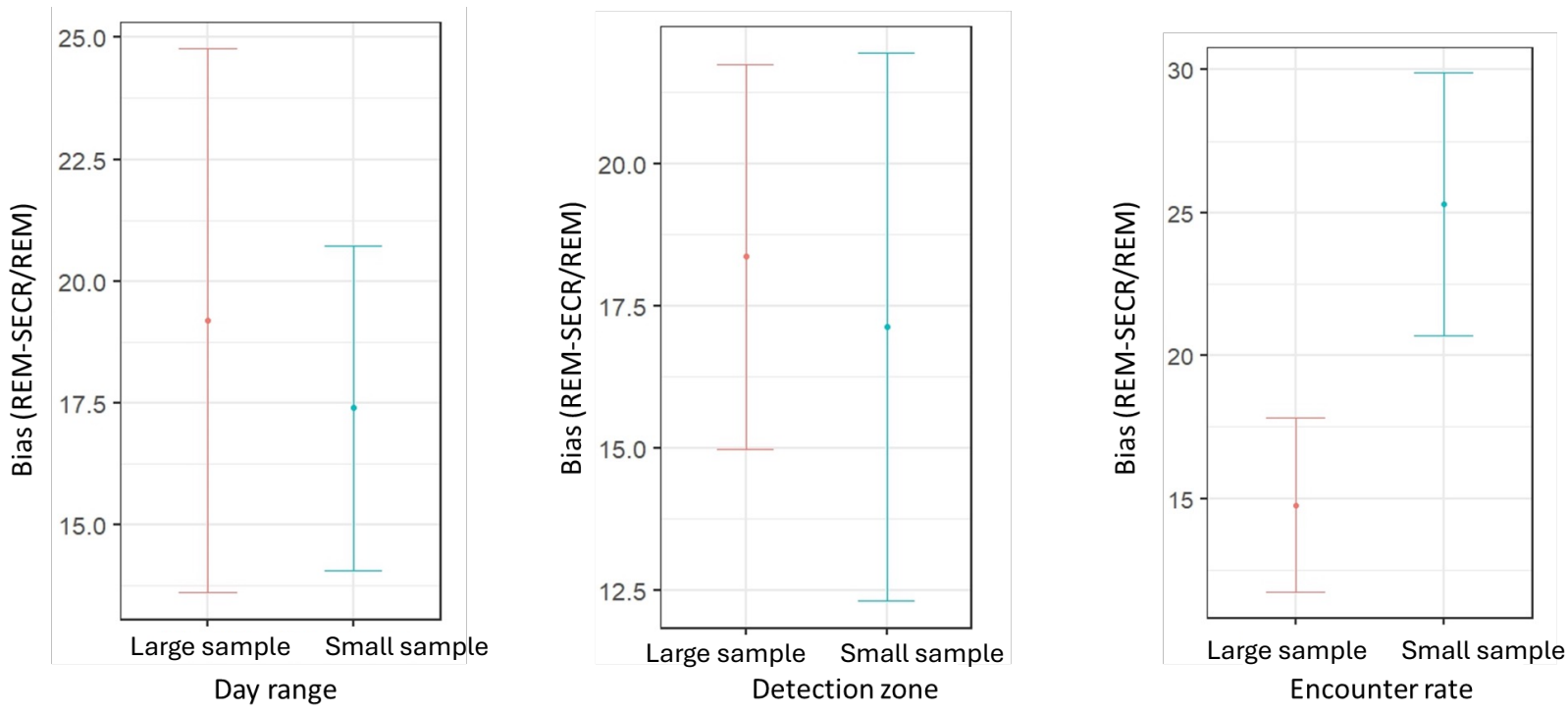

Figure 3.4. Predicted values for day range, detection zone and encounter rate considering large sample and small sample, and its effect on bias for clouded leopard, leopard cat, and marbled cat. Error bars represent the lower and upper 95% confidence interval.

3.3.5 REM density estimates of Asiatic golden cat from different combination of trail and random camera stations

We estimated densities of Asiatic golden cat by REM only, as it differs from the spotted felid species in lacking individually identifiable patterns. We obtained a more precise density estimate from the 0T + 100R deployment than from other deployments (Table 3.3). This estimate was considered as a reference for comparisons between different combinations of

trail and random stations. Deploying 25 trail stations alongside 50 random stations gave a density estimate that aligns most closely with the reference estimate (Table 3.3). The station combination of 100 trails and 100 random yields the most precise estimate. However, the estimate is precisely wrong compared to the reference density (1st row Table 3.3).

Table 3.3. Density estimates of Asiatic golden cat from different combinations of the trail (T) and random stations (R) with a total availability of 100 camera traps. Paired cameras at trail and a single camera at random. The number in the bracket shows the standard error of estimates.

Station combination	**REM Parameters**				$\widehat{D}$ **(Nos/100 km^2)**
	y/t	***V*(km/day)**	***r*(m)**	***θ*(radians)**	
0T + 100R	**0.001**	**7.71(1.56)**	**3.56 (0.23)**	**0.17 (0.02)**	**7.62(3.24)**
100T + 100R	0.006	7.17(0.75)	3.46 (0.10)	0.18 (0.01)	**43.08 (12.39)**
12T + 76R	0.001	6.03(1.36)	3.66(0.24)	0.17(0.02)	**12.42 (4.79)**
25T + 50R	0.002	12.98 (1.99)	3.61(0.24)	0.16(0.02)	**9.27(3.02)**
33T + 34R	0.002	11.53(1.89)	3.81(0.16)	0.15(0.01)	**9.68(3.62)**
50T+ 0R	0.01	10.83(1.52)	3.61(0.24)	0.20(0.03)	**38.27 (15.92)**

With availability of 100 grid cells, the density estimates closest to the reference density (from 0T + 100R in Table 3.3) was given by the deployment of 50 trail plus 50 random stations (Table 3.4) and farthest from reference density while deploying a paired cameras across 100 trail stations (4th row, Table 3.4). The inclusion of additional random stations decreases the disparities in density when compared to the reference density. The density estimates were highest from 100 trail-only stations, indicating a likely bias combined with reduced precision.

Table 3.4. Density estimates of Asiatic golden cat from different combinations of trail (T) and random stations (R), with a total availability of 100 stations. Paired cameras at trail and a single camera at random.

Station combination	**REM Parameters**				$\widehat{D}$ **(Nos/100 km^2)**
	y/t	***V*(km/day)**	***r*(m)**	***θ* (radians)**	
25T & 75R	0.002	5.67(9.97)	4.00(0.20)	0.15(0.14)	**9.87(5.79)**
50T & 50R	0.002	8.01(1.14)	3.39(0.20)	0.19(0.02)	**7.01(1.14)**
75T & 25R	0.003	8.02(1.38)	3.66(0.25)	0.16(0.01)	**19.31(1.38)**
100T & 0R	0.004	7.15(0.72)	0.47(0.03)	0.17(0.01)	**29.19(15.77)**

3.3.6 Abundance of prey and sympatric carnivore species

We used REM to estimate the abundance of prey and sympatric carnivores in our study area from the deployment of 100 random-only stations (0T + 100R). These reference estimates were then used to evaluate estimates from deployments of 100 trail-only stations (100T + 0R) and 100T + 100R stations, to test for influences of non-random sampling, and 0T + 50R stations, to test for an influence of sample size. We found that muntjac was the most abundant prey species in the study area followed by wild boar and sambar deer (Table 3.5). The Himalayan serow and goral were the second most abundant prey species in the study area. Gaur was the least abundant prey (prey for dhole and tiger) found in the study area (Table 3.5). Dhole and bear were the sympatric carnivores recorded in the study area. The density of dhole was comparatively higher than the Himalayan black bear in the study area (Table 3.5).

Trail-based and full deployments of cameras result in > 2-fold overestimation of population densities for all the prey species including the sympatric carnivores, relative to the random-only deployment of 100 stations (Table 3.5). The density estimates from the deployment of 50 random-only stations also overestimated the densities for sympatric carnivore (dhole), whereas it underestimated the densities for sympatric carnivore (bear) and prey species except for gaur and Himalayan goral (where model failed to converge). However, the bias in density estimate was minimal compared to that from trail and full deployment. This suggests that in the event of having a total availability of only 50 camera traps or 50 grid cells, REM estimation can still be useful with suitable cautions about likelihood of over-estimation. On the other hand, REM estimation would be unwise from non-random deployments.

Table 3.5. Density estimates of prey and sympatric carnivores from full deployment (100T +100R), trail-only (100T + 0R) and random-only (0T + 100R, and 0T + 50R) deployments of camera traps, with paired cameras at trail (T) and a single camera at random (R) stations. Body weight is the range of average weights in kg of each species given in the literature. REM parameters (y/t = encounter rate; V= the average speed (day range); r=radius of detection; and θ= angle of detection) and n contacts shows the number of encounters of the animal at the camera traps. The speed was calculated from daylight hour. Density estimates are given with standard error in brackets. The species are presented in the alphabetical order.

Species	**Body weight**	**Station combination**	**REM parameters**					**REM $\widehat{D}$ (nos/100-km^2)**
			y/t	***V* (km/day)**	***r* (m)**	***θ* (radians)**	**n (contacts)**	
Asiatic black bear	70-200[1]	100T + 100R	0.006	5.34(0.81)	2.61 (0.06)	0.21 (0.01)	301	**132.31(47.39)**
		100T + 0R	0.006	5.02(0.44)	2.60(0.06)	0.22(0.03)	244	**60. 72(16.69)**
		0T + 100R	0.001	5.62(0.83)	2.73(0.25)	0.23(0.04)	61	**11.46(3.85)**
		0T + 50R	0.0006	3.07(0.57)	3.03(0.36)	0.22(0.04)	12	**8.87(3.43)**
Dhole	12-18[2]	100T + 100R	0.017	6.15(0.67)	3.24 (0.03)	0.34 (0.01)	649	**121.85(39.12)**
		100T + 0R	0.020	2.55(0.21)	3.33(0.04)	0.34(0.01)	567	**277.89(70.43)**
		0T + 100R	0.002	4.58(0.79)	3.24(0.03)	0.34(0.01)	82	**17.95(7.32)**
		0T + 50R	0.001	3.09(0.65)	2.53(0.29)	0.47(0.06)	37	**18.08(10.14)**
Gaur	650-1000[3]	100T + 100R	0.001	2.55(0.57)	2.62 (0.27)	0.25 (0.02)	46	**20.21 (8.61)**
		100T + 0R	0.001	1.65(0.44)	2.61(0.29)	0.26(0.02)	37	**22.45(11.09)**

[1] (Kozakai et al., 2021)
[2] (Hayward, Lyngdoh, & Habib, 2014)
[3] (Ahrestani & Karanth, 2014)

		0T + 100R	0.0001	0.84(0.24)	2.62(0.28)	0.25(0.02)	8	**8.27(7.49)**
		0T +50R	NA	NA	NA	NA	NA	NA
Himalayan goral	35-42[4]	100T + 100R	0.001	6.84(0.29)	2.06 (0.13)	0.23 (0.02)	122	**98.11(34.74)**
		100T + 0R	0.001	1.57(0.32)	1.89(0.12)	0.23(0.02)	75	**29.71(12.78)**
		0T + 100R	0.001	1.47(0.26)	2.06(0.12)	0.23(0.02)	47	**30.01(10.52)**
		0T + 50R	NA	NA	NA	NA	NA	NA
Himalayan serow[5]	30-45	100T + 100R	0.007	2.92(0.24)	2.54(0.07)	0.24(0.01)	516	**138.58 (33.62)**
		100T + 0R	0.007	2.80(0.24)	2.58(0.07)	0.23(0.01)	370	**107.64(28.42)**
		0T + 100R	0.003	2.28(0.34)	2.54(0.06)	0.24(0.01)	145	**59.30(15.15)**
		0T + 50R	0.001	1.89(0.27)	2.52(0.31)	0.28(0.04)	60	**31.95(11.86)**
Muntjac[6]	9-16	100T + 100R	0.06	4.77(0.21)	2.49(0.28)	0.16(0.002)	4999	**905.56 (135.40)**
		100T + 0R	0.064	3.58(0.18)	2.46(0.03)	0.16(0.002)	3134	**813.69(140.40)**
		0T + 100R	0.040	3.41(0.18)	2.49(0.02)	0.15(0.002)	1867	**512.78(78.13)**
		0T + 50R	0.021	2.65(0.13)	2.56(0.07)	0.17(0.01)	389	**425.06(87.41)**
Sambar[7]	150-300	100T + 100R	0.002	2.13(0.14)	2.39(0.08)	0.29(0.01)	505	**164.69(42.71)**

[4] (Bashir, Bhattacharya, Poudyal, Roy, & Sathyakumar, 2014)
[5] (Bashir et al., 2014)
[6] (Wegge & Mosand, 2015)
[7] (Keneisenuo et al., 2022)

Deer		100T + 0R	0.004	1.66(0.26)	2.50(0.04)	0.29(0.01)	408	**90.70(30.44)**
		0T + 100R	0.002	1.86(0.40)	2.39(0.08)	0.29(0.01)	97	**33.80(10.79)**
		0T + 50R	0.0009	1.54(0.25)	2.31(0.30)	0.30(0.04)	38	**30.47(10.91)**
Wild boar[8]	50-90	100T + 100R	0.057	6.56(0.37)	2.77(0.03)	0.23(0.003)	2137	**502.01(102.07)**
		100T + 0R	0.059	5.64(0.20)	2.82(0.04)	0.23(0.004)	1640	**417.32(73.81)**
		0T + 100R	0.017	5.91(0.64)	2.64(0.06)	0.21(0.01)	489	**123.27 (25.52)**
		0T + 50R	0.012	4.87(0.24)	2.64(0.08)	0.20(0.01)	224	**126.56(33.19)**

[8] (Baruzzi et al., 2023)

3.4 Discussion

Historically density estimation from camera traps are mostly limited to those animals with uniquely identifiable body markings. Recent developments of new protocols to estimate population densities without requirement of individual recognition has enabled demographic study of a wider range of wildlife species (Palencia et al., 2022; Wearn et al., 2022). These techniques have also broadened the applicability of camera trapping studies for wildlife population monitoring (Palencia et al., 2022). Nevertheless, there have been few, or no comparative studies conducted to evaluate the reliability of density estimates derived from these methods (Gilbert et al., 2021; Moeller et al., 2018; Palencia et al., 2022). In this study, we compared the density estimates derived from REM with best estimates from SECR for marked felid species to evaluate the differences in the estimates that corresponds to the reliability of REM estimates, considering SECR as a standard density estimation technique for marked species. We further evaluated the influence on REM estimates from inclusion of trail camera traps to confirm the need of randomization of detectors for REM. Additionally for REM estimates of density of prey and sympatric carnivores, we estimated the influence of including trail as well as random stations in the deployment.

Overall, we observed differences in the density estimates derived from REM and SECR for four felid species. Difference in density estimates by REM and SECR were observed for non-feline species in previous studies, while equivalence in estimates between the two techniques were also observed by other studies (Chauvenet et al., 2017; Palencia et al., 2022). The REM and other unmarked population estimation technique such as time-to-event model was found to provide precise results, but REM tends to overestimate the density while the time-to-event model underestimates the population density (Santini et al., 2022). We observed that differences of REM density from SECR were high when the speed of movement was estimated as low, and that speed as a REM input parameter has a major influence on the density estimate for almost all the felid species. The sensitivity of REM to the speed parameter has been observed in a previous study in ungulates and canids, where biased density estimates resulted from an improper estimation of animal speed (Santini et al., 2022). LLM revealed the effect on REM accuracy of other poorly estimated REM parameters, including detection zone, encounter rate and day range. Despite observing large difference in density estimate between REM and SECR for common leopard, detection zone and encounter rate have less influence on REM bias for common leopard, compared to the speed parameter. A previous study has found REM parameters such as day range, detection zone and encounter rate caused bias in REM estimates when applied on smaller sample size (Palencia et al.,

2022). Speed measurement was compromised in our study as Panthera V7 camera traps cannot be configured to take a rapid sequence of photos at night, forcing us to use only daylight photographs for estimating the animal's representative speed.

Our study revealed that the addition of trail stations induces overestimation of REM densities for all the cat species as well as prey and sympatric carnivores. This overestimation is caused by trail stations increasing the values of encounter rate. Non-random placement of camera traps is very common amongst earlier studies, where camera traps are placed in locations with higher encounter of animal signs, which often means on trails (Palencia et al., 2022; Rahman et al., 2017; Rovero & Marshall, 2009). The estimates from such studies have high potential of overestimation of animal densities due to inflation of encounter rates (Palencia et al., 2022). One of the key considerations required for REM is randomization of the detector with respect to animal movement, which means avoidance of over-representing places with high animal traffic, and avoidance of lures to attract animals towards camera traps (Rowcliffe et al., 2013). The REM assumption of random placement of camera traps is often misinterpreted in the field by choosing a random location but then deploying camera traps at the nearest location with high incidences of wildlife presence (Palencia et al., 2022; Rahman et al., 2017). Such deviations from true randomization of the detectors may lead to increased encounter rates and biased estimation of REM parameters (Rowcliffe et al., 2016).

We observed relatively low precision in REM estimates compared to those from SECR for all the cat species. Similar observations were made by previous studies concerning the precision of REM estimates (ENETWILD-consortium et al., 2019; Palencia et al., 2022; Palencia et al., 2021). We found that precision of our REM estimates increased with an increase in the number of camera traps, except for marbled cat. An increase in the number of camera stations increases the number of records and the sampling effort, thereby increasing the precision of estimates (Schaus et al., 2020). For animals that are non-uniformly distributed (i.e., spatially aggregated), more detectors are required to improve the precision and thus, REM is generally recommended for applications to population with low aggregation (Palencia et al., 2022; Pollock et al., 1990). One of the strongest assumptions in the REM approach is that all animals in the study population are active and at their peak of activity (Rowcliffe et al., 2014; Wearn et al., 2022). We recommend putting a greater number of random camera traps across space and time to improve the accuracy and precision of estimates. Best practice for REM is the proper estimation of all REM input parameters, applying reliable protocols and random placement of camera stations, and considering the variability of all the parameters when evaluating the precision of density estimates (Palencia et al., 2022; Rowcliffe et al., 2013).

We estimated the density of Asiatic golden cats solely from REM, as this species lacks unique body markings, unlike other wildcats in our study area. Little is known regarding the population densities and abundances of the near-threatened Asiatic golden cat (Kamler et al., 2020). If we consider our density estimate from the 100-station random-only deployment as the most accurate estimate, camera combinations with fewer trail stations and more random stations could have achieved similar density estimates to this reference (Table 3.3 and Table 3.4). The density estimates derived from REM for Asiatic golden cats has the same order of magnitude as density estimates from SECR for the similar sized marbled cat (Table 3.1) which has been recorded in similar habitats in Myanmar and in North-East India (respectively 8.80 ± SD 2.06 and 5.03 ± SD 2.07 individuals per 100 km^2: (Naing et al., 2019; Singh & Macdonald, 2017).

Similarly, our density estimate of Asiatic black bear was close to that recorded from camera-trap studies in Thailand (8 ± SD 3.04 individuals per 100 km^2: (Ngoprasert et al., 2012), but almost 5-fold that recorded in North-west India (2.50 individuals per 100 km^2: (Bhattacharya et al., 2022). Our density estimate of dhole is a little higher than estimates in similar habitat in the Indian state of Arunachal Pradesh from camera trap studies (10.6 ± SD 3.04 individuals per 100 km^2: (Selvan et al., 2014) and Western Ghats (9.15 individuals per 100 km^2: (Punjabi et al., 2022). Previous studies on demography of guar have mostly focused on group size and sex composition rather than true population estimation (Debata & Swain, 2019; Pitimol & Srikosamatara, 2023). One study in the Indian state of Tripura found a higher density of gaur (1.25 individuals per km^2: (Mary et al., 2015) compared to our REM estimate. Our density estimate of Himalayan goral was smaller than estimates in the Azad Jammu and Kashmir areas of Pakistan (4-4.7 individual per km^2: (Ashraf et al., 2015; Shakeel et al., 2015). We observed a density estimate of Himalayan serow a little higher than an line-transect estimate from the same area (36 individuals per 100 km^2: (Wang, 2010). Similarly, our density estimates for muntjac was 2-fold higher than the density estimated in same location with line transect (Wang, 2010). The density estimates of sambar deer from line transect in same area by Wang, 2010 was 3 times higher than our REM estimate. The density wild boar from same study area by line transect (Wang, 2010) was also almost 3 times higher than our REM.

3.5 Conclusion

This study has compared density estimates of rare wild cats from REM and SECR models for the first time. We observed that REM can be used as a viable alternative with less resource (camera traps in this case), to obtain ecologically important information on densities of wild felids. However, it requires accurate measurement of REM parameters and proper randomization of the detector (camera traps). The results presented in this study were constrained in accuracy by the detector design, which cannot take multiple nocturnal photos in a single trigger as required by REM protocol for nocturnal species, and which have a centring algorithm that restricts the detection zone of camera traps. The need for rapid sequences of photographs presents a substantial technological challenge for studies of nocturnal animals, because of the inevitably large drain on the camera batteries caused by flash lighting. Our REM density estimates of sympatric carnivores and prey species reveal that REM can obtain ecologically sensible density estimates, given careful measurement of REM parameters and randomization of detectors. We recommend further comparative study between different density estimation techniques to improve methodological approaches and survey design.

Chapter 4 Movement behaviour and resource use pattern of montane carnivores

Contributions

The aims and objectives of this study were originated by Dr Oliver Richard Wearn and my principal supervisor Professor C. Patrick Doncaster. I developed standard operating procedure for live trapping of wild carnivores with advice from Dr Lon Grassman, Jr. from Texas A & M university-Kingsville. The document was reviewed by Professor Doncaster and Dr Grassman. Dr Grassman visited the field sites and advised on and approved the field methodologies. All fieldwork was approved by the University of Southampton Ethics and Research Governance panel (ERGO 53715). I trained the field staff of Jigme Singye Wanghcuck National Park and Royal Manas National Park with additional experts from the Wildlife Rescue Centre of the Department of Forests and Park Services of Bhutan, on chemical immobilization of wildlife and live trapping of wildlife. I led the fieldwork with veterinary support from the Department of Forest and Park Services of Bhutan. The purchase of GPS-Collars and fieldwork were supported by a WWF Innovation grant to Dr Wearn at the Zoological Society of London, and grants from Panthera International and World Wildlife Fund Bhutan Office. I analysed the data with support from Dr. Ugyen Penjor of Flora and Fauna International. The chapter was reviewed by Professor Doncaster, Dr Wearn, and Dr Grassman. Sonam Wangdi, Tandin Tandin, and Lethro from the Nature Conservation Division of Bhutan's Department of Forests and Park Services, shared data on dhole and common leopard collared from Western Bhutan.

Abstract

An understanding of animal movement patterns is crucial for their effective ecological management and conservation. Yet knowledge of wildlife movement ecology is constrained by limited technological capabilities of animal tracking, ethical concerns regarding research methods, and vastness of habitats for many species, including carnivores. Montane carnivores are the least studied of all carnivores due to the remoteness of their habitats and uncertain movement behaviours. In this study of montane carnivores in Bhutan, we live trapped seven individuals: three (2 male and 1 female) common leopards (*Panthera pardus*), one female Asiatic golden cat (*Cattopuma temminckii*), one male leopard cat (*Prionailurus bengalensis*), and two female Asiatic wild dogs (dhole; *Cuon alpinus*). We fitted larger animals (common

leopard and dhole) with GPS collars and smaller animals (Asiatic golden cat and leopard cat) with VHF collars and tracked each for more than 150 days.

We estimated the home range of each animal using the area-corrected and weighted autocorrelated kernel density method. We found larger home range sizes for male leopards compared to female and the home range of a male leopard from coniferous habitat was seven times larger than that of a male leopard found in lower warm broadleaved forests. Asiatic golden cat and leopard cat had similar home range sizes, and almost double the size of the female leopard range. The home range of the female wild dog collared in lower warm broad-leaved forest was almost 6 times larger than that of the female collared in cool temperate forest.

We quantified the resource selection function (RSF) of all the collared animals, based on available site covariates. The resource selection by all the collared common leopards was negatively influenced by gain in elevation. The male leopard collared in Royal Manas National Park-tended to select resources with higher incidences of human-carnivore conflict recorded in the past 5-years. The Asiatic golden cat selected resources in habitat that were away from human settlements. Similarly, the leopard cat preferred habitat away from human settlements. The dholes tended to select resources in the habitat where there were higher incidences of human-carnivore conflicts, avoiding sites with higher occupancy of common leopards. The findings from this chapter provide benchmarks for information on home range and resource selection by montane carnivores in Bhutan, and are useful for formulating human-carnivore co-existence strategies.

4.1 Introduction

Distances moved by an animals are directly influenced by the availability of the resources in the surrounding environment (Dickie et al., 2022). Almost all organisms faces fundamental trade-offs between maximization of energy acquisition and minimization of energy expenditure (Charnov, 1976; Dickie et al., 2022). One of the fundamental characteristics of ranging by many animals is that they each restrict their movements within a specific home range, which is smaller than one might expect based on observed levels of mobility (Börger et al., 2008; Darwin, 1860). Several studies suggest that home-range size is inversely proportional to the resource density (Dickie et al., 2022). The size of home-range reflects a trade-off between the cost and benefits associated with acquiring all necessary resources, including mates as well as food (McNab, 1963). In this chapter, we quantified the home ranges of montane carnivores including canids in Bhutan and modelled their resource use in

relation to their habitat and anthropogenic covariates. We also identified on-trail and off-trail site preferences by wild felids in our study area to assess the site preferences of different sexes of wild felids.

Knowledge of animal movement can inform a wide range of wildlife characteristics including population abundance and distribution, community ecology, animal physiology, disease spread, geneflow, and wildlife management (Calabrese et al., 2016; Nathan et al., 2008). Home range is typically defined as the spatial expression of behaviours animals perform in order to survive and reproduce (Burt, 1943). Home-range formation and maintenance by individuals is linked to the space used to meet life-history requirement (Burt, 1943; Dickie et al., 2022). There are empirical findings on home range behaviour for a large range of invertebrates and vertebrates (Börger et al., 2008; Laver & Kelly, 2008; White & Garrott, 2012), varying from a few square centimetres (e.g., small intertidal snails) (Skov et al., 2011) to thousands of kilometres (Börger et al., 2008). An animal might occupy a particular home range for a single season or for multiple years (Börger et al., 2008). It might defend a territory against conspecifics. Territorial behaviour is observed in many vertebrates. In large wild felids, it may be exhibited in the form of vocalizations and scent marking while patrolling (Lehmann et al., 2008). For species defending a territory, resource use has to be balanced against the costs of defensive behaviours and aggressive interactions (Cubaynes et al., 2014). The movement paths taken by the different sexes of the big cat families varies due to different life history trade-offs between males and females. Males tigers (*Panthera tigris*) are more territorial and have comparatively larger home ranges than females (Hernandez-Blanco et al., 2015). Common leopards (*Panthera pardus*) show a similar pattern, with the male tending to have a more linear movement path than the female (Martins & Harris, 2013). Female big cats also are generally more diurnal in their activity compared to males (Wang et al., 2015).

Space use by organisms is fundamental in ecology with its implications for wildlife conservation and management (Aliperti et al., 2021). The territoriality is central to animal behaviourists' providing various perspectives of animal behaviour, including resource acquisition, space use, communication, and matting systems (Kamath & Wesner, 2020). Resource availability to an organism is related to its ability to exploit those resources through movement (Dickie et al., 2022; Pyke et al., 1977). When resource density is high in a particular area, it will influence the consumption rate and when the resource density is low, there will be higher competition for resource consumption (Dickie et al., 2022; Holling, 1959). Habitat types, habitat heterogeneity, landscape permeability and anthropogenic habitat alteration influences the resource exploitation capability of wildlife (Johnson et al., 1992;

Tucker et al., 2018). Resource selection is further influence by the inter and intraspecific competition of the resources and interaction within the landscape (Wysong et al., 2020). Individual behaviours of animals across time or contexts, a concept known as animal personality, behavioural types, temperament or copying styles all influence the habitat use by animals, determining movement and dispersal (Gosling, 2001; Kamath & Wesner, 2020; Koolhaas et al., 1999; Réale et al., 2010). Potential overlap in the use of food resources has been observed in species with similar ecological requirements (Donadio & Buskirk, 2006). If the available resources are not a limiting factor, species would coexist without competition. However, if the availability of resources is limited, there will be competition amongst species, where one species will be dominant over the other (Lovari et al., 2015).

Home range sizes across felids are broadly proportional to its body size, reflecting food-resource need (Harestad & Bunnel, 1979). Large territorial male tigers (body weight of 100-260 kg) have mean home range sizes of 267 – 294 km^2 and females (body weight of 75- 177 kg) have 70- 84 km^2 calculated from 95% and 100% minimum convex polygon (MCP) (Simcharoen et al., 2014). Dhendup et al., (2023) estimated the home ranges of montane tiger of Jigme Dorji Wangchuck National Park of Bhutan as 150 km^2 for male and 90 km^2 for female with the 50% kernel density estimator from camera trapping records (Dendup et al., 2023). The home range of two male common leopards (*Panthera pardus*) with 100% MCP in Sariska Tiger Reserve in India was 84.3 and 63.2 km^2 (Mondal et al., 2013). Studies from across the globe have estimated the average home range of common leopard (body weight of male: 30 – 72 kg, female: 20-43kg) from 14.5 km^2 in India to 885.6 km^2 in Nambia (Snider et al., 2021). The annual home range size of mainland clouded leopards (body weight: 12 – 23 kg) (*Neofelis nebulosa*) in Thailand is estimated at 22.9 – 45.1 km^2 (95% MCP)(Grassman et al., 2005a). Similarly, Austin et at., (2007) measured average home range of male clouded leopard at 42.2 km^2 and 39.4 km^2 for female from 95% Fixed-Kernel estimator (Austin & Tewes, 1999). Only one study in Thailand has measured the average home range of Asiatic golden cat (*Cattopuma temminckii*), at 32.6 – 47.7 km^2 from 95% MCP (Grassman et al., 2005a; Kamler et al., 2020). The range of marbled cat (*Pardofelis marmorata*; body weight: 3 – 7 kg) was 5.3 km^2 for one month in Thailand but the information on home-range size still remains unclear since only one individual was radio-tracked (Grassman et al., 2005a; Hendry et al., 2023). The mean home-range size of leopard cat (*Prionailurus bengalensis*; body weight 2 – 6 kg) in Thailand was estimated at 12.4 km^2 for male and 14 km^2 for females from 95% MCP (Grassman et al., 2005b). In an oil-palm landscape of Borneo, the home range of male was 1.47 km^2 (n=4; SD = 0.63 km^2) and for female was 1.29 km^2 (n=4; SD = 0.28 km^2)

(Silmi et al., 2021). For dhole (*Cuon alpinus*), the home range of an adult female from Autocorrelated Kernel Density Estimation (AKDE) was 64.6 km^2 and for a male was 132.9 km^2 (Suksavate et al., 2020).

Resource use and selection by the common leopard is influenced by habitat types, prey abundance, and presence of domestic preys (Mondal et al., 2013). The common leopard, unlike other carnivores, is termed a 'generalist' because it can prey on a wide range of species and in various habitat types (Sunquist & Sunquist, 2002). Habitat use and resource selection by the common leopard is negatively impacted by presence of larger cat species in the locality (Lovari et al., 2015). Habitat domination by tiger over the common leopard is observed in Southeast Asia and avoidance of tiger by the common leopard (Lovari et al., 2015; Odden et al., 2010; Palomares & Caro, 1999). In tropical deciduous forests of India leopard prefers habitat with a higher encounter rate of sambar (*Rusa unicolor*) and chital (*Axis axis*) (Mondal et al., 2022). Mondal et al., 2022 also observed higher habitat preference for moderate to thick vegetation cover with reduced encounter rate with domestic prey species.

Little is known about the ecology of the Asiatic golden cat, compared to other small wild felids including leopard cat (Kamler et al., 2020). The dietary habit of the Asiatic golden cat mostly includes small ungulates followed by murid rodents and smaller carnivores (Kamler et al., 2020). Adult Asiatic golden cats are solitary hunters and primarily ground-based with capability to climb trees if required (Kawanishi & Sunquist, 2008). The species is found to be active in closed cover, typically having an irregular activity pattern coexisting with other medium size cat species including clouded leopard, marbled cat and leopard cat (Haines et al., 2022). Bhutan has recorded more than six coat morphs of the Asiatic golden cat distributed from subtropical forest to alpine forest up to 3,600 masl (Norbu et al., 2022; Sangay et al., 2014). The leopard cat consumes smaller prey species compared to other wild cats. Studies have found murid rodents comprising 79 - 85% of dietary composition of leopard cats (Grassman et al., 2005b; Kamler et al., 2020). In China, the leopard cat has been found to prefer habitat with less tree cover, tree density and fallen-wood, and it preferred habitat near areas of moderate levels of human disturbance intensity (Wu et al., 2020). In Khangchendzonga Biosphere Reserve, India, there was higher occupancy of leopard cat in low elevation, with high rodent abundance and tree cover (Bashir et al., 2014). Prey species of dhole mainly consists of larger ungulates to domestic livestock. A study in Western Ghats, India, found more than 90% of dhole diet comprising guar (*Bos gaurus*), sambar, chital, wild pig (*Sus scrofa*), and muntjac (*Muntiacus muntjac*) (Srivathsa et al., 2014). Livestock forms a sizable portion of the dhole's diet in most of its natural habitat (Srivathsa et al., 2020). In

Dhorpatan Hunting Reserve in Nepal, 20% of dietary composition of dhole was livestock (Aryal et al., 2015). In Thailand, a high degree of prey overlap (98%) was observed between dhole and common leopard indicating high competition for prey (Grassman et al., 2005). Social dominance of dhole is observed over the common leopard, as leopards avoid kill sites upon encounter with dhole groups, but solitary dholes are often ambushed and preyed upon by tigers and leopards (Karanth & Sunquist, 2000).

In this study, we explored home range size and Resource Selection Function (RSF) of four montane-carnivore species of Bhutan. Resource selection function is a fundamental tool in ecology that describes the distribution of animals to their preference for specific habitat conditions and yields values proportional to the probability of use of a resource unit (Boyce et al., 2002; Street et al., 2021). Firstly, we evaluated home range sizes and compared differences in home range size between sexes and habitat types. Next, we assessed the RSF of seven individuals collared with GPS and VHF radio collars. We modelled RSF with habitat and anthropogenic covariates. Detection heterogeneity is widespread in wild felids and between male and female wild felids. To evaluate the on-trail and off-trail habitat preferences by the felids, we estimated the differences in site occupancy of different sexes of felids from trail-based and full deployment of camera traps. We hypothesized that the inclusion of randomly placed cameras with respect to habitat would increase the site occupancy of females compared to their occupancy estimates from trail-based deployment of camera traps.

4.2 Methodology

4.2.1 Live-trapping site

We conducted live-trapping exercises in Bhutan's Jigme Singye Wangchuck National Park and Royal Manas National Park (Fig.4.1) in two phases, the first from January 2022 to March 2023, and the second form June 2022 to January 2023. The location of live traps was chosen based on our records of clouded leopard from camera traps studies (reported in chapter 2) and having high occupancy of clouded leopards. We achieved 600 trap nights (75 days x 8 live traps) in the first phase of the fieldwork and 2,240 trap nights (160 days x 14 traps) in the second phase.

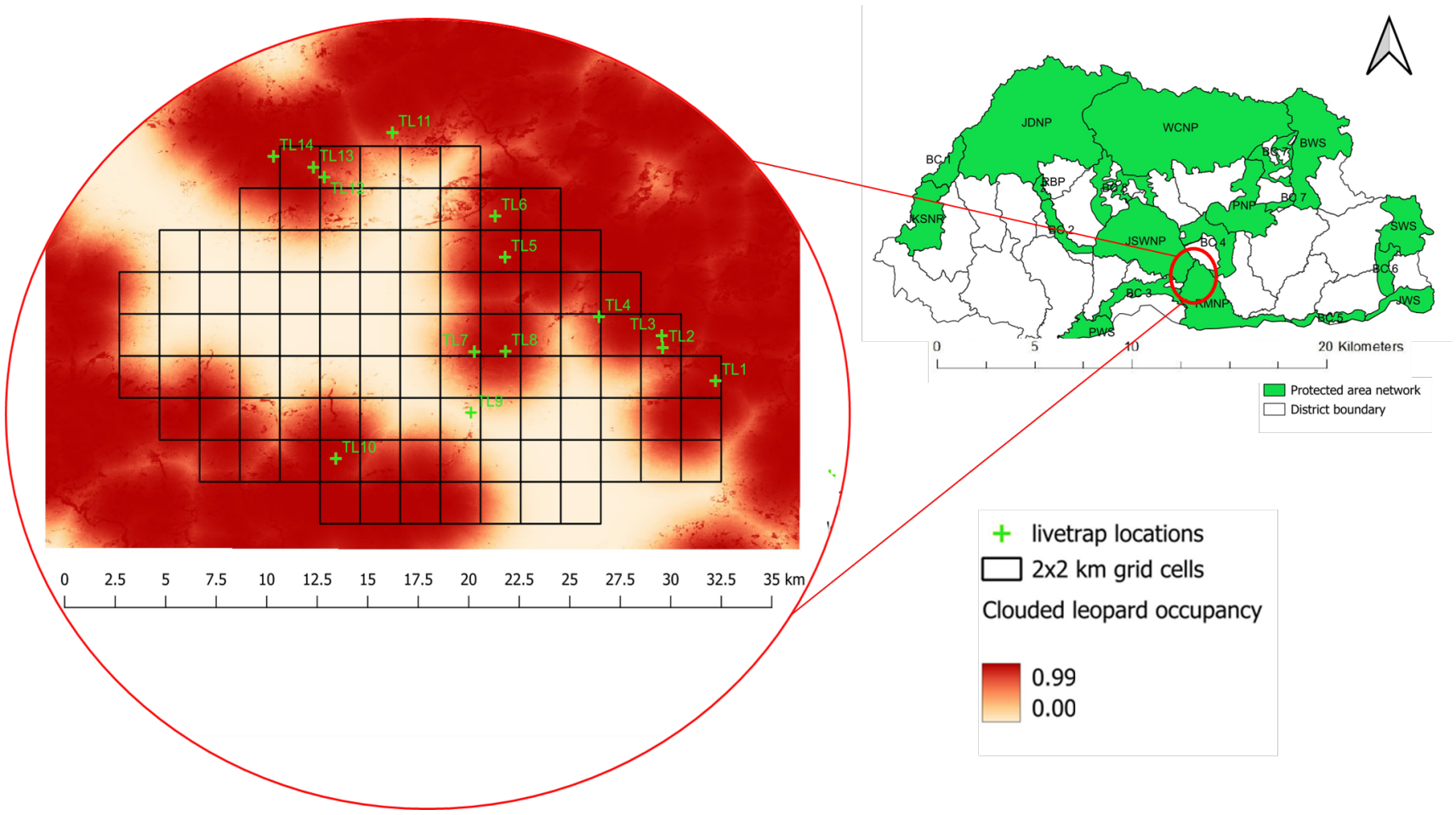

Figure 4.1. Live trapping sites numbered 1-14 (TL = Trap Location) showing location of livetraps (green plus sign). The heat map shows the predicted occupancy of clouded leopard in Jigme Singye Wangchuck National Park and Royal Manas National Park from camera trap studies. The 100 2x2-km grid cells make up the camera-trapping grid described in chapters 2 and 3, and those cells having higher captures of wild felids were used for setting livetraps. The inset map on the right shows the protected area network of Bhutan (BWS: Bumdeling Wildlife Sanctuary, JDNP: Jigme Dorji National Park, JKSNR: Jigme Khesar Strict Nature Reserve, JWS: Jomotsangkha Wildlife Sanctuary, PNP: Phrumsengla National Park, SWS: Sakteng Wildlife Sanctuary, WCNP: Wangchuck Centennial National Park) including biological corridors (Biological corridors are identified by numbers BC 1-7).

4.2.2 Live trapping of carnivores

We used baited sliding door box-traps, each 50 cm high x 40 cm wide x 160 cm long with a door drop mechanism, and foot treadle located about 100 cm within the trap (appendix 3a). Initially the livetrap box was designed to capture clouded leopard and smaller sized wild cats in the study area. Its dimensions nevertheless allowed safe capture of small to medium sized wild felids and sympatric carnivores (bear, Yellow-throated marten, and dhole) (Grassman et al., 2005a, 2005b). We placed a separate bait box behind each trap, with dimensions of 51 cm high x 46 cm wide x 30 cm long, to hold a live chicken. We deployed each livetrap at a predefined location of high encounter rate in camera traps with clouded leopard and common leopard (Figure 4.1), to maximize the capture success. We also assessed the presence of

indirect signs (i.e., scats, pug marks and scraps on trees) of clouded leopard and other wild cats. The livetraps were covered with local vegetation for camouflage with the surrounding vegetation (Grassman et al., 2005a).

Each bait box was fitted with a plastic cup and food container for a live chicken and was replenished with the food and water supplies every after 2-3 days by a team of trained local forest rangers. Accessibility of 2G network in all the trap locations enabled use of remote electronic door monitoring devices. We used Catch AliveOne™ version 1 trap alarms (https://catchalive.com/) for all the livetraps, which enabled 24-h monitoring of live trap with 99% monitoring success (only 1 trap alarm failed due to hardware issues). The trap monitor sends an SMS and e-mail alarm immediately upon the closing of traps doors, reducing the period of capture stress to captured wild animals. The study and trap design received approval from University of Southampton Animal Ethic committee vide University's Ethics and Research Governance Online (ERGO) approval number 53715. All live-trapping fieldwork was carried out in accordance with the Standard Operating Procedure (SOP) for live-trapping approved by the Department of Forests and Park Services of Bhutan, and by academic supervisors (appendix 3a).

4.2.3 Chemical restraints and collaring of carnivores

We used Tiletamine-Zolazepam (4mg/kg, tradename Telazol) as a chemical restraint for felids and canids. Previous studies have found safe performance of Telazol with the focal wild felids, and it is used as an alternative to ketamine combinations (e.g., ketamine-xylazine), which does not require reversal agents (Grassman et al., 2004; Lester et al., 2012). We also used etorphine hydrochloride 1mg/kg as a chemical restraint for Asiatic black bear (*Ursus thibetanus*) with 4mg/kg of naloxone as the reversal drug. We used a DAN-INJECT CO_2 pistol (https://daninjectdartguns.com/product/co2-pistol/) to deliver the drug. This pistol is easy to handle and allows minimal physical contact with the animal, unlike a pole syringe. The dart gun was loaded with a 10 ml DAN-INJECT dart syringe (https://shop.daninject.com/products/dart-syringes.di72/10.0ml-dart-syringe-with-stabilizer.diS10) with needle length of 1.5 mm x 25 mm for smaller cats and 2.0 mm x 40 mm for animals with body weight more than 25 kg. We used chemical restraint only for targeted species that are fit for GPS/VHF collaring and larger carnivores posing a threat to field staff. The entire procedure of chemical immobilization and post aesthetic monitoring were performed in accordance with the SOP (Appendix 3a) by a trained veterinarian from the local wildlife rescue unit under the Department of Forests and Park Services of Bhutan, and by the

principal investigator who was also trained in chemical immobilization of wild animals (Appendix 3b). In addition, all field assistants were trained in wildlife handling and chemical immobilization by the veterinarian and principal investigator.

We used an ATS G5-D Iridium/GPS collar weighing 500 g for common leopard and dhole, and a VHF radio collar weighing 50 g for Asiatic golden cat and leopard cat. GPS collars were calibrated to transmit 6 fixes (locations) per day and to upload data to the server every 48 hours. The 'VHF on' feature of the GPS collar was set to transmit VHF signals from 10 am to 2 pm Bhutan Standard Time. VHF collars had VHF frequency between 140-149 MHz. We recorded 2-3 VHF signal locations within 30 minutes every 2-3 days for Asiatic golden cat and leopard cat using a handheld collapsible Yagi antenna. The GPS location, time, date and bearing of VHF signals were recorded as shown in, appendix 3c.

4.2.4 Quantifying home range size

We estimated home range sizes of two common leopards (one female and one male) collared in the study site and one male common leopard collared by Department of Forests and Park Services of Bhutan in Western Bhutan. The female common leopard transmitted data from 9th March 2022 to 7th August and the male from 6th June 2022 to 30th April 2023. The male leopard collared outside the study site transmitted data from 23rd August 2022 to 16th January 2023. Likewise, we used data from a female dhole collared in the study site and a female dhole collared by Department of Forests and Park Services of Bhutan in Western Bhutan. The female from our study site transmitted GPS data from 26th February 2022 to 16th June 2022 and the female collared outside the study area transmitted data from 11th June 2022 to 08 September 2022. We tracked Asiatic golden cat (female) from 6th July 2022 till 20th February 2023 and leopard cat (female) from 26th November 2022 to 7th June 2023, both caught within the study site. Animal locations were determined from triangulation of VHF bearing using the LOAS software program (https://www.ecostats.com/LOAS) (Grassman et al., 2005a). Unlike GPS collared animals, we could track Asiatic golden cat and leopard cat only after a gap of 2-3 days, with one location on the day of tracking.

Estimation of home range is an important component of the analysis of animal tracking data, which is frequently complicated due to autocorrelation, sampling irregularity and small effective sample size (Fleming et al., 2018). We used the Autocorrelated Kernel Density Estimation (AKDE) technique to calculate home range sizes (Fleming & Calabrese, 2017; Fleming et al., 2015). Kernel density estimation (KDE) is statistically the most efficient and widely used range estimation technique (Fleming et al., 2015). It assumes that sequential

locations are independent and identically distributed (IID) (Worton, 1989), which is not always the case with animal tracking data that have inherent autocorrelation, leading to underestimation of home range (Fleming et al., 2015). Autocorrelation refers to an animal's position, velocity measured at one point of time being statistically correlated with the same measurement in the past and in the future, which arises from animal movement being a continuous process and from particular movement behaviours such as revisiting the same foraging area, den or nesting sites (Fleming et al., 2015).

The conventional KDEs are also the most efficient nonparametric estimators of the probability density function (PDFs) of animal movement (Fleming et al., 2015; Worton, 1989). With given observed locations $\mathbf{r}(t_i)$ at times t_i with $i \in \{1, \ldots, n\}$, and in q dimensions with the location vector $\mathbf{r}$, the kernel-density estimate $\hat{p}(\mathbf{r})$ of the true probability-density function (PDF) of $\mathbf{r}$, $p(\mathbf{r})$ is taken to be

$$\hat{p}(\mathbf{r}) = \frac{1}{n}\sum_{i=1}^{n} k\big(\mathbf{r} - \mathbf{r}\,(t_i)\big)$$

where $k(\mathbf{r})$ is a kernel that smooths the empirical distribution of the data, which is chosen as Gaussian with zero mean and q x q covariance matrix $\boldsymbol{\sigma}_{\mathrm{B}}$

$$k\,(\mathbf{r}) = \mathcal{N}(\mathbf{r}; \mathbf{0}, \boldsymbol{\sigma}_{\mathrm{B}}\,) = \frac{e^{-\frac{1}{2}\mathrm{r}^{\mathrm{T}}\sigma_{\mathrm{B}}^{-1}\mathrm{r}}}{\sqrt{\det(2\pi\boldsymbol{\sigma}_{\mathrm{B}})}}$$

KDE places small kernels of covariance of bandwidth $\boldsymbol{\sigma}_{\mathrm{B}}$ at each sampled location and the average of these kernels provides the PDF estimate, $\hat{p}$. It controls the spread of each kernel around each recorded location by influencing the degree of smoothing of the resulting distribution (Péron, 2019; Silverman, 2018). A large bandwidth smooths out these peaks and yields a more spread-out distribution and small bandwidth yields a distribution with numerous peaks around each cluster of recorded locations (Péron, 2019). It is crucial to select the right bandwidth, and the optimal bandwidth minimizes the mean integrated squared error (MISE) between true p and estimate $\hat{p}$, hereafter denoted $\varepsilon(\boldsymbol{\sigma}_{\mathrm{B}})$. The MISE can be given in terms of covariance of the locations $\boldsymbol{\sigma}_0$, number of spatial dimensions q, and number of data points n and bandwidth $\boldsymbol{\sigma}_{\mathrm{B}}$. This relation gives an asymptotically consistent estimate and an asymptotically optimal order of error (Péron, 2019):

$$\varepsilon(\boldsymbol{\sigma}_B) = \frac{1}{(2\pi)^{\frac{q}{2}}}\left(\frac{\frac{1}{2}}{\sqrt{\det(2\boldsymbol{\sigma}_{\mathrm{B}})}} + \frac{\frac{n-1}{n}}{\sqrt{\det(2\boldsymbol{\sigma}_0 + 2\boldsymbol{\sigma}_{\mathrm{B}})}} - \frac{2}{\sqrt{det(2\boldsymbol{\sigma}_0 + 2\boldsymbol{\sigma}_{\mathrm{B}})}} + \frac{1}{\sqrt{det(2\boldsymbol{\sigma}_0)}}\right)$$

In AKDE, animal movement is generally considered as a non-stationary process that allows both the mean velocity and the autocorrelation function to vary in time, which might result from spatial dependence (Fleming et al., 2015). For AKDE, the reference-function approximation for animal's probability of being at location **r** at time *t* is given by,

$$p(\mathbf{r},t) \approx \mathcal{N}\big(\mathbf{r};\boldsymbol{\mu}(t),\boldsymbol{\sigma}(t,t)\big) = \frac{e^{-\frac{1}{2}(\mathbf{r}-\boldsymbol{\mu}\,(t))^{T}\boldsymbol{\sigma}(t,t)^{-1}(\mathbf{r}-\boldsymbol{\mu}(t))}}{\sqrt{\det(2\pi\boldsymbol{\sigma}(t,t))}}$$

which is a function of the mean and autocorrelation function (ACF):

$$\boldsymbol{\mu}(t) = \langle \mathbf{r}(t) \rangle, \qquad \boldsymbol{\sigma}(t,t') = \langle (\mathbf{r}(t) - \boldsymbol{\mu}(t))(\mathbf{r}(t') - \boldsymbol{\mu}(\boldsymbol{t}))^{T} \rangle$$

The mean and ACF is estimated from the data, and as the data pertain to a particular set of times, $\{t_1, \ldots, t_n\}$, the corresponding time-averaged density is considered as the reference function:

$$p(\mathbf{r}) \approx \frac{1}{n}\sum_{i=1}^{n} \mathcal{N}\big(\mathbf{r};\boldsymbol{\mu}(t_i),\boldsymbol{\sigma}(t_i,t_i)\big) = \sum_{i=1}^{n} \frac{e^{-\frac{1}{2}(\mathbf{r}-\boldsymbol{\mu}\,(t_i))^{T}\boldsymbol{\sigma}(t_i,t_i)^{-1}(\mathbf{r}-\boldsymbol{\mu}(v))}}{\sqrt{\det(2\pi\boldsymbol{\sigma}(t_i,t_i))}}$$

For a stationary stochastic process, where temporal variation is absent from both mean and the ACF governing animal movement, the autocorrelated MISE is given by

$$\varepsilon(\boldsymbol{\sigma}_B) = \frac{1}{(2\pi)^{\frac{q}{2}}} = \left(\frac{1}{n^2}\sum_{\tau}\frac{n(\tau)}{\sqrt{\det(2\gamma(\tau)+2\boldsymbol{\sigma}_{\mathrm{B}})}} - \frac{2}{\sqrt{\det(2\boldsymbol{\sigma}_0+2\boldsymbol{\sigma}_{\mathrm{B}})}} + \frac{1}{\sqrt{det(2\boldsymbol{\sigma}_0)}}\right)$$

where $\gamma(\tau)$ is the semi-variance function, $n(\tau)$ is the number of location pairs with the time lag τ between them (Fleming et al., 2015). We used area corrected ADKE ($ADKE_C$) as it produces more accurate area estimates when the sample size is small and its confidence interval more reliable compared to a Gaussian reference function (GRF) method that generally overestimates the areas(Fleming & Calabrese, 2017; Worton, 1995). Similarly, we use weighted autocorrelated kernel density estimation ($wAKDE_C$) that includes weights on data points that have more influence over others, and its inclusion helps to correct biases that might arise due to uneven sampling effort or varying reliability of location data (Fieberg, 2007). The analyses were run as a continuous-time stochastic process (CTSP) that accommodates multiscale autocorrelation by separating the continuous-time movement process from the discrete-time sampling process (Fleming et al., 2019). CTSP can accommodate different kinds of autocorrelation in data spanning from no autocorrelation, through Markovain (position) autocorrelation, to multiscale non-Markovain autocorrelation (position and velocity autocorrelation) (Fleming & Calabrese, 2017; Fleming et al., 2015)

We used perturbative Hybrid Residual Maximum Likelihood (pREML) to fit independent identically distributed, Brownian motion, Ornstein – Uhlenbeck Foraging models, and selected the model with the Akaike Information Criterion (AIC) score (Fleming et al., 2015; Fleming et al., 2019). Conventional use of Maximum Likelihood (ML) based estimation has inherent weaknesses such as a tendency for ML to systematically underestimate variance and variance-related parameters at small sample sizes (Cressie, 2015) where underestimation of variance in AKDE translates into underestimation of home range (Fleming et al., 2019; Noonan et al., 2019). Analyses were performed using the 'ctmm' package in R (Calabrese et al., 2016).

4.2.5 Habitat selection by carnivores

We determined habitat selection by carnivores using the resource selection function (RSF), where the resources available to the carnivores from their known location collected by collars were compared to the resources available to them within the study area as a whole (Klaassen & Broekhuis, 2018; Manly et al., 2007; Manly et al., 2002). Habitat selection by an animal is a behavioural process by which the individual chooses the best suitable locations for maximizing its fitness (Fretwell & Calver, 1969; Northrup et al., 2013). The most common method for estimating habitat selection pattern from GPS radio collar data is the resource selection function (Manly et al., 2007; Northrup et al., 2013). A resource selection function is a model of the likelihood that an available spatial unit will be used by an animal, given its resource value (Avgar et al., 2016; Boyce, 2006). The RSF typically fits into a use-availability framework, whereby environmental covariates (e.g., elevation) at the locations where the animal was present (the used locations) are compared to covariates at random locations taken from an area considered to be available for selection (Manly et al., 2007; Manly et al., 2002).

We computed the Maximum Convex Polygon (MCP) around the locations collected by each collar (Figure 4.2, appendix 3d) and generated a random sample of points to characterize availability within the MCP (Johnson, 1980; Morris et al., 2016; Northrup et al., 2013; Stabach et al., 2016). The common method of resource selection entails generating a random sample of points to characterize availability within a buffer around each used location (Northrup et al., 2013).

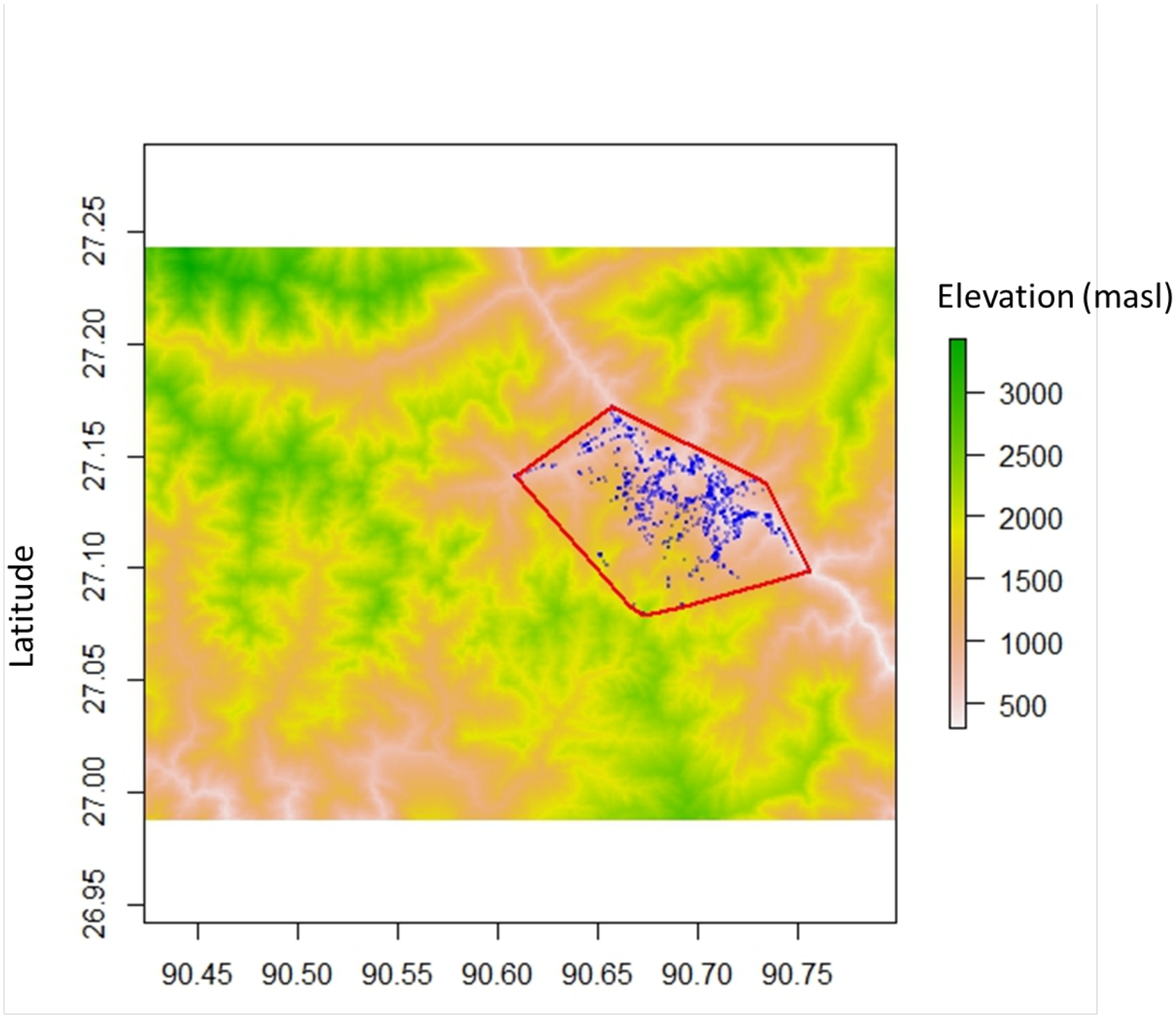

Figure 4.2. Maximum Convex Polygon (MCP) around the data points of leopard_1, which was used to generate random points of available site and the site used by an animal. The background raster represents elevation in meters above sea level.

A more practical and accurate approach is to draw a sample of used resource units and a sample of available resources unit (can be used or unused) and to estimate an RSF that is proportional to the probability of use (Johnson et al., 2006; Nielsen et al., 2002). For our data, we sampled 200 animal locations recorded by GPS collars (used site = 1) and 1000 random locations (available = 0) within the 100% MCP (Figure 4.3., appendix 3e).

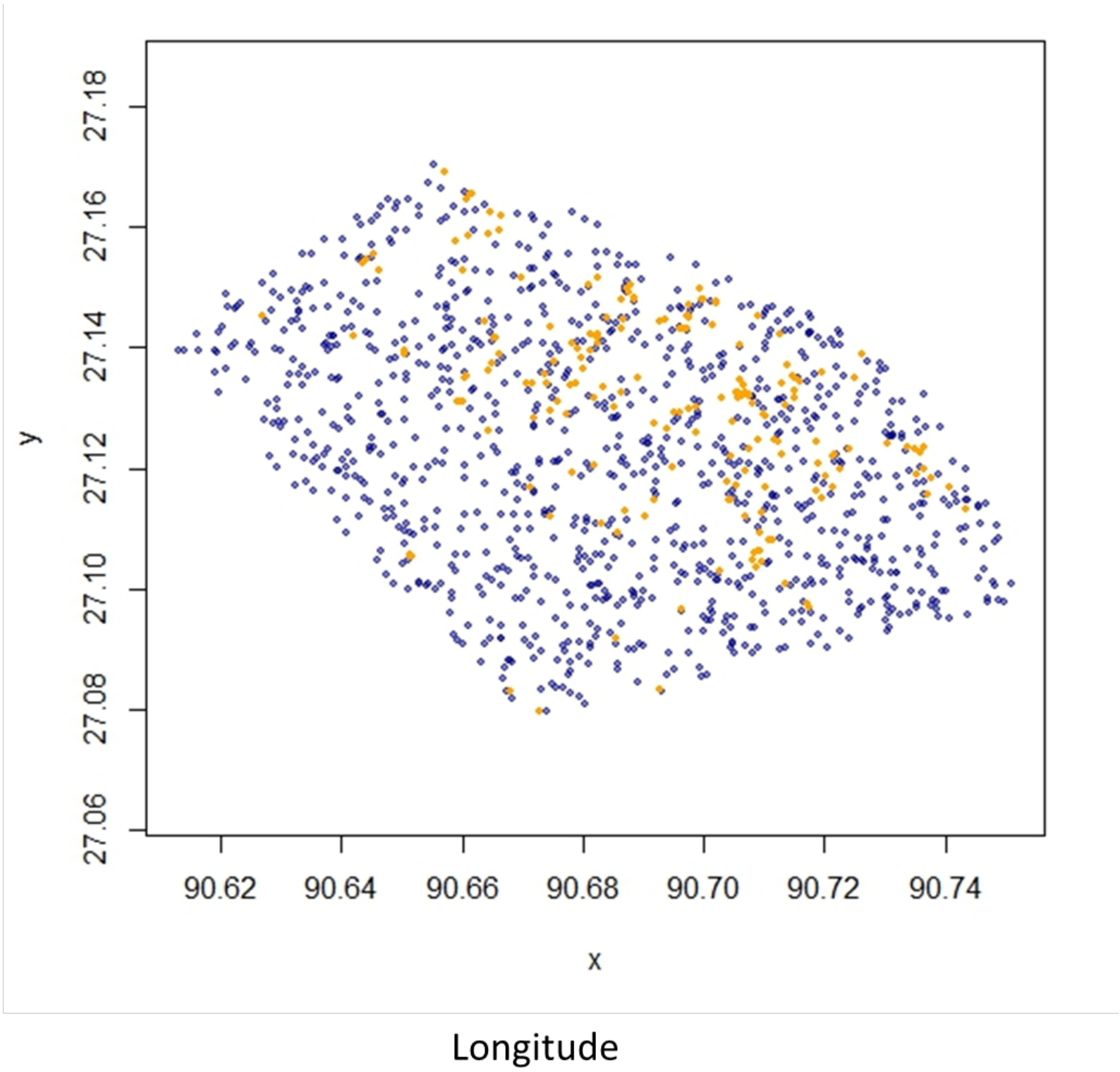

Figure 4.3. Random points generated for modelling resource use function for leopard_1, where blue points represent random points available for resource exploitation by an animal and orange points are the sites that were used by the animal recorded by GPS collar.

We applied use-availability framework for fitting RSF of our data, where the used locations are a realization from the used distribution $f^{\mathrm{U}}(\mathbf{x})$, which can be written as a weighted version of the availability distribution. $f^{\mathrm{A}}(\mathbf{x})$ (Johnson et al., 2006; Northrup et al., 2013)

$$f^{\mathrm{U}}(\mathbf{x}) = \frac{w(\mathbf{x}'\boldsymbol{\beta}) f^{\mathrm{A}}(\mathbf{x})}{\int w(\mathbf{x}'\boldsymbol{\beta}) f^{\mathrm{A}}(\mathbf{x}) d\mathbf{x}}$$

where $\mathbf{x}$ is a vector of environmental covariates, with corresponding vector of coefficients, β and $w(\mathbf{x}'\boldsymbol{\beta})$ is the RSF which is interpreted as how the animal selects habitat from $f^{\mathrm{A}}(\mathbf{x})$. Studies have proved that, provided $w(\mathbf{x}'\boldsymbol{\beta})$ takes exponential form (i.e., $w(\mathbf{x}'\boldsymbol{\beta}) = e^{\mathrm{x}'\beta}$), logistic regression can provide unbiased estimates of $\boldsymbol{\beta}$ (Johnson et al., 2006). RFS can be also estimated from Bayesian random-effect model or random-effect designs for logit-link GLM

(McLoughlin et al., 2010). For our study we used logistic regression, because it is a powerful and robust tool that has been much used in wildlife habitat studies (Johnson et al., 2006; Manly et al., 2002). We constructed the RSF from the following logistic equation:

$$w(\mathbf{x}'\boldsymbol{\beta}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k)$$

where $w(\mathbf{x}'\boldsymbol{\beta})$ is a RSF for a vector x of k predictor covariates. The β_i is model coefficient for the ith habitat covariate, whilst x_i can be estimated using the corresponding coefficient from logistic regression (Manly et al., 2002). Based on the availability of environmentally meaningful variables from the literature, we constructed lists of a *priori* models (Morris et al., 2016). We selected the most parsimonious model using Akaike's Information Criterion (AIC) (Burnham et al., 2011). The parameters from the best model were used to create the habitat suitability map using the resource selection function by the exponential form (appendix 3i).

4.2.5.1 Habitat covariates

We constructed a habitat model of RSF with the habitat covariates, which included elevation (ELE), distance to river (RIVDIST), distance to settlement (SETDIST), forest cover (TREECOVER), and distance from human-wildlife conflict location (HWCDIST). The elevation and river data were extracted from Digital Elevation Model (DEM) data of Bhutan. We used settlement data from National Housing and Population Census of Bhutan 2017 (NSB, 2017) by rasterizing the spatial point of settlement followed by calculating raster distance using a raster-proximity calculator in Q-GIS 3.32.2 (QGIS.org, 2023). We used forest cover data from 30-m resolution global forest cover change for the year 2001 (Hansen et al., 2013). The distance from nearest location of human-wildlife conflict was calculated from the spatial location of incidences of human-wildlife conflict recorded by forest ranger offices from 2015-2021 in Q-GIS 3.32.2 (QGIS.org, 2023). We modelled RSF of carnivores captured in the southern part of Bhutan (study site shown in Figure 4.1) using all the habitat covariates. We could not model those captured outside the study area, due to lack of data on habitat covariates. We rasterized all these covariates and produced a Raster Brick using raster package in R (Hijmans et al., 2013), which was used for RSF modelling:

$$RSF_{(Habitat)} = \exp(\beta_0 + \beta_1 ELE_{scaled} + \beta_2 RIVDIST_{scaled} + \beta_3 SETDIST_{scaled} + \beta_4 TREECOVER_{scaled} + \beta_5 HWCDIST_{scaled})$$

The subscript 'scaled' refers to the spatial scale of variables that were rescaled to have zero means and unit variance. We also ran the habitat interaction model by hypothesizing that

distance from settlement and distance from nearest conflict incident interact, such that habitat use might be especially high near conflict areas when they are close to settlements. :

$$RSF_{(Interaction)} = \exp(\beta_0 + \beta_1 ELE_{scaled} + \beta_2 RIVDIST_{scaled} + \beta_3 SETDIST_{scaled} + \beta_4 TREECOVER_{scaled} + \beta_5 HWCDIST_{scaled} + \beta_6 SETDIST \times HWCDIST)$$

4.2.5.2 Species interaction model

We modelled sex-based influences on resource selection for common leopards, which we term here an intraspecific model. From the detection histories of male and female leopard from camera trap studies in chapter 2 and section 2.6 of this chapter, we produced an occupancy map for the male ($OCCU_{MALE}$)and female leopard ($OCCU_{FEMALE}$). Similarly, to the habitat model, we could construct models for species depending upon availability of data from the particular location where the animal was captured. The maps were rasterized with each pixel of raster representing the occupancy at that location. The RSF model was constructed to check the intraspecific interaction amongst common leopards as follows:

$$RSF_{(Itraspecific)} = \exp(\beta_0 + \beta_1 OCCU_{MALE} + \beta_2 OCCU_{FEMALE})$$

In addition, we modelled RSF based on occupancy of prey species in the locality that includes occupancy of gaur ($OCCU_{GAUR}$), Himalayan Goral ($OCCU_{GORAL}$), Himalayan serow ($OCCU_{SEROW}$), muntjac (($OCCU_{MUN}$), sambar deer ($OCCU_{SAMBAR}$) and wild boar ($OCCU_{BOAR}$).

$$RSF_{(Prey)} = \exp(\beta_0 + \beta_1 OCCU_{GAUR} + \beta_3 OCCU_{GORAL} + \beta_4 OCCU_{SEROW} + \beta_5 OCCU_{MUN} + \beta_6 OCCU_{SAMBAR} + \beta_7 OCCU_{BOAR})$$

Further, we modelled influences on RSF from presence of sympatric carnivores in the locality. We used occupancy of dhole ($OCCU_{DHOLE}$) and Himalayan black bear ($OCCU_{BEAR}$) as explanatory variables for the RSF of collared animals as:

$$RSF_{(Iterspecific)} = \exp(\beta_0 + \beta_1 OCCU_{DHOLE} + \beta_2 OCCU_{BEAR})$$

4.2.6 Trail and random site preferences by animals

We ran single-species single-season occupancy models to evaluate the trail and random site preferences by the different felid species (Fiske & Chandler, 2011). Individual detection histories (0/1 representing absence/presence of species detection by each camera-trap station

on a specific day) were prepared using the 'camtrapR' R package (Niedballa et al., 2016). The total length of survey was >200 days starting from 15th October 2020 to 5th May 2021. We used only the first 90 days of each camera trap session to minimize the risk of violating the population closure assumption (i.e., no birth, no death, no immigration, and emigration during the survey period: (Rota et al., 2009; Tan et al., 2017). The 90-day data subset was collapsed to a 7-day period based on chi-square goodness-of-fit test (as shown in appendix 3l) for the multivariate global model to reduce overdispersion of data (Mackenzie & Bailey, 2004; Wright et al., 2016).

Occupancy ψ is defined as the probability that a species will occupy a random site at a given period (MacKenzie et al., 2017; Penjor et al., 2018). It is an important state variable in ecological research (Fiske & Chandler, 2011), and is also referred to as the probability of site use, which is the probability of an animal using a sampling unit (MacKenzie et al., 2017; Penjor et al., 2018). Occupancy modelling involves identifying the factors (i.e., site-covariates) that are associated with variation in the probability of sites being occupied (i.e., $\psi = Pb$ at $Z_i = 1$), where the binary state variable $Z = 1$ if site i is occupied by an animal and $Z = 0$ if it is not occupied. We deployed camera traps to M sites, which record the binary response Y_{ij} of species detection ($Y = 1$) or non-detection ($Y = 0$) during $j = 1……., J_i$ camera sampling occasions at the ith site (Fiske & Chandler, 2011; Mackenzie et al., 2002). To maintain independent detection enclosure (where current detection does not influence subsequent detection, which would otherwise inflate false positives), we considered 60-minute time gaps between successive captures of individuals of the same species by the camera (Choki et al., 2023; Tan et al., 2017; Warton et al., 2017). We considered detection probability parameter p in the model, which accounts for the probability of detecting a species that is present in the survey area, as there are chances of recording false absences. The camera might not capture the species presence ($Y_{ij} = 0$) even if it is present in the survey area ($Z_i = 1$) (Fiske & Chandler, 2011). The main assumptions involved in estimating occupancy probability (ψ) are that there should be more than one detection at a site ($J_i > 1$), the probability of detection p is the same for all sites throughout the season, and successive detections are independent of each other (Mackenzie & Royle, 2005). The joint distribution of animal observations, conditional on the latent occupancy state and the marginal distribution of the latent occupancy state variable, is described by the following hierarchical model:

$$Z_i \sim Bernoulli(\psi) \text{ for } i = 1,2,....., M$$

$$Y_{kj}/Z_i \sim Bernoulli\ (Zip) \text{ for } j = 1, 2,....J_i$$

Removing *Z* latent variables with marginalization yields the following likelihood formula:

$$L(\psi, p \mid \{Y_{ij}\}) = \prod_{i=1}^{M} \left\{ \prod_{j-1}^{Ji} (p^{Y_{ij}} (1-p)^{1-Y_{ij}}) \psi \; + I(Y_i = 0)(1-\psi) \right\}$$

I(.) is the indicator function, which takes value of 1 if its argument is true, and 0 otherwise (Fiske & Chandler, 2011; MacKenzie et al., 2017).

Occupancy models can be incorporated with site- and survey-specific covariates, to consider the difference in occupancy and detection probabilities (MacKenzie et al., 2017). We ran single-species occupancy models for different sexes of marked felids in trail deployment (100T) and full deployment (100T +100R). We ran null models for the probability of occupancy and detection, to evaluate the occupancy of trail and random habitats by different sexes of marked felid species (clouded leopard, common leopard, leopard cat and marbled cat) in our study area. Further we ran single-species occupancy models with site-specific covariates for five different felid species, which are incorporated as supplementary material in appendix 3l.

Forest cover, elevation, human density, distance from settlement, and distance from river were selected as the site covariates based on previous studies (Penjor et al., 2018; Tan et al., 2017). Forest-cover data from 30-m resolution global forest cover change for the year 2001 (Hansen et al., 2013) were used for the forest cover covariate. This is freely available for Bhutan, and we classified forest cover into open forest (21-40% tree cover), closed forest (>40% tree cover) and non-forest for 0-20% tree cover)(Choki et al., 2023). The elevation and stream data were extracted from the Digital Elevation Model (DEM) of Bhutan available at the Bhutan Geospatial Portal including spatial files on settlement , human density and stream networks of Bhutan (NLCS, 2010). We used the ‘raster’ R package (Hijmans et al., 2013) to extract the site covariate value (Johnston et al., 2019), which was the mean of raster cells bound within concentric circles calculated at four scales: 500-m, 1-km, 2-km and 4-km radius around each camera-trap station (Penjor et al., 2018; Tan et al., 2017). To choose the best scale for each variable, we ran a univariate model and selected the variable at the scale with lowest ΔAIC. We modelled detection probability *p* as an intercept-only model considering that all camera traps have equal probability of capturing an animal on every sampling occasion. All the continuous site covariates were z-standardised to a mean 0 and unit standard deviation before analysis for model convergence and comparison amongst covariates (Choki et al., 2023; Stanton et al., 2015). The final models for occupancy and detection probability are:

$$Logit\ (\psi) = \beta_0 + \beta_1 Openforest_1 + \beta_2 Elevation_1 + \beta_3 Closedforest_1 + \beta_4 Openforest_1 + B_5 Settlement\ distance_1 + \beta_6 River\ distance_1 + \beta_7 Human\ density_1$$

$$logit(p) = \alpha_0 + \alpha$$

We ran single-species, single-season occupancy models using the R package 'unmarked' (Fiske & Chandler, 2011) to estimate maximum-likelihood occupancy probability and detection probability. All possible global models were constructed using the 'MuMin' R package (Barton & Barton, 2015) and comparisons amongst all possible models were made using the 'AICcmodavg' R package (Mazerolle & Mazerolle, 2017). We estimated mean occupancy probability and detection probability from models with $\Delta AIC < 2$ (Bumham & Anderson, 2002) using the 'predict' function in the 'unmarked' package.

4.3 Results

4.3.1 Home range sizes of montane carnivores

The home-range size of common leopard was larger for male leopards compared to that of the female (Table 4.1, Figure 4.4, appendix 3f.). The home-range size of the leopard in Royal Manas National Park (leopard_1) was 7 times smaller than the leopard collared at higher altitude in Western Bhutan. Smaller home range size can be due to higher availability of prey or of mates in the surrounding areas (Table 4.2, appendix 3f). Leopard cat and Asiatic golden cat had similar home range sizes, which were almost double the size of the female leopard's range (Table 4.2).

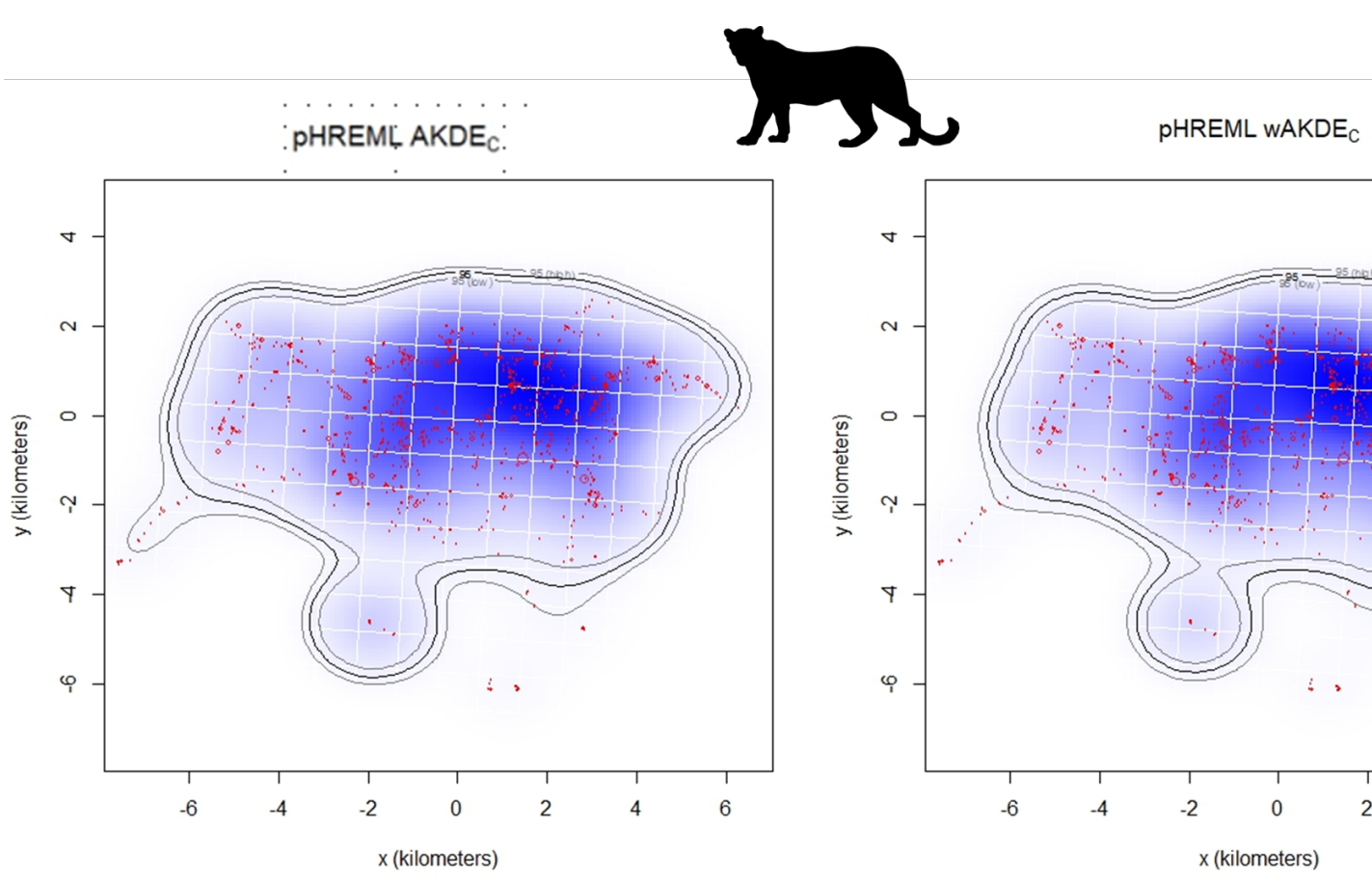

Figure 4.4. Autocorrelated kernel density estimates for common leopard_1 with area corrected AKDE ($AKDE_C$) left and weighted AKDE ($wAKDE_C$) right by using perturbative Hybrid Residual Maximum Likelihood estimator (pREML). The thick black contour represents the 95% home range area estimate, the inner lighter one represents the lower confidence interval, and the outer lighter contour represents the upper confidence interval.

Home range size of the female dhole collared in warm broad-leaved forests of Jigme Singye Wangchuck National Park was almost 6-fold higher than that of the female dhole collared in cool temperate forests of Western Bhutan (Table 4.2). A large home range for dhole_2 could be due to a smaller pack size and correspondingly lower hunting success. Camera trap photos from various locations after collaring recorded only 3 individuals in its pack. The best fitting model for common leopard and dhole was the Anisotropic version of Ornstein-Uhlenbeck Foraging (OUF) process (Appendix 3g). For Asiatic golden cat and leopard cat, the best-fitting model was the anisotropic model of independent identically distributed (IID), which assumes uncorrelated positions and velocities (Appendix 3g).

Table 4.1. Home range estimates of carnivores from area corrected and weighted AKDE. UCL and LCL are the lower and upper confidence limit of 95% confidence interval. Location represents the capture site of animal during collaring. Where WTFD: Wangdue Territorial Forest Division; JSWNP: Jigme Singye Wangchuck National Park; RMNP: Royal Manas National Park.

Animal ID (sex)	**Location**	**Method for estimating HR**	**Estimate (km^2)**	**LCL (km^2)**	**UCL (km^2)**
Leopard_1 (male)	RMNP	$AKDE_C$ (p-HERML)	74.18	65.78	83.06
		$wAKDE_C$ (p-HERML)	72.23	64.06	80.89
Leopard_2 (male)	WTFD	$AKDE_C$ (p-HERML)	538.37	455.99	627.48
		$wAKDE_C$ (p-HERML)	531.59	450.25	619.57
Leopard_3 (female)	RMNP	$AKDE_C$ (p-HERML)	14.84	12.67	17.17
		$wAKDE_C$ (p-HERML)	14.61	12.48	16.91
Golden_1 (female)	JSWNP	$AKDE_C$ (p-HERML)	32.21	26.03	39.04
		$wAKDE_C$ (p-HERML)	32.21	26.03	39.04
Leopard cat_1 (male)	JSWNP	$AKDE_C$ (p-HERML)	30.10	24.57	36.19
		$wAKDE_C$ (p-HERML)	30.10	24.57	36.19
Dhole_1 (female)	WTFD	$AKDE_C$ (p-HERML)	58.20	47.22	70.31
		$wAKDE_C$ (p-HERML)	57.24	46.45	69.14
Dhole_2 (female)	JSWNP	$AKDE_C$ (p-HERML)	342.34	283.55	406.59
		$wAKDE_C$ (p-HERML)	359.44	297.71	426.89

4.3.2 Behavioural patterns in resource selection by montane carnivores

4.3.2.1 Resource selection by common leopard

Resource selection by common leopard_1 was best described by the habitat interaction model (Table 4.2, Figure 4.5). Resource selection by leopard_1 was negatively and significantly influenced by gain in elevation (Figure 4.5, Table S1 appendix 3h, Figure S1 appendix 3k). Leopard_1 selected location with incidences of human-carnivore conflicts, including incidences of livestock depredation by carnivores in the past 5-years (Figure 4.5, Table S1 appendix 3k, Figure S3 appendix 3k). Other habitat variables including tree cover, distance to settlement and river distance did not detectably influences resource selection by leopard_1 (i.e., $\boldsymbol{p} > 0.05$). In terms of interaction, increasing distance from settlement correlates with decreasing incidences of human-carnivore conflict and with decreasing resource selection by leopard_1 (Figure S1, appendix 3j). Presence of the female leopard positively influenced the resource selection by leopard_1 (Figure 4.2). Leopard_1 tended to prefer muntjac over other prey species and presence of sambar negatively influences its resource selection (Figure 4.5). There was significant evidence of avoidance of dhole by leopard_1, and sites with higher occupancy of dhole were less preferred for selection by leopard_1 (Figure 4.5, Figure S6 appendix 3k).

Table 4.2. Resource selection model of common leopard. The presented models are the best-fitting resource selection model, as determined by smallest delta AIC (dAIC). Where RSF represents resource selection function, K is number of model parameters and LL is loglikelihood.

Animal ID (sex)	RSF model	K	AICc	dAICc	LL
Leopard_1 (male)	Habitat interaction	7	948.1	0	-467
	Habitat	6	950.98	2.88	-469.45
	Prey	6	985.56	37.47	-486.75
	Sympatric carnivores	3	1004.42	56.33	-499.2
	Intraspecific	3	1020.55	72.46	-507.27
Leopard_2 (male)	Habitat interaction	6	990.05	0.00	-488.99
	Habitat	5	991.27	1.22	-490.61
Leopard_3 (female)	Intraspecific	3	1020.16	0	-507.07
	Habitat	6	1021.28	1.11	-504.6
	Habitat interaction	7	1023	2.84	-504.46
	Prey	6	1071.8	51.64	-529.86

Sympatric carnivores	3	1073.5	53.33	-533.74

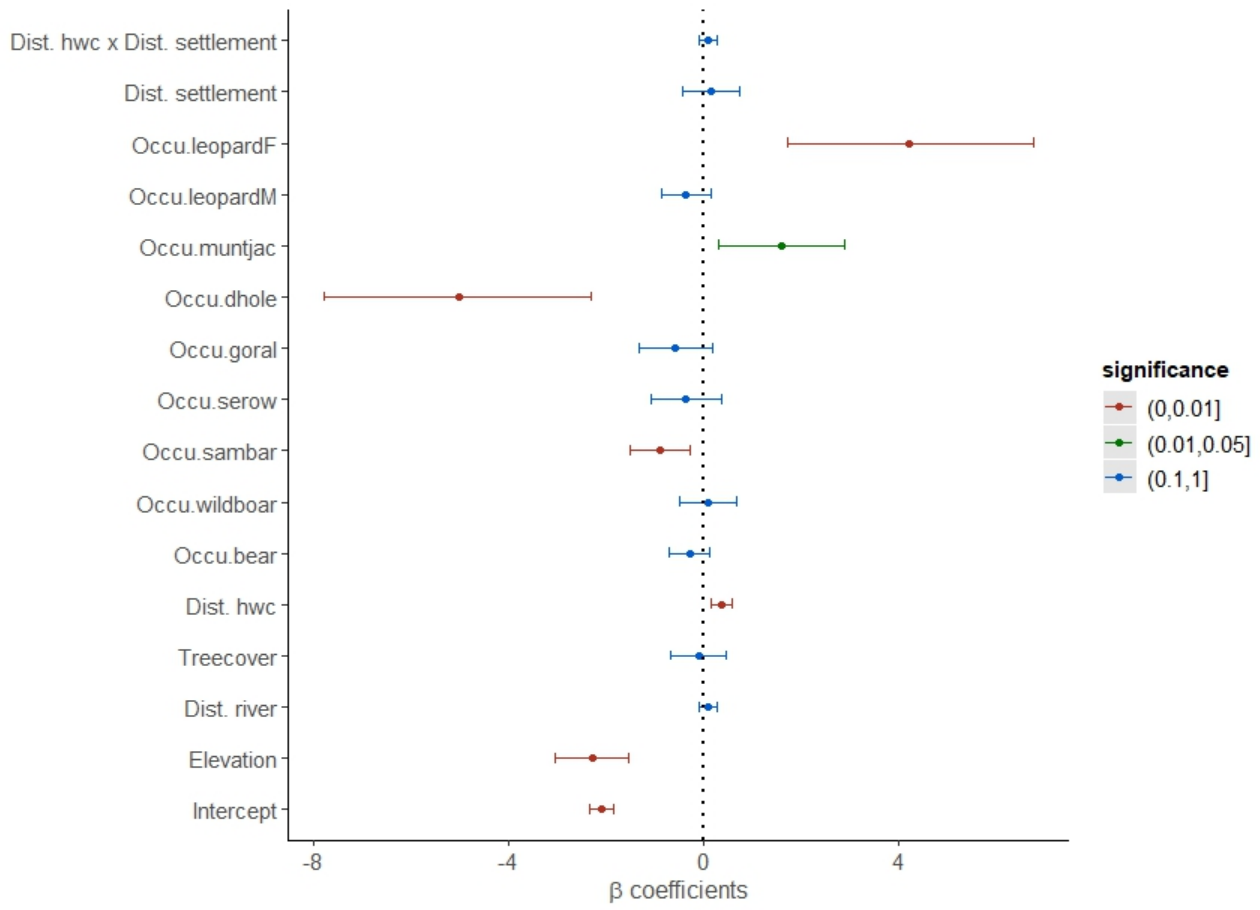

Figure 4.5. Influence of predictor variables on resource selection function of Leopard_1. Abbreviation Dist. represents distance, Occu. represents occupancy, M and F represents male and female sexes, and hwc represents human wildlife (here carnivore) conflicts. Different colours of the lines depict significance level as shown in legend on the right. Error bar represents lower and 95% confidence intervals.

The habitat interaction (distance to settlement *x* Tree cover) model was the top-ranking model for resource selection function for leopard_2 (Table 4.6.). Unlike leopard_1, resource selection was negatively influenced by increasing distance from human settlement (Figure 4.6, Figure S 18 appendix 3k, Table S2 appendix 3h). Resource selection by leopard_2 decreased with increasing elevation (Figure 4.6, Figure S16 appendix 3k, Table S2 appendix). Resource selection by leopard_2 increased with increasing distance from river (Figure 4.6, Figure S15 appendix 3k), Table S2 appendix 3h). Leopard_2 possibly selected sites with higher tree cover but with low confidence in a relationship ($p > 0.05$; Figure 4.6, Figure S17 appendix 3k, Table S2 appendix 3h). The interaction model shows an increase in resource selection by leopard_2 near settlement with higher tree cover (Figure 4.6, Figure S2 appendix 3j).

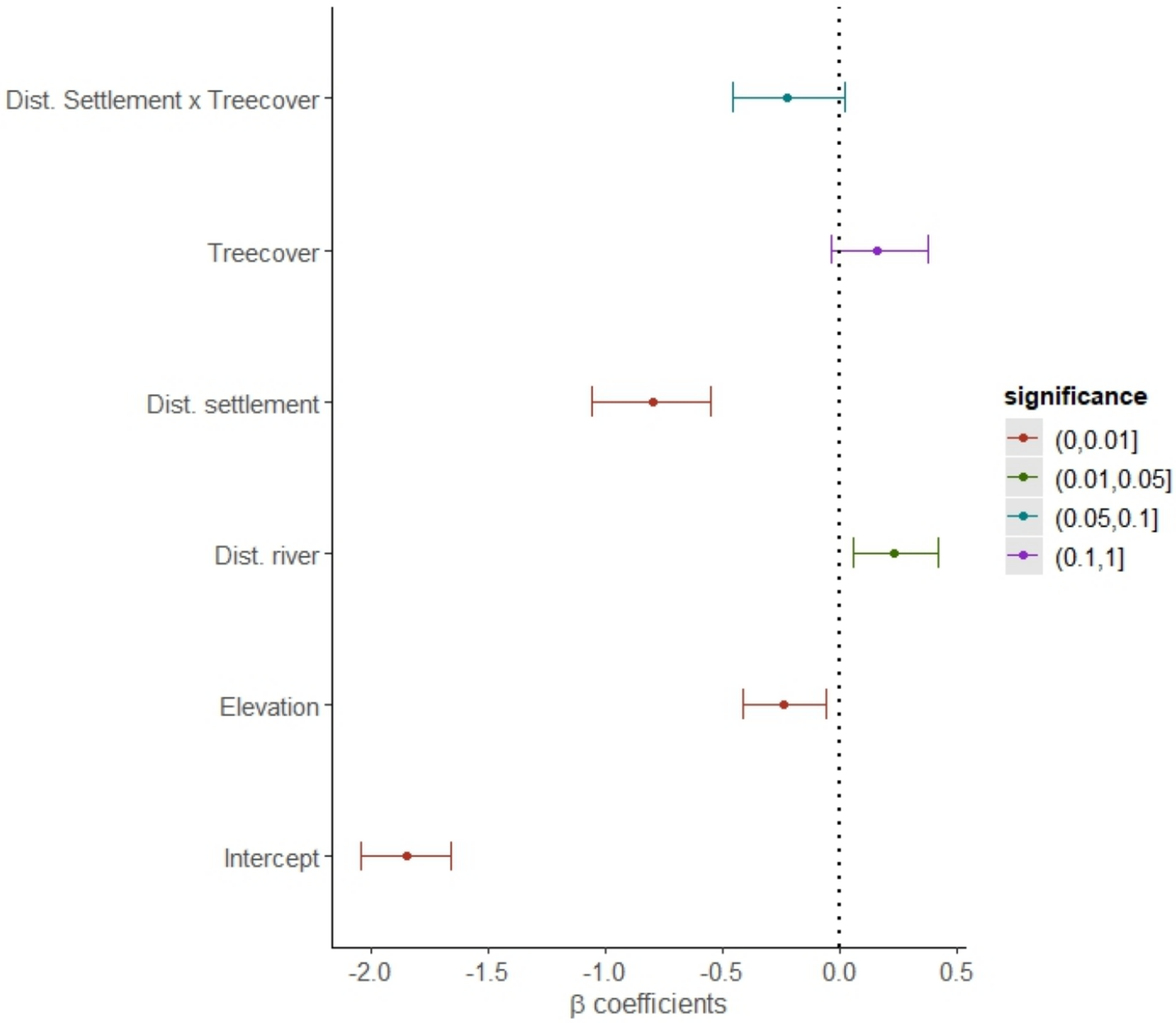

Figure 4.6. Influence of predictor variables on resource selection function by leopard_2. Figure legend are as for figure 4.5.

The intraspecific influence model was selected as the best model for describing resource selection by leopard_3. Leopard_3 possibly tended to avoid both presence of male and female leopard in its vicinity but with weak evidence of a relationship ($p > 0.05$; Figure 4.7, Figure S26 appendix 3k, Table S3 appendix 3h). Avoiding sites with higher occupancies of other males and females may be a strategy to prevent cub infanticides, as observed in the case of leopard_3 when a sub-adult cub was found after collaring. Increase in distance from river positively influenced the resource selection by leopard_3. While leopard_3 selected resources where there was less tree cover (Figure 4.7, Figure S22a appendix 3k, Table S3 appendix 3h). Unlike leopard_1, increase in distance from human-carnivore conflict favoured resource selection by leopard_3. Other habitat covariates including elevation and distance to human settlement were less evidently influences on resource selection by leopard_3 ($p > 0.05$; Figure 4.7, Figure S19-22 appendix 3k, Table S3 appendix 3h). Higher site occupancy of bear positively influenced resource selection by leopard_3. A similar tendency was observed for dhole but with weaker evidence ($p > 0.05$; Figure 4.7, Figure S23 appendix 3k, Table S3 appendix 3h). Leopard_3 selected resources in site where there were higher occupancies of

goral, muntjac, and wild boar (low confidence: $p > 0.05$) and site less occupied by sambar (low confidence: $p > 0.05$) and serow (high confidence: $p < 0.05$; Figure 4.7, Figure S27-29 appendix 3k, Table S3 appendix 3h).

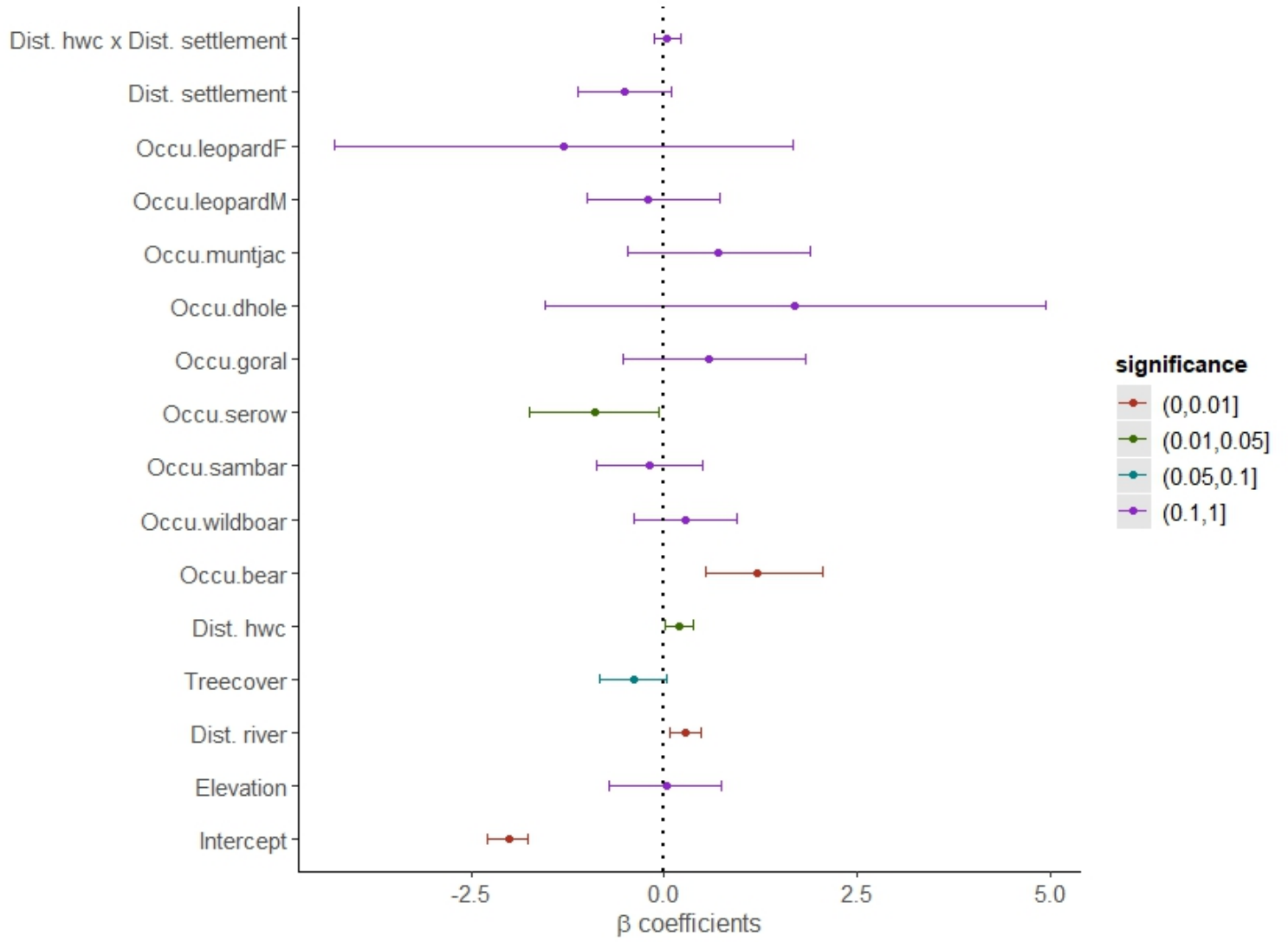

Figure 4.7. Influence of predictor variables on resource selection function by leopard_3. Figure legend are as for figure 4.5.

4.3.2.2 Resource selection by Asiatic golden cat and leopard cat

The habitat interaction model was the top-ranking resource selection function for both Asiatic golden cat and leopard cat (Table 4.3). In terms of interaction between distance to human carnivore conflicts and distance to settlement, Asiatic golden cat preferred sites away from human settlement but nearer to human-carnivore conflicts (Figure 4.8, Figure S4 appendix 3j, Table S4 appendix 3h). There were possible negative associations between resource selection and increase in elevation and tree cover, although weakly evidenced ($p > 0.05$; Figure 4.8, Figure S35 appendix 3k, Table S4 appendix 3h). Asiatic golden cat preferred to select resources in habitat away from rivers and streams (Figure 4.8, Figure S33 appendix 3k, Table S4 appendix 3h). It may have avoided site with higher occupancies of large predators including bear, dhole, common leopard, clouded leopard, and marbled cat (low confidence: $p > 0.05$; Figure 4.8, Figure S36 -39 appendix 3k, Table S4 appendix 3h). However, presence of

muntjac indicated a possible positive correlation with its resource selection function (low confidence: $p > 0.05$; Figure 4.8, Figure S40 appendix 3k, Table S4 appendix 3h).

Table 4.3. Resource selection model of Asiatic golden cat and leopard cat. Table legends are as for Table 4.2.

Animal ID	RSF model	K	AICc	Delta_AICc	LL
Asiatic golden cat_1	Habitat interaction	7	313.77	0	-149.78
	Habitat	6	318.1	4.34	-152.97
	Large carnivores	4	336.88	23.11	-164.4
	Sympatric carnivores	5	342.66	28.89	-166.28
Leopard cat_1	Habitat interaction	7	316.97	0	-151.38
	Large carnivores	3	333.4	16.43	-163.68
	Habitat	6	334.36	17.39	-161.1
	Sympatric carnivores	5	337.49	20.52	-163.69

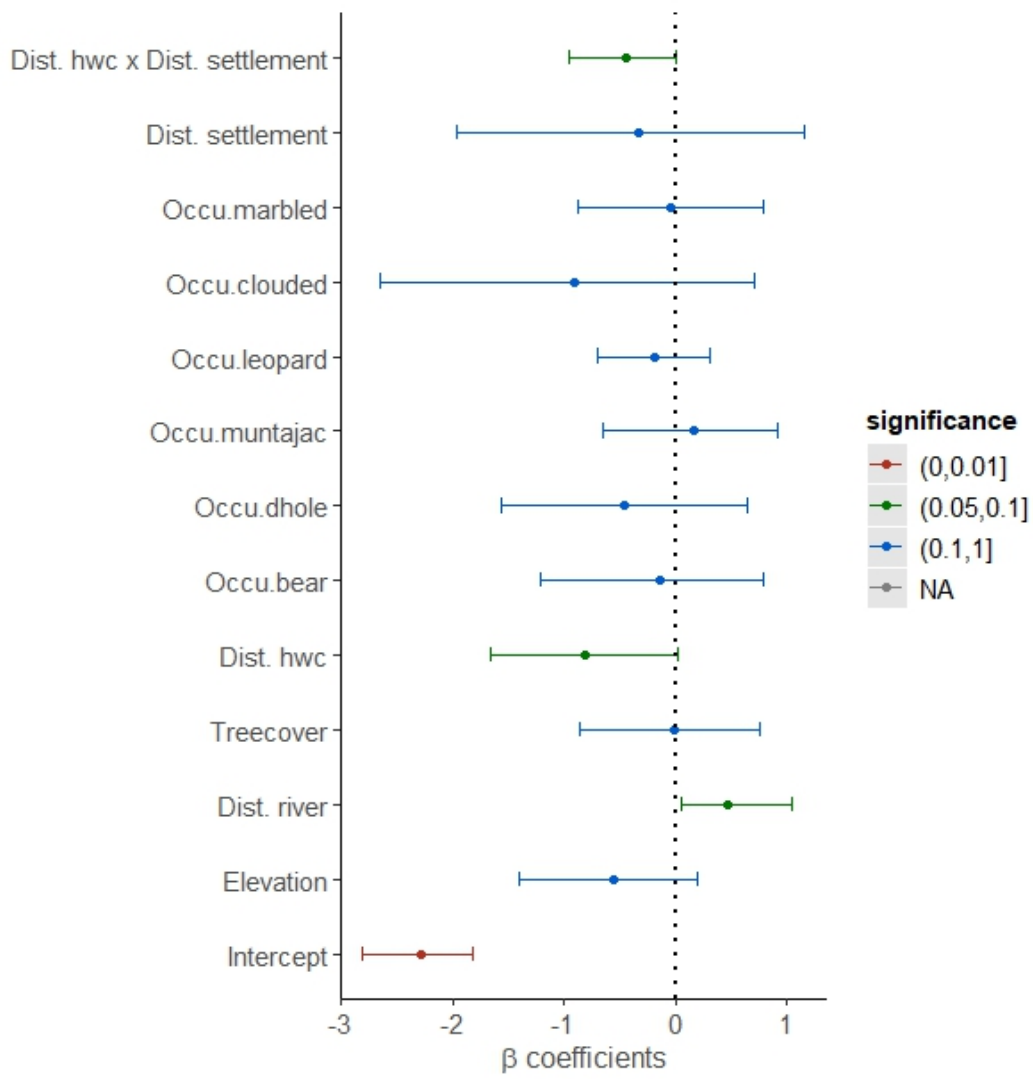

Figure 4.8. Influence of predictor variables on resource selection function by Asiatic golden cat. Figure legend are as for figure 4.5.

Resource selection by leopard cat_1 increased with increasing distance from human settlement ($p > 0.05$) and decreased with increasing distance from incidences of human-carnivore conflicts (Figure 4.9, Figure S5 appendix 3j, Table S4a appendix 3h). Unlike common leopard habitat, the interaction model showed decreasing resource selection with

distance from human settlements where there was evidence of human-carnivore conflicts (Figure 4.9, Figure S5 appendix 3j, Table S4a appendix 3h). Leopard cat_1 possibly selected resource in habitat where there was less tree cover significant (low confidence: $p > 0.05$; Figure 4.9, Figure S appendix, Table S4a appendix 3h). Presence of larger predators including bear, clouded leopard, common leopard, dhole, and marbled cat did not negatively impact resource selection by leopard cat_1 ($p > 0.05$; Figure 4.9, Figure S55-57, S59-60 appendix 3k, Table S4a appendix 3h). Leopard cat_1 did not select resources in habitat with higher occupancy of Asiatic golden cat ($p > 0.05$; Figure 4.9, Figure S58 appendix 3k, Table S4a appendix 3h).

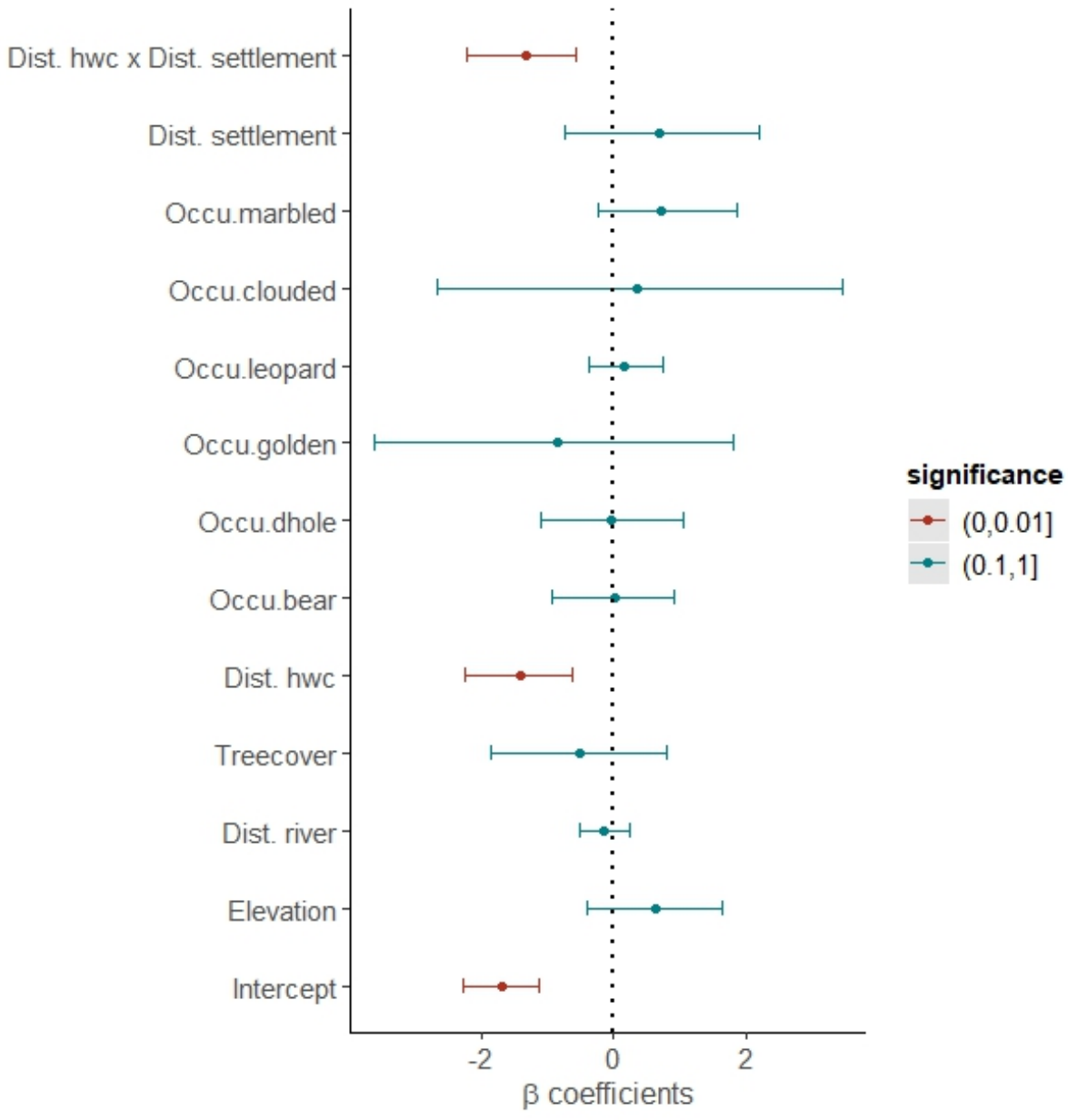

Figure 4.9. Influence of predictor variables on resource selection function by leopard cat. Figure legend are as for figure 4.5.

4.3.2.3 Resource selection by dhole

The habitat interaction model best explains the resource selection function of dhole_1 (Table 4.3). Dhole_1 selected resource in site away from human settlement with lower forest cover as shown by the interaction model (Figure 4.10, Figure S6 appendix 3j, Table S5 appendix 3h). However, the variable tree cover had positive correlation with the resource selection dhole_1. Resource selection decreased with increasing elevation (Figure 4.10, Figure S64

appendix 3k, Table S5 appendix 3h). Dhole_1 possibly selected resource further from rivers and settlements (low confidence: $p > 0.05$; Figure 4.7, Figure S68 appendix 3k, Table S5 appendix 3h).

Table 4.7. Resource selection model of common leopard_3. Table legends are as for Table 4.2.

Animal ID	RSF model	K	AICc	Delta_AICc	LL
Dhole_1	Habitat interaction	6	1026.25	0	-507.09
	Habitat	5	1040.32	14.07	-515.14
Dhole_2	Habitat	6	958.84	0	-473.38
	Habitat interaction	7	959.55	0.71	-472.73
	Sympatric carnivores	4	987.88	29.04	-489.92
	Prey	6	992.01	33.17	-489.97

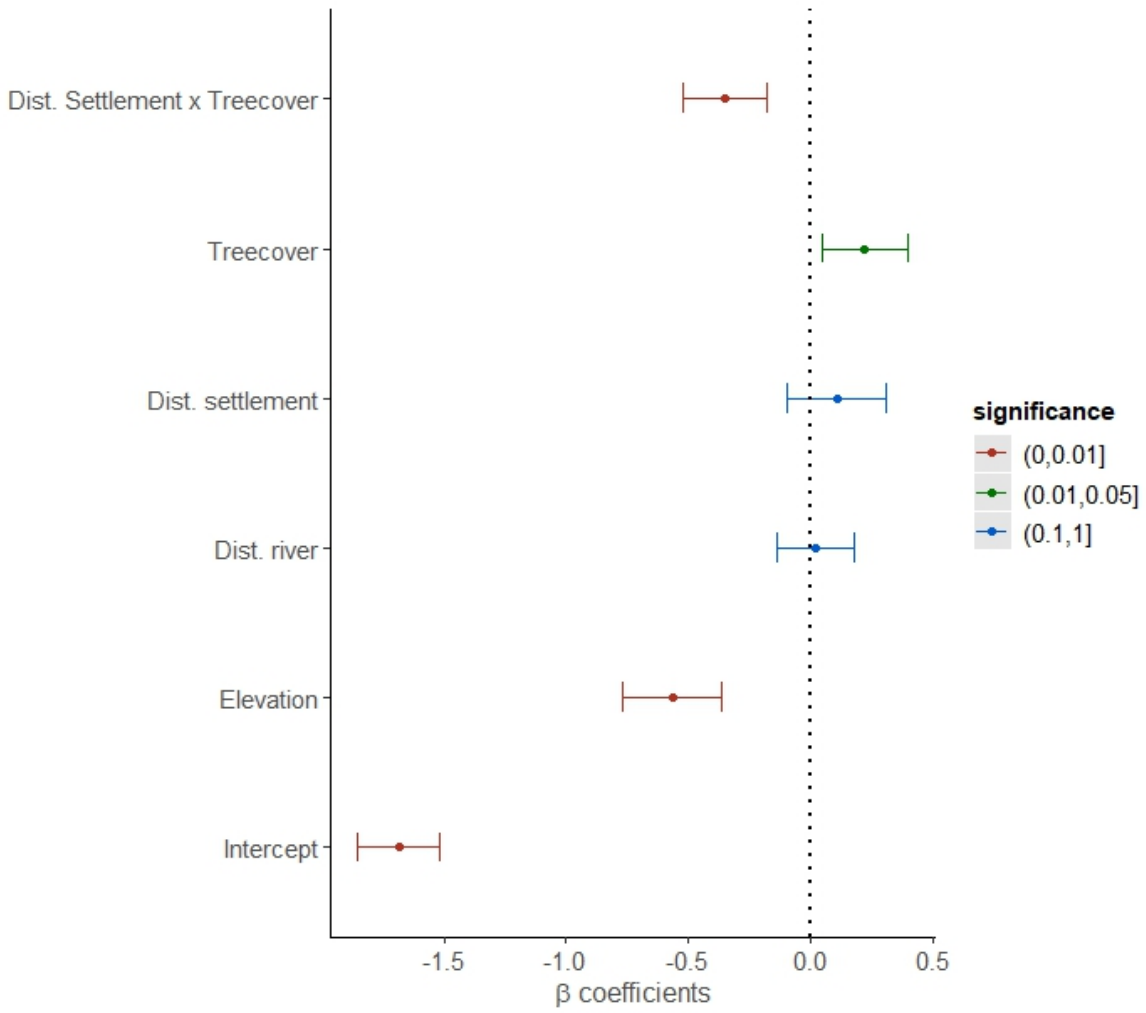

Figure 4.10. Influence of predictor variables on resource selection function by dhole_1. Figure legend are as for figure 4.5.

The habitat model was the top-ranking resource selection model for dhole_2 and resource use declined with increasing elevation (Figure 4.11, Figure S66 appendix 3k, Table S6 appendix 3h). Resource use by dhole_2 correlated positively with incident of human-carnivore conflicts and negatively with distance from human-carnivore conflict (Figure 4.11, Figure S67 appendix 3k, Table S6 appendix 3h). The interaction model revealed that resource selection by dhole_2 was highest at the distance farthest from human settlement and near to human-

carnivore conflict (Figure 4.11, Figure S67 appendix 3k, Table S6 appendix 3h). Resource use by dholes correlated negatively with tree cover (Figure 4.11, Figure S appendix, Table S appendix 3k). Dhole_2 preferred resource selection in sites with higher occupancy of bear (Figure 4.11, Figure S70 appendix 3k, Table S6 appendix 3h). However, it tended to avoid sites with higher occupancies of male and female common leopards (Figure 4.11, Figure S72 appendix 3k, Table S6 appendix 3h). Dhole_2 selected resources in habitat with higher occupancies of muntjac over gaur and goral (Figure 4.11, Figure S71-72 appendix 3k, Table S appendix). Dhole_2 did not select resources in sites with higher occupancies of serow, sambar and wild boar ($p > 0.05$; Figure 4.11, Figure S75 -77 appendix 3k, Table S6 appendix 3h). The parameters from the best model of dhole_1 was used to create the habitat suitability map using the resource selection function by the exponential form (Figure 4.12)

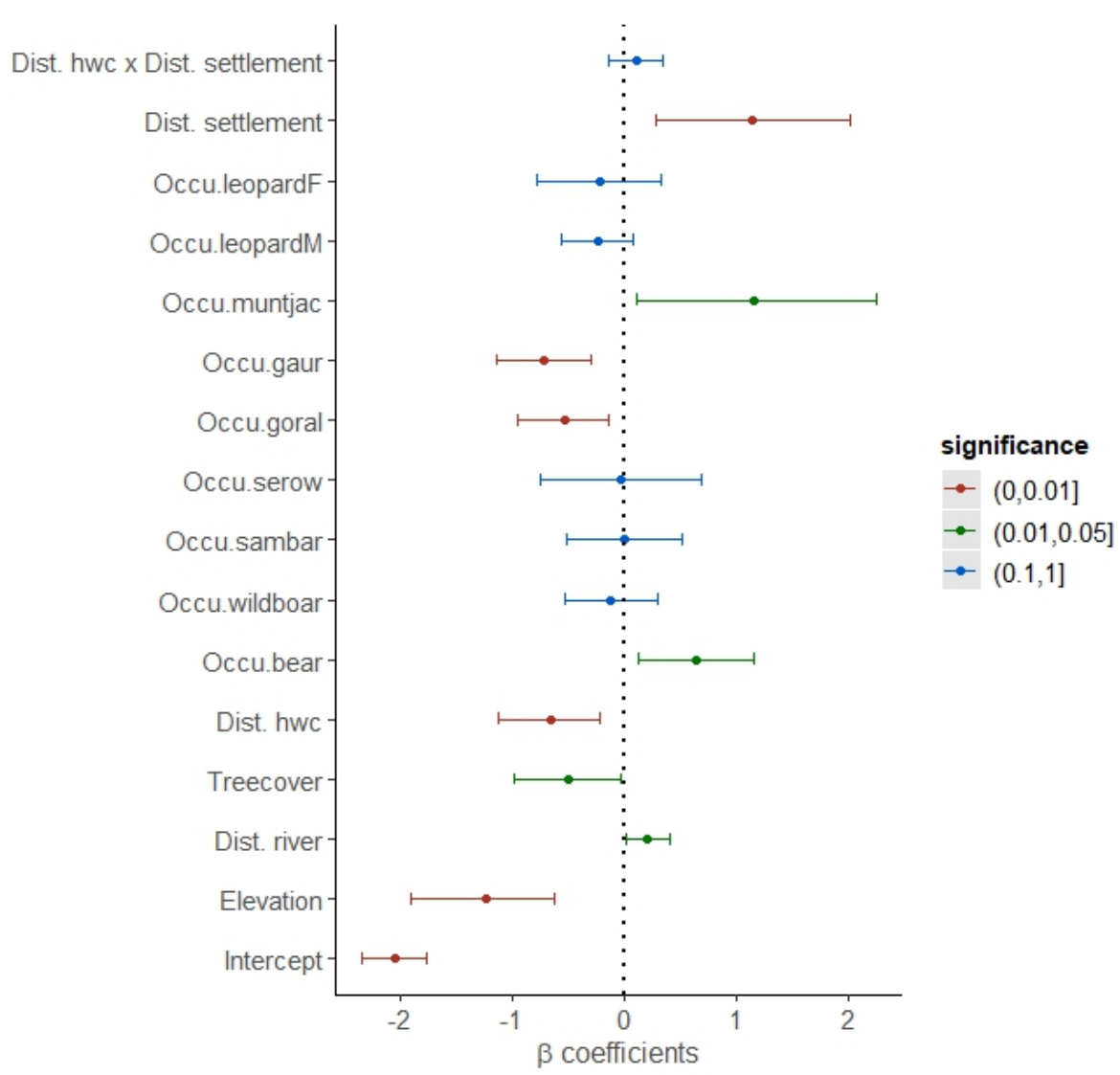

Figure 4.11. Influence of predictor variables on resource selection function by dhole_2.

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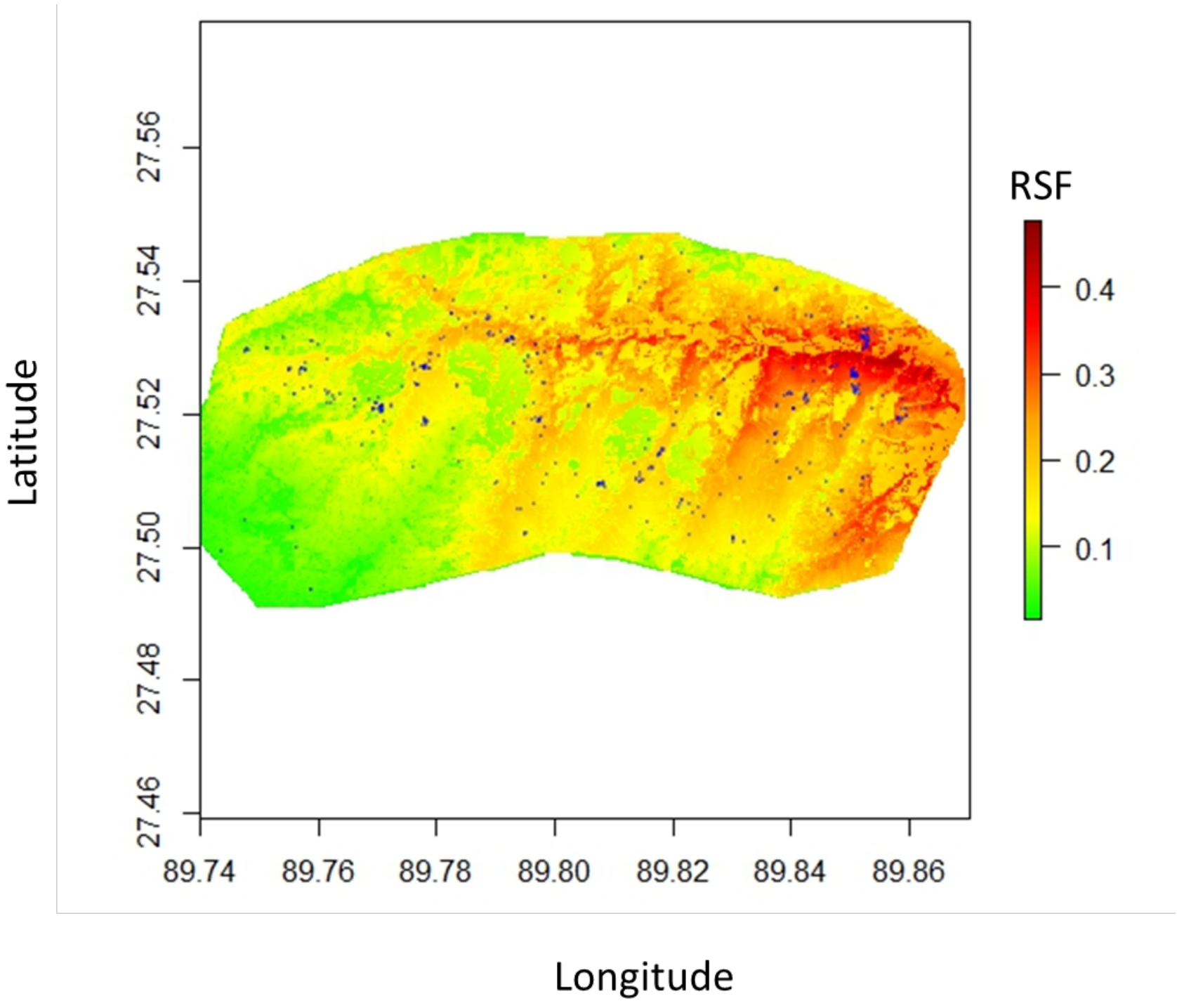


Figure 4.12. Resource selection function map of dhole_1. The colour scale from green to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

4.3.3 Trail and Random site preferences of wildcats

For all species, we observed higher site occupancy by males than females in both the trail-only deployment of 100 stations (100T + 0R) and the combined deployment of 100T + 100R stations, as shown in Figure 4.13. Nevertheless, the random-only deployment of 100 stations (0T + 100R) significantly improved the occupancy of females for all the cat species (Figure 4.13). Similarly, the detection probability of females increased with inclusion of random camera with the trail deployment, except for the clouded leopard (Figure 4.14).

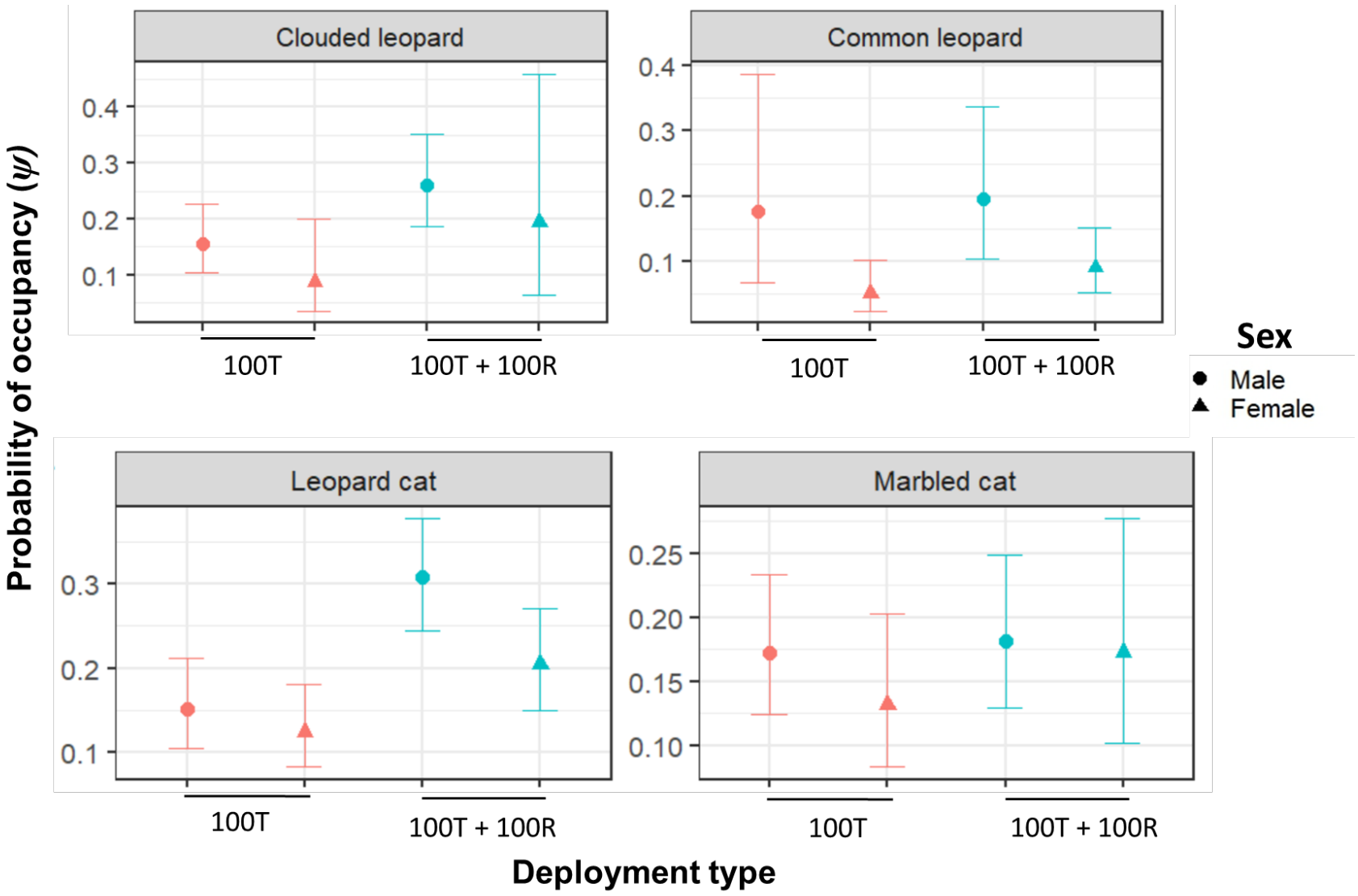


Figure 4.13. Effect on the probability of occupancy of male and female with inclusion of random cameras. Probability of occupancy of male and female were calculated from 100 trail deployment (100T) and full deployment (100T +100R). The error bar represents the 95% confidence interval.

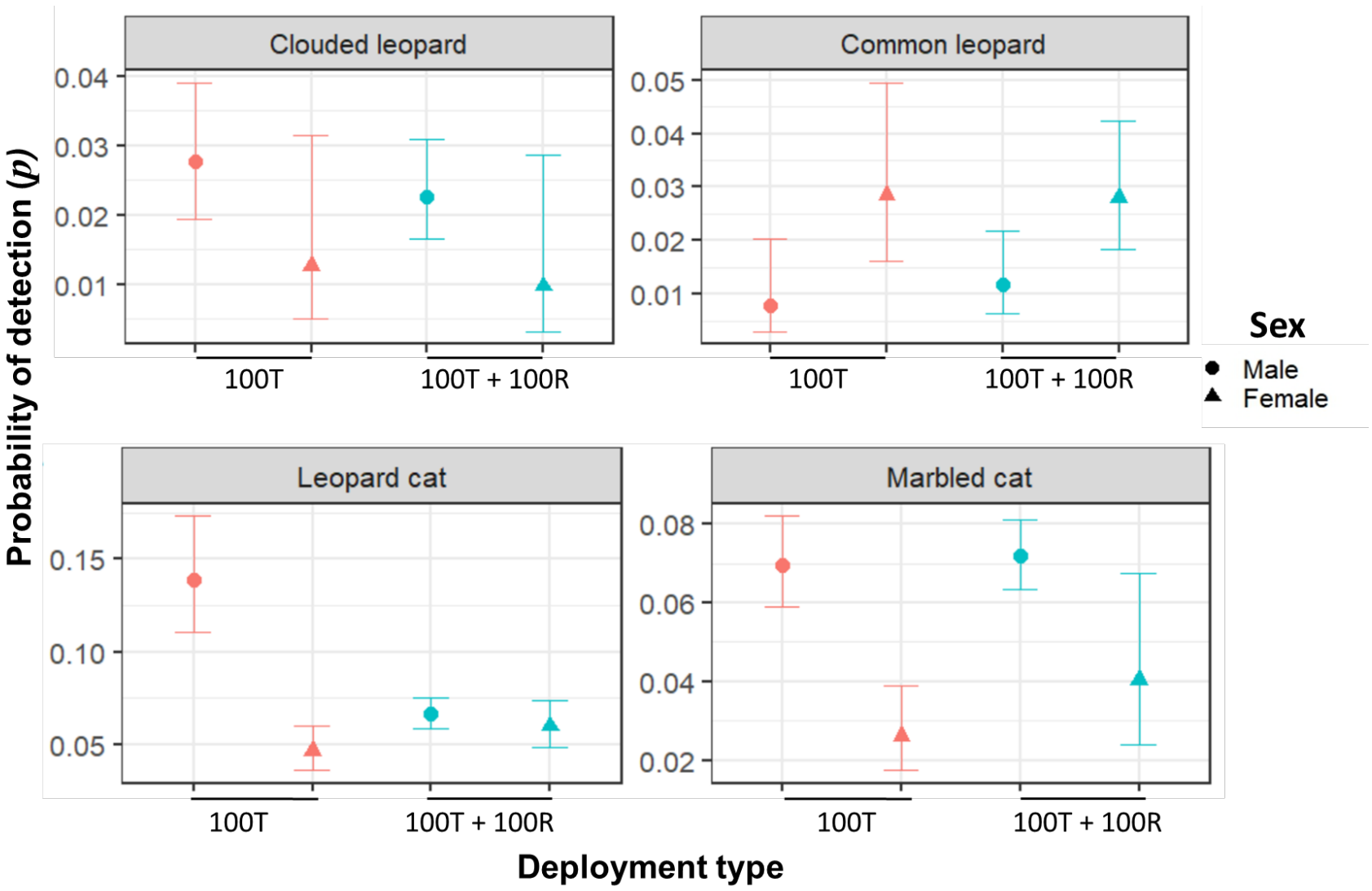


Figure 4.14. Effect on the probability of detection of male and female with inclusion of random cameras. Probability of detection of male and female were calculated from 100 trail deployment (100T) and full deployment (100T +100R). The error bar represents the 95% confidence interval.

4.4 Discussion

Montane carnivores of Southeast Asia are the least studied of all the carnivores, and little is known about their home range and resource needs, which is essential for conservation planning and management. For example leopards are endangered species in Southeast Asia and there is limited information regarding their resource needs required for long-term conservation planning (Mondal et al., 2013). The spatial ecologies of tigers, leopards, and snow leopards have recently been explored in Bhutan, yet there are no scientific publications available for references. We collared three species of wild cats and one species of canid from lower mountainous terrain of Bhutan. Our study also used data from the high Himalayas of the Western part of Bhutan, to compare differences in home range and resource use by carnivores between lower and upper Himalayas. Heterogenous habitat selection has been observed between different species of carnivores as well between the sexes within the same species (Harmsen et al., 2010; Montalvo et al., 2023). To evaluate heterogeneity in habitat selection, we assessed occupancies of wild felids between trail and off-trail (random) habitat.

The home ranges of common leopard in our study spanned 14 to 540 km^2, with a comparatively smaller home range for the female. Home ranges of leopards in desert habitat of Israel were 84 km^2 and 137 km^2 for two males. In Russia, two adult females had home ranges of 33 and 63 km^2, and an adult male had a home range of 280 km^2 (Miquelle et al., 1996). The home range of leopards in India varied from 10 to 451 km^2 (Mondal et al., 2013). Smaller home ranges for the common leopard in our study area may be influenced by restricted access to suitable refugia for raising young cubs. We saw a female leopard from our study site with a subadult cub a few months after collaring (Figure 5, appendix 3). In polygynous species, each sex is expected to have a different ranging strategy in acquiring resources to maximize reproductive success (Sandell & Gittleman, 1989). Nursing mothers are found to prioritise refugia in suitable sites while raising you cubs, and this behaviour is seen in almost all carnivores (Macdonald, 1983; Rodríguez-Recio et al., 2022). We observed an almost 7x larger home range for male the leopard collared in Western Bhutan, which occupied habitat mostly consisting of coniferous forest thought to have lower prey density. Male leopards are large and solitary carnivores that require extensive space use for their polygynous mating system, influenced by the availability prey (Happold & Happold, 2013). Leopard home-range size also depends on the primary productivity of the site, being much larger in arid and less productive sites (Mondal et al., 2013).

The female Asiatic golden cat had a home range that was almost double the size of female leopard (leopard_3) and similar was observed in the case of male leopard cat where home range size was double the size of female leopard_3. Home range size can vary among and within populations depending on access to resources and cost for defending resources in the case of territorial species such as cat species recorded in our study area (Herfindal et al., 2005; Nilsen et al., 2005). Within populations, the home range size varies due to both intrinsic and extrinsic factors such as food, reproductive resources, intraspecific density, and competition (Rodríguez-Recio et al., 2022). The home range sizes of the two smaller cats may be larger than the female leopard due to lower prey choice and hunting success. The habitat use by Asiatic golden cat was found to be influenced mostly by presence of prey species rather than presence of potential competitors (Rasphone et al., 2020). The home range of Asiatic golden cat was similar to that recorded in Thailand, which ranged from 32.6 to 47.7 km^2. The home range size of male leopard cat in our study area had almost double the size of home range estimated in Thailand (12 4 km^2 for male and 14 km^2 for female) (Grassman et al., 2005b). Mountainous habitat with lower prey diversity and hunting efficiency can again explain the larger home range size compared to that of plain areas.

The home range size of the female dhole collared in southern warm broadleaved montane forest was 5 times larger than that collared from cool temperate forest of Western Bhutan. We anticipate that the pack size of dholes might have an influence on their hunting success. The pack size of dhole may vary between 3 and 7 individuals (Karanth, 1993). The female we collared (dhole_2) had pack size of 3, which was recorded in several camera trap locations. Smaller pack size may require larger effort for hunting, and reduces chances of prey availability, thereby requiring larger home ranges. The home range size of male dholes collared in north central Thailand was 12 km^2 and 46 km^2 respectively (Grassman et al., 2005). Similarly, the home range of dhole collared in central India ranged from 60-70 km^2, much smaller than the dhole_2, with home range size of 342 km^2 observed in our study (Acharya et al., 2010).

Resource use by the two male leopards was best explained by the habitat model, whereas resource use by the female was determined by influence from the presence of other leopards in the locality. Elevation was the major habitat factor determining resource selection where resource selection is influenced negatively over its rise. Larger home range sizes are found in leopards recorded from higher elevation, likely due to inconsistent prey availability under harsh environmental conditions, when leopards require broader and larger movement incurring higher energy expenditure (Rodríguez-Recio et al., 2022). Our male leopard (leopard_1) selected resources near places where incidences of human-carnivore conflict were recorded in the past 5 years. We expect that common leopard likely favour domestic animals as a prey species (supported by reports from the social survey in Chapter 5). Presence of a female positively influences the resource selection by male leopards, likely a response to perceived mating opportunity. The home range pattern of females has been found to be the chief driver of resource selection by male leopards and by felids in general (Bailey, 1993; Snider et al., 2021). Male home range size is found to encompasses several female home range sizes (Rodríguez-Recio et al., 2022). Resource selection by our female was negatively influenced by the presence of males and by human settlements. Here we foresee that the female tends to avoid human disturbance and other leopards to minimise the risk of cub infanticides. As with the larger cats, resource selections by Asiatic golden cat and leopard cat are mostly influenced by habitat features. The Asiatic golden cat avoided larger carnivores while selecting resources, and likewise the leopard cat. The two dholes had similar resource selection patterns to the male leopards that we collared. Resource selection by dholes was negatively influenced by elevation and was positively influenced by the presence of human-carnivore conflict incidences. However, we observed dhole and leopard tend to avoid each

other while selecting resources, as the presence of each negatively influenced their resource selection.

Climate change is a global issue that influences biodiversity distribution and the interactions of human communities cohabiting with wildlife (Gizachew, 2022). Knowledge of the movement ecology of carnivores is crucial for developing effective management responses to climate change (Gizachew, 2022; Westley et al., 2018). For example, carnivores are highly sensitive to changes in temperature and habitat, leading to shifts in their ranges (Khosravi et al., 2021; Ripple et al, 2014). Information on these shifts may help to predict where carnivores may move in response to climate change, which can be vital for conservation planning and managing negative interactions between human and carnivores. Our study on the movement ecology of carnivores in Bhutan is the first of its kind to explore four cohabiting carnivore species that play key roles in ecosystem dynamics as predators. Carnivores regulate or limit prey populations, which further influence vegetation structure (Dorresteijn et al., 2015). Changes in their movement pattern may have cascading effects on other species and on ecosystem processes (Dorresteijn et al., 2015). Developmental activities often threaten habitat connectivity in landscapes such as those in Bhutan. Knowledge of movement patterns and site use by carnivores will help in maintaining or restoring these connections to facilitate adaptation to changing environmental conditions, ensuring their long-term survival.

The information from this study will help to inform policy makers on the ways that carnivores in Bhutan exploit their resources and the movement path they take. This will be crucial for environmental impact assessments for developmental projects, and mitigation of adverse impacts on carnivore habitat from developmental projects. Knowledge on the pattern of resource use by the carnivores will be crucial in the formulation of habitat management strategies within the protected area system of Bhutan and those areas that lie outside it. This information will also be crucial in formulating mitigation strategies for negative interactions between humans and carnivores. By understanding the way carnivores move in response to environmental changes, conservationist can develop climate adaptation strategies such as creation of wildlife corridors or protected areas to adapt to the climate change impacts.

4.5 Conclusion

This report is the first of its kind in Bhutanese landscapes pertaining to the movement ecology of carnivores. The empirical results presented in this chapter are based on a limited sample size. Additionally, the home range and resource usage patterns discussed here are specific to individual animals, making them subjective. Therefore, our findings are not generalized to a

national or regional level. We urge conservation authorities and researchers to conduct detailed studies of the movement ecologies of wild carnivores of Bhutan, as these are the least studied mammals, and studies to date have often focused on population estimates rather than spatial ecology and interaction with local communities.

Chapter 5 Evaluation of social factors influencing community-level attitudes to wild felids

Contributions

I developed the aims, objectives, and method for this study, in collaboration with Vijay Kumar Moktan, Kuenley Tenzin and Nagdrel Lham from World Wildlife Fund Bhutan (WWF Bhutan) Project office. The proposal was reviewed by my supervisor Professor C. Patrick Doncaster and was later submitted to WWF Bhutan for approval. I developed both the Knowledge, Attitude, and Practice (KAP) and Key Informant Survey (KIS) questionnaires, which were reviewed by WWF-Bhutan and by Professor Doncaster, prior to approval by the University of Southampton Ethics and Research Governance panel (ERGO 76113.A1). Field assistants were trained on the questionnaire and on how to collect data through a mobile phone-based application. I received funding support from the World Wildlife Fund Bhutan office to conduct the entire fieldwork. I analysed the data and drafted the report, which was reviewed by Professor Doncaster and Dr Oliver Richard Wearn from Flora and Fauna International.

Abstract

Successful management of wild felids depends on knowledge of factors responsible for social acceptance by co-habiting communities. Conservation that discounts societal attitudes and perceptions about wild felids may foster indiscriminate treatment of the felids by local communities, whereas consideration of community attitudes can provide the foundations for human-felid coexistence. In order to evaluate the social elements contributing to positive or negative human-felid interactions, we modelled human behaviours underpinning the social acceptance of wild felids and dhole (*Canis alpinus*), hereafter referred to as our focal carnivores, in Bhutan's Jigme Singye Wanghcuck National Park and Royal Manas National Park. We interviewed 330 householders from four communities with a Knowledge, Attitude and Practice (KAP) questionnaire, and 33 local leaders with a Key Informant Survey (KIS).

We found that almost 90% of the residents of local communities in RMNP and JSWNP are aware of human-carnivore conflicts in their locality. Common leopard was ranked as the carnivore in their locality associated with most conflicts, followed by tiger; small felids caused the least conflict. Residents ranked the tiger as the most important, and small felids as the least important in the ecosystem, amongst wild carnivores that influence their lives. We

modelled social acceptance of carnivores by communities using Structural Equation Modelling (SEM). Social acceptance was found to be significantly influenced by government incentives on carnivore conservation and positive attitudes of local communities to carnivores. Negative attitudes towards carnivores were associated with rates of conflict with common leopards. In the presence of conflict with tigers, community support for carnivores conservation was positively influenced by higher compensation. Communities perceived that future risks of livestock depredation were significantly raised by a rising frequency of conflicts with common leopards.

Over the last 5 years, the surveyed communities suspected loss of 412 domestic animals, worth 81,185 USD, to carnivores. Direct compensation for loss of livestock, and insurance schemes, were found to be the most effective mitigation measure for the community in terms of improving attitude towards carnivore conservation. We found that almost all the key informants understood the causes of human-carnivore conflict in these protected areas. According to key informants, the common leopard was the wild felid most associated with conflicts, and the main causes of human-carnivore conflict were the proximity of a human settlement to carnivore habitat, habitat encroachment, the decline in prey populations and climate change. Mitigation measures most frequently suggested by key informants were creating awareness of positive roles or benefits of species to communities, awareness of compensation schemes, awareness of protection levels and the law, awareness of punitive sanctions for retaliatory killing (e.g., fines or prison) and technological advancement by providing heat sensing devices, chain-link and electric fencing. This study recommends initiating a sustainable financing system for livestock loss and technological advancement to strengthen co-habitation with wild felids.

5.1 Introduction

Thirty-seven different species of wild felids (family: Felidae) are present across all continents except Australasia and Antarctica, and sixty percent of the living wild felids (21 species) occur in Asia (Macdonald et al., 2010). Wild felids shape the structure and function of diverse ecosystems worldwide (Holland et al., 2018). Large felids, including tigers, lions, leopards, jaguars, and snow leopards, are keystone species essential for maintaining biodiversity and ecosystem balance (Newsome et al., 2017). Nevertheless, the Felidae are the most threatened mammalian family due to ever declining populations from human-induced habitat degradation and poaching (Loveridge et al., 2010). The dhole, also, is threatened with extinction and livestock predation is main source of conflict between humans and dholes (Srivathsa et al.,

2020; Thinley et al., 2021). Government and conservation NGOs are investing substantial effort and resources globally into reducing the negative impacts on wild carnivores from anthropogenic activities (Bhattarai & Fischer, 2014). The success or failure of these efforts depends on the managerial capacity of conservation authorities and the social behaviours of cohabiting communities (Karanth et al., 2017). Here we evaluate sociocultural factors that influence community-level experiences of positive and negative human-carnivore interactions in central Bhutan, focussing on the seven species of co-occurring felids, as well as the dhole. This questionnaire-based study develops a methodology for detecting the influence of multiple interacting drivers of attitudes, which has wide applicability to other questionnaire surveys.

Eleven different wild felids inhabit the range of habitats present in Bhutan, from subtropical forests to snow-capped mountains (Wang & Macdonald, 2006). They form an integral part of the rich biodiversity that makes Bhutan one of the biological hotspots of the world (Wang & Macdonald, 2009). Wild felids receive substantially more conservation investment worldwide than any other carnivores, due to their declining populations and degrading habitats (Holland et al., 2018). In Bhutan, they enjoy political and religious support for their upkeep across large tracts of undisturbed natural habitat (Wang & Macdonald, 2009). Bhutan has committed to conserving wild felids, notably to doubling the current number of tigers (*Panthera tigris*) and snow leopards (*Panthera uncia*) by 2030 (NCD, 2018). In 2019, two protected areas of Bhutan, Jigme Singye Wangchuck National Park and Royal Manas National Park, received accreditation from the Conservation Assured Tiger Standards (CA|TS) for global Tiger Conservation standards (WWF, 2019). In 2023, Bhutan recorded a 27% increase in its wild tiger population compared to the baseline of the first national tiger survey using camera trapping in 2015 (WWF, 2023). Bhutan also recorded almost 40 % increase in population of snow leopard compared to the records from 2016 (DoFPS, 2023).

Due to their requirement of an extensive home range and need for live-caught food, wild felids rank amongst the mammals coming most frequently associated in conflict with humans (Inskip & Zimmermann, 2009). The tiger and common leopard alone account for 82% of livestock depredation in Bhutan's South-central region (Wang & Macdonald, 2006). The snow leopard is a major subject of conflict in the country's Northern region (Lham et al., 2021), causing losses of more than 10% of yak herders' earnings. In a 7-month period in 2020, Bhutan recorded more than 200 livestock depredation events by tigers, causing massive losses to the livelihoods of farmers (Dorji, 2020). Depredations by snow leopards in Wangchuck Centennial National Park of Bhutan accounted for the loss of more than 10% of yak herders'

yearly income (Jamtsho & Katel, 2019). Such interactions between felids and humans negatively impact the livelihoods of forest-dependent communities, and negatively impact the wild animals from retaliatory killing (Lham et al., 2021; Sangay & Vernes, 2008).

There are various mitigation measures to reduce incidences of human-felid conflict worldwide, from financial compensation to modifying animal husbandry practices (Holland et al., 2018). However, these management interventions have limited success in reducing conflicts with felids. The interventions rarely align with the conflict situations, due to a lack of in-depth study on the nature of the conflicts (Baynham-Herd et al., 2018). A lack of fundamental understanding of the social and ecological factors influencing human-wildlife conflicts also hampers proper mitigation planning (Dickman, 2010). In Bhutan, the government formulated a strategy over a decade ago to mitigate conflicts by providing compensation and alternative livelihoods to livestock husbandry (NCD, 2008). Nevertheless, there has been a rise in human-felid conflicts over the years, posing an important concern to the government (Sharma et al., 2021). Therefore, there is a need to properly analyse human-felid interactions in Bhutan to review and revise the current mitigation measures.

In this study we evaluate the relationships amongst social factors likely to influence acceptance of carnivores, to characterize causes and mitigation of human-felid conflict. This first assessment for Bhutan will help policymakers and wildlife managers to understand the nature of interactions between humans and felids. We identify factors that positively or negatively influence social acceptance of, and attitudes towards, wild felids by local communities. We identify factors that lead to support for conservation of wild felids by the local communities, including their perceptions of risks from cohabiting with wild felids. We also evaluate key informants' knowledge about human-carnivore conflicts and their recommendations for mitigating negative impacts from human-carnivore conflict.

Conceptual framework

In the conservation science of large carnivores, public willingness to accept the policies developed by the conservation authorities is recognised as important for social acceptance of large carnivores and for conservation in general (Barmoen et al., 2021). We consider that incentives in the form of financial or in-kind assistance from government agencies and conservation authorities will positively impact the social acceptance of wild felids by the communities. Governments throughout the world have been using incentives to address socially important issues through the ages (Silverman et al., 2016). In biodiversity conservation, economic incentives have progressively gained prominence in the conservation

of environment and biodiversity (Rode et al., 2015; WBCSD, 2011). Incentive-based conservation is now a popular and significant part of how forest and biodiversity is governed, despite criticism for its potential impact on local and indigenous populations (McWherter et al., 2022; Wiik et al., 2020). We defined social acceptance of wild felid as the ability and willingness of communities to cohabit with wild felids despite impacts from negative interactions with them. To test how financial or policy incentives impact community-level acceptance of felid conservation, we formulated a first hypothesis $\boldsymbol{H_1}$ of a total of nine hypotheses (Figure 5.2):

H_1: Incentives from conservation authorities (f6) positively influence the social acceptance of wild carnivores (f1).

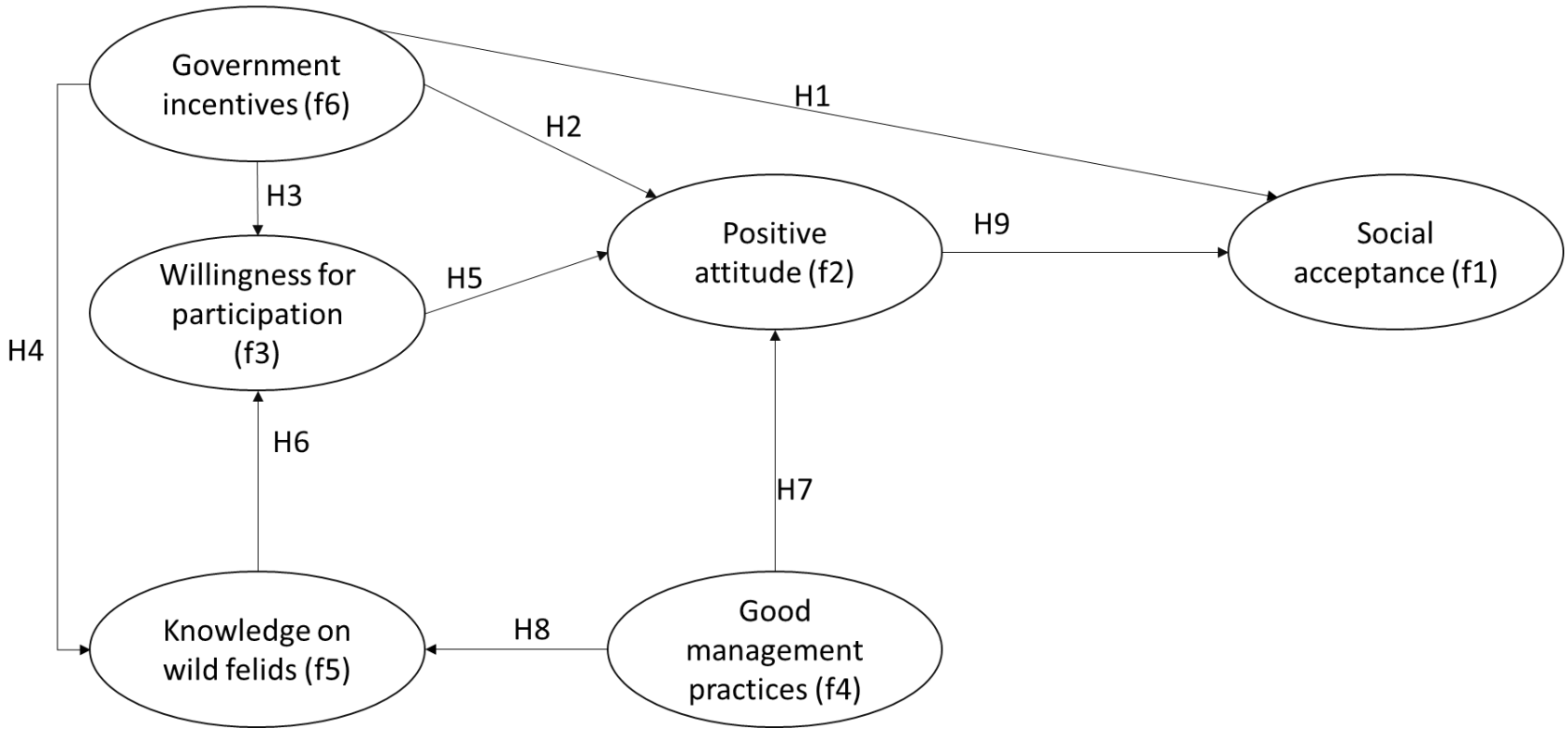


Figure 5.1. Conceptual framework for a hypothesized structural model illustrating the relationship between factors responsible for social acceptance of carnivore presence by the local communities of JSWNP and RMNP. The arrow represents how one factor (f) positively determines the other factor (e.g., f1, social acceptance of wild felids is positively influenced by positive attitude towards wild felid from local communities f2 and government incentives f6). Each of these factors is measured by a set of questions as shown in Table 3.1. The hypotheses tested are represented by H1- H9.

Aside from incentives, the intrinsic value placed upon wildlife by a community is also found to be an important determinant of public participation in conservation (Jones, 1999). Endorsing the inherent importance of the natural world fosters a moral responsibility in humans for the conservation of wildlife and their habitat, which we term here as a positive attitude towards wild felids (Batavia & Nelson, 2017; Ghasemi & Kyle, 2021). Studies have

reported that moral concern for wildlife conservation motivates individuals for conservation of endangered species, habitat protection and donations towards conservation (Batavia & Nelson, 2017; Ghasemi & Kyle, 2021; Lute & Attari, 2017). Morality considerations influence positive attitudes towards wildlife conservation, and attitudes vary globally depending on the economy, geographical location, religion, utility of wildlife, and human culture (Driscoll, 1992; Su & Martens, 2017). We define a positive attitude toward wild felids as a favourable perception of wild felids by local communities measured in its embedding in moral ethics and cultural practices. We hypothesize that government incentives in the form of financial or policy incentives will positively motivate community to conserve wildlife:

H_2: Incentives from conservation authorities will positively impact community-level attitudes toward wildlife conservation ("positive attitude")

Effective conservation requires a combined effort based on scientific evidence and the time-tested wisdom of the local communities living within the ecosystem (Sagoe et al., 2021). Engaging communities in conservation through the assessment of their attitude toward wildlife can help in enhancing ecosystem conservation (Xu et al., 2022). The future engagement of communities for conservation is predetermined by how much they have been involved in previous conservation activities (Xu et al., 2022). Involving communities in conservation activities through ecotourism activities and co-management of wildlife habitat has been shown to enhance local guardianship towards biodiversity (Bhalla et al., 2016; Han et al., 2016). Furthermore, studies have found that perceived pressures to conserve wildlife come not only from friends and family, but also from the social environment, such as government and society (Zhang, 2016). We define community-level willingness to participate in wild felid conservation as how likely community members are to participate in conservation planning and implementation of conservation measures for carnivores (e.g., member of human-wildlife conflict rapid response team, gewog tiger conservation group). We therefore set a hypothesis with respect to the influence of incentives from conservation authorities on community-level willingness to participate in wild felid conservation (Figure 5.2):

H_3: Government incentives positively motivate community-level willingness to participate in wild felid conservation.

We define community-level knowledge of wild felid conservation as the level of community members' knowledge on the cultural and ecological significance and threats to wild felid conservation. The knowledge gap between conservation authorities and the communities is one of the main issues of concern in the field of wildlife conservation (Karanth et al., 2017). Incorporating community knowledge into the conservation of wildlife and conservation authority to educate community on importance of wildlife conservation are now a general consideration in the field of wildlife conservation (Gandiwa et al., 2014; Goldman, 2003). Through education and awareness-raising programmes, there is a growing understanding of the importance of wildlife and habitat. Nevertheless, understanding of the moral motivations for wildlife conservation through the lens of moral psychology still remains unstudied (Ghasemi & Kyle, 2021). In this regard, we set the following hypothesis regarding the influence of government interventions on enhancing knowledge of wild felid conservation:

H_4: Incentives from the conservation authorities positively impact community-level knowledge of wild felid conservation.

Moral psychologists argue that moral reasoning, which is based on criteria for right and wrong, acts as a primary driver for individuals to engage in morally right actions (Ghasemi & Kyle, 2021; Kohlberg, 1969). Further, moral psychologists have explored the role of emotions concerned with interest in, and welfare of, others as a stimulus for moral behaviour (Ghasemi & Kyle, 2021; Haidt, 2003). We believe that community-level willingness to participate in wild felid conservation is influenced by individual morality, which directly relates to positive attitudes towards wild felid conservation. For example, past personal experiences of participating in wildlife conservation positively affected the willingness of people in China to protect the African elephant in Africa (Yang et al., 2022; Zhang, 2016). With this in mind, we hypothesize that:

H_5 Willingness to participate in wild felid conservation will positively influence community-level attitudes towards wild felid conservation.

Ecologically conscious behaviour is primarily motivated by enhanced understanding of the topic (Lo et al., 2012; Zhang, 2016). Studies have found that people's knowledge of biodiversity was positively correlated with their willingness to pay for biodiversity conservation (Turpie, 2003). We consider that a higher level of knowledge of wild felids will

positively influence community-level willingness to participate in wild felid conservation, motivating the hypothesize that:

H_6 : knowledge on the importance of wild felid conservation will positively influence the willingness of participation in wild felid conservation by park communities.

Successful wildlife conservation is often backed by good management practices of conservation authorities, which influence public attitudes and support towards wildlife conservation (Karanth et al., 2017; Pomeranz et al., 2021). A desired outcome of wildlife conservation can be achieved by good wildlife governance principles that embody considerations of holistic public trust and norms of effective governance (Decker et al., 2012; Pomeranz et al., 2021). Good governance has also become important in the realm of biodiversity management where an approach of consensus-driven stakeholder participation is most common (Pomeranz & Stedman, 2020). We define good management practice as efficient grievance redressal mechanisms and their implementation in the field of wild felid conservation. This evidence enables us to formulate two hypothesis (Figure 5.2):

H_7: Good management practice by conservation authorities directly and positively influences community-level attitudes towards wild felid conservation.

H_8: Good management practice by conservation authorities positively increases community-level know-how on wild felid conservation.

According to the classical theory of planned behaviour, an individual's attitude towards a behaviour refers to the extent to which the individual holds a favourable or unfavourable evaluation of the behaviour in the question (Ajzen, 1991; Manstead & Parker, 1995). It has been observed that positive attitude was an important predictor of intention to conserve manatees and Asian turtles (Aipanjiguly et al., 2003; Lo et al., 2012; Yang et al., 2022; Zhang, 2016). Additionally, favourable attitudes towards the focal species was associated with high behavioural intention to conserve them (Zhang, 2016). We considered that positive (or negative) values (Decker & Purdy, 1988) of variables f6 and f2 (Fig. 5.2) will positively (or negatively) influence the social acceptance of wild felids by the communities. Theories related to human cognition and research suggest that wildlife, risks associated with wildlife, and how these risks are perceived significantly impact an individual's willingness to accept wildlife (Ajzen, 1991; Decker et al., 2012; Fulton et al., 1996). An early definition states that 'the wildlife acceptance capacity is the maximum wildlife population level in an area

acceptable to people' (Decker & Purdy, 1988). Social acceptance of wild felids will be determined by the community's attitude towards it. Therefore, we hypothesize that:

H_9: Positive attitudes towards wild felids will directly and positively influences social acceptance of wild felids by communities.

5.2 Methodology

5.2.1 Study site

The project site spans two protected areas of Bhutan: Jigme Singye Wangchuck National Park and Royal Manas National Park, which have a high density of wild felids and recorded incidences of human-felid conflicts (Figure 5.1) over the past five years as recorded by the park offices.

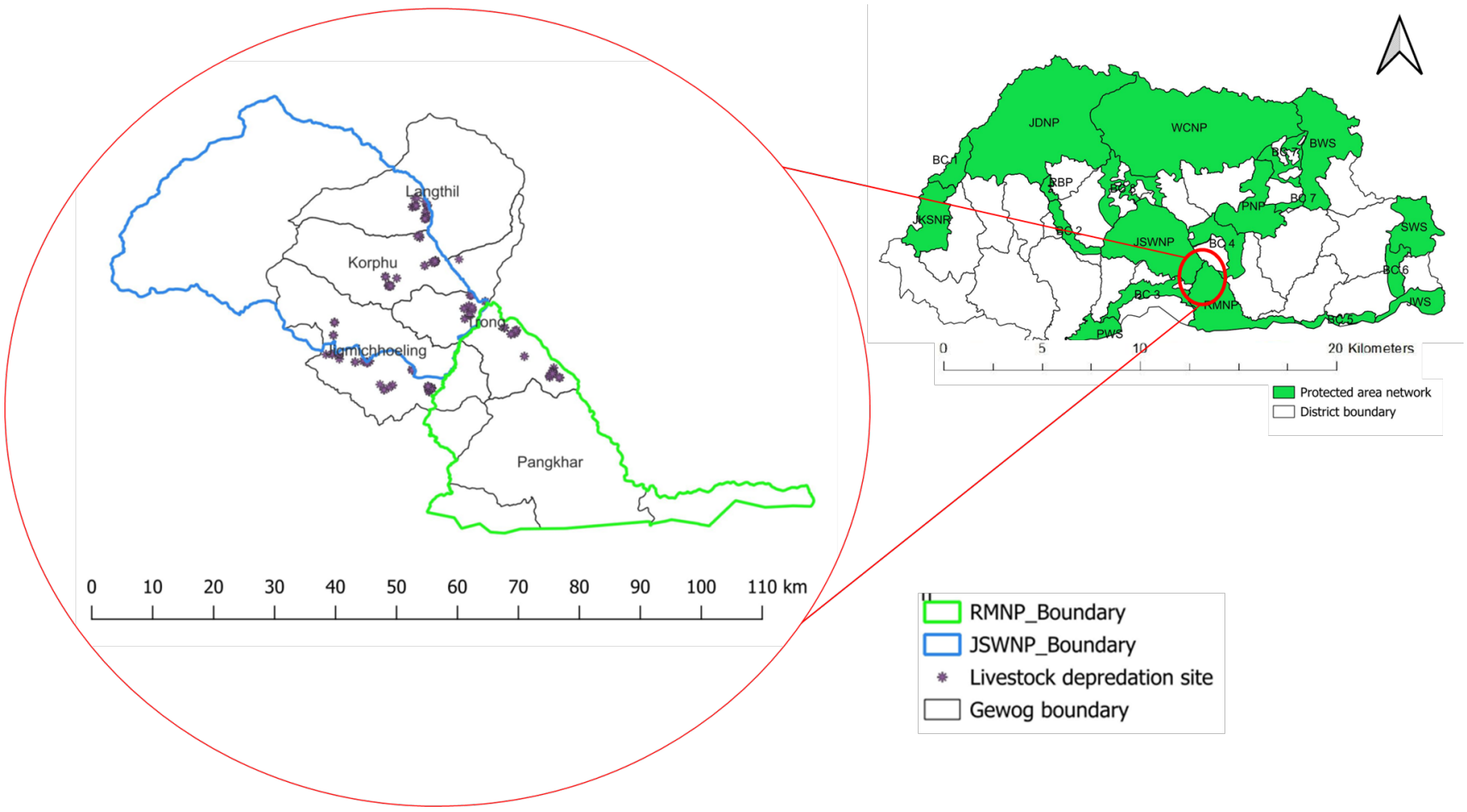


Figure 5.2. Study site in Jigme Singye Wangchuck National Park (JSWNP) and Royal Manas National Park (RMNP) showing incidences of livestock depredation in the past 5 years (2017-2022). The key identifies boundaries of the protected areas in the study site and the gewogs (village blocks). The map on the right shows the protected area network of Bhutan (BWS: Bumdeling Wildlife Sanctuary, JDNP: Jigme Dorji National Park, JKSNR: Jigme Khesar Strict Nature Reserve, JWS: Jomotsangkha Wildlife Sanctuary, PNP: Phrumsengla National Park, SWS: Sakteng Wildlife Sanctuary, WCNP: Wangchuck Centennial National Park) including biological corridors (Biological corridors are identified by numbers BC 1-7).

5.2.2 Research ethics and approval

This study conducted two major social interviews: a survey of 'Knowledge Attitude and Practice on wild felid conservation' with communities, and a 'Key Informant Survey' on wild felid conservation with local stakeholders (elected local government officials and civil servants). We received approval to conduct these questionnaire surveys from the University of Southampton Ethics and Research Governance Online (ERGO-II number: 76113.A1) and Ugyen Wangchuck Institute of Conservation and Environmental Research of Bhutan (research permit number: 8423233545E33B9316C6F7, Figure S1 appendix 4).

5.2.3 Focal population

We identified park communities, civil servants, and elected local leaders as our focal population for this study. Park communities include individuals residing inside and within a 15-km buffer around the protected areas, whose livelihoods may depend partially or fully on natural resources from the protected areas. We involved park communities as the respondents for the Knowledge Attitude and Practice (hereon 'KAP') survey and the elected local leaders and civil servants as the respondents of Key Informant Survey (hereon 'KIS'). We identified local leaders, government officials, and NGO personnel as Key Informants. These individuals have a direct impact on community well-being and are involved in implementing government plans and policies in the field. The marginalized groups in these communities were the old aged, the disabled, nomads, and hunters. We ensured confidentiality of individual respondents and proportionate involvement of marginalized groups in the survey in accordance with the research ethics approval (S1, appendix 4).

To assist the process of running the KAP survey, which involved some sensitive questions, we employed non-forestry personnel (i.e., staff not employed by the Bhutan Department of Forests), in order to minimize the risk of bias from the respondents and to maintain respondents' confidentiality.

5.2.4 Determination of sample size

For choosing an adequate sample size, the Royal Manas National Park and Jigme Singye Wangchuck National Park boundaries were selected as the sampling frame from which the households falling within the park boundary were chosen as sampling units. The total population of the two protected area as enumerated in their conservation management plan was 2,271 (JSWNP, 2016, 2022; RMNP, 2015), which included those living within the protected areas. We selected 330 households for the KAP survey and 60 individuals for the

KIS survey. We calculated the sample size for the KAP survey using an open-access web program (https://www.surveysystem.com/sscalc.htm), which is based on the following formula:

$$n = \frac{\frac{Z^2.P(1-P)}{e^2}}{1 + \left(\frac{Z^2.P(1-P)}{e^2 N}\right)}$$

Z is the standard error of the 95% confidence interval, calculated from the proportion of population *P* and marginal error e. We assigned the general conservative social science values of 50% and 3% for *P* and *e*, respectively, to determine our sample size of 330 households of 2,171 total households. We sampled following probability-based stratified random sampling, a straightforward sampling method for small populations (Acharya et al., 2013). The village blocks (Gewogs) falling under each protected area are selected as the sub-strata, and the households falling within these sub-strata are sampled following Probability Proportional to Size (PPS) method as shown in Table 5.1. PPS is a sampling technique for a finite population in which size measures (attributes of population, e.g., number of households) are available for each population unit prior to sampling and the probability of selecting a unit is proportional to its size (Skinner, 2014). We determined the sampling weight for each stratum to represent its entire household population (HHs) as shown in Table 5.1. The probability (π_{ij}) of selecting j^{th} household in i^{th} stratum is computed with:

$$\pi_{ij} = \frac{x_{ij}}{X_{ij}}$$

where x_{ij} is the sampled household in the corresponding stratum *i* and X_{ij} is the total number of households belonging to the corresponding stratum. $\frac{x_{ij}}{X_{ij}}$ is also referred to as the sampling fraction (*SF*) and the inverse of it provides the sampling weight (w_b) of items in the stratum (Table 5.1).

Table 5.1. Sampled households and their statistical weights for KAP and KIS survey. HHs represents the total number of households in each stratum (gewogs) and sampled HHs represents the total number of sampled households for the KAP survey. SF represents the sampling fraction, inverse of which is sampling weight (W_b)

Protected area	Gewog	HHs	Sampled HHs	SF	W_b	Respondents for KIS
JSWNP	Jigmechoeling	746	113	0.15	6.60	15
	Korphu	525	80	0.15	6.60	15
	Langthel	322	49	0.15	6.60	15
RMNP	Trong	578	88	0.15	6.60	15
Total		**2,171**	**330**	**0.15**	**6.60**	**60**

We selected 15 key informants from local government functionaries and public servants working in the locality. The KAP survey achieved a 100% response rate, covering communities from three dzongkhangs (districts), and 4 gewogs (village-blocks). The KIS survey obtained 33 responses out of the 60, with many key informants unavailable during the survey period. Details of the sampling techniques and sampling plan are provided in the ERGO-II ethics form in S1, appendix 4.

5.2.5 Pretesting of survey questionnaire

Prior to the survey, we tested our questionnaire with the local communities that were later sampled for the main study. During pretesting of the survey questionnaire, we trailed a draft survey with at least 4 individuals from 4 different village blocks (gewogs), which were same villages used for main survey, who had similar profiles to the target population. We identified issues with the questionnaire's clarity and wording, and the time required for full implementation of the questionnaire to ensure the survey's reliability and validity.

5.2.6 Evaluating factors responsible for the societal approval of wild felids by communities in the area

Social approval of large carnivores and the risk posed by communities is found to be crucial for their successful conservation (Bruskotter & Wilson, 2014). We applied Structural Equation Modelling (SEM), a powerful, multivariate technique to investigate and test the multivariate causal relationships, in order to identify social factors that favour acceptance (or lack of acceptance) of wild felid co-habitation with the local communities (Fan et al., 2016; Pugesek et al., 2003). SEM is ideal for evaluating a multi-level framework since it simultaneously measures associations among several independent (exogenous) and dependent (endogenous) variables (Carter et al., 2012). We formulated variables both endogenous and exogenous from questions from the KAP survey, and those variables does not explicitly falls under the domain of KAP survey.

Statistical model

Statistically speaking, SEM is a linear-model framework for simultaneous regression equations with both measured and latent variables, where 'latent' means constructed as opposed to measured from the data (Jöreskog et al., 2016). Some of the special cases of SEM are linear regression, multivariate regression, path analysis, confirmatory factor analysis, and structural regression (Jöreskog et al., 2016; Kline, 2023). We developed a conceptual framework outlining the factors that influence the level of societal acceptance of wild felids among the communities residing in the park and its buffer area (Figure 5.2). A SEM demands the creation of a set of hypotheses within this conceptual framework (Hair et al., 2021; Schreiber et al., 2006). To test our hypotheses, we followed the two-step procedure for SEM recommended by Anderson & Gerbing (1988): first a Confirmatory Factor Analysis (CFA) to test the measurement model, and then structural equation models to measure the direct and indirect effects of variables on one another according to the path diagram (Carter et al., 2012; Ghasemi & Kyle, 2021; Kline, 2023). The measurement model specifies relationships between the survey items and the latent variables. The model is also known as an *x*-side model, defined as (Kline, 2023):

$$x = \tau_x + \Lambda_x \xi + \delta \qquad \text{eqn 1}$$

Where $x = (x_1, \ldots\ldots, x_q)$ is a vector of *x*-side indicators (items), τ_x is a vector of q intercepts for *x*-side indicators, ξ is a vector of n latent exogenous variables, Λ_x is a matrix of loadings (q x n) corresponding to the latent exogenous variables, $\delta = (\delta_1, \ldots\ldots, \delta_q)'$ is a vector of residuals of *x*-side indicators. If in the formula, term τ_{x1} means the intercept of the first item, and $\lambda_{\frac{x}{2}}$ is the loading of the second item with the factor and δ_3 is the residual of the third item when only one factor is accounted. Factor loadings are regression parameter values that quantify the strength of the relationship between a latent variable and an observed variable. They each indicate how much of the variation in the observed variable is explained by the underlying latent variable. In SEM, factors can be endogenous, and, in this case, we rename the factor by Greek letter eta (η), corresponding to y-side models defined by:

$$y = \tau_y + \Lambda_y \eta + \epsilon \qquad \text{eqn 2}$$

Where $y = (y_1, \ldots\ldots, y_q)'$ is a vector of *y*-side indicators (items), τ_y is a vector of q intercepts for *y*-side indicators, η is a vector of m latent endogenous variables, Λ_y is matrix of loadings (m x q) corresponding to the latent exogenous variables, $\epsilon = (\epsilon_1, \ldots\ldots, \epsilon_q)'$ is a vector of

residuals of *y*-side indicators, and θ_ϵ is variance or covariance of residuals for *y*-side indicators.

The second part of the SEM is the structural regression model, which specifies relationships between latent variables, whether endogenous or exogenous. The full structural regression model is given by (Kline, 2023):

$$\eta = \alpha + \mathrm{B}\eta + \Gamma\xi + \zeta \qquad \text{eqn 3}$$

Where α is a vector of *m* intercepts, B is a matrix of regression coefficients (*m* x *m*) of latent endogenous to latent endogenous variables with *i*-th row indicating the target endogenous variable and *j*-th column indicating the source endogenous variable, Γ is a matrix of regression coefficients (*m* x *n*) of latent exogenous to latent endogenous variables with *i*-th row indicating the target endogenous variable and *j*-th column indicating the source endogenous variable, and $\zeta = (\zeta_1, \ldots\ldots, \zeta_m)'$ is vector of residuals for the latent endogenous variable. The general assumption of a structural regression model is that η and ξ are not observed, ϵ and δ are errors of measurement for *y* and *x* respectively, and the error terms for *x* and *y* are uncorrelated.

The measurement equations and structural models can be expressed in matrix algebra terms as follows: For example, if a latent exogenous model having six items ($x_1, x_2, x_3, x_4, x_5, x_6$), where the first three are measured by exogenous factor ξ_1 and the rest are measured by exogenous factors (ξ_2), we the get *x*-sided measurement model:

$$\begin{pmatrix} x_1 \\ x_2 \\ \cdot \\ \cdot \\ x_6 \end{pmatrix} = \begin{pmatrix} \tau_{x1} \\ \tau_{x2} \\ \cdot \\ \cdot \\ \tau_{x6} \end{pmatrix} + \begin{pmatrix} \lambda_{11}^{x} & \lambda_{12}^{x} \\ \lambda_{21}^{x} & \lambda_{22}^{x} \\ \vdots & \vdots \\ \lambda_{61}^{x} & \lambda_{62}^{x} \end{pmatrix} \begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix} + \begin{pmatrix} \delta_1 \\ \delta_2 \\ \vdots \\ \delta_6 \end{pmatrix} \qquad \text{eqn 4}$$

Similarly, if the latent endogenous model has three items (y_1, y_1, y_1) measured by one factor η_1, the *y*-sided measurement model is

$$\begin{pmatrix} y_1 \\ y_2 \\ y_3 \end{pmatrix} = \begin{pmatrix} \tau_{y1} \\ \tau_{y2} \\ \tau_{y3} \end{pmatrix} + \begin{pmatrix} \lambda_{11}^{y} \\ \lambda_{21}^{y} \\ \lambda_{31}^{y} \end{pmatrix} (\eta 1) + \begin{pmatrix} \epsilon_1 \\ \epsilon_2 \\ \epsilon_3 \end{pmatrix} \qquad \text{eqn 5}$$

As a structural regression model specifies the relationship between latent variables, substituting x-side and y-side of eqn 3, the new regression model where one latent endogenous (η1) variable is predicted by two latent exogenous (ξ_1, ξ_2) variables is as follows:

$$H1 = \alpha_1 + (\gamma_{11}\ \gamma_{12}) \begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix} + 0.\eta 1 + \zeta_1 \qquad \text{eqn 6}$$

The Γ matrix which represents the relationship between exogenous and endogenous variables is substituted by γ_{11}, a regression path between endogenous variable η1and the first exogenous variable ξ_1, and γ_{12}, a regression path between η1 and the second exogenous variable ξ_2. Since there were no endogenous variables predicting each other, B in equation 3 is substituted with 0. Depending upon the number of items describing the latent variable and reliability of each latent variable, the structural regression model can measure the relationship between various combinations of exogenous and endogenous variables. Our study had six latent variables, 4 of which were exogenous and 2 endogenous.

Data measurement for SEM

We had sufficient sample size required for running SEM in accordance with a general rule of thumb, which states that: sample size of 50 is treated as very poor, 100 as poor, 200 as fair, 300 as good, 500 as very good, and above 1000 as excellent (Comrey & Lee, 2013; Harman, 1976). For this survey, factors 1 to 6 were measured on a five-point Likert scale, providing response values from 1: strongly agree to 5: strongly disagree. For the analysis, we reversed the coding of each response so that the scale of measurement was consistent with the scale used to measure other factors (Carter et al., 2012). With this retransformation, the scale was reversed from 5: strongly agree to 1: strongly disagree.

Measurement model and validation with Confirmatory Factor Analysis (CFA)

CFA is an inherent procedure in SEM, which we constructed to assess the degree to which 18 survey items (i.e., observed variables) loaded on six pre-defined latent variables, also known as factors: f1 (social acceptance), f2 (positive attitude), f3 (willingness for participation), f4 (good management practices), f5 (knowledge on wild felids), and f6 (government incentives). We optimized each item to load on only one latent factor (Carter et al., 2012). The factor analysis of the measurement model is essentially a linear regression except the main predictor, the factor, is exogenous or endogenous, unobserved (latent) and multivariate with multiple outcomes (Jöreskog et al., 2016). We performed CFA to evaluate the model's psychometric properties, meaning the validity and reliability of our factors as loadings for the structural equation model (Ghasemi & Kyle, 2021; Hair et al., 2014). The composite reliability test was performed in R package 'semtools' (Jorgensen et al., 2016), and a composite reliability value above 0.7 was deemed acceptable for running the structural regression model (Jorgensen et

al., 2016). Factors with a loading value of ≤ 0.5 are generally accepted for running structural models to test the hypothesis (Kline, 2023). We further validated CFA results with model fit indices described in Table 5.2 (Dash & Paul, 2021; Kline, 2023; Schermelleh-Engel et al., 2003).

Structural Equation Model

We estimated the structural model to test the hypotheses. Model parameters were estimated using maximum likelihood with robust standard errors (MLR), and full information maximum likelihood (FIML) estimation, which accounts for normality and missing data issues in SEM (Ghasemi & Kyle, 2021; Kline, 2023). We assessed model fit using the procedure described in the previous section (Table 5.2). The relationships of the latent variables to the predicting items inform the path diagram, which describes causal relationships between each variable and the items describing the variable (West et al., 2012). All the analyses were performed in R package 'lavaan' (Rosseel, 2012) and the path diagram from CFA to SEM was drawn with the 'semPlot' package (Epskamp, 2015).

Table 5.2. Fit indices for assessing model fit of CFA (measurement model) and the structural regression (structural model), adapted from previous studies (Schreiber et al., 2006). Thresholds represent the set of criteria for model assessment from the model residuals.

Fit indices	Threshold		
	Excellent fit	Midcore fit	Poor fit
Model $\chi 2$ (degree of freedom)	>0.05		
Comparative Fit Index (CFI)	>0.95	>0.90	>0.089
Trucker-Lewis Index (TLI)	>0.95	>0.90	>0.089
Root Mean Square Error of Approximation (RMSEA)	≤ 0.05	0.05-0.08	≥ 0.10
Standardized Root Mean Square Residuals	≤ 0.05	0.05-0.08	≥ 0.10

Table 5.3. Item means and standard deviations and factor loadings from Confirmatory factor analysis. Q represent the survey item numbers derived from the KAP detailed in S4, appendix 4, (e.g., Q33 is question number 33). Mean and SD represents mean and standard deviation in the measurement of survey items (measured on a five-point Likert scale 1-5, which was

reverse coded for each item). Parameter λ enumerates the factor loading, which explains the relationship between the observed and latent variables.

Latent variable	**Observed variable**	**Item in the questionnaire**	**Mean**	**SD**	**λ**
Social acceptance	Q33	I can tolerate livestock depredation by carnivores	2.90	1.14	0.99
	Q34	I am happy living in proximity of carnivores	2.60	1.12	0.98
	Q52	Tiger and other iconic species are our local deities	2.31	0.98	0.99
Positive attitude	Q36	Blaming wildlife for Human-carnivore conflict is not good	2.58	0.91	0.89
	Q37	Communities blaming low livestock productivity due to carnivores is an excuse	3.07	1.06	0.98
	Q40	I will not retaliate against carnivores	2.43	1.22	0.95
Willingness for participation	Q38	It is important to discuss and plan with communities for proper management of Human-carnivore conflicts	2.10	1.01	0.86
	Q39	Communities should be responsible for reducing livestock depredation from carnivores	2.21	0.96	0.73
Proper management	Q41	Authorities and government are responsible for managing human-carnivore conflicts	1.94	0.79	0.74
	Q42	The government is addressing human-carnivore conflicts effectively	2.56	1.04	0.77
	Q44	There should be compensation from the government for the loss of livestock	1.83	0.82	0.99
	Q46	Government authorities respond to our complaints and requests	2.33	0.94	0.93

Knowledge of carnivores	Q24a	Conservation of carnivores and interaction with humans is good for the ecosystem	4.02	0.88	0.88
	Q24b	Conservation of carnivores and interaction with humans is good for ecotourism	4.00	0.79	0.85
	Q24c	Conservation of carnivores and interaction with humans is good for controlling herbivores	4.05	0.82	0.84
	Q24d	Conservation of carnivores and interaction with humans have cultural significance	3.60	0.80	0.90
Government incentives	Q75a	Timely compensation will increase tolerance of the community	3.78	1.13	0.73
	Q75b	Projects on human-carnivore conflicts will increase the community's interest in conservation of carnivores	3.71	1.19	0.79

5.2.7 Determinants of negative attitude and support for wild-felid conservation

We measured negative attitudes towards wild felids by communities from their responses on the importance of wild felids conservation (i.e., question 32 “carnivores in the forests are not important to everybody”) on the five-point Likert scale, where ‘1’ is strongly agree to ‘5’ strongly disagree. To evaluate the causes of negative attitude towards the wild felids, we ran ordinal logistic regression with attitude as the response variable followed by chi-square tests to indicate model fit in the R package ‘ordinal’ (Christensen & Christensen, 2015; Miller et al., 2016). Predictor variables included the socio-economic status of respondents (occupation, level of education, involvement in conservation activities), type of interaction (rate of negative interaction by different wild felid species), knowledge on the importance of wild felids for the ecosystem, level of satisfaction towards conservation authorities, and level of tolerance towards wild felids from negative interaction (detailed in Table S1 appendix4, (Esmaeili et al., 2019; Miller et al., 2016). We used R package ‘rcompanion’ for pseudo R^2 to assess association of dependent and predictor variables (Mangiafico & Mangiafico, 2017). In

ordinal logistic regression, predictor variables should uphold the parallel assumption, which means the effect of predictor variables on the odds of moving from one category (strongly agree to strongly disagree) to the another remains constant on the ordinal scale (Harrell & Harrell, 2015).We computed the parallel assumption of our predictor variables and the residual statistics of the model in R package 'MASS' (Ripley et al., 2013).

Similarly, we measured support for wild-felid conservation from the response on tolerance of livestock depredation by wild felids (i.e., question 33, "I can tolerate livestock depredation by carnivores"). For predictor variables, we used socio-economic status (education level and occupation), level of species-specific negative interaction with wild felids, importance ranking (response on perceived importance of wild felids), and satisfaction with the interventions of conservation authorities (Table S2, appendix 4). All the variable items were measured on the five-point Likert scale ('1' strongly agree to '5'strongly disagree). As for negative attitudes towards wild felids, we ran ordinal regression with support for conservation as the response variable. Model fitness and residual statistics were calculated following similar methods.

5.2.8 Local understanding of the factors influencing risk of livestock depredation from wild felids

To assess the perceptions of livestock owners about the risk of attack on their livestock from wild felids, respondents were interviewed on their experiences over the last 5 years regarding livestock depredation by wild felids. We ran a logistic regression model to test the relationship between past experience of livestock depredation and livestock grazing practices. The yes/no response on the experience of livestock depredation by wild felids was treated as the response variable; predictor variables included perceptions regarding the cause of negative-human felid interaction (encroachment of habitat by humans, carnivore population expulsion, ecosystem imbalance), ranking of species which cause negative interaction, perceptions of the locations of livestock depredation events, and livestock grazing practices (Table S3 appendix 4).

Prior to fitting the model, we checked for missing values in our data. This check revealed that only 2% of our data had missing values (plotted using R package 'Amelia' in Figure S2, appendix 4; (Honaker et al., 2010). The data with missing values were removed using list-wise deletion, as recommended for logistic regression (Harrell, 2001; Meeyai, 2016). We ran

binomial logistic regression using R package ‘caret’ and performed ANOVA with a chi-square test to check the deviance of variables from null and intercept-only models. The importance of each variable was tested with the R package ‘vip’ (as detailed in Figure S3 appendix 4, (Greenwell et al., 2020). We assessed model fit with McFadden’s pseudo R^2 in R package ‘pscl’, with values of 0.02 to 0.04 showing excellent distinction of the model from the null (Domencich & McFadden, 1975; Jackman et al., 2015). The model's predictability was computed from the Area Under Curve (AUC) metric using R package 'ROCR' (Sing et al., 2015).

Additionally, we conducted binary recursive partitioning based on conditional inference tress using the R package ‘party’ (Hothorn, Hornik, Strobl, et al., 2015), to compare the response variable with each explanatory variable and identify significant covariates with the highest explanatory power through adjusted Bonferroni tests at $p < 0.05$ (Hothorn et al., 2015; Thinley et al., 2021; Tighe et al., 2012). Conditional trees provide a more straightforward approach to understanding the hierarchical importance of explanatory variables in explaining variations in the categorical response variables, and they work with more than one categorical variables (Hothorn et al., 2015; Levshina, 2020). We tested ‘risk of livestock depredation by felids’ (response variable) against the following explanatory variables: encroachment of habitat, carnivore population explosion, ecosystem imbalance, rate of conflict (common leopard, dhole, small felids, and tiger), risk to free-ranging livestock, mode of livestock grazing, and conflict habitat (near human settlement and in the livestock habitat).

5.2.9 Key Informant perspectives on human-carnivore interactions

We explored key informants’ know-how on human-carnivore interactions in our study area, as a perceived congruency between key informants and communities is found to be essential for successful human-wildlife coexistence (Riley et al., 2018). Our survey interviewed about half of the key informants from the initial list of known key informants. Key Informants were asked both quantitative and qualitative questions (detailed in S5, appendix 4) ranging from their knowledge on carnivores to polices related to carnivore conservation in Bhutan. The questionnaire was circulated to the key informants through Google forms and by printed copies sent to those residing in villages (for later transcription into electronic format). The questionnaire consisted of three structured questions covering knowledge on human-carnivore conflicts, importance of carnivores in an ecosystem and know-how on the existing policies for mitigating human-carnivore conflicts. These were followed by seven open-ended questions

covering 1) causes of human-carnivore conflicts, 2) species in conflict, 3) positive and negative impacts from human-carnivore interactions, 4) reasons for the recent rise in human-carnivore conflicts, 5) means and measure of mitigating human-carnivore conflicts, 6) ways to reduce retaliatory killings, and 7) general comments on human-carnivore conflicts. There are no specific guidelines for the analysis of qualitative data, which can be a complex task (Baskarada, 2014). We followed conventional content analysis techniques whereby key words from respondents were recorded and coded for subsequent analysis of responses (Hsieh & Shannon, 2005; Rodríguez et al., 2012). The key responses that were highlighted during the content analysis were categorized into 1) perceived causes of human-carnivore conflicts, 2) positive impacts from human-carnivore interaction, 3) negative impact of human-carnivore interaction, and 4) recommendations for reducing human-carnivore conflicts.

5.3 Results

Sections 5.3.1-13 below analyse the KAP survey; Sections 5.3.14-15 analyse the KIS survey.

5.3.1 Socio-demographic characteristics of KAP respondents

For each of the SEM and regression responses, we tested for influences of gewogs and dzongkhags using two-way ANOVAs followed by Tukey post-hoc tests, finding no detectable effects (all $p > 0.05$). We therefore treated these nested levels as random factors that equally represent the 330 sampled households.

The KAP survey was completed by 330 individuals, each representing one household, with a median household size of 5 ($\sigma = 2.90$) individuals. We recorded respondents with ages ranging from 18-84 years, and the median age of respondents was 40 ($\sigma = 13.50$) years. Of all 330 respondents, 86% were farmers, 3 % government employees, 3% students and 8% other occupation groups. Of all respondents 45% were members of a single community forestry group, 11% were members of three conservation groups (Community Forestry Group, Human-Wildlife Conflict Rapid Response Team, and Eco-Camp Group), 2% were members of only the Eco-Camp Group, and the remaining 42% were not members of any forestry conservation groups. For 95% of the households, the main source of household income was generated from selling agricultural products, namely fruits and livestock products, with 30% of the respondents owning livestock. The average annual household income of the respondents was 137,382 BTN (Bhutanese Ngultrums, equivalent to 1,675 USD) and average expenditure per year was 94,94,685 BTN (1,154 USD).

5.3.2 Knowledge of wild felids

Respondents were asked for their agreement or otherwise on the definition of human-carnivore conflict: "human-carnivore conflicts are the negative interaction between humans and carnivores residing in the same location". This (valid) statement was supported by 89% of the 330 respondents (composite mean and SD of responses from 5-point Likert scale: $\bar{x}$ = 4.14, σ = 0.73) as shown in Figure 5.3. The modal value 4 corresponds to 'agree', signifying that most respondents have know-how regarding human-carnivore conflicts. Amongst the four types of importance of carnivores, the highest mean was attributed to 'controls herbivores' ($\bar{x}$ = 4.05, σ = 0.82) followed by 'good for ecosystem' ($\bar{x}$ = 4.02, σ = 0.88) and 'good for ecotourism' ($\bar{x}$ = 4.00, σ = 0.79). Cultural significance had comparatively lower support ($\bar{x}$ = 3.60, σ = 0.80). When asked about the location of human-carnivore conflict, respondents reported that it occurs mostly inside carnivore habitat ($\bar{x}$ = 4.63, σ = 1.05), followed by near human settlement. Whereas 67% of respondents took the view that it occurs in both the locations ($\bar{x}$ = 3.63, σ = 0.75). When asked about the causes of human-carnivore conflicts, increase in carnivore population ($\bar{x}$ = 3.57, σ = 0.90) received most support, followed by human encroachment on felid habitat ($\bar{x}$ = 3.51, σ = 0.91), ecosystem imbalance ($\bar{x}$ = 3.47, σ = 1.04) and curse of local deities ($\bar{x}$ = 3.29, σ = 1.02).

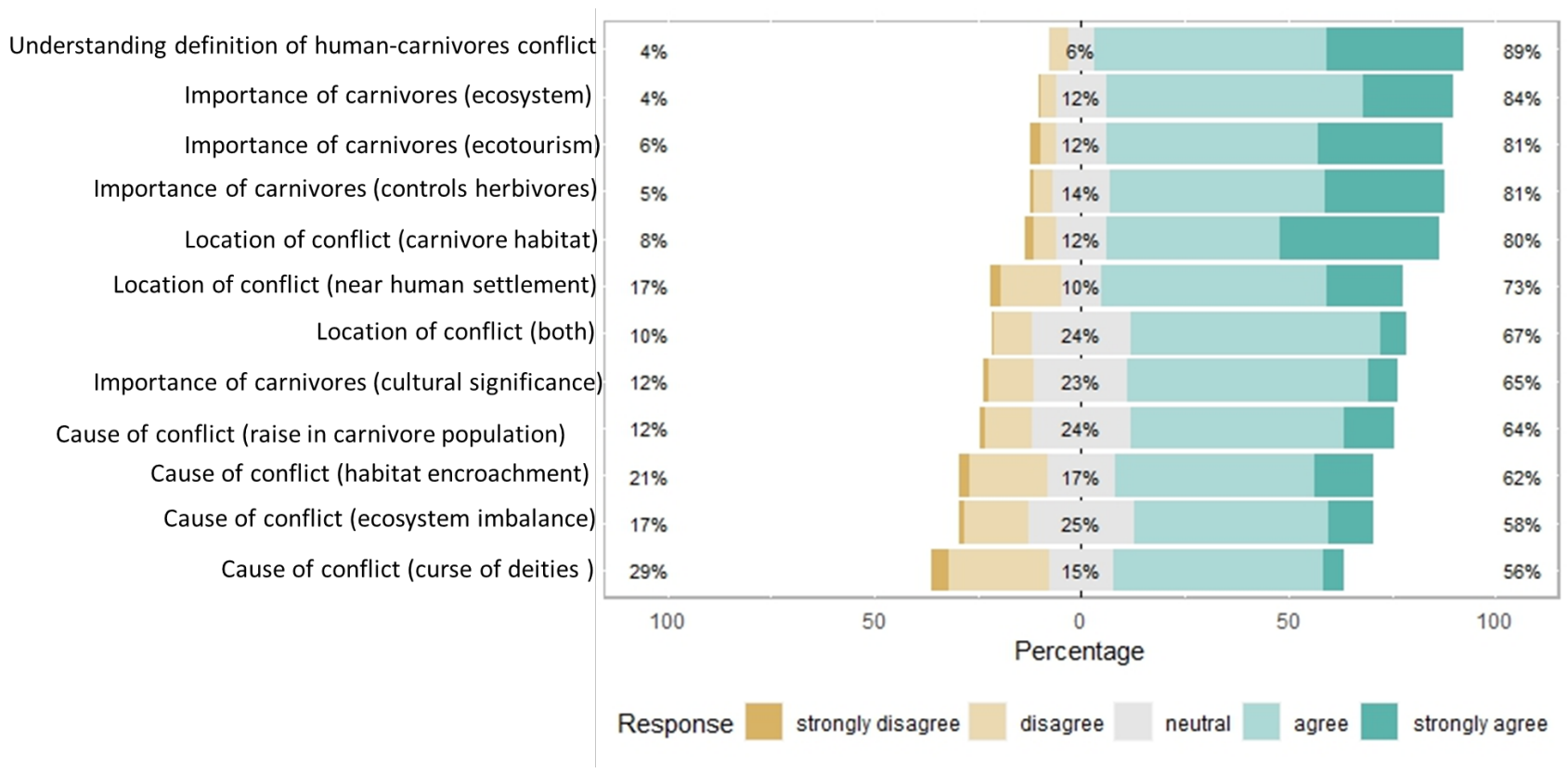


Figure 5.3. Responses on opinions regarding definition of human-carnivore conflict, importance of carnivores to the ecosystem, and causes and location of human-carnivore conflicts (each on five-point Likert scale). The left-side % represents the percentage of all 330 respondents choosing options 'strongly disagree' to 'disagree', middle % shows percentage

of respondents choosing neutral (neither agree nor disagree) and the right-side % shows respondents choosing option 'strongly agree' to 'agree'.

More than 65% of respondents had heard about human-carnivore conflicts (n = 216), either from elders (n = 162), friends (n = 113), television (n = 29), social media (n = 27), forestry personnel (n = 20), or personal observation (n = 34). The survey sought respondents' knowledge of conflicts with felid species in the locality. The majority of respondents reported common leopard ($\bar{x}$ = 3.68, σ = 1.20) as a conflict species in their locality followed by tiger ($\bar{x}$ = 3.62, σ = 1.21), dhole ($\bar{x}$ = 3.28, σ = 1.14) and small felids ($\bar{x}$ = 3.01, σ = 1.24), as shown in Fig. 5.4. The corresponding modal value of 4 indicates that the most frequent response was to consider one or more of these species as conflicted species. More than 87% of respondents reported the tiger as making important contributions to ecosystem health ($\bar{x}$ = 4.34, σ = 0.93, modal value of 5: strongly agree), followed by leopard ($\bar{x}$ = 3.72, σ = 0.75), dhole ($\bar{x}$ = 3.50, σ = 0.91) and clouded leopard ($\bar{x}$ = 3.31, σ = 1.04), as shown in Fig. 5.5. Small felids were reported less often by respondents as contributing to ecosystem health ($\bar{x}$ = 2.69, σ = 0.99, modal value of 3: neither agree nor disagree).

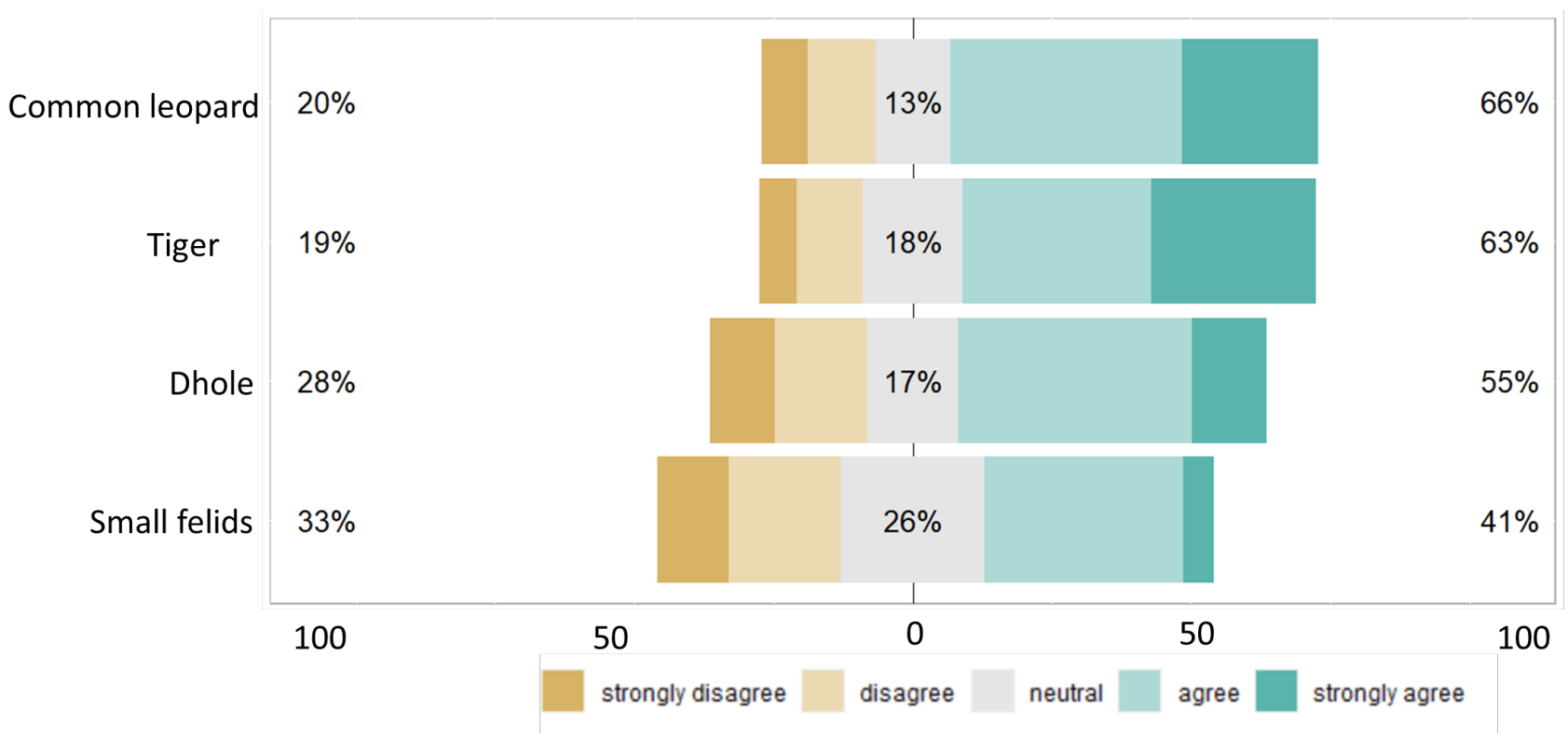


Figure 5.4. Opinion on the level of conflict with carnivore species (on five-point Likert scale). Meaning of percentages as for Fig. 5.3. Species are ordered by perceived level of conflict.

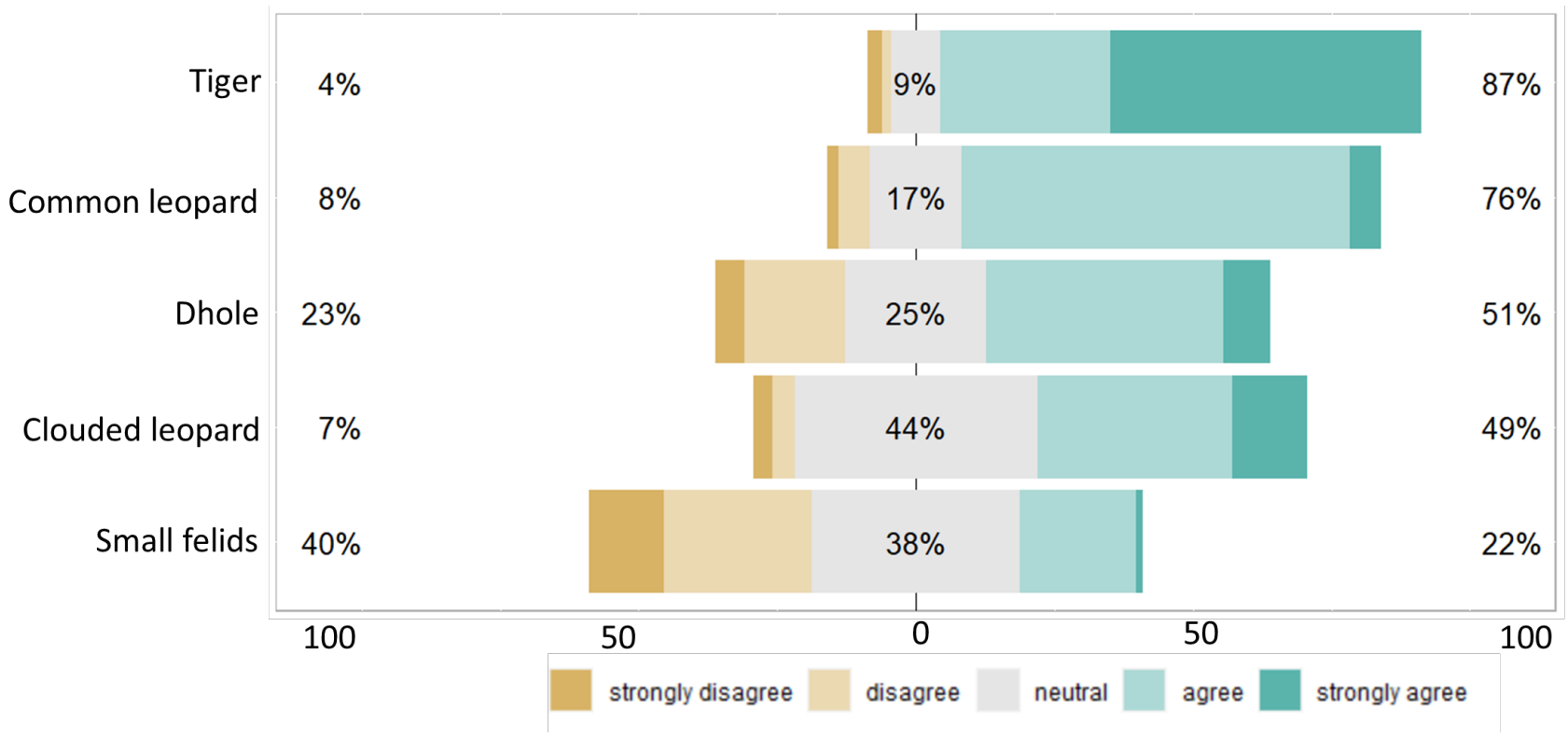


Figure 5.5. Perception of the importance of species in the ecosystem (on five-point Likert scale). Meaning of percentages as for Fig. 5.3. Species are ordered by perceived level of importance.

5.3.3 Perceptions of human-felid interactions

When asked about the negative consequences of human-felid interactions, 64% of respondents took the view that there are negative impacts from human-felid interactions, and the remaining 36% responded that there are no negative impacts. The 210 respondents perceiving negative impacts were further asked about negative or positive impact on the set of socio-economic factors from human-felid conflicts. Most respondents (86%) perceived retaliatory killing as a negative impact from human-felid conflict, and only 37% took the view that human-felid conflict led to negative impacts on livelihoods (Fig. 5.5). The highest positive impact from human-felid conflict was given as a positive impact on the ecosystem.

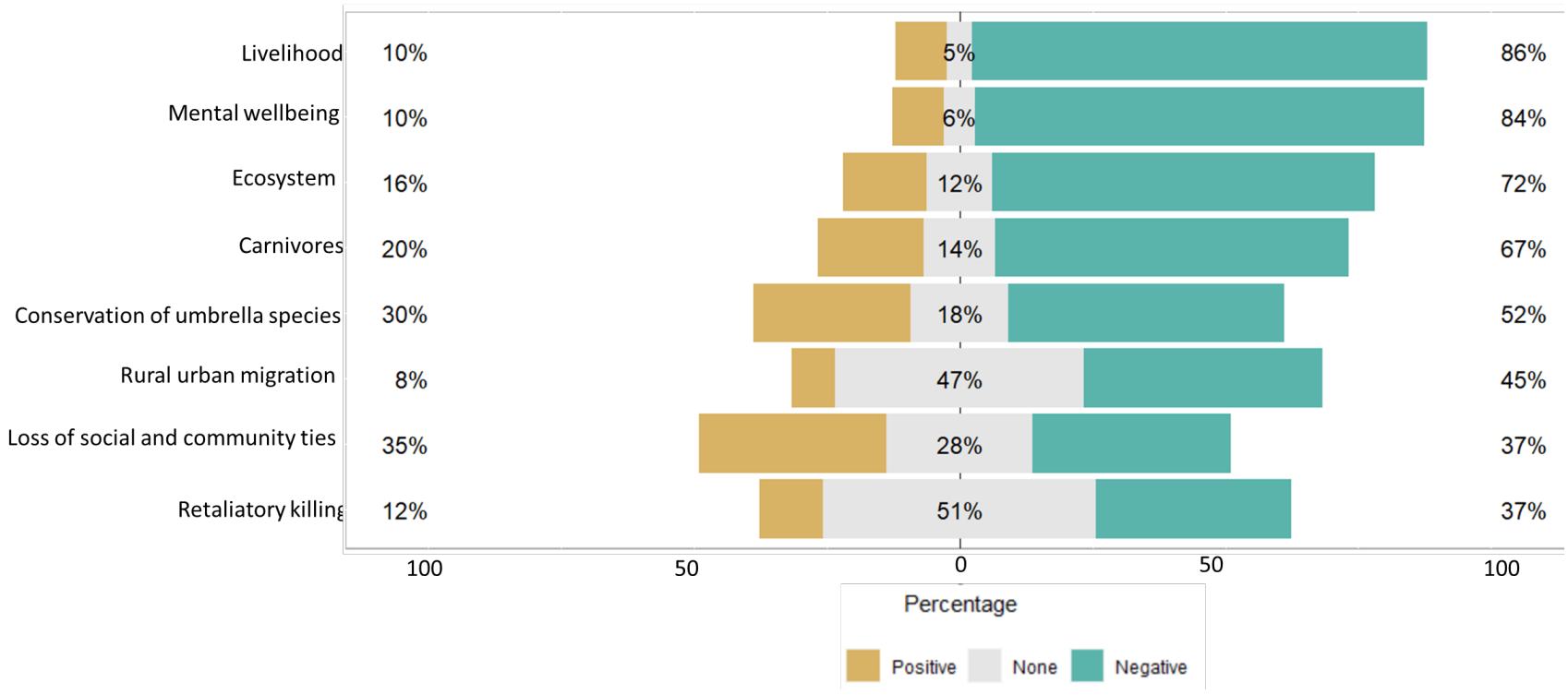


Figure 5.5. Perceptions regarding positive (shaded in brown) and negative impacts (shaded in grey) from human-felid conflicts on the set of socio-economic indicators listed on the y-axis. The left-side % represents percentage of all 210 respondents choosing options 'positive impact', middle % shows percentage of respondents choosing 'negative impact' and the right-side % shows respondents choosing option 'none'.

5.3.4 Attitudes

Respondents were asked for their opinions on not allowing domestic cattle to enter the core forest. More than half of respondents did not support the statement "cattle/domestic animals should not be allowed to enter the core forests" ($\bar{x}$ = 2.52, σ = 1.27, mode = 2: 'disagree'; Q28 in Fig. 5.6). Similarly, more than 90% of respondents do not believe that domestic animals entering forests are at high risk of depredation from carnivores ($\bar{x}$ = 1.66, σ = 0.73, mode = 2: 'disagree'; Q29 in Fig. 5.6). In contrast, most respondents (76%) believed that farmers develop negative attitude towards carnivores as a result of livestock depredation ($\bar{x}$ = 4.40, σ = 1.09, mode = 5: 'strongly agree'; Q30 in Fig. 5.6). Comparably, respondents supported the view that wildlife should not be allowed to come towards the village periphery ($\bar{x}$ = 4.40, σ = 1.09, mode = 4; Q31 in Fig. 5.6). Regarding their perception on importance of carnivores, the majority of respondents (60%) did not agree with the statement "carnivores in the forests are not important to everybody" ($\bar{x}$ = 2.63, σ = 1.08, mode = 2; Q32 in Fig. 5.6). When considering their stance on livestock depredation by carnivores, surprisingly almost 40% of respondents agreed or strongly agreed that they can tolerate livestock depredation from carnivores. However, the majority (60%) took the view that they cannot tolerate livestock depredation by the carnivores ($\bar{x}$ = 2.89, σ = 1.14, mode = 2; Q33 in Fig.5.6).

Respondents did not prefer having carnivores living in their proximity, and mostly (57%) disagreed with the statement “I am happy to live in close proximity to carnivores” ($\bar{x}$ = 2.60, σ = 1.11, mode = 2; Q34 in Fig. 5.6). Furthermore, the majority of respondents (75%) did not agree that they feel depressed by human-carnivore conflicts ($\bar{x}$ = 2.25, σ = 0.86, mode = 2; Q35 in Fig. 5.6). Most of the respondents seemed to believe that carnivores should be blamed for livestock losses (61%), as a majority disagreed with the statement “blaming wildlife for human-carnivore conflict is not good” ($\bar{x}$ = 2.57, σ = 0.90, mode = 2; Q36 in Fig. 5.6). There were almost equal proportion of respondents agreeing (43%) and disagreeing (40%) to the statement “communities blaming low livestock productivity due to carnivores is an excuse” ($\bar{x}$ = 3.07, σ = 1.02, mode = 2; Q37 in Fig. 5.6). Respondents’ interest in participating in mitigating human-carnivore conflicts appeared to be limited, with most expressing disagreement regarding the importance of discussing plans with the community ($\bar{x}$ = 2.10, σ = 1.01, mode = 2; Q38 in Fig. 5.6) and the community's responsibilities for reducing livestock depredation by carnivores ($\bar{x}$ = 2.21, σ = 0.96, mode = 2; Q39 in Fig. 5.6). Respondents expressed a willingness to resort to retaliatory actions in response to livestock depredation, given that a significant majority (66%) disagreed with the statement "I will not retaliate against carnivores" ($\bar{x}$ = 2.40, σ = 1.17, mode = 2; Q40 in Fig. 5.6). Retaliatory killing of wildlife outside farmland is illegal by law in Bhutan. However, laying of snares to protect agricultural land and livestock is allowed only in one’s legal properties (NAB, 2023). Respondents took the view that government and authorities are responsible for managing human-carnivore conflict ($\bar{x}$ = 4.06, σ = 0.78, mode = 4; Q41 in Fig. 5.6). It is conceivable that the government is not sufficiently addressing issues of human-carnivore conflict despite communities’ complaints, since the majority of respondents disagreed with the statement that government is addressing human-carnivore conflict effectively ($\bar{x}$ = 2.55, σ = 1.03, mode = 2; Q42 in Fig. 5.6) and with the statement that the community fails to report incidents to the concerned authorities ($\bar{x}$ = 2.86, σ = 1.07, mode = 2; Q43in Fig. 5.6).

Respondents strongly believed that there should be compensation from the government on the loss of livestock due to carnivores ($\bar{x}$ = 2.86, σ = 1.07, mode = 4; Q44 in Fig. 5.6). It appears that respondents were uninformed regarding the government wildlife insurance scheme (gewog wildlife endowment fund), or that they lack other opportunities for wildlife insurance, as they disagreed with the statement “communities should also invest in insurance schemes for livestock” ($\bar{x}$ = 1.97, σ = 0.83, mode = 2; Q45 in Fig. 5.6). Moreover, when asked about the response from government and about government incentives, respondents disagreed with the statement “government authorities respond to our complaints and requests” ($\bar{x}$ = 2.31, σ =

0.93, mode = 2; Q46 in Fig. 5.6) and agreed with the statement “there is no technological advancement from the government or from communities to reduce and mitigate human-carnivore conflicts” ($\bar{x}$ = 3.40, σ = 1.09, mode = 4; Q47 in Fig. 5.6). Respondents disagreed that people should be allowed to kill the conflicted animals ($\bar{x}$ = 2.45, σ = 1.07, mode = 2; Q48 in Fig. 5.6); they also disagreed that people miss household chores by guarding their livestock ($\bar{x}$ = 2.32, σ = 0.93, mode = 2; Q49 in Fig. 5.6). Respondents have mixed feeling on the statement “people should not be allowed to raise cattle in the forests or herding practices”, where 47% of respondents agreed and 46% were neutral to the statement ($\bar{x}$ = 2.95, σ = 1.13, mode = 2; Q50 in Fig. 5.6). Almost half of the respondents agreed that the compensation they get from government is insufficient ($\bar{x}$ = 3.35, σ = 1.25, mode = 3; Q51 in Fig. 5.6), with the rest neutral on the matter. The majority of respondents (72%) disagreed with the statement “tigers and other iconic species are our local deities” ($\bar{x}$ = 2.31, σ = 0.93, mode = 2; Q52 in Fig. 5.6), and the majority disagreed that conservation of carnivores is more important than losing livestock ($\bar{x}$ = 2.31, σ = 0.93, mode = 2; Q53 in Fig. 5.6). Some of the respondents (47%) believed that rural-urban migration might be a cause of human-carnivore conflict ($\bar{x}$ = 3.03, σ = 1.14, mode = 4; Q54 in Fig. 5.6), and that this migration has risen over the last 5 years ($\bar{x}$ = 3.03, σ = 1.13, mode = 4; Q55 in Fig. 5.6).

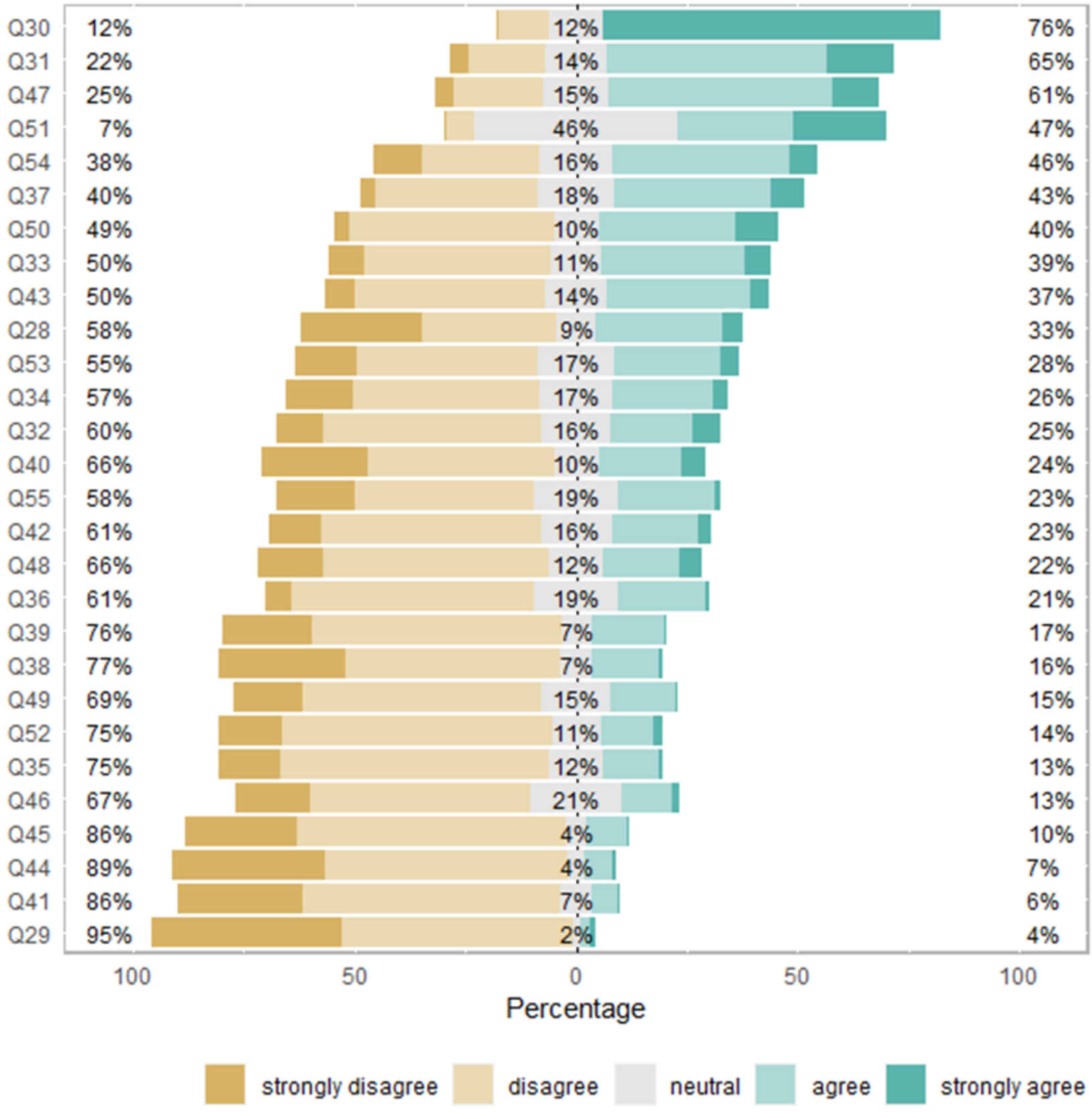


Figure 5.6. Attitudes of local communities towards wild felid conservation. Q# represents the KAP survey question in S4 appendix4, (e.g., Q33 corresponds to question 33). They are arranged in decreasing order of agreement (i.e., strongly agree to strongly disagree) with the statement by the respondents. Meaning of percentages as for Fig. 5.3.

5.3.5 Social acceptance of wild felids

Measurement model

The measurement model shows good fit to the data, with values for fit indices introduced in Methods Table 5.2: χ^2 (df) = 7495 (120), CFI = 0.95, TLI = 0.94 and SRMR = 0.036, RMSEA = 0.09. All the variable constructs used for the analysis were found reliable as shown in Table 5.4. The average Variance Extracted (AVE) for each variable is above 0.5, the recommended threshold, and the composite reliability values are higher than the recommended threshold 0.7 (Table 5.4). Cronbach's $\boldsymbol{\alpha}$ values are higher than 0.7, indicative of high internal consistency,

which shows that the items in each variable group are closely related (Table 5.4). The factor loadings given in Methods Table 5.3 confirm that observed variables hold convergent validity, defining how well they measure the hypothetically defined latent variable or construct. The loading ranges from 0.73 to 0.99 as shown in Table 5.3 are all above the required theoretical threshold of 0.7.

Table 5.4. Reliability of measurement items used for the structural model.

Latent Variable	Average Variance Extracted (AVE)	Composite Reliability	Cronbach's α
Social acceptance	0.98	0.99	0.99
Positive attitude	0.89	0.96	0.96
Willingness for participation	0.67	0.77	0.77
Proper management	0.75	0.92	0.91
Knowledge on carnivores	0.75	0.92	0.92
Government incentives	0.56	0.72	0.72

Structural model

The structural model results showed reasonably fit to the data (χ^2(df) = 7495(153), CFI = 0.95, TLI = 0.94, SRMR = 0.03, RMSEA = 0.09). Overall social acceptance of wild felids is positively influenced by a positive attitude of respondents towards wild felids ($\beta = 0.11$, $p < 0.03$) and by incentives from government ($\gamma = 0.51$, $p < 0.001$) as shown in the path diagram (Figure 5.7), which supports hypotheses $\mathbf{H_1}$ and $\mathbf{H_8}$. The likelihood of respondents having a positive attitude towards wild felid conservation was increased by their willingness to participate in wild-felid conservation ($\gamma = 0.10$, $p < 0.02$), and by proper management of wild felids by government authorities ($\beta = 0.96$, $p < 0.001$, Figure 5.7), supporting hypotheses $\mathbf{H_5}$ and $\mathbf{H_7}$.

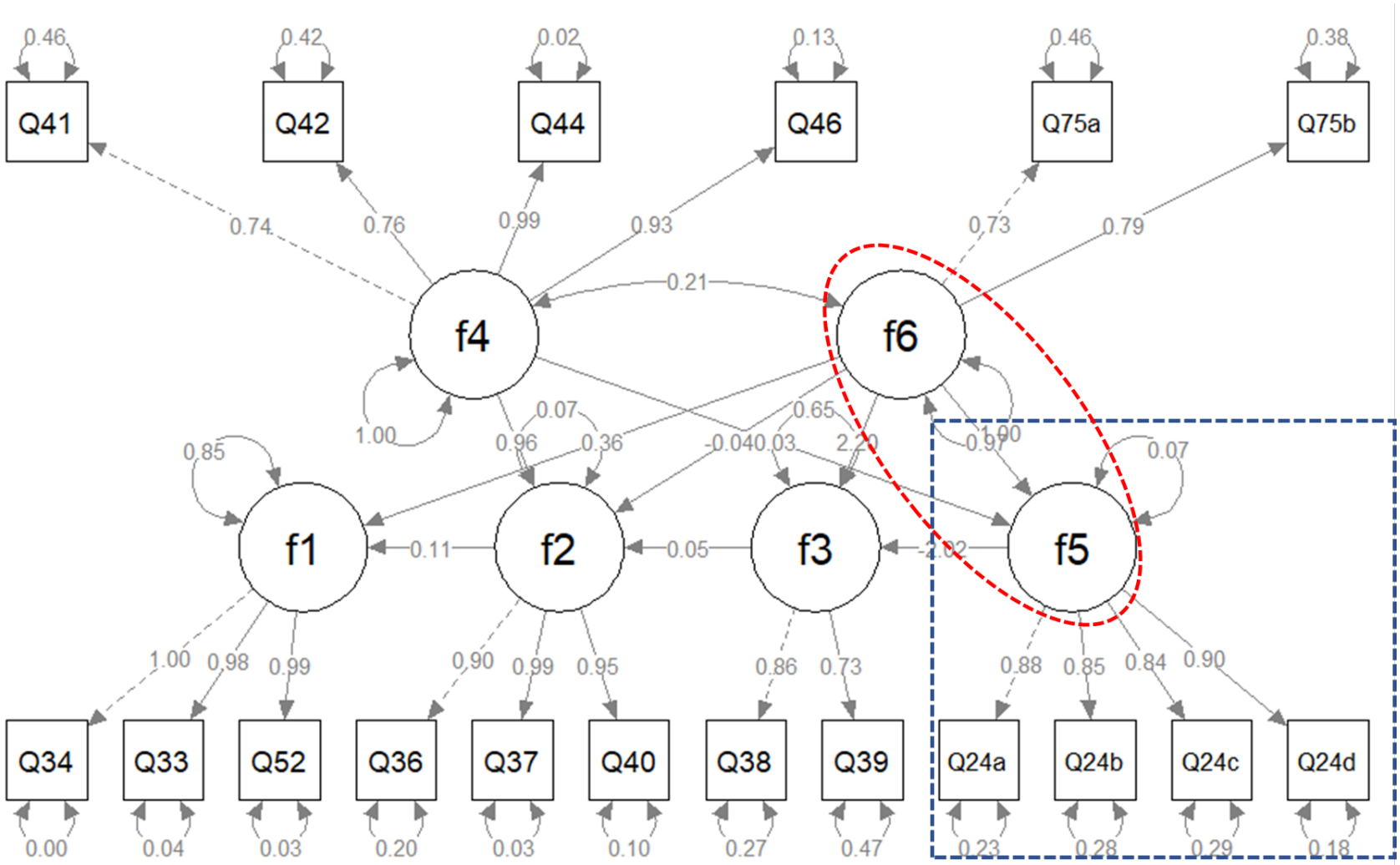


Figure 5.7. Path diagram showing structural relationships between endogenous variables defined as f1: social acceptance, f2: positive attitude, f3: willingness for participation, and exogenous variables defined as f4: proper management, f5: knowledge on carnivores, f6: government incentives. Items represented by Q## are the KAP survey questions (detailed in Table 5.3). For example, the red highlighted path explains relationships between exogenous variable f6 and endogenous variable f5. The arrow from f6 to f5 depicts regression of factor f6 on factor f5 (referred to as factor loading). Its positive value (coefficient) shows positive relationship between f5 and f6. The direction of arrow signifies the direction of influence or effect that one variable has on the other. Similarly, the blue highlighted path shows how latent variables influences the survey question items (Q24a and Q24b-d). The dashed arrow indicates a lower significance in the relationship (e.g., low confidence in influence of f5 on survey item Q24a), and solid arrows indicate higher significance (e.g., high confidence in f5 influencing Q24b). Looped arrows enumerate correlation and autocorrelation.

Government incentives negatively influence the positive attitude of respondents towards wild felids, rejecting hypothesis $\mathbf{H_2}$ (Figure 5.7). Respondents' willingness to participate in wild-felid conservation is positively influenced by government incentives ($\beta = 2.20$, $p < 0.07$, Fig. 5.7), supporting hypothesis $\mathbf{H_3}$, and negatively influenced by knowledge of wild felids, rejecting hypothesis $\mathbf{H_6}$. Knowledge of wild felids is positively influenced by government incentives ($\gamma = 0.10$, $p < 0.02$, Fig. 5.7), which supports hypothesis $\mathbf{H_7}$. Knowledge of wild-

felid conservation is perhaps negatively influenced by proper management of wild felids by government, although with weak statistical support, possibly rejecting hypothesis **H_9**.

Table 5.4: Results of structural equation model, showing path standardised estimates of coefficients and support for hypothesis (with weak support/rejection indicated by brackets).

Variable	Path	Estimate	*p*	Hypothesis
Social acceptance	← Positive attitude	0.11	0.03*	Supported
Social acceptance	← Government incentives	0.36	0.001***	Supported
Positive attitude	←Willingness to participate	0.10	0.02*	Supported
Positive attitude	←Government incentive	-0.04	0.06	(Rejected)
Positive attitude	←Proper management	0.95	0.001***	Supported
Willingness to participate	←Government incentives	2.20	0.07	(Supported)
Willingness to participate	←Knowledge of carnivores	-2.02	0.09	(Rejected)
Knowledge of carnivores	← Proper management	-0.30	0.27	(Rejected)
Knowledge of carnivores	← Government incentives	0.97	0.001***	Supported

**** p-value <0.001; * p-value <0.05*

5.3.6 Determinants of negative attitude towards wild felid conservation

The model of factors influencing negative attitudes towards the conservation of wild felids revealed that respondents belonging to conservation groups (Community Forestry Group, Human-Wildlife Conflict Rapid Response Team, and Eco-Camp Group) show positive attitudes towards conservation of wild felids. A higher frequency of conflict with leopard (or tiger) leads to a strongly (or weakly) resolved negative attitude towards conservation of wild felids (Table 5.7). The importance ranking of dhole from 1-4 (1: Not at all important; 2: Not important; 3: neither not important nor important; 4 important) on the five-point Likert scale shows a negative association with respondent's attitude towards wild felid conservation (Table 5.7). The importance ranking has no positive or negative association with attitude towards wild felid conservation. Respondents' tolerance of the loss of productive cattle breeds (high milk yielding cattle breed) positively associates with the negative attitude towards wild felid conservation.

Table 5.7. Model output of factors influencing positive attitudes towards conservation of wild felids. Columns show the variable coefficient β, its standard error, and the probability *p* of making an error in rejecting the null hypothesis of no influence. Emboldened variables have strongly evidenced influence.

Variable	β	SE	*p*
Occupation	0.00	0.09	0.98
Education level	-0.06	0.08	0.44
Conservation group members	0.52	0.29	0.08*
Rate of conflict, Leopard	-0.38	0.13	0.001***
Rate of conflict, Tiger	0.16	0.12	0.19
Rate of conflict, small felids	-0.11	0.13	0.40
Rate of conflict, Dhole	-0.14	0.13	0.28
Species importance, Tiger	-0.28	0.21	0.18
Species importance, Leopard	0.15	0.26	0.56
Species importance, Clouded leopard	-0.28	0.18	0.12
Species importance, Dhole	-0.34	0.16	0.03**
Species importance, small felids	-0.05	0.15	0.73
Missing household chores	0.06	0.15	0.68
Lower compensation	0.21	0.17	0.22
Satisfaction with government	-0.32	0.22	0.15
Frequency of monitoring by authorities	0.08	0.15	0.62
Tolerance, loss of high yielding breeds	0.38	0.15	0.01**
Tolerance of not attending to complains	-0.11	0.15	0.45
Tolerance of lower compensation	-0.09	0.18	0.62
Tolerance of late compensation	0.04	0.13	0.75

**** p-value <0.001; ** p-value <0.05; * p-value <0.1*

5.3.7 Factors determining support towards wild felid conservation

Generally, respondents show stronger support for larger wild felids than smaller ones. For instance, the rate of conflict with tiger shows a positive influence for wild felid conservation, in contrast to weak evidence of a negative influence for small felids (Table 5.8). Similarly, respondents consider larger cats more important than smaller cats, and large cats positively influences respondents' support for wild felid conservation (Table 5.8).

Table 5.8. Model output of factors influencing support towards conservation of wild felids. Parameters for Table 5.7.

Variable	β	SE	*p*
Occupation	-0.04	0.07	0.57
Education level	-0.02	0.07	0.74
Rate of conflict, Leopard	0.02	0.10	0.84
Rate of conflict, Tiger	0.22	0.10	0.03 **
Rate of conflict, small felids	-0.13	0.11	0.22
Rate of conflict, Dhole	-0.17	0.11	0.11
Species importance, Tiger	0.08	0.16	0.63
Species importance, Leopard	0.46	0.22	0.03 **
Species importance, Clouded leopard	0.04	0.15	0.78
Species importance, Dhole	0.25	0.13	0.06 *
Species importance, small felids	-0.27	0.13	0.04 **
Missing household chores	0.32	0.13	0.02 **
Lower compensation	-0.29	0.13	0.02 **
Satisfaction with government	0.00	0.15	0.99
Frequency of monitoring by authorities	0.11	0.11	0.32

*** *p-value <0.001;* ** *p-value <0.05;* * *p-value <0.1*

5.3.8 Factors influencing perceived risk for livestock depredation by wild felids

The model on perceived risk of livestock depredation by wild fields shows excellent fit to the data (McFadden pseudo-R^2=0.28; AUC= 0.80; accuracy=0.71). Depredation by leopard is considered most likely, followed by tiger, with weaker evidence for dhole and small felids (Table 5.9). The risk of livestock depredation rises with proximity to human settlement, and with proximity to carnivore habitat. Risk of livestock depredation by wild felids decreases with free grazing of livestock and with improved mode of grazing.

Table 5.9. Model output of factors influencing respondents' perceived risk of livestock depredation by wild felids. Parameters as for Table 5.7.

Variable	β	SE	*p*
Intercept	-4.77	1.66	0.001 ***
Encroachment of habitat	-0.25	0.16	0.12
Carnivore population expulsion	0.12	0.20	0.56
Ecosystem imbalance	-0.07	0.18	0.71
Rate of conflict, Leopard	0.47	0.15	0.001 ***
Rate of conflict, Tiger	0.43	0.16	0.01 **
Rate of conflict, small felids	-0.08	0.15	0.57
Rate of conflict, Dhole	0.04	0.14	0.80
Risk of free grazing	-0.45	0.21	0.03**
Daily free grazing practice	-0.22	0.13	0.09*
Proximity to human settlement	0.59	0.18	0.001***
Proximity to carnivore habitat	0.48	0.19	0.01**

**** p-value <0.001; ** p-value <0.05; * p-value <0.1*

The regression tree analysis reveals that the proximity to carnivore habitat was a primary determinant of respondents' perception of risk of livestock depredation by wild felids (Fig. 5.8). Of 241 respondents who strongly agreed or disagreed (1 or 5 on the five-point Likert scale) with livestock depredation occurring in carnivore habitat, 38% (n = 92) believed that the risk is further influenced by ecosystem imbalance. However, 62% (n = 149) who moderately agreed or disagreed (2 to 4 on the Likert scale) with livestock depredation occurring in carnivore habitat were influenced by the rate of livestock depredation by leopard (Fig. 5.8). Of those who did not disagree with an influence of ecosystem imbalance (neutral or agrees; 3-4 on the point Likert scale), the rate of conflict with leopards significantly influenced their perception on risk of livestock depredation (Figure 5.8).

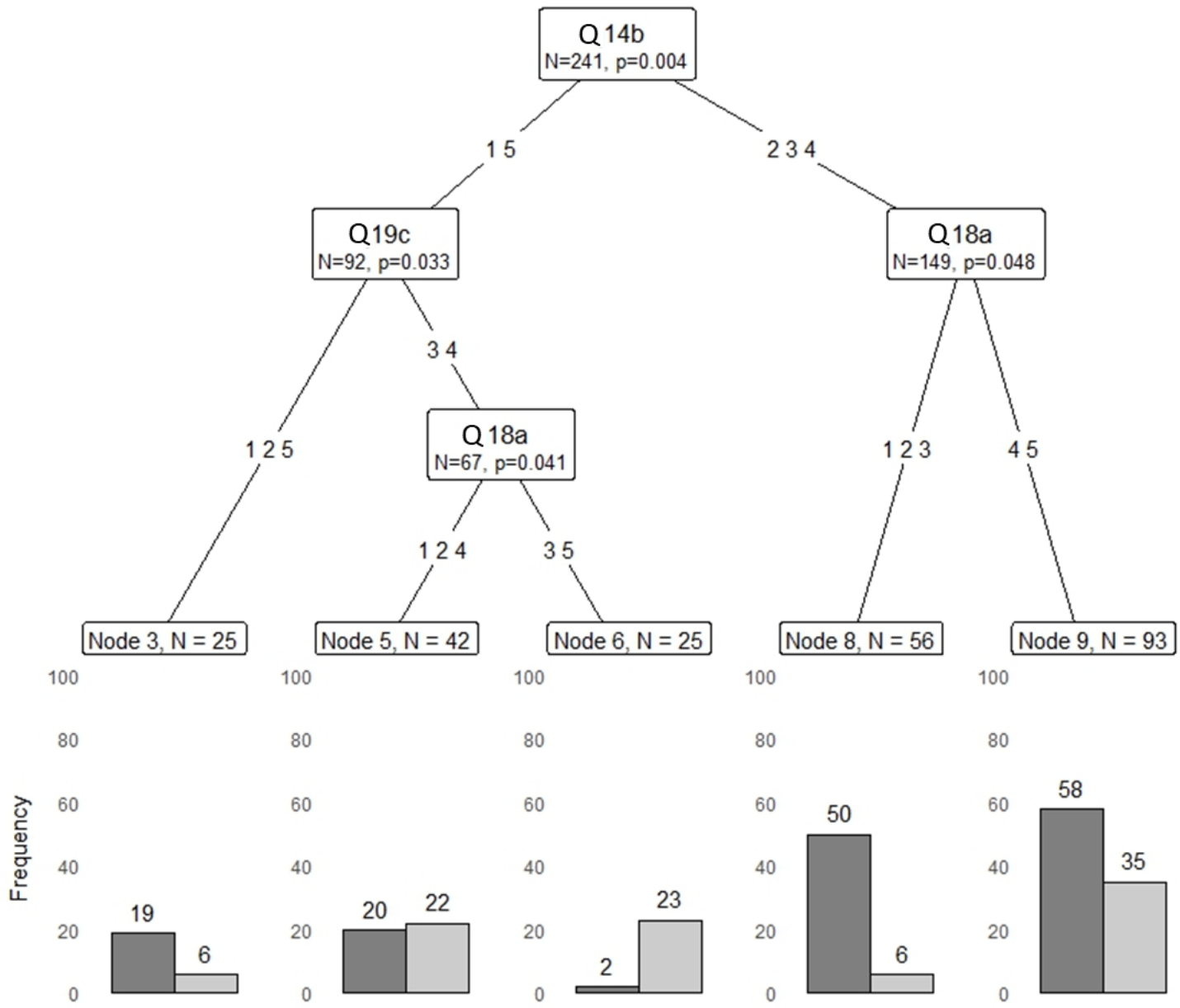


Figure 5.8. Conditional inference tree showing significant predictors of people's perception of the risk of livestock depredation by wild felids. Item Q14b: proximity to carnivore habitat; Q18a: rate of conflict with leopard; Q19c: increase in wild felid population; *n*: number of respondents; *p*: statistical significance; histograms show numbers of respondents with (dark bar) or without (light bar) experience of livestock depredation by wild felids.

5.3.9 Livestock grazing practice

The 99 respondents owning cattle were asked about the grazing practices, revealing that 43% practiced free roaming in the forests and collecting in the evening, followed by 40% who used stall feeding (animals kept in a cattle barn), and 17% still followed traditional herding practices in which cattle are accompanied at all times by cowherd. When asked about their preference, 45% preferred stall feeding followed by 42% preferring free roaming in the forests and collecting it in the evening, with only 13% preferring herding practices. This study also sought to probe the respondents' observations on grazing practices in their locality. We

found that 39% of cattle-owning respondents observed daily free roaming in their locality, 11% saw it weekly, 15% who observed it no more than once a month or in a year, and 35% never saw free roaming in their locality. We found that 67% of cattle-owning respondents never leave their cattle unattended in the forests, 18% reported leaving their cattle unattended every day in the forests, and the remaining 15% said they leave their cattle unattended once a week or a month.

5.3.10 Negative interactions with carnivores

Of the 99 livestock-owning respondents, 34% had lost livestock to wild carnivores during the last 5 years, with 1 of them reporting a weekly loss of livestock, while 5 respondents reported monthly losses, and 28 respondents faced livestock predation by carnivores over the past five years. Respondents reported a total of 412 livestock animals lost to wild carnivores during the last 5 years, worth approximately 6.576 million BTN (81,185 USD) or 66,424 BTN (820 USD) per livestock owner. This equates to 9.8% of average annual income for a household in this region of Bhutan. Of the 99 livestock-owning respondents, 43% of respondents complained to concerned authorities regarding the livestock loss. Of the 43 reporting their loss to the authorities, 73% reported to the Forest Rangers Office, and 27% to local government and gewog livestock extension office. When asked about the response from the authorities, 54% of complainants agreed that the authorities responded to their complaint. Respondents were asked to rank their perception on effectiveness of different relevant offices for mitigating human-carnivore conflicts. Two-thirds of all (330) respondent agreed that the forest ranger office ($\bar{x}$ = 3.78, σ = 1.13, mode = 4). and local government office ($\bar{x}$ = 3.56, σ = 0.72, mode = 4) were effective in mitigating human-carnivore conflicts. Almost half of respondents agreed that the livestock office ($\bar{x}$ = 3.44, σ = 0.80, mode = 4) was effective in mitigating human-carnivore conflicts, and two-thirds were neutral in their perception of NGOs ($\bar{x}$ = 3.03, σ = 0.68, mode = 3), as shown in Figure 5.9. When asked about projects on mitigation of human-carnivore conflicts, 32% of respondents agreed that government and conservation authorities implement projects.

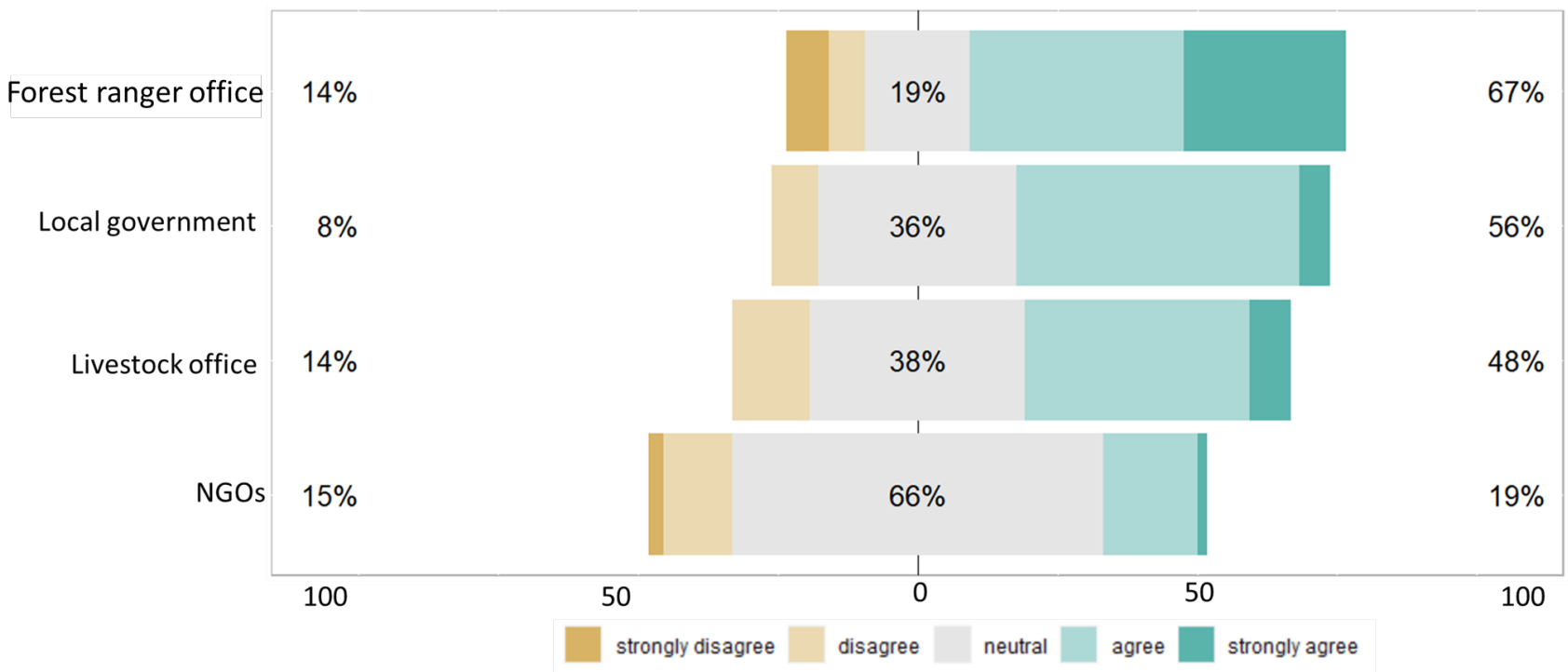


Figure 5.9. Local perception on effectiveness of different conservation authorities (shown on y-axis) in mitigating human-carnivore conflicts. Figure annotations as for Fig. 5.3.

5.3.11 Perceptions of the effectiveness of mitigation measures

When questioned about the effectiveness of mitigation measures, most respondents strongly agreed that the most effective measures were insurance schemes (84% scoring 5 on the Likert scale) and compensation for losses (75% scoring 5 for experienced, 86% for perceived), as depicted in the Figure 5.10. Respondents further strongly agreed that effective mitigation included improving grazing practice such as stall feeding (86% scoring 5) and education and awareness on human-wildlife conflicts (88%, Figure 5.10). In the experience of respondents, proper inspection (e.g., ranger confirming carnivore species involved in conflict and reporting to authorities within timeframe) of human-felid conflict was considered effective (75% scoring 5) followed by provision of high yielding breeds (73%) and replacement of lost livestock (70%). The majority of respondents (54%) were strongly disagreed in their view on relocation of conflicted animal as a mitigation for human-carnivore conflict (Figure 5.10).

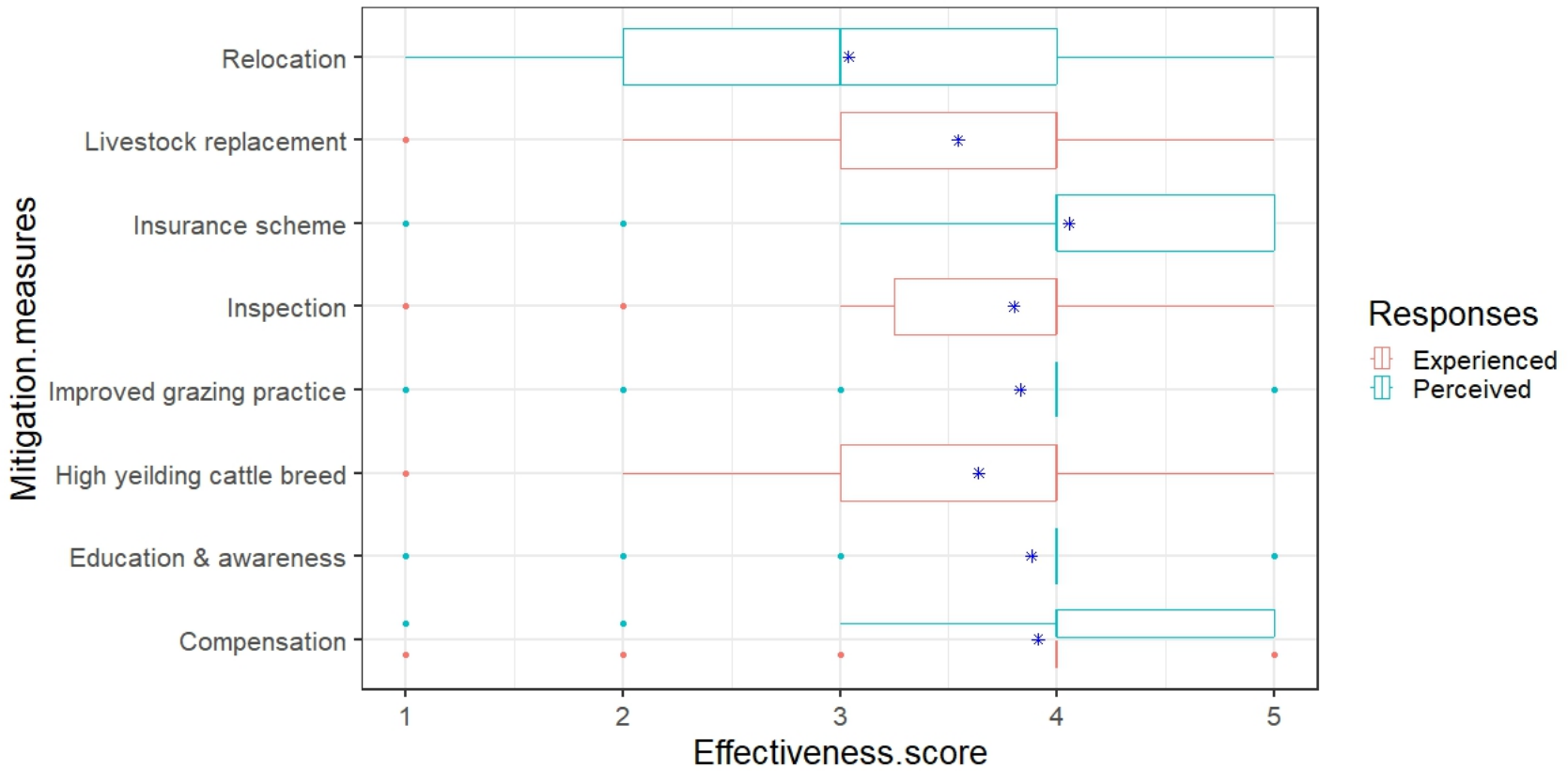


Figure 5.10. Experienced and perceived effectiveness score for mitigation measures for human-carnivore conflicts (5-point Likert scale). Box-and-whiskers show quartiles 1-3 and range, with outliers as dots. Blue asterisk depicts the mean score. Effectiveness scores above 3 are deemed effective, while those below are considered not effective.

5.3.12 Tolerance towards negative human-carnivore interactions

Respondents were asked about their experience of retaliation to livestock depredation by carnivores. Despite being a sensitive issue, and their option to skip answering the question, 4 (1.2%) of the respondents agreed that they had retaliated against the predator in their lifetime. Similarly, respondents were asked about the prevalence of retaliation, with 46 (14%) reporting having heard of retaliation in their locality and in nearby communities. Of those with personal experience or hearing about retaliation, 26 respondents reported the method as leg trapping for carnivores, 8 respondents as snaring, and 4 respondents as poisoning carcasses. Respondents also reported multiple use of retaliation methods as 8 respondents reported use of leg traps, snares and poisoning of carcases. Concerning the prevalence of human-carnivore conflicts in their locality, 4% of all 330 respondents reported hearing such news daily or weekly, with 16% hearing it monthly, and 50% annually, while the remaining 30% were unaware of any human-carnivore conflicts in the past 5 years in their locality.

The majority of respondents agreed that community-level tolerance of livestock depredation by carnivores will be increased by timely compensation ($\bar{x}$ = 3.77, σ = 1.33, mode = 4; Q75a in Fig. 5.11) and by projects on human wildlife conflicts ($\bar{x}$ = 3.70, σ = 1.18, mode = 4; Q75b in Fig. 5.11). Respondents were interested in carnivore conservation, with most not agreeing to the statement “I am not at all interested in the conservation of carnivores” ($\bar{x}$ = 2.61, σ =

1.10, mode = 2; Q75c in Fig. 5.11). When asked about the factors that reduce their tolerance, respondents remained tolerant even if their complaints were not addressed by the authorities ($\bar{x}$ = 2.86, σ = 1.02, mode = 2; Q76a in Fig. 5.11). However, they agreed that their tolerance towards carnivores reduces when they lose high yielding livestock breed ($\bar{x}$ = 3.41, σ =1.09, mode = 4 ;Q76b in Fig. 5.11) and with lower amounts of compensation ($\bar{x}$ = 3.36, σ = 1.07, mode = 4 ;Q76c in Fig. 5.11). Respondents remain neutral to the term "when compensation reaches late" ($\bar{x}$ = 3.19, σ = 0.09, mode = 3; Q76d). Most of the survey enumerators recorded in their additional notes section of the questionnaire that *"Respondent would rather have late compensation than no compensation."*

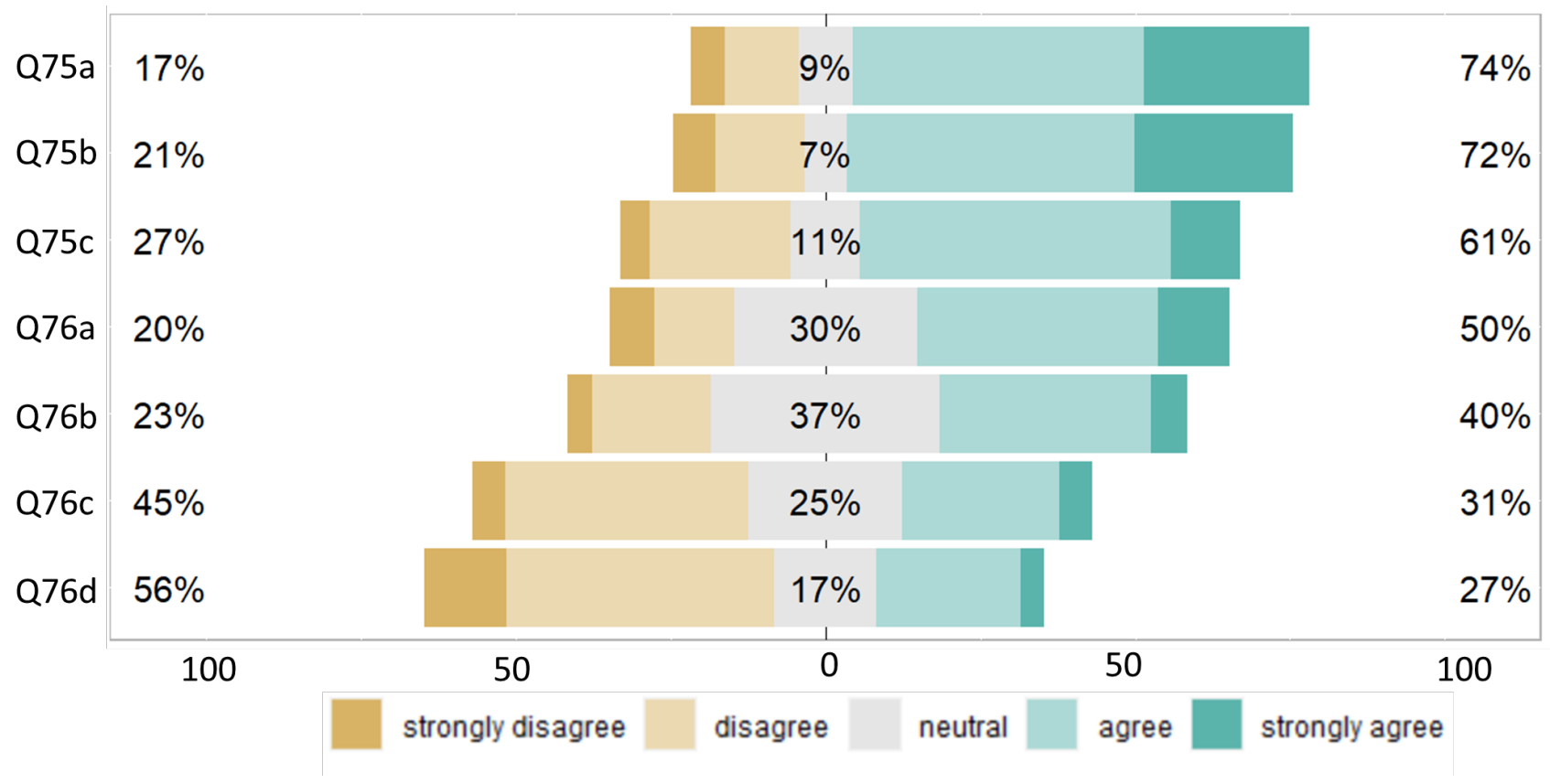


Figure 5.11. Influences on the tolerance of communities to livestock depredation by carnivores. Figure annotations as for Fig. 5.3.

5.3.13 Preventive measures and level of satisfaction with authorities

We found that 15% of all 330 respondents (50% of livestock owners) had invested in the government insurance scheme for livestock losses to carnivores. About one-third (n = 35) of respondents still followed traditional methods of preventing livestock depredation by carnivores. Of these, 25% reported using only noise to drive away the carnivores, 21% only appeased local deities by performing rituals, and the remaining 54% used all forms of conventional practices including making noise, burning firewood, crackers, and herbs, and appeasing local deities. Other preventive measures included avoiding free roaming of cattle by guarding them in the forest (28%), and stall feeding with high yielding breeds of cattle (72%).

More than two-thirds of all 330 respondents had been involved in conservation-related work during the past five years. Of all involved in conservation related work, 9% worked as a rapid response to human-wildlife conflict, 26% as a porter to foresters in the field, 39% in education and awareness programs, and 25% of respondents were involved in all these activities. When respondents were asked about the frequency of monitoring human-carnivore interactions by authorities, 20% of them saw frequent monitoring, 39% saw less frequent, 20% said authorities never inspected the human-carnivore interactions in their locality, and the remaining 21% were unsure.

5.3.14 Quantitative findings from key informants

The 33 key informants in the KIS survey were asked about their level of understanding of issues in human-carnivore conflict. All 33 responded that they understand about the issue (44% understand, 66% fully understand). Regarding the importance of carnivores, 30% responded that carnivores control herbivore populations, 28% that carnivores are endangered, 20% that carnivores are keystone species, 19% that carnivores are ecosystem engineers, and only 3% responded that people like carnivores. When questioned on their knowledge of policies and strategies pertaining to mitigation of human-carnivore conflicts in Bhutan, 59% of key informants were aware to fully aware of the national Human-Wildlife Conflict Strategy (2008), while 31% admitted to not being aware of this strategy; 72% were aware of the conservation management plans for the two National Parks and only 9% admitted to not being aware of these plans. Similarly, 72% of key informants were aware to fully aware of the gewog (village-block) human-wildlife conflict endowment fund, while 22% admitted to not being aware of this fund. Key informants appeared more aware of the recent programme of the gewog tiger conservation fund, which was initiated in 2021, with 91% aware to fully aware of this fund. The common leopard was reported by 40% of key informants as the wild felid most commonly associated with conflict in their locality; the tiger had this status for 36%, and the dhole for 12% of key informants, with the remaining 12% taking the view that no one species predominates in conflicts and conflict cases are rare.

5.3.15 Qualitative findings from key informants

Perceived causes of Human-carnivore conflict

Most of the 33 key informants in the KIS survey reported being aware of the causes of human-carnivore conflicts in their areas. Almost all considered habitat degradation as the main cause of human-carnivore conflicts, followed by encroachment of settlements into

wildlife habitat (which they refer to as deep forests). Habitat encroachment by agricultural expansion and impact of developmental activities were other major causes reported by the key informants. Climate change was also reported by the majority of key informants as one of the causes. They also perceived that declines in the numbers of prey species in carnivore habitat leads to depredation of domestic animals including pets. Some key informants reported incidences of direct attacks on humans by common leopards. According to their understanding, the presence of dense bushes and inadequate sanitation in the surroundings was identified as a potential cause of these incidents. Similarly, rural-to-urban migration creating fallow land for overgrowth was also perceived as a cause of human-carnivore conflicts. A park ranger working in our study area reported (Appendix 4, Table S4, row 28):

> "The majority of people nowadays prefer free ranging methods for livestock grazing, unlike the past. Young people are more inclined to choose urban living over residing in rural communities. As a result, there is an increase in human-carnivore conflict due to the absence of younger individuals in the villages who would normally carry out necessary work (cattle herding). This leaves only the elderly parents behind to handle all responsibilities and tasks."

One of the gewog administrative officers further mentioned (Appendix 4, Table S4, row 25):

> "Due to rural urban migration the lands remained uncultivated, forming wildlife habitat in and around the settlement, causing increase of herbivore population in the locality."

In contrast to this statement, one of the park rangers said (Appendix 4, Table S4, row 21):

> "Encroachment of habitat by humans leads to carnivore population increase in the community. Loss of habitat increases the population of wild animals in the community. Letting their livestock freely roam in the forest encourages attacks by the carnivores."

Additionally, most of the key informants consider that increasing numbers of carnivores in the forests has in the past caused increases in human-carnivore conflict. Some mentioned that projects are mostly focused only on carnivore conservation, and there is no proper coordination between stakeholders. A gewog livestock extension officer said (Appendix 4, Table S4, row 7):

> "The management and solution don't match with the scale of problem, and management are often implemented with just a conservation focus. There is a lack of

> support and coordination amongst the sectors despite the issue being so important and global in nature."

One of the village heads (*Tsogpa*) said (Appendix 4, Table S4, row 8):

> "A greater number of protected areas around the human settlements has caused the human-carnivore conflict to rise over past years."

Most of the rangers considered that declines in prey species can be caused by hunting herbivores and illegal trade in wildlife products, which in turn lead to human-carnivore conflicts. Key informants perceived that lack of awareness about the importance of wild-carnivore conservation might be a contributing factor in human-carnivore conflicts.

Positive impacts of human-carnivore interactions

Reductions in herbivore populations was one of the most frequently perceived positive impacts from human-carnivore interactions by key informants. Presence of carnivore in the locality would benefit farmers by reducing crop depredation by wild herbivores. Some key informants mentioned that with more carnivores in the locality, the community will be eligible to receive funds for alternative livelihood opportunities. One ranger cited (Appendix 4, Table S4, row 4) as an example the gewog tiger conservation fund, which is an opportunity for the community to obtain compensation for livestock losses. Additional perceived positive impacts of human-carnivore interactions included benefits to ecotourism, ecosystem balance and regulation of ecosystem services. Some key informants considered that the presence of large carnivores such as the tiger will not only control herbivore populations, but also other carnivore populations. A teacher said Appendix 4, Table S4, row 6):

> "Presence of tiger will drive other carnivore to deeper forests. People's fear will be reduced if the carnivores move deeper into the forests, herders will take extra care of cattle, and people will learn to use stall feeding instead of free roaming."

Negative impacts from human-carnivore interactions

Most of the key informants were more aware about negative impact of human-carnivore interactions than the positive impacts. Almost all key informants mentioned livestock depredation by carnivores and threat to human life as negative impacts. Some key informants mentioned that farmers face huge financial losses from carnivore depredation on high-yielding breeds of cattle, and indirect damage through diminished or lost interest in livestock rearing.

Insights from key informants on strategies to mitigate human carnivore conflicts

Most of the key informants recommended advocacy and awareness programmes about the importance of carnivores in the wild and management strategies. They took the view that local people should be involved in awareness training, from village level to district (dzongkhag) level. Key informants were more concerned about developing case-specific management strategies through appropriate consultation with farmers, rather than providing generic strategies for mitigating human-carnivore conflicts. An administrative officer for one of the gewogs identified appropriate mitigation strategies for carnivores as (Appendix 4, Table S4, row 5):

> "Preserving their habitat strictly and not letting humans destroy their habitat. Compensating farmers for the actual loss of their cattle due to carnivores. Overall, I find it important to conserve the carnivores, as they are endangered and may go extinct, and future generations may not see them, like dinosaurs. Creating awareness face to face rather than sending notifications. Creating awareness of the carnivores as endangered species. Strictly monitoring wild species and human behaviour and imposing strict fines as per the rules and regulations. Giving training or financial subsidies to improve livestock."

Similarly, a teacher reported the need for logical and holistic plans, saying Appendix 4, Table S4, row 6):

> "Communities and carnivores share the same landscape; therefore, poor co-existence strategies lead to rising human-carnivore conflicts over the years. There are needs for well-planned and holistic and integrated management plans and strategies. [Good plans require] compensating farmers for the livestock kills [by carnivores], maintaining good relationships with carnivores and maintaining a healthy co-existence strategy, making people aware about the direct and indirect benefits of having carnivores in the forest. People should be made more aware about the importance of carnivores in the ecosystem. A proper, integrated, and holistic plan is required to manage human-carnivore conflicts."

A gewog livestock extension officer mentioned (Appendix 4, Table S4, row 7):

> "To reduce human wildlife conflict, we need to assess the relationship between humans and wildlife, especially the direct relationship between humans and wildlife to improve their coexistence in the future. We need to identify the approaches that will

address the deeper cause of the human-carnivore conflicts, developing systematic and context-specific solutions, with affected communities as equal participants for solutions and equal involvement of communities in decision making."

Key informants further proposed technological applications and advancements in the field of wildlife conservation, such as provision of chain-link fencing to avoid trespassing by carnivores into human settlements. Most of the key informants took the view that there should be strict monitoring, with fines and penalties for retaliation against carnivores by humans. Direct compensation of livestock loss was recommended by most of the key informants, and some suggested direct transfer of compensation to farmers to simplify the bureaucratic process. Key informants also recommended soft relocation of conflict animals to reduce the frequency of conflicts.

5.4 Discussion

In this study we examined the factors responsible for maximizing positive and minimize negative interactions of human with carnivores. We assessed the level of knowledge, and the attitudes and practices of communities residing inside protected areas and within a 15-km buffer zone surrounding the protected areas. Perceptions of wildlife by a community determine the participation of the community in wildlife conservation. These perceptions are influenced by factors such as individual moral responsibilities (willingness for participation in wildlife conservation) and positive or negative attitudes towards wildlife, which are driven by know-how on the value of wildlife and the wider benefits of conservation (e.g., through government incentives) and good governance (Barmoen et al., 2021; Ghasemi & Kyle, 2021; Silverman et al., 2016; Yang et al., 2022). However, there are few studies that describe socio-economic factors determining positive cohabitation of wildlife and communities.

The majority (60%) of respondents on this survey considered carnivores as important wildlife species to the ecosystem. The structural equation model revealed that the willingness of communities to participate in carnivore conservation was not positively influenced by government incentives as we had hypothesized. Neither were attitudes towards carnivore conservation positively influenced by government incentives. We interpret these outcomes to signify that that government incentives reduce human-wildlife interactions to an economic transaction in the perception of communities. Community equity is the main issue posed by economic incentives that involve environmental conservation (Schelling, 1984). Incentives are mostly in the form of group activities such as Eco-Camp groups, payments to a local human-wildlife rapid response team, and payments to local nature guides for tourism. The

effectiveness of group incentives depends on the efficiency of policy design and the nature of the interaction within the group (Segerson, 2022). Despite negative attitudes attributable to the government incentives, they are nonetheless important in achieving the objectives of improving social acceptance (Rode et al., 2015). We recommend conservation managers and authorities review the redesign of incentives to maximise positive attitude and social acceptance by the communities.

We observed that positive attitudes towards carnivores positively influences social acceptance of carnivores by the communities. Positive attitudes were positively influenced by effective management of human-carnivore conflicts by the government and conservation authorities. Communities took the view that proper inspection by field rangers and timely reporting by their organization were most effective measures for mitigating impacts from human-carnivore conflicts. Good governance has become an imperative for decision making and programme implementation for many nations across the globe and it is also important in the realm of natural resource management in which the consensus-driven process of stakeholder participation is currently most common (Pomeranz & Stedman, 2020). Good governance is widely seen as a determinant of effective natural resources management in a world is facing environmental decline from increasing anthropogenic pressures (Turner et al., 2014). There is strong evidence of a positive influence on public attitudes and support towards wildlife conservation from good management practices (Karanth et al., 2017; Pomeranz et al., 2021). We therefore recommend that conservation authorities develop standard operating procedure to deal with human-carnivore conflicts, reducing bureaucratic backlogs to increase positive attitude and positive social acceptance of carnivores by communities.

Respondents in communities that belong to wildlife or environmental conservation groups show comparatively more positive attitudes towards carnivore conservation than the other respondents. Community-based conservation has been on the rise over the past two decades mostly through integrated conservation and development projects (Horwich & Lyon, 2007). The fences-and-fines approach (American National Park model) for conservation fails in protected areas that encompass human habitations, and its more modern alternative of community-level involvement in wildlife conservation is more successful (Songorwa, 1999). The engagement and inclusion of stakeholders and local communities in mainstream conservation is now a proven best practice for effective conservation (Viollaz et al., 2022). In our study area, we see an opportunity in encouraging more community members to engagement in conservation related activities. Our study found more than 45% respondents were not involved in any of the local conservation groups. To enhance conservation-group

membership and to improve local livelihoods, we recommend that conservation authorities initiate innovative conservation activities, such as sustainable ecotourism, development of nature-based entrepreneurship, and initiation of payments for ecosystem services (e.g., on the well-established Mexican model) (Ramirez-Reyes et al., 2018).

The common leopard was mentioned both by communities and by the local key informants as being the source of most human-wildlife conflicts. Our study also revealed that communities perceived predation of cattle by leopard and tiger as the most likely conflict issue in their locality. They took the view that livestock depredation risk is higher from leopards near to human settlements and risk from tigers in closer proximity to the carnivore's habitat. Similar studies in India found villagers perceiving a high risk of livestock attack by common leopards near to villages and agriculture field, and risk of tiger increasing with denser forest and fewer human structures (Miller et al., 2016). Study of the movement patterns of leopard and tiger can be recommended to reduce risks of livestock depredation, by identifying patterns of carnivore interactions with humans. Humans can draw lessons from behavioural ecology of animals, insofar as wild prey tend to adapt their tactics for escaping predation by shifting away from habitats favoured by predators, which requires knowledge of predator movement behaviours in the landscape (Miller et al., 2014; Preisser & Bolnick, 2008). Conservation managers can map resource use by carnivores in the human dominated landscape, to highlight areas with high habitat use by carnivores. Local herders and communities can be restricted from entry to these areas or cautioned about risk of livestock depredation by carnivores. We recommend deploying remote camera traps that can warn local rangers about the possibility of livestock depredation by carnivores currently in their area. This technological advancement in mitigating human-carnivore conflicts was suggested by most of the respondents and key informant in this study.

5.5 Conclusion

The communities and key informant in our study area have considerable know-how on carnivores present in their locality. Structural equation modelling revealed that government incentives had a positive influence on community's knowledge on the importance of carnivore conservation and carnivores in an ecosystem. We recommend more education and awareness training for communities on the species-specific values of wildlife to ecosystems, to increase the knowledge base of the communities on carnivore conservation. Key informants likewise preferred more education and advocacy on the value of carnivores, and on rules and regulations. Communities preferred a sustainable livestock insurance scheme and government

compensation scheme over any other kinds of human-carnivore conflict mitigation measures. We urge conservation authorities, NGOs, financial institutions, and government to initiate sustainable insurance schemes and endowment funds for compensating livestock losses caused by carnivores. Conservation of carnivores is comparatively favoured in southern Asia and the region is renowned for its general tolerance towards carnivores, which is shaped by ethical cultural values (Bagchi & Mishra, 2006; Karanth et al., 2010; Negi, 2005). The structural equation model also revealed that willingness to participate in conservation (likely driven by moral responsibility) positively influenced carnivores. In this respect, we recommend more research on community-level values and cultural ties with carnivores. Although our study included a large total number of respondents, it sampled from few communities, representing a narrow segment of the general population. We recommend that more such studies be conducted across a broader geographical range, to enable generalisation of findings beyond the two studied national parks.

Chapter 6 General Discussion

This thesis aims to improve the design of camera-trap deployments for conservation monitoring of wild felids, and to evaluate social perceptions of wild felids amongst rural communities in Bhutan. We analysed the abundances and movement patterns of montane carnivores and prey of Bhutan for the first time and determined the social acceptance of wild felids by communities residing in the protected areas. The comparative density estimates of marked felids form trail and random deployments of camera traps in Chapter 2 suggested that a combination of trail and random camera deployments could yield the least biased density estimates compared to trail only or random only deployment of camera traps. The density comparison between marked and unmarked methods in Chapter 3 revealed that REM method for unmarked animals overestimates the density for some species of wild felids, but can nevertheless be a useful technique when it is hard to recognize the individuals of species due to lack of bodily markings. The analysis in Chapter 4 reveals previously unknown aspects of the movement ecology of wild carnivores of Bhutan in montane landscapes, and their selection of habitat based on availability of resources. The structured interviews with local communities of protected areas reported in Chapter 5 suggested that their social acceptance of wild felids depends on government incentives and activities that positively influence attitudes towards wild felids and carnivores.

6.1 Main Findings from Chapters

The main take home message from Chapter 2 was a sex skewed detection difference in trail and random camera stations, where a trail-based deployment favoured more male detections and a random deployment favoured more female detections. The combination of trail and random deployment of camera traps reduced sex-based bias in detection. We estimated population densities of four species of naturally marked felids using the Spatially Explicit Capture Recapture (SECR) method from trial and random deployments of camera traps and compared their estimates. We observed that combining trail and random deployments enhances the density estimates for all the cat species. Our model of the influences of deployment type, sex type and their interaction on population density confirmed that population density generally depends on type of deployment and on the sex of individuals. When we estimated densities from trail-only or random-only deployments of camera traps,

we observed that each type missed some individuals. Non-consideration of sex-specific detection heterogeneity underestimated the density from the trail deployment, which gets mitigated by including sex-dependent detection in the density model. We observed from the analysis that robust density estimates can be obtained with camera traps deployed both randomly and on trails but can be substituted with a sex-based model for a trail-only deployment, which will be less expensive. However, addition of random cameras is the only way to reduce bias for marked animals with difficulty in sex differentiation. For some wild felid species, analysis of density using data from a single sex yields reasonable estimates for males from the trail deployment and for females from the random deployment. This can be an alternative option for density estimation where capture is heavily male biased and random deployment is not possible.

We estimated densities of four marked wild felids with Random Encounter Modelling in Chapter 3, and compared these estimates to our most robust density estimates derived from SECR modelling of the full trail plus random deployment in Chapter 2. Our comparison revealed higher density estimates from REM over SECR for clouded leopard, common leopard and marbled cat and lower density estimates from REM compared to SECR for leopard cat. Additionally, we tested bias in the REM estimates induced by addition of trail stations, finding an increase in density bias with addition of more trail stations. When compared to SECR, REM estimates were less precise for all four marked wild felid species. Our analysis further revealed that conservative REM parameter values of day range and detection zone underestimated the density, while conservative encounter rates overestimated the density. Of all the REM parameters, animal movement speed had the strongest influence on the accuracy of REM density estimates, where lower speed overestimated the density and higher speed decreased the density estimates. We estimated density of Asiatic golden cat with REM, and found the most precise density from the full random deployment of 100 camera traps. As with the spotted cats, the addition of trail stations increased the density bias. REM was further used to estimate density of prey species and sympatric carnivores found in the study area.

The main outcome of Chapter 4 was estimates of the home ranges of Asiatic golden cat, clouded leopard, common leopard, leopard cat, and dhole along with their resource use functions. The home range size of a female Asiatic golden cat was similar to that of a male leopard cat and was larger than the female common leopard. A male common leopard from

Western Bhutan, with habitat comprising of mixed coniferous forests, had a home range almost seven times larger than that of the male leopard found in warm broad-leaved forests of South-Central Bhutan. The female dhole collared in lower warm broad-leaved forest had a home range that was six times larger than that of the female collared in cool temperate forest of Bhutan. The resource selection function of common leopard revealed that its resource selection was more influenced by habitat factors than by the presence of other carnivores and prey. Both the male leopards' resource selection was negatively influenced by elevation. The male leopard in South-Central Bhutan preferred to select resources in places with higher incidences of livestock depredation by carnivores in the past. We found common leopard as most conflicted wild carnivore from interviews with local communities and key informants as highlighted in the findings of chapter 5. Unlike leopards, the Asiatic golden cat selected resources where there was less disturbance from human activities. We found that resource selection by leopard cat was also more towards deeper forests than nearby human settlement. Dhole selected resources where there were higher incidences of human-carnivore conflicts but avoided sites with higher occupancy of common leopards.

In Chapter 5 we analysed local communities' knowledge and perceptions on wild felid conservation, and factors responsible for their social acceptance of wild felids. We found that a very high proportion of the residents of local communities in RMNP and JSWNP are aware of human-carnivore conflicts in their locality. More than half of the respondents in the survey were members of one or more conservation groups (Community Forestry Group, Human-Wildlife Conflict Rapid Response Team, and/or Eco-Camp Group). More than 80% of respondents were aware of the importance of carnivore conservation. Common leopard was ranked as the carnivore in their locality associated with most conflicts, either in the form of livestock depredation or direct attack on human, followed by tiger; small felids caused the least conflict. However, unlike common leopard, tiger, small felids, and wild dogs are not associated with direct attack on human. Communities ranked the tiger as the most important, and small felids as the least important in the ecosystem, amongst wild felids that influence their lives. Social acceptance was found to be significantly influenced by government incentives on wild felid conservation and positive attitudes of local communities to wild felids. Negative attitudes towards wild felids were associated with rates of conflict with common leopards and predicted higher future risk of conflict. In the presence of conflict with

tigers, community support for wild-field conservation was positively influenced by higher compensation.

Direct compensation for loss of livestock, and insurance schemes, were found to be the most effective mitigation measure for the community in terms of improving attitudes towards carnivore conservation. Our analysis reported that almost all the key informants understood the causes of human-carnivore conflict in these protected areas. According to key informants, the common leopard was the wild felid most associated with conflicts, and the main causes of human-carnivore conflict were perceived to be the proximity of a human settlement to carnivore habitat, habitat encroachment, the decline in prey populations and climate change. Key informants suggested creating awareness amongst communities to improve knowledge regarding importance of conservation of carnivores. The key informants further suggested increasing fines and penalties and higher prison terms poachers.

6.2 Unexplored avenues: initiatives requiring amplified commitment

Our analysis in Chapter 2 confirmed the presence of widespread detection heterogeneity between males and females, which could be effectively addressed by deploying detectors (camera traps) randomly with respect to habitat (in our case at the centre of each 2 x 2 km grid cell). For further authentication of influences on density estimates, we recommend comparisons to density estimates from full randomization of detector stations without structuring by grid cells, to explore a potential difference between randomisation with respect to habitat (our design) and randomisation with respect to animal movement (the REM assumption). We know from Chapter 4 the wild felids in our study area have species-specific resource-use functions, and therefore may not move randomly with respect to habitat. Randomized placement of detectors often accumulates new species faster than the detectors that are placed on trails (Fonteyn et al., 2021). We further recommend conducting comparative density estimates from trail and random deployment of camera traps in different seasons to understand intra and interspecific avoidance in different period and influence on density estimates. Different species may have different behaviours with respect to avoiding core activity periods of other carnivores (Iannarilli et al., 2021; Smith et al., 2023).

Information regarding Adult Sex Ratio (ASR) is vital for ecological understanding of population dynamics in time and space, risk of extinction and success in perpetuation through reproduction (Anile & Devillard, 2018). ASR is generally expected to have a female bias in some areas, and female bias is observed in species such as cougar (*Puma concolor*) (Anile & Devillard, 2018; Martin et al., 2023). However, ASR is more usually balanced or male biased in felids (Anile & Devillard, 2018). Our simulation in Chapter 2 suggested using single-species density estimation as an alternative to factoring in sex to a SECR model on a trail deployment. This method needs more exploration of adult sex ratios amongst wild felids, especially in mountainous habitat like that in Bhutan. Apart from its use in density estimation, ASR can provide key information for wildlife conservation on the viability of animal populations for better management policies (Ancona et al., 2017).

In Chapter 3, we observed that the accuracy of REM density estimates depends on accuracies in measurement of REM parameters. Of all the REM parameters, we found that animal movement speed had the largest influence on REM density estimates. We recommend building a reference database of speed from the camera trap studies for different species of wildlife. The speed of an animal detected in a camera trap study is calculated by dividing the length of passage by its duration (observed speed) and fitting a size-based probability distribution to a sample observed speeds (Rowcliffe et al., 2016). This method of wildlife speed estimation is found to yield accurate estimates of the day range of wildlife (Rowcliffe et al., 2016). Hence, building a speed database of different species of wildlife in varied landscapes could provide a valuable resource for calculating density using REM wherever local speed calculations are constrained by camera performance and animal behaviours. In our own case, for example, the camera-flash recharge time ruled out use of nocturnal detections for species with nocturnal habits.

We observed rare capture of elusive wild felids including Asiatic golden cat, marbled cat, and clouded leopard. Little is known of the movement ecology of these cat species, leaving us ignorant of their daily energetics and dietary requirements. Such information is crucial to the effective allocation of areas for conservation, and for understanding ecosystem functioning (Habib et al., 2021; Reshamwala et al., 2022). Very little is known about the movement ecology of montane tigers anywhere in their remaining geographic distribution (Tempa et al., 2019). Information on movement ecology of tigers helps to understanding their ecological behaviour, the formulation of conservation strategies, and informed decision making relevant

to all the wild felid species present in same area as the tiger (Brum-Bastos et al., 2022; Malishev & Kramer-Schadt, 2021). For Instance, Bhutan has seen a decade-long famous political debate about road construction through one of its national parks. The road is designed to pass through core habitat of the Royal Bengal Tiger, restricting its environment through forestry clearance. However, evidence for opposing the road issuing from the forestry and environment authorities is often debated for its reliability (Penjor, 2012). In such instances, unbiased information gathering would help policy makers in speedy and just decision-making.

Our initial plan was to live-capture clouded leopard and study its movement ecology. However, due to its elusive nature and arboreal behaviour, we had zero success in live trapping this species across a total of 2,840 trap nights. We recommend investing resources in studying movement ecology of clouded leopards in Bhutan. Capture success could be increased by setting a larger number of live traps across different clouded-leopard habitat. Clouded leopard is one of the most threatened and least known big-cat species in this region (Tashi, 2018). It is the smallest of all the big cats (Austin et al., 2007), and the less well-known due to its nocturnal, semi-arboreal and secretive habits, and low density (Gordon & Stewart, 2007). There has been a notable increase in population studies of clouded leopard with advancements in statistical methods (including SECR models) for density estimation and associated software packages (Chiang, 2017). SECR models can yield density estimates of clouded leopard, as individuals are easily identified by their distinctive cloud-like coat pattern (Borah et al., 2014). The population of this species is seen to be in constant decline from anthropogenic activities (Rasphone et al., 2021) .The species is widely distributed over the region, in ecosystem types that are representative also of many other big-cats (Kitchener et al., 2006).

Clouded leopard is a scheduled species in the 2023 Forest and Nature Conservation Act of Bhutan, and hunting is strictly prohibited, warranting criminal prosecution under the law (NAB, 2023). It is listed in Appendix-I of the Convention on International Trade of Endangered Species (CITES, 2023). It is mostly distributed along the sub-tropical areas of South-east Asia, which are undergoing the fastest deforestation in the region (Petersen et al., 2020), and the main threat to its population is from illegal hunting for its coat combined with habitat loss (Ghimirey & Acharya, 2018). Due to a decreasing trend of its population in the wild, it is listed as Vulnerable by the International Union for Conservation of Nature (IUCN)

Red List (Grassman et al., 2015). Little is known about the species in Bhutan, giving urgency to the need for ecological data from its rapid changing of environment (Penjor et al., 2018). The Standard Operating Procedure (SoP) for live trapping of clouded leopard given in Appendix 3 can be easily adapted to future live-trapping of clouded leopards in Bhutan and elsewhere.

Our findings from Chapter 5 have recorded perceptions of wild cat conservation from four different communities falling under three districts of Bhutan. We recommend replication of such surveys across different protected areas in Bhutan. Surveys should also be replicated in non-protected areas where there are higher frequencies of human-carnivore conflicts, which may support higher densities of wild cats. Bhutan has recorded higher densities of wild tiger from areas outside national parks, wildlife sanctuaries and strict wildlife reserves (DoFPS, 2015, 2023c). Ignoring the communities residing outside the protected areas will undermine overall human perceptions towards conservation of wild felids in places like Bhutan. Efficient management of human-carnivore conflicts involves multidisciplinary approaches connecting across the natural and social sciences (Lozano et al., 2019; Pooley et al., 2014; Tallis & Lubchenco, 2014).

6.3 Role of Bhutan in maintaining healthy population of wild felids

Asia is home to over half (21 species) of the worldwide total of 39 extant wild felid species, distributed from tropical sea level to freezing Himalayas (IUCN, 2023; Macdonald et al., 2010). Of these 21 species, the larger-sized felids are particularly vulnerable due to the extensive spatial requirements of their populations, which usually span geopolitical borders requiring management of transboundary populations often with heterogeneity in conservation challenges (Farhadinia et al., 2021). Mid-sized cats are threatened by deforestation and habitat fragmentation (Decœur et al., 2023). However, smaller cats can persist to become abundant in fragmented and degraded habitat, due to their smaller home ranges and their adaptability to changing foraging conditions (Prugh et al., 2009). Eleven of Asia's 21 wild felid species are found in Bhutan, from subtropical forests to snow-capped mountains (Wang & Macdonald, 2006).

Bhutan is one from the 234 globally outstanding ecoregions of the world, with its rich diversity of flowering plants and flourishing populations of some of the rarest animals on Earth (Banerjee & Bandopadhyay, 2016). Bhutan has healthy populations of ungulates

capable of supporting healthy population of wild felids (Wang, 2010). Bhutan has recently increased its geographical land cover under protection from 51.44% to 52.00%, with the addition of a new biological corridor connecting Sakteng Wildlife Sanctuary with Bumdeling wildlife Sanctuary in the extreme east of the country (NCB, 2023). Geographically, 69% of land area in Bhutan is under tree cover and almost 80% of land area falls under state reserve forest land (DoFPS, 2023a). Bhutan has strong government regulations and policies related to conservation management (Lham et al., 2019). For example, the constitution of Bhutan mandates a minimum of 60% of forest cover in perpetuity (NAB, 2007), and the government has committed to remain carbon neutral (Tobgay, 2016). Carbon neutrality remains a distant aspiration for every other country in the world except for Bhutan and Suriname, which achieved it at least by 2019 (ECIU, 2019).

Is Bhutan a potential global gene pool for in-situ conservation of wild felids? Conservationist could agree to this proposition, as Bhutan can easily sustain healthy wild-felid populations, given current national population trends of big cats and political support gained by big cats. Bhutan has recently observed a 27% rise in tiger population abundance since its first systematic survey in 2015, and almost 40% rise in snow leopard abundance compared to its findings in 2016 (DoFPS, 2023b, 2023c). Study of Bhutan's protected area networks and it tiger carrying capacity shows that 138 – 151 tigers can be supported within 46% of the protected area network (Thinley et al., 2021). However, Bhutan's tiger population is not confined to the protected area systems, as both the nationwide surveys in 2015 and 2022 observed higher densities of tiger outside protected areas, in territorial forest division (forests areas that does not falls under protected area regime in Bhutan) that is sometimes logged for scientific purposes (DoFPS, 2015, 2023c). Bhutan has 7,206 km^2 of habitat suitable for harbouring healthy population of snow leopard, of which 40% falls in national parks and wildlife sanctuaries and 8% in biological corridors (Lham et al., 2021). To maintain healthy populations of snow leopards and tigers, Bhutan has committed to monitor these two iconic big cats every five years (DoFPS, 2016; Thinley et al., 2015). Bhutan has further committed to double the population of tigers and snow leopards by 2030 from their status in 2015. The country has strategized conservation of these two big cats and secured a budget for monitoring of their populations every five years (NCD, 2018, 2019).

What is the role of Bhutan in wild felid conservation at the global scale? Bhutan has an exemplary role to play in global wild felid conservation. Bhutan's continuous protected area

system connected by biological corridors and key biodiversity areas outside protected areas can function as a global gene pool for wild felids (Choki et al., 2023; Lham et al., 2021; Thinley et al., 2021). Besides habitat suitability, Bhutan's political boundaries are connected to various transboundary landscapes. Bhutan's Royal Manas National Park (RMNP) is one of the oldest protected areas of Bhutan, which shares a continuous border with India's Manas Tiger Reserve, and is one of the hot spots for wild felids in Bhutan (Tempa et al., 2013). RMNP can act as a buffer to the increasing anthropogenic pressures and forest loss threatening protected areas such as the Manas Tiger Reserve (Allan et al., 2017). Governance is one of the major factors found to be limiting the likelihood of wild felid conservation, followed by human population pressure and economy (Dickman et al., 2015). Conservation is also a politically challenging endeavour, particularly in developing countries where government have to frequently balance economic development with the conservation funding (Srivathsa et al., 2020). Unlike its neighbours, Bhutan has political support, a robust legal framework and economic development does not compromise conservation of nature, as enshrined in the economic development principle of Gross National Happiness (Ura & Galay, 2004). With this infrastructure, Bhutan can expand its role in the global forum on conservation of wild felids.

6.4 Next step for wild felid conservation in Bhutan

Enhancing wild felid conservation in Bhutan requires multidisciplinary approaches that address the ecological, social, and economic aspects of conservation. Bhutan needs to invest more resources in scientific monitoring of all the species of wild felid, using modern technologies such as thermal heat seeking drones, remotely operated camera traps and DNA technologies. Updated information on species population dynamics and resource use would help conservation managers to plan and allocate resources for implementing conservation strategies. Currently increases or decreases in populations are judged based on one-time, one-season information, gathered once every 5 to 6 years. Monitoring of wild felids is expensive and resource-intensive, with current monitoring standards requiring deployment of massive numbers of camera traps across the entire nation (Dröge et al., 2020). We urge authorities to explore application of unmanned aerial vehicles (UAVs) to monitor wild felids living above tree lines, such as snow leopards. UAVs have capability to collect high quality data and have increasing cost effectiveness in the monitoring of wildlife population (Lyons et al., 2019).

UAVs fitted with thermal sensors might be feasible for monitor larger sized wild felids in the southern part of country, even in forested areas. A pilot study on the potential effectiveness of UAVs for monitoring snow leopard and its prey suggested that they will play an important role in snow leopard conservation with continuous improvement in drone technologies (Hunter et al., 2023). However, such methods remain untested on the wild carnivores and larger sized mammals in rugged terrains like Bhutan (Lyons et al., 2019). Field offices should pilot uses to reduce costs in human resource. Apart from direct population monitoring, drone technology can be used to monitor prey, antipoaching and habitat assessment.

Bhutan can also explore non-invasive techniques such as environmental DNA (eDNA) techniques to quantify wild-felid abundances distributions. For all rare species, including wild felids, monitoring is an arduous job that is often associated with false positives (misidentification) and false negatives (missed detection), and new techniques such as eDNA applied to rare terrestrial species have potential to eliminate misidentifications and missed detections (Franklin et al., 2019). The information on distribution and extent of site use from eDNA can be used for strategizing mitigation measures for human-felid conflicts (Arbieu et al., 2021). Besides assessing animal abundance and distribution, eDNA can also contribute to building DNA databases for wild felids and other sympatric carnivores of Bhutan.

Poaching and negative interactions between humans and wild felids are the top challenges for wild felid conservation in Bhutan, which require large-scale managerial operations to reduce their impacts on wild population (Tempa et al., 2019; Wangmo et al., 2021). Bhutan can explore the use of remotely operated camera traps capable of sending real-time photographs from the field for monitoring illegal activities within felid habitat. Different brands of camera traps are now available that can be programmed to detect specific animals or human disturbance using artificial intelligence, that can transmit real-time data though cellular networks, or can be adjusted to send data through the Iridium satellite system (Laughlin et al., 2023; Whytock et al., 2023). These technologies can be also explored from the perspective of resolving human-carnivore conflicts, by using real time data on animal positions and movements to mitigate depredation on livestock by wild felids and direct conflicts of humans with wild felids. Other measures for combatting illegal activities against wild felids can include strategic patrolling using modern tools such as SMART patrolling and theme-based patrolling (e.g., focused on wild felids generally, or on individual species). We also urge conservation authorities to explore the wider angle of ecotourism, to turn occasional negative

interactions of humans and wild felids into a sustainable benefit for local communities in the form of income from ecotourism projects. Co-existence of humans and wild felids will ultimately be determined by the collective efforts of wildlife managers and local communities.

Appendix 1. Supplementary materials for Chapter 2

Figure S1: Conceptual framework of camera trap data management. The figure shows processing raw data from camera trap till production of detection histories in comma separated csv files for population and site use modelling.

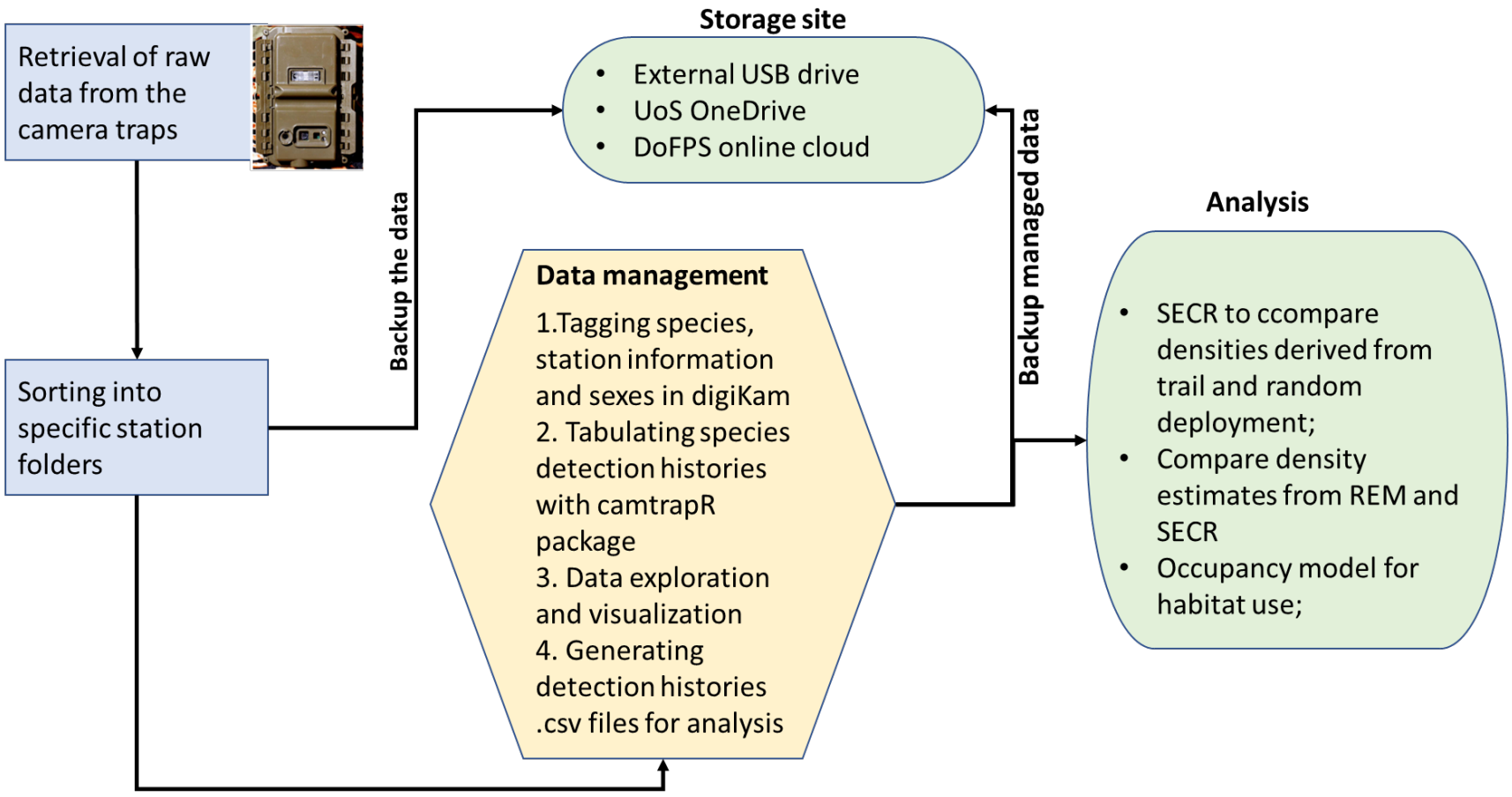


Table S1: AIC comparison of density models from full deployment of camera traps (100T +100R). Interaction model (sex *placement), placement (trail or random deployment of camera traps), sex (male or female). In the model specification, we kept the scale parameter sigma ~ sex constant for all the model with prior information about difference in the home range of male and female wild felids.

Species	Model	Model specification	DF	K	AIC	dAIC
Clouded leopard	Interaction	D~1, g0~sex*placement	hn	7	584.41	0
	Placement	D~1, g0~placement	hn	5	588.61	4.2
	Sex dependent	D~1, g0~sex	hn	5	589.18	4.8
	Null	D~1, g0~1	hn	4	594.74	10.3
Common leopard	Null	D~1, g0~1	hn	4	491.21	0
	Sex dependent	D~1, g0~sex	hn	5	492.14	0.93
	Placement	D~1, g0~placement	hn	5	492.29	1.1
	Interaction	D~1, g0~sex*placement	hn	7	493.77	2.57
Leopard cat	Interaction	D~1, g0~sex*placement	hnl	7	1382.30	0
	Sex dependent	D~1, g0~placement	hn	5	1402.86	20.56
	Placement	D~1, g0~sex	hn	5	1411.37	29.10
	Null	D~1, g0~1	hn	4	1424.74	42.45
Marbled cat	Interaction	D~1, g0~sex*placement	hn	7	1135.68	0
	Placement	D~1, g0~placement	hn	5	1139.45	3.77
	Sex dependent	D~1, g0~sex	hn	5	1166.13	30.45
	Null	D~1, g0~1	hn	4	1169.03	33.35
Tiger	Placement	D~1, g0~placement	hn	5	128.60	0
	Null	D~1, g0~1	hn	4	130.37	1.77
	Sex dependent	D~1, g0~sex	hn	5	131.85	3.25
	Interaction	D~1, g0~sex*placement	hn	7	131.98	3.38

Table S2. Density estimates of clouded leopard, common leopard, leopard cat and marbled cat based on maximum likelihood models incorporating latent covariates and the sex covariates. The camera trap combination 100 T & 100 R identifies the full deployment of paired cameras at 100 Trail stations and single cameras at 100 Random stations (totaling 300 cameras at 200 stations in 100 contiguous grid-cells each of 2x2 km). The models presented are the best-fitting models for the species, as determined by smallest dAIC. The no-sex model does not account sex-based effect on detection probability and sigma, whereas the sex-based models assume an effect of sex on detection probability and sigma. *np* is the number of estimated parameters; df is the detection function; density is the number of individuals per 100 km^2, with SE in brackets.

Camera Combination (Species)	**Model**	**model specification**	**df**	**np**	**logLik**	**AIC**	**AICc**	**dAIC**	**AICwt**	**Density**
100 T & 100 R Clouded leopard	No_sex	CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-279.31	568.63	571.78	0	0.93	3.5 (0.96)
		CL_M0 D~1 g0~1 sigma~1	hn	3	-284.30	574.60	575.75	5.97	0.04	2.7 (0.60)
		CL_MK D~1 g0~K sigma~1	hn	4	-284.30	576.60	578.60	7.97	0.01	2.7 (0.60)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-329.45	666.91	668.91	98.28	0	2.8 (0.64)
		CL_bk D~1 g0~bk sigma~1	hn	4	-331.61	671.22	673.22	102.59	0	2.8(0.64)
		CL_Mk D~1 g0~k sigma~1	hn	4	-342.62	693.25	695.25	124.62	0	2.9(0.64)
		CL_MTD~1 g0~T sigma~1	hn	4	-343.32	694.64	696.64	126.01	0	2.8(0.61)
		CL_Mt D~1 g0~t sigma~1	hn	6	-343.02	698.04	702.71	129.41	0	2.7 (0.61)
		CL_Mb D~1 g0~b sigma~1	hn	4	-345.96	699.93	701.93	131.30	0	2.4(0.54)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-343.00	700.00	706.59	131.37	0	2.8(0.72)
		CL_MB D~1 g0~B sigma~1	hn	4	-347.35	702.71	704.71	134.08	0	2.5(0.58)
	Model _sex	CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-292.12	594.24	597.4	0	0.71	3.5(0.91)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-292.12	596.24	600.90	1.99	0.26	3.5(0.85)
		CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-295.90	601.80	604.96	7.56	0.01	3.3(0.72)
100 T & 100 R Common leopard	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-237.20	480.40	482.24	0.00	0.67	1.8(0.48)
		L_MK D~1 g0~K sigma~1	hn	4	-237.20	482.40	485.73	2.00	0.24	1.8(0.48)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-237.20	484.40	489.85	4.00	0.09	1.8(0.48)
		L_bk D~1 g0~bk sigma~1	hn	4	-296.12	600.24	603.58	119.85	0.00	1.8(0.49)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-297.75	603.50	606.84	123.11	0.00	1.8(0.49)
		L_MT D~1 g0~T sigma~1	hn	4	-297.83	603.66	606.99	123.26	0.00	1.9(0.50)
		L_Mt D~1 g0~t sigma~1	hn	6	-297.80	607.60	616.00	127.21	0.00	1.9(0.50)
		L_Mb D~1 g0~b sigma~1	hn	4	-300.52	609.04	612.37	128.65	0.00	1.6(0.44)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-297.69	609.39	621.83	128.99	0.00	1.9(0.55)
		L_Mk D~1 g0~k sigma~1	hn	4	-301.69	611.38	614.71	130.98	0.00	1.8(0.49)
		L_MB D~1 g0~B sigma~1	hn	4	-302.66	613.31	616.64	132.92	0.00	1.7(0.46)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-243.94	497.89	503.34	0.00	0.59	1.7(0.47)

	Model_sex	L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-243.41	498.82	507.22	0.93	0.37	1.8(0.48)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-246.78	503.56	509.02	5.68	0.03	1.8(0.48)
	No_sex	LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-648.57	1307.1	1307.7	0.00	1.00	26.4(2.6)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-663.45	1332.8	1333.1	25.75	0.00	21.8(2.3)
100 T & 100 R		LC_MK D~1 g0~K sigma~1	hn	4	-663.45	1334.8	1335.3	27.75	0.00	21.1(2.3)
Leopard cat		LC_Mbk D~1 g0~bk sigma~1	hn	4	-705.22	1418.4	1418.8	111.31	0.00	27.7(3.6)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-706.57	1421.1	1421.5	113.99	0.00	26.7(3.4)
		LC_Mk D~1 g0~k sigma~1	hn	4	-797.58	1603.1	1603.5	296.02	0.00	28.9(3.9)
		LC_MT D~1 g0~T sigma~1	hn	4	-805.88	1619.7	1620.1	312.61	0.00	21.6(2.2)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-803.55	1621.1	1622.2	313.96	0.00	24.2(3.0)
		LC_Mt D~1 g0~t sigma~1	hn	6	-805.65	1623.3	1624.1	316.17	0.00	21.6(2.2)
		LC_Mb D~1 g0~b sigma~1	hn	4	-818.92	1645.8	1646.2	338.69	0.00	20.0(2.1)
		LC_MB D~1 g0~B sigma~1	hn	4	-820.74	1649.4	1649.8	342.34	0.00	21.1(2.2)
	Model_sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-701.82	1415.6	1416.5	0.00	1.00	24.4(2.3)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-711.61	1433.2	1433.8	17.57	0.00	22.9(2.4)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-717.73	1445.4	1446.0	29.81	0.00	21.8(2.3)
	No_sex	MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-535.57	1081.1	1082.6	0.00	1	7.7(1.2)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-557.99	1121.9	1122.5	40.85	0	6.7(1.03)
100 T & 100 R		MC_MK D~1 g0~K sigma~1	hn	4	-557.99	1123.9	1124.9	42.85	0	6.7(1.03)
Marbled cat		MC_MBk D~1 g0~Bk sigma~1	hn	4	-623.05	1254.1	1255.0	172.96	0	6.8(1.09)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-624.61	1257.2	1258.1	176.08	0	6.8(1.09)
		MC_Mk D~1 g0~k sigma~1	hn	4	-636.39	1280.7	1281.7	199.63	0	8.0(1.2)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-670.52	1355.0	1357.9	273.91	0	7.2(1.15)
		MC_Mt D~1 g0~t sigma~1	hn	6	-672.52	1357.0	1359.1	275.90	0	6.6(1.03)
		MC_MT D~1 g0~T sigma~1	hn	4	-675.55	1359.1	1360.0	277.96	0	6.6(1.03)
		MC_MB D~1 g0~B sigma~1	hn	4	-675.95	1359.9	1360.8	278.77	0	6.9(1.08)
		MC_Mb D~1 g0~b sigma~1	hn	4	-676.35	1360.6	1361.6	279.55	0	6.7(1.06)
	Model_sex	MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-581.14	1172.2	1173.7	0.00	0.64	6.8(1.06)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-580.91	1173.8	1175.9	1.55	0.29	6.8(1.06)
		MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-583.36	1176.7	1178.1	4.45	0.07	6.8(1.07)

Table S3. Density estimates of clouded leopard from different combinations of trail (T) and random (R) stations, given a total availability of 100 camera traps. The T & R combination identifies the number of trail stations with paired cameras trail and random stations with single cameras. The models presented are the best-fitting models for the deployment, as determined by smallest dAIC. Parameters as for table 1 of Annexure II

Camera Combination	Model	model specification	df	np	logLik	AIC	AICc	dAIC	AICwt	Density
50 T & 0 R	No_sex	CL_M0 D~1 g0~1 sigma~1	hn	3	-117.51	241.03	242.88	0	0.6488	3(1.09)
		CL_MK D~1 g0~K sigma~1	hn	4	-117.51	243.03	246.36	2	0.2387	3(1.09)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-117.27	244.54	249.99	3.505	0.1125	4.2(2.65)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-134.20	276.41	279.74	35.374	0	3.3(1.47)
		CL_bk D~1 g0~bk sigma~1	hn	4	-134.99	277.99	281.33	36.961	0	3.3(1.47)
		CL_Mk D~1 g0~k sigma~1	hn	4	-135.02	278.05	281.38	37.019	0	4.24(1.9)
		CL_MT D~1 g0~T sigma~1	hn	4	-136.79	281.59	284.92	40.559	0	3(1.06)
		CL_Mt D~1 g0~t sigma~1	hn	6	-135.4	282.80	291.20	41.765	0	3(1.07)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-135.39	284.79	297.23	43.758	0	3(1.46)
		CL_Mb D~1 g0~b sigma~1	hn	4	-138.91	285.82	289.15	44.784	0	1.9(0.76)
		CL_MB D~1 g0~B sigma~1	hn	4	-140.05	288.11	291.45	47.082	0	2.5(0.93)
	Model_sex	CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-126.01	262.01	267.47	0.00	0.55	3.4(1.46)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-125.72	263.44	271.84	1.43	0.27	3(1.51)
		CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-127.14	264.28	269.74	2.27	0.18	3(1.10)
33T & 34R	No_sex	CL_M0 D~1 g0~1 sigma~1	hn	3	-116.40	238.79	242.22	0.00	0.47	1.3(0.52)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-115.36	240.73	252.73	1.94	0.18	1.2(0.50)
		CL_MK D~1 g0~K sigma~1	hn	4	-116.40	240.79	247.46	2.00	0.17	1.3(0.52)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-137.61	283.22	289.89	44.43	0.00	1.3(0.55)
		CL_MT D~1 g0~T sigma~1	hn	4	-137.78	283.55	290.22	44.76	0.00	1.3(0.53)
		CL_bk D~1 g0~bk sigma~1	hn	4	-137.92	283.84	290.51	45.05	0.00	1.3(0.55)
		CL_Mb D~1 g0~t sigma~1	hn	6	-136.69	285.38	306.38	46.59	0.00	1.3(0.53)
		CL_Mt D~1 g0~b sigma~1	hn	4	-139.09	286.17	292.84	47.38	0.00	1(0.44)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-136.51	287.03	324.36	48.24	0.00	1.7(1.07)
		CL_Mk D~1 g0~k sigma~1	hn	4	-139.52	287.05	293.71	48.25	0.00	1.4(0.54)
		CL_MB D~1 g0~B sigma~1	hn	4	-139.78	287.57	294.24	48.78	0.00	1.2(0.52)
	Model_Sex	CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-118.01	248.03	269.03	0.00	0.61	1.2(0.51)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	6	-120.10	252.20	273.20	4.17	0.08	1.8(1.11)
		CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-121.40	252.80	264.80	4.77	0.06	1.1(0.39)
25T & 50R	No_sex	CL_M0 D~1 g0~1 sigma~1	hn	3	-136.46	278.93	280.53	0.00	0.58	3.6(0.98)
		CL_MK D~1 g0~K sigma~1	hn	4	-136.46	280.93	283.79	2.00	0.21	3.5(0.98)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-135.47	280.95	285.56	2.02	0.21	4.9(2.29)
		CL_Mk D~1 g0~k sigma~1	hn	4	-153.71	315.42	318.28	36.49	0.00	4.7(1.66)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-157.26	322.52	325.38	43.59	0.00	3.8(1.18)
		CL_bk D~1 g0~bk sigma~1	hn	4	-158.06	324.13	326.98	45.20	0.00	3.8(1.18)
		CL_MT D~1 g0~T sigma~1	hn	4	-164.55	337.09	339.95	58.16	0.00	3.5(0.96)
		CL_MB D~1 g0~B sigma~1	hn	4	-164.98	337.97	340.82	59.04	0.00	4(1.48)
		CL_Mb D~1 g0~b sigma~1	hn	4	-165.19	338.38	341.24	59.45	0.00	3.6(1.18)
		CL_Mt D~1 g0~t sigma~1	hn	6	-164.06	340.11	347.11	61.19	0.00	3.5(0.96)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-163.40	340.81	350.99	61.88	0.00	4.7(2.10)

	Model _Sex	CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-140.02	290.04	294.65	0.00	0.66	5.28(2.5)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-139.76	291.52	298.52	1.48	0.31	8.01(5.0)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-143.30	296.60	301.22	6.56	0.02	9.81(7.0)
	No_sex	CL_M0 D~1 g0~1 sigma~1	hn	3	-108.40	222.79	225.19	0.00	0.63	2.93(0.9)
		CL_MK D~1 g0~K sigma~1	hn	4	-108.40	224.79	229.24	2.00	0.23	2.93(0.9)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-107.92	225.84	233.34	3.05	0.14	4.00(2.9)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-122.03	252.05	256.50	29.26	0.00	3.32(1.1)
		CL_bk D~1 g0~bk sigma~1	hn	4	-122.95	253.91	258.35	31.12	0.00	3.32(1.1)
12T & 76R		CL_Mk D~1 g0~k sigma~1	hn	4	-125.19	258.38	262.82	35.59	0.00	3.47(1.2)
		CL_MB D~1 g0~B sigma~1	hn	4	-128.88	265.76	270.20	42.97	0.00	Err
		CL_Mb D~1 g0~b sigma~1	hn	4	-129.29	266.58	271.02	43.79	0.00	Err
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-128.27	270.54	289.20	47.75	0.00	Err
		CL_MT D~1 g0~T sigma~1	hn	4	-131.62	271.24	275.68	48.45	0.00	2.92(0.9)
		CL_Mt D~1 g0~t sigma~1	hn	6	-130.84	273.67	285.67	50.88	0.00	2.91(0.8)
	Model _Sex	CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-112.70	235.39	242.89	0.00	0.60	9.92(9.4)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-112.36	236.71	248.71	1.32	0.31	6.03(4.7)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-114.59	239.18	246.68	3.79	0.09	3.87(2.0)
	No_sex	CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-104.71	219.42	226.92	0.00	0.66	4(1.99)
		CL_M0 D~1 g0~1 sigma~1	hn	3	-107.67	221.33	223.73	1.91	0.25	2.5(0.85)
		CL_MK D~1 g0~K sigma~1	hn	4	-107.67	223.33	227.78	3.91	0.09	2.5(0.85)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-116.21	240.42	244.86	21.00	0.00	2.9(1.33)
		CL_bk D~1 g0~bk sigma~1	hn	4	-116.73	241.46	245.90	22.04	0.00	2.9(1.32)
0T & 100R		CL_Mk D~1 g0~k sigma~1	hn	4	-120.32	248.64	253.08	29.22	0.00	3.5(1.53)
		CL_MB D~1 g0~B sigma~1	hn	4	-128.66	265.32	269.77	45.91	0.00	4.7(3.9)
		CL_Mt D~1 g0~b sigma~1	hn	4	-129.22	266.45	270.89	47.03	0.00	4(3.10)
		CL_MT D~1 g0~T sigma~1	hn	4	-130.19	268.38	272.83	48.97	0.00	2.5(0.85)
		CL_Mb D~1 g0~t sigma~1	hn	6	-129.75	271.51	283.51	52.09	0.00	2.5(0.84)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-128.82	271.63	290.30	52.22	0.00	4.3(1.06)
	Model _sex	CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-112.26	234.52	242.02	0.00	0.45	26(29.0)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-112.39	234.78	242.28	0.26	0.40	15(140.7)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-112.37	236.74	248.74	2.21	0.15	3.8(9.33)

Table S4. Density estimates of common leopard from 100 camera traps. Parameters as for

Table S2

Camera Combination	**Model**	**model specification**	**df**	**np**	**logLik**	**AIC**	**AICc**	**dAIC**	**AICwt**	**Density**
	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-50.10	106.20	118.20	0.00	0.73	1.2(0.75)
		L_MK D~1 g0~K sigma~1	hn	4	-50.10	108.20	148.20	2.00	0.27	1.2(0.75)
		L_Mb D~1 g0~b sigma~1	hn	4	-58.00	123.99	163.99	17.79	0.00	0.8(0.46)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-58.11	124.23	164.23	18.03	0.00	1.3(0.95)
		L_MT D~1 g0~T sigma~1	hn	4	-58.22	124.44	164.44	18.24	0.00	1.2(0.79)
		L_bk D~1 g0~bk sigma~1	hn	4	-58.37	124.75	164.75	18.55	0.00	1.3(0.94)
50 T & 0 R		L_Mt D~1 g0~t sigma~1	hn	6	-56.73	125.46	NA	19.26	0.00	1.3(0.82)
		L_MB D~1 g0~B sigma~1	hn	4	-59.01	126.02	166.02	19.82	0.00	0.9(0.54)
		L_Mk D~1 g0~k sigma~1	hn	4	-59.02	126.04	166.04	19.84	0.00	1.3(0.92)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-56.68	127.37	NA	21.17	0.00	1.2(0.83)
		L_Mh2 D~1 g0~t sigma~1	hn	6	-59.98	131.95	NA	25.76	0.00	1.2(0.76)

	Model_sex	L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-52.10	114.20	NA	0.00	0.46	1.3(0.82)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-52.35	114.70	NA	0.50	0.36	1.2(0.75)
		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-51.99	115.98	NA	1.79	0.19	1.3(0.78)
33T & 34R	No_sex	L_Mk D~1 g0~k sigma~1	hn	4	-58.17	124.35	144.35	0.00	0.54	4.49(5.6)
		L_M0 D~1 g0~1 sigma~1	hn	3	-59.82	125.65	133.65	1.30	0.28	1.57(0.7)
		L_MK D~1 g0~K sigma~1	hn	4	-59.82	127.65	147.65	3.30	0.10	1.57(0.7)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-59.20	128.41	188.41	4.06	0.07	6.51(6.5)
		L_bk D~1 g0~bk sigma~1	hn	4	-67.35	142.71	162.71	18.36	0.00	1.17(1.0)
		L_MB D~1 g0~B sigma~1	hn	4	-69.06	146.12	166.12	21.77	0.00	1.25(0.5)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-69.61	147.23	167.23	22.88	0.00	1.63(0.8)
		L_Mb D~1 g0~b sigma~1	hn	4	-70.10	148.19	168.19	23.84	0.00	1.23(0.6)
		L_MT D~1 g0~T sigma~1	hn	4	-70.41	148.83	168.83	24.48	0.00	1.61(0.8)
		L_Mt D~1 g0~t sigma~1	hn	6	-69.84	151.68	NA	27.33	0.00	1.62(0.8)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-69.26	152.53	NA	28.18	0.00	1.10(0.6)
	Model_Sex	CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-60.22	130.4	190.4	0.00	0.55	15.2(17)
		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-59.54	131.0	NA	0.65	0.40	6.1(5.8)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-62.53	135.0	195.0	4.61	0.05	2.0(1.4)
25T & 50R	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-76.11	158.22	170.22	0.00	0.67	0.85(0.4)
		L_MK D~1 g0~K sigma~1	hn	4	-76.11	160.22	200.22	2.00	0.24	0.85(0.4)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-76.11	162.22	NA	4.00	0.09	0.85(0.4)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-83.38	174.76	214.76	16.55	0.00	0.93(0.5)
		L_Mk D~1 g0~k sigma~1	hn	4	-87.46	182.93	222.93	24.71	0.00	0.99(0.5)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-88.76	185.51	225.51	27.30	0.00	0.87(0.4)
		L_MT D~1 g0~T sigma~1	hn	4	-89.68	187.36	227.36	29.15	0.00	0.88(0.4)
		L_Mb D~1 g0~b sigma~1	hn	4	-90.76	189.52	229.52	31.30	0.00	0.65(0.3)
		L_Mt D~1 g0~t sigma~1	hn	6	-89.26	190.52	NA	32.30	0.00	0.88(0.4)
		L_MB D~1 g0~B sigma~1	hn	4	-91.64	191.28	231.28	33.07	0.00	0.74(0.3)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-89.21	192.43	NA	34.21	0.00	0.98(0.6)
	Model_Sex	L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-79.27	168.55	NA	0.00	0.36	0.85(0.4)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-79.31	168.63	NA	0.08	0.34	0.87(0.4)
		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-78.44	168.87	NA	0.33	0.30	0.82(0.4)
12T & 76R	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-75.63	157.26	160.69	0.00	0.67	2.40(1.0)
		L_MK D~1 g0~K sigma~1	hn	4	-75.63	159.26	165.93	2.00	0.24	2.40(1.0)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-75.63	161.26	173.26	4.00	0.09	2.30(1.0)
		L_Mt D~1 g0~t sigma~1	hn	6	-85.38	182.75	203.75	25.49	0.00	2.69(1.2)
		L_MT D~1 g0~T sigma~1	hn	4	-87.52	183.05	189.72	25.79	0.00	2.64(1.2)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-88.29	184.58	191.25	27.32	0.00	2.79(1.5)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-85.32	184.63	221.97	27.37	0.00	2.95(1.6)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-88.87	185.75	192.41	28.48	0.00	2.76(1.5)
		L_Mb D~1 g0~b sigma~1	hn	4	-89.98	187.96	194.63	30.70	0.00	1.56(0.6)
		L_Mk D~1 g0~k sigma~1	hn	4	-90.49	188.97	195.64	31.71	0.00	2.84(1.4)
		L_MB D~1 g0~B sigma~1	hn	4	-91.57	191.15	197.81	33.88	0.00	1.92(0.8)
	Model_Sex	L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-77.34	164.69	176.69	0.00	0.64	5.68(4.0)
		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-77.03	166.07	187.07	1.38	0.32	4.59(2.9)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-80.04	170.08	182.08	5.39	0.04	3.04(1.8)
	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-72.56	151.13	155.13	0.00	0.67	2.11(0.9)

		L_MK D~1 g0~K sigma~1	hn	4	-72.56	153.13	161.13	2.00	0.24	2.11(0.9)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-72.56	155.13	170.13	4.00	0.09	2.11(0.9)
		L_MT D~1 g0~T sigma~1	hn	4	-83.49	174.98	182.98	23.85	0.00	2.30(1.0)
		L_Mt D~1 g0~t sigma~1	hn	6	-81.83	175.66	203.66	24.53	0.00	2.35(1.1)
0T & 100R		L_MBk D~1 g0~Bk sigma~1	hn	4	-84.37	176.73	184.73	25.61	0.00	2.43(1.3)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-81.78	177.57	233.57	26.44	0.00	2.53(1.4)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-84.97	177.94	185.94	26.81	0.00	2.41(1.3)
		L_Mb D~1 g0~b sigma~1	hn	4	-86.05	180.09	188.09	28.96	0.00	1.38(0.5)
		L_Mk D~1 g0~k sigma~1	hn	4	-86.58	181.16	189.16	30.03	0.00	2.48(1.3)
		L_MB D~1 g0~B sigma~1	hn	4	-87.68	183.36	191.36	32.23	0.00	1.7(0.7)
	Model _sex	L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-75.98	161.97	176.97	0.00	0.45	2.43(1.3)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-76.20	162.39	177.39	0.43	0.36	2.36(1.1)
		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-75.86	163.73	191.73	1.76	0.19	2.55(1.3)

Table S5. Density estimates of leopard from cat 100 camera traps. Parameters as for Table S2

Camera Combination	Model	model specification	df	np	logLik	AIC	AICc	dAIC	AICwt	Density
	No_sex	LC_M0 D~1 g0~1 sigma~1	hn	3	-176.41	358.83	359.53	0.00	0.67	16.1(3.3)
		LC_MK D~1 g0~K sigma~1	hn	4	-176.41	360.83	362.04	2.00	0.24	16.1(3.5)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-176.41	362.83	364.70	4.00	0.09	16.1(3.5)
		LC_Mbk D~1 g0~bk sigma~1	hn	4	-189.34	386.69	387.90	27.86	0.00	61.9(47)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-192.34	392.69	393.90	33.86	0.00	44.23(25.55)
		LC_MT D~1 g0~T sigma~1	hn	4	-210.43	428.87	430.08	70.04	0.00	14.35(2.89)
50 T & 0 R		LC_MB D~1 g0~B sigma~1	hn	4	-211.61	431.22	432.43	72.39	0.00	16.42(5.27)
		LC_Mb D~1 g0~b sigma~1	hn	4	-211.74	431.48	432.70	72.66	0.00	15.59(5.03)
		LC_Mt D~1 g0~t sigma~1	hn	6	-210.25	432.49	435.20	73.67	0.00	14.33(2.88)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-209.28	432.56	436.30	73.74	0.00	20.12(8.67)
	Model _sex	L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-193.37	396.74	398.62	0.00	0.55	17.4(4.1)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-194.19	398.38	400.26	1.64	0.24	16.5(3.7)
		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-193.36	398.73	401.44	1.98	0.20	17.2(4.1)
	No_sex	LC_M0 D~1 g0~1 sigma~1	hn	3	-239.48	484.96	485.43	0.00	0.65	22.7(3.8)
		LC_MK D~1 g0~K sigma~1	hn	4	-239.48	486.96	487.76	2.00	0.24	22.7(3.8)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-239.27	488.54	489.76	3.58	0.11	23.9(4.6)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-279.14	566.28	567.08	81.32	0.00	40.2(12)
		LC_Mbk D~1 g0~bk sigma~1	hn	4	-279.78	567.57	568.37	82.61	0.00	43.8(15)
		LC_MT D~1 g0~T sigma~1	hn	4	-287.65	583.29	584.09	98.33	0.00	20.7(32)
		LC_Mt D~1 g0~t sigma~1	hn	6	-286.84	585.68	587.43	100.72	0.00	20.7(3.2)
33T & 34R		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-286.37	586.74	589.12	101.78	0.00	23.1(4.7)
		LC_Mb D~1 g0~b sigma~1	hn	4	-295.25	598.50	599.30	113.54	0.00	16.9(2.7)
		LC_MB D~1 g0~B sigma~1	hn	4	-297.12	602.24	603.04	117.28	0.00	19.4(3.5)
	Model _Sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-118.01	248.03	269.03	0.00	0.61	23.0(4.5)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	6	-120.10	252.20	273.20	4.17	0.08	23.1(4.0)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-121.40	252.80	264.80	4.77	0.06	22.7(3.9)
	No_sex	LC_M0 D~1 g0~1 sigma~1	hn	3	-219.19	444.39	445.09	0.00	0.67	10.1(2.0)

		LC_MK D~1 g0~K sigma~1	hn	4	-219.19	446.39	447.60	2.00	0.24	10.1(2.4)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-219.19	448.39	450.26	4.00	0.09	10.1(2.0)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-238.69	485.39	486.60	41.00	0.00	14.5(4.4)
		LC_Mbk D~1 g0~bk sigma~1	hn	4	-241.33	490.65	491.86	46.27	0.00	14.4(4.3)
25T & 50R		LC_Mk D~1 g0~k sigma~1	hn	4	-244.33	496.67	497.88	52.28	0.00	27.8(14)
		LC_MT D~1 g0~T sigma~1	hn	4	-263.07	534.14	535.35	89.75	0.00	9.9(1.95)
		LC_Mt D~1 g0~t sigma~1	hn	6	-263.00	538.00	540.71	93.62	0.00	9.9(1.96)
		LC_Mb D~1 g0~b sigma~1	hn	4	-265.97	539.94	541.15	95.55	0.00	8.30(1)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-262.97	539.94	543.67	95.55	0.00	10.3(2.4)
		LC_MB D~1 g0~B sigma~1	hn	4	-266.91	541.81	543.02	97.43	0.00	19.6(2.1)
	Model _Sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-226.78	465.56	468.27	0.00	1.00	12.0(2.6)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-233.54	477.07	478.95	11.51	0.00	14.5(4.0)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-240.91	491.81	493.69	26.25	0.00	10.1(2.0)
	No_sex	LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-300.75	611.50	612.84	0.00	0.83	15.27(2.966)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-304.64	615.28	615.79	3.78	0.13	12.91(2.13)
		LC_MK D~1 g0~K sigma~1	hn	4	-304.64	617.28	618.15	5.78	0.05	12.91(2.13)
		LC_Mbk D~1 g0~bk sigma~1	hn	4	-308.02	624.05	624.92	12.55	0.00	21.22(6.09)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-309.13	626.25	627.12	14.75	0.00	29.36(5.57)
12T & 76R		LC_Mk D~1 g0~k sigma~1	hn	4	-339.23	686.45	687.32	74.95	0.00	30.88(10.72)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-358.08	730.17	732.77	118.66	0.00	17.82(4.58)
		LC_MT D~1 g0~T sigma~1	hn	4	-361.32	730.64	731.51	119.14	0.00	13.09(2.14)
		LC_Mt D~1 g0~t sigma~1	hn	6	-360.47	732.93	734.84	121.43	0.00	13.11(2.14)
		LC_Mb D~1 g0~b sigma~1	hn	4	-369.97	747.95	748.82	136.44	0.00	11.56(2.09)
		LC_MB D~1 g0~B sigma~1	hn	4	-370.37	748.75	749.62	137.24	0.00	13.09(2.61)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-330.38	670.76	672.09	0.00	0.50	13.8(2.3)
	Model _Sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-329.43	670.85	672.76	0.10	0.48	13.4(2.2)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-333.47	676.95	678.28	6.19	0.02	13.0(2.1)
	No_sex	LC_Mbk D~1 g0~bk sigma~1	hn	4	-268.95	545.90	546.88	0.00	0.90	18.7(6.4)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-271.10	550.19	551.17	4.29	0.10	17.6(5.6)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-274.73	559.47	560.97	13.57	0.00	13.0(2.7)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-278.36	562.72	563.29	16.82	0.00	10.9(1.9)
		LC_MK D~1 g0~K sigma~1	hn	4	-278.36	564.72	565.70	18.82	0.00	10.9(1.9)
0T & 100R		LC_Mk D~1 g0~k sigma~1	hn	4	-295.96	599.92	600.90	54.02	0.00	47.1(27)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-323.16	660.33	663.28	114.43	0.00	17.4(5.5)
		LC_MT D~1 g0~T sigma~1	hn	4	-327.83	663.65	664.63	117.75	0.00	11.0(1.9)
		LC_Mt D~1 g0~t sigma~1	hn	6	-327.05	666.10	668.26	120.20	0.00	11.0(1.9)
		LC_MB D~1 g0~B sigma~1	hn	4	-334.44	676.87	677.85	130.97	0.00	11.8(2.7)
		LC_Mb D~1 g0~b sigma~1	hn	4	-334.71	677.42	678.39	131.52	0.00	10.8(2.3)
	Model _sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-291.48	594.96	597.11	0.00	0.98	11.7(2.1)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-296.41	602.81	604.31	7.85	0.02	13.(2.7)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-303.16	616.33	617.83	21.37	0.00	11.0(1.9)

Table S6. Density estimates of marbled cat from 100 camera traps. Parameters as for Table

S2

Camera Combination	Model	model specification	df	np	logLik	AIC	AICc	dAIC	AICwt	Density
50 T & 0 R	No_sex	MC_M0 D~1 g0~1 sigma~1	hn	3	-232.45	470.90	471.83	0.00	0.46	6.01(1.1)
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-230.69	471.38	473.88	0.48	0.37	6.20(1.2)
		MC_MK D~1 g0~K sigma~1	hn	4	-232.45	472.90	474.50	2.00	0.17	6.01(1.1)
		MC_Mk D~1 g0~k sigma~1	hn	4	-246.45	500.89	502.49	29.99	0.00	9.80(2.8)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-249.07	506.14	507.74	35.24	0.00	6.77(1.5)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-251.23	510.47	512.07	39.57	0.00	6.76(1.5)
		MC_MT D~1 g0~T sigma~1	hn	4	-276.72	561.43	563.03	90.53	0.00	5.88(1.1)
		MC_Mb D~1 g0~b sigma~1	hn	4	-277.40	562.81	564.41	91.90	0.00	5.74(1.1)
		MC_MB D~1 g0~B sigma~1	hn	4	-277.66	563.31	564.91	92.41	0.00	6.01(1.2)
		MC_Mt D~1 g0~t sigma~1	hn	6	-276.24	564.49	568.14	93.59	0.00	5.92(1.1)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-276.19	566.39	571.48	95.48	0.00	6.04(1.2)
	Model_sex	MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-247.30	504.60	507.10	0.00	0.50	5.98(1.1)
		MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-247.76	505.51	508.01	0.91	0.32	5.98(1.1)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-247.30	506.60	510.25	2.00	0.18	5.98(1.1)
33T & 34R	No_sex	MC_Mk D~1 g0~k sigma~1	hn	4	-208.40	424.80	426.46	0.00	1.00	61.3(77)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-225.11	458.23	459.89	33.43	0.00	6.9(2.2)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-226.32	460.64	462.31	35.85	0.00	6.9(2.2)
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-225.54	461.09	463.70	36.29	0.00	7.0(1.8)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-230.73	467.45	468.41	42.65	0.00	5.7(1.2)
		MC_MK D~1 g0~K sigma~1	hn	4	-230.73	469.45	471.12	44.65	0.00	5.7(1.2)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-264.19	542.38	547.71	117.58	0.00	7.3(2.2)
		MC_Mt D~1 g0~t sigma~1	hn	6	-265.42	542.85	546.67	118.05	0.00	5.7(1.2)
		MC_MB D~1 g0~B sigma~1	hn	4	-268.11	544.23	545.89	119.43	0.00	6.2(1.6)
		MC_MT D~1 g0~T sigma~1	hn	4	-268.19	544.38	546.04	119.58	0.00	5.7(1.2)
		MC_Mb D~1 g0~b sigma~1	hn	4	-268.32	544.64	546.31	119.84	0.00	6.0(1.5)
	Model_Sex	MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-248.11	506.22	508.83	0.00	0.45	6.18(1.4)
		MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-248.31	506.62	509.23	0.40	0.37	6.12(1.4)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-248.05	508.10	511.92	1.88	0.18	6.28(1.5)
25T & 50R	No_sex	MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-191.70	393.41	395.81	0.00	0.50	8.86(1.9)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-194.03	394.06	394.95	0.65	0.36	8.21(1.6)
		MC_MK D~1 g0~K sigma~1	hn	4	-194.03	396.06	397.60	2.65	0.13	8.21(1.6)
		MC_Mk D~1 g0~k sigma~1	hn	4	-203.08	414.16	415.70	20.75	0.00	27.66(15)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-219.91	447.83	449.37	54.42	0.00	10.5(2.6)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-221.01	450.03	451.56	56.62	0.00	10.4(2.6)
		MC_MB D~1 g0~B sigma~1	hn	4	-235.06	478.13	479.67	84.72	0.00	8.8(2.2)
		MC_Mb D~1 g0~b sigma~1	hn	4	-235.37	478.75	480.29	85.34	0.00	8.45(2.0)
		MC_MT D~1 g0~T sigma~1	hn	4	-235.49	478.98	480.52	85.57	0.00	7.95(1.5)
		MC_Mt D~1 g0~t sigma~1	hn	6	-234.40	480.80	484.30	87.40	0.00	7.97(1.5)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-233.83	481.66	486.53	88.26	0.00	9.20(2.4)
	Model_Sex	MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-204.36	420.71	424.21	0.00	0.67	8.59(1.7)
		MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-206.05	422.10	424.50	1.39	0.33	9.31(2.0)
		MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-210.91	431.82	434.22	11.10	0.00	8.45(1.7)
	No_sex	MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-299.48	608.95	610.77	0.00	0.96	7.97(1.6)

12T & 76R		MC_M0 D~1 g0~1 sigma~1	hn	3	-304.99	615.99	616.67	7.03	0.03	6.64(1.1)
		MC_MK D~1 g0~K sigma~1	hn	4	-304.99	617.99	619.16	9.03	0.01	6.64(1.1)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-329.04	666.09	667.27	57.14	0.00	7.31(1.5)
		MC_Mk D~1 g0~k sigma~1	hn	4	-329.06	666.13	667.30	57.17	0.00	11.8(2.8)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-329.38	666.76	667.94	57.81	0.00	7.28(1.5)
		MC_MT D~1 g0~T sigma~1	hn	4	-368.41	744.82	745.99	135.86	0.00	6.60(1.1)
		MC_Mt D~1 g0~t sigma~1	hn	6	-366.53	745.06	747.68	136.11	0.00	6.61(1.1)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-366.38	746.76	750.37	137.81	0.00	6.84(1.3)
		MC_Mb D~1 g0~b sigma~1	hn	4	-369.49	746.98	748.16	138.03	0.00	6.27(1.1)
		MC_MB D~1 g0~B sigma~1	hn	4	-370.02	748.04	749.22	139.09	0.00	6.52(1.2)
	Model_Sex	MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-326.57	663.14	664.96	0.00	0.47	6.82(1.2)
		MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-326.87	663.74	665.56	0.60	0.35	6.77(1.2)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-326.57	665.14	667.76	1.99	0.18	6.83(1.2)
0T & 100R	No_sex	MC_Mk D~1 g0~k sigma~1	hn	4	-173.48	354.96	356.96	0.00	0.99	47.0(59)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-179.06	364.11	365.25	9.15	0.01	17.6(5.6)
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-177.55	365.10	368.26	10.14	0.00	13.0(2.7)
		MC_MK D~1 g0~K sigma~1	hn	4	-179.06	366.11	368.11	11.15	0.00	10.9(1.9)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-189.95	387.90	389.90	32.93	0.00	10.9(1.9)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-190.44	388.88	390.88	33.91	0.00	47.1(27)
		MC_MB D~1 g0~B sigma~1	hn	4	-210.48	428.95	430.95	73.99	0.00	17.4(5.5)
		MC_Mb D~1 g0~b sigma~1	hn	4	-210.53	429.05	431.05	74.09	0.00	11.0(1.9)
		MC_MT D~1 g0~T sigma~1	hn	4	-210.64	429.28	431.28	74.32	0.00	11.0(1.9)
		MC_Mt D~1 g0~t sigma~1	hn	6	-210.18	432.35	437.02	77.39	0.00	11.8(2.7)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-209.98	433.96	440.55	78.99	0.00	10.8(2.3)
	Model_sex	MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-192.49	394.98	398.14	0.00	0.49	6.65(1.86)
		MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-192.91	395.82	398.98	0.84	0.32	6.21(1.71)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-192.43	396.87	401.53	1.89	0.19	6.48(1.80)

TableS7. Density estimates of clouded leopard from different combination of trail (T) and random (R) cameras, given a total availability of 100 stations. The T & R combination identifies numbers of trail stations with paired cameras and random stations with single cameras. Parameters as for Table S2.

Camera Combination	**Model**	**model specification**	**df**	**np**	**logLik**	**AIC**	**AICc**	**dAIC**	**AICwt**	**Density**
75 T & 25 R	No_sex	CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-157.42	324.83	329.12	0.00	0.82	4.56(2.3)
		CL_M0 D~1 g0~1 sigma~1	hn	3	-161.23	328.46	329.96	3.63	0.13	2.76(0.7)
		CL_MK D~1 g0~K sigma~1	hn	4	-161.23	330.46	333.13	5.63	0.05	2.76(0.7)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-188.25	384.50	387.16	59.67	0.00	2.90(0.8)
		CL_Mbk D~1 g0~bk sigma~1	hn	4	-189.27	386.53	389.20	61.70	0.00	2.89(0.8)
		CL_MT D~1 g0~T sigma~1	hn	4	-189.90	387.80	390.46	62.97	0.00	2.77(0.7)
		CL_Mt D~1 g0~t sigma~1	hn	6	-188.30	388.60	395.07	63.77	0.00	2.76(0.7)
		CL_Mk D~1 g0~k sigma~1	hn	4	-190.54	389.09	391.75	64.26	0.00	3.11(0.9)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-188.51	391.03	400.36	66.20	0.00	2.70(0.9)
		CL_Mb D~1 g0~b sigma~1	hn	4	-192.95	393.90	396.57	69.07	0.00	2.06(0.6)
		CL_MB D~1 g0~B sigma~1	hn	4	-194.92	397.84	400.51	73.01	0.00	2.30(0.6)

	Model_sex	CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-163.57	337.14	341.42	0.00	0.67	9.61(1.2)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-163.30	338.60	345.06	1.46	0.32	7.42(4.5)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-167.46	344.91	349.20	7.78	0.01	4.30(2.0)
25T & 75R	No_sex	CL_M0 D~1 g0~1 sigma~1	hn	3	-120.24	246.48	248.48	0.00	0.59	2.83(0.9)
		CL_MK D~1 g0~K sigma~1	hn	4	-120.24	248.48	252.12	2.00	0.22	2.83(0.9)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-119.40	248.80	254.80	2.32	0.19	3.61(1.6)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-134.67	277.34	280.97	30.85	0.00	3.13(1.2)
		CL_bk D~1 g0~bk sigma~1	hn	4	-135.40	278.79	282.43	32.31	0.00	3.15(1.2)
		CL_Mk D~1 g0~k sigma~1	hn	4	-135.42	278.83	282.47	32.35	0.00	3.87(1.5)
		CL_MB D~1 g0~B sigma~1	hn	4	-144.00	295.99	299.63	49.51	0.00	3.35(1.6)
		CL_Mb D~1 g0~b sigma~1	hn	4	-144.07	296.14	299.78	49.66	0.00	3.37(1.9)
		CL_MT D~1 g0~T sigma~1	hn	4	-144.20	296.41	300.04	49.93	0.00	2.82(0.9)
		CL_Mt D~1 g0~t sigma~1	hn	6	-143.41	298.82	308.15	52.34	0.00	2.82(0.9)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-143.22	300.43	314.43	53.95	0.00	3.71(2.6)
	Model_Sex	CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-125.65	263.31	272.64	0.00	0.47	2.50(1.6)
		CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-126.80	263.60	269.60	0.30	0.41	13.27(35)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-127.98	265.96	271.96	2.65	0.13	3.88(2.1)
50T & 50R	No_sex	CL_M0 D~1 g0~1 sigma~1	hn	3	-157.59	321.17	323.02	0.00	0.64	2.57(0.7)
		CL_MK D~1 g0~K sigma~1	hn	4	-157.59	323.17	326.51	2.00	0.24	2.57(0.7)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-157.29	324.57	330.03	3.40	0.12	3.04(1.3)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-174.16	356.32	359.65	35.14	0.00	2.77(0.8)
		CL_bk D~1 g0~bk sigma~1	hn	4	-175.69	359.38	362.71	38.21	0.00	2.76(0.8)
		CL_Mk D~1 g0~k sigma~1	hn	4	-179.45	366.90	370.23	45.73	0.00	2.94(0.8)
		CL_MT D~1 g0~T sigma~1	hn	4	-186.21	380.43	383.76	59.25	0.00	2.57(0.6)
		CL_Mt D~1 g0~t sigma~1	hn	6	-185.99	383.97	392.37	62.80	0.00	2.57(0.6)
		CL_Mb D~1 g0~b sigma~1	hn	4	-188.52	385.05	388.38	63.88	0.00	2.23(0.6)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-185.85	385.70	398.15	64.53	0.00	2.79(0.9)
		CL_MB D~1 g0~B sigma~1	hn	4	-189.07	386.13	389.47	64.96	0.00	2.42(0.7)
	Model_Sex	CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-158.75	329.51	337.91	0.00	0.82	3.30(0.9)
		CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-161.26	332.52	337.97	3.01	0.18	4.04(1.4)
		CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-165.19	340.38	345.83	10.87	0.00	2.77(0.8)
100T & 0R	No_sex	CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-204.06	418.11	422.11	0.00	0.91	5.7(1.47)
		CL_M0 D~1 g0~1 sigma~1	hn	3	-208.69	423.39	424.80	5.28	0.07	2.5(0.66)
		CL_MK D~1 g0~K sigma~1	hn	4	-208.69	425.39	427.89	7.28	0.02	2.5(0.66)
		CL_MBk D~1 g0~Bk sigma~1	hn	4	-235.55	479.10	481.60	60.99	0.00	2.6(0.74)
		CL_bk D~1 g0~bk sigma~1	hn	4	-237.13	482.25	484.75	64.14	0.00	2.6(0.74)
		CL_MT D~1 g0~T sigma~1	hn	4	-241.42	490.85	493.35	72.74	0.00	2.5(0.67)
		CL_Mt D~1 g0~t sigma~1	hn	6	-239.45	490.90	496.90	72.79	0.00	2.5(0.67)
		CL_Mbt D~1 g0~b + t sigma~1	hn	7	-239.42	492.83	501.45	74.72	0.00	2.6(0.77)
		CL_Mk D~1 g0~k sigma~1	hn	4	-244.05	496.11	498.61	78.00	0.00	2.7(0.75)
		CL_Mb D~1 g0~b sigma~1	hn	4	-246.54	501.08	503.58	82.97	0.00	1.9(0.55)
		CL_MB D~1 g0~B sigma~1	hn	4	-249.10	506.20	508.70	88.09	0.00	2.2(0.61)
	Model_Sex	CL_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-216.61	443.21	447.21	0.00	0.64	3.1(0.97)
		CL_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-216.60	445.21	451.21	1.99	0.24	3.2(1.01)
		CL_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-218.27	446.55	450.55	3.34	0.12	2.9(0.75)

TableS8. Density estimates of common leopard from different combination of trail (T) and random (R) cameras, given a total availability of 100 stations. The T & R combination identifies numbers of trail stations with paired cameras and random stations with single cameras. Parameters as for Table S2.

Camera Combination	Model	model specification	df	np	logLik	AIC	AICc	dAIC	AICwt	Density
75 T & 25 R		L_M0 D~1 g0~1 sigma~1	hn	3	-139.25	284.49	287.16	0.00	0.67	1.6(0.5)
		L_MK D~1 g0~K sigma~1	hn	4	-139.25	286.49	291.49	2.00	0.24	1.6(0.5)
		CL_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-139.25	288.49	297.06	4.00	0.09	1.61(0.5)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-158.11	324.21	329.21	39.72	0.00	1.67(0.5)
	No_sex	L_Mk D~1 g0~k sigma~1	hn	4	-159.45	326.91	331.91	42.41	0.00	1.9(0.63)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-162.06	332.11	337.11	47.62	0.00	1.64(0.5)
		L_Mb D~1 g0~b sigma~1	hn	4	-167.36	342.72	347.72	58.23	0.00	1.45(0.4)
		L_MB D~1 g0~B sigma~1	hn	4	-168.09	344.18	349.18	59.69	0.00	1.49(0.4)
		L_MT D~1 g0~T sigma~1	hn	4	-168.29	344.58	349.58	60.09	0.00	1.63(0.5)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-166.87	347.75	370.15	63.25	0.00	1.39(0.4)
		L_Mt D~1 g0~t sigma~1	hn	6	-167.99	347.97	361.97	63.48	0.00	1.63(0.5)
	Model_sex	L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-144.73	301.47	315.47	0.00	0.54	1.6(0.52)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-146.29	302.57	311.14	1.11	0.31	1.62(0.5)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-147.06	304.13	312.70	2.66	0.14	1.59(0.5)
25T & 75R	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-76.05	158.11	162.11	0.00	0.67	1.41(0.5)
		L_MK D~1 g0~K sigma~1	hn	4	-76.05	160.11	168.11	2.00	0.24	1.41(0.5)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-76.05	162.11	177.11	4.00	0.09	1.41(0.59
		L_Mk D~1 g0~k sigma~1	hn	4	-83.81	175.62	183.62	17.51	0.00	2.55(1.8)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-87.00	181.99	189.99	23.88	0.00	1.56(0.9)
		L_MT D~1 g0~T sigma~1	hn	4	-87.52	183.04	191.04	24.93	0.00	1.54(0.6)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-84.83	183.67	239.67	25.56	0.00	3.21(4.9)
		L_Mt D~1 g0~t sigma~1	hn	6	-87.25	186.51	214.51	28.40	0.00	1.54(0.7)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-89.30	186.60	194.60	28.49	0.00	1.50(0.7)
		L_Mb D~1 g0~b sigma~1	hn	4	-91.10	190.20	198.20	32.09	0.00	1.01(0.4)
		L_MB D~1 g0~B sigma~1	hn	4	-92.50	193.00	201.00	34.89	0.00	1.22(0.6)
	Model_Sex	L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-77.12	166.25	194.25	0.00	0.67	2.36(1.1)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-78.90	167.80	182.80	1.56	0.31	3.2(2.3)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-81.77	173.53	188.53	7.29	0.02	1.45(0.6)
50T & 50R	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-103.71	213.43	215.61	0.00	0.67	2.9(0.96)
		L_MK D~1 g0~K sigma~1	hn	4	-103.71	215.43	219.43	2.00	0.25	2.9(0.96)
		L_Mh2r D~1 g0~h2 sigma~1 pmix~h2	hn	5	-103.83	217.66	224.33	4.24	0.08	3.54(1.2)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-124.08	256.17	260.17	42.74	0.00	3.29(1.2)
		L_Mk D~1 g0~k sigma~1	hn	4	-124.50	257.00	261.00	43.57	0.00	3.95(1.6)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-125.63	259.27	263.27	45.84	0.00	3.15(1.1)
		L_MT D~1 g0~T sigma~1	hn	4	-126.20	260.41	264.41	46.98	0.00	3.06(1.0)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-124.10	262.20	278.20	48.77	0.00	7.8(7.8)
		L_Mt D~1 g0~t sigma~1	hn	6	-125.86	263.71	274.21	50.29	0.00	3.04(1.0)
		L_Mb D~1 g0~b sigma~1	hn	4	-128.81	265.63	269.63	52.20	0.00	2.25(0.7)
		L_MB D~1 g0~B sigma~1	hn	4	-129.39	266.79	270.79	53.36	0.00	3.23(1.5)
	Model_Sex	L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-111.72	233.44	240.11	0.00	0.44	2.93(0.9)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-111.86	233.73	240.39	0.29	0.39	2.90(0.9)

		L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-111.68	235.35	245.85	1.91	0.17	2.90(0.9)
100T & 0R	No_sex	L_M0 D~1 g0~1 sigma~1	hn	3	-123.54	253.09	255.76	0.00	0.67	1.63(0.5)
		L_MK D~1 g0~K sigma~1	hn	4	-123.54	255.09	260.09	2.00	0.24	1.63(0.5)
		L_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-123.54	257.09	265.66	4.00	0.09	1.63(0.5)
		L_Mbk D~1 g0~bk sigma~1	hn	4	-139.73	287.45	292.45	34.36	0.00	1.73(0.6)
		L_Mk D~1 g0~k sigma~1	hn	4	-139.89	287.79	292.79	34.70	0.00	2.12(0.7)
		L_MBk D~1 g0~Bk sigma~1	hn	4	-143.91	295.81	300.81	42.72	0.00	1.68(0.5)
		L_Mb D~1 g0~b sigma~1	hn	4	-148.07	304.14	309.14	51.05	0.00	1.41(0.4)
		L_MT D~1 g0~T sigma~1	hn	4	-148.71	305.43	310.43	52.34	0.00	1.67(0.5)
		L_MB D~1 g0~B sigma~1	hn	4	-148.76	305.52	310.52	52.43	0.00	1.45(0.4)
		L_Mt D~1 g0~t sigma~1	hn	6	-147.56	307.12	321.12	54.03	0.00	1.68(0.5)
		L_Mbt D~1 g0~b + t sigma~1	hn	7	-146.60	307.19	329.59	54.10	0.00	1.36(0.4)
	Model _Sex	L_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-129.98	271.96	285.96	0.00	0.39	1.64(0.5)
		L_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-131.21	272.43	281.00	0.46	0.31	1.64(0.5)
		L_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-131.23	272.47	281.04	0.51	0.30	1.61(0.5)

Table S9. Density estimates of leopard cat from different combination of trail (T) and random (R) cameras, given a total availability of 100 stations. The T & R combination identifies numbers of trail stations with paired cameras and random stations with single cameras. Parameters as for Table S2.

Camera Combination	**Model**	**model specification**	**df**	**np**	**logLik**	**AIC**	**AICc**	**dAIC**	**AICwt**	**Density**
75 T & 25 R	No_sex	LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-353.20	716.40	717.31	0.00	0.96	22.2(3.1)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-358.74	723.48	723.84	7.08	0.03	20.8(2.7)
		LC_MK D~1 g0~K sigma~1	hn	4	-358.74	725.48	726.08	9.08	0.01	20.8(2.7)
		LC_Mk D~1 g0~k sigma~1	hn	4	-405.27	818.55	819.14	102.15	0.00	59.6(2.1)
		LC_Mbk D~1 g0~bk sigma~1	hn	4	-405.38	818.75	819.35	102.35	0.00	30.6(5.8)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-405.86	819.71	820.31	103.31	0.00	29.3(5.3)
		LC_MT D~1 g0~T sigma~1	hn	4	-435.69	879.38	879.97	162.98	0.00	20.3(2.6)
		LC_Mt D~1 g0~t sigma~1	hn	6	-434.95	881.89	883.18	165.49	0.00	20.3(2.6)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-434.38	882.77	884.52	166.37	0.00	22.4(3.8)
		LC_Mb D~1 g0~b sigma~1	hn	4	-443.23	894.46	895.05	178.06	0.00	17.4(2.2)
		LC_MB D~1 g0~B sigma~1	hn	4	-445.41	898.82	899.42	182.42	0.00	18.(2.64)
	Model _sex	LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-393.74	797.48	798.39	0.00	0.63	21.8(3.0)
		LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-393.62	799.24	800.53	1.76	0.26	21.6(3.0)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-395.55	801.11	802.02	3.62	0.10	21.2(2.8)
25T & 75R	No_sex	LC_Mbk D~1 g0~bk sigma~1	hn	4	-310.01	628.01	628.90	0.00	1.00	14.0(4.8)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-315.31	640.62	641.99	12.61	0.00	12.5(2.5)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-316.98	641.96	642.85	13.95	0.00	13.5(4.1)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-318.15	642.31	642.83	14.30	0.00	10.6(1.9)
		LC_MK D~1 g0~K sigma~1	hn	4	-318.15	644.31	645.20	16.30	0.00	10.6(1.)
		LC_Mk D~1 g0~k sigma~1	hn	4	-346.83	701.66	702.55	73.65	0.00	29.9(11)
		LC_MT D~1 g0~T sigma~1	hn	4	-377.17	762.34	763.23	134.32	0.00	10.7(1.9)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-375.03	764.06	766.72	136.05	0.00	15.5(4.9)
		LC_Mt D~1 g0~t sigma~1	hn	6	-377.11	766.23	768.18	138.22	0.00	10.7(1.9)
		LC_MB D~1 g0~B sigma~1	hn	4	-380.02	768.04	768.93	140.02	0.00	13.2(3.6)
		LC_Mb D~1 g0~b sigma~1	hn	4	-381.00	770.00	770.89	141.99	0.00	10.7(2.5)

		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-345.50	701.00	702.37	0.00	0.52	11.9(2.3)
	Model _Sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-344.89	701.77	703.73	0.77	0.36	11.1(2.1)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-346.94	703.89	705.25	2.89	0.12	10.8(2.0)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-648.57	1307.1	1307.7	0.00	1.00	23.6(2.6)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-663.45	1332.8	1333.1	25.75	0.00	21.8(2.3)
		LC_MK D~1 g0~K sigma~1	hn	4	-663.45	1334.8	1335.3	27.75	0.00	21.8(2.3)
	No_sex	LC_Mbk D~1 g0~bk sigma~1	hn	4	-705.22	1418.4	1418.8	111.31	0.00	27.2(3.6)
		LC_MBk D~1 g0~Bk sigma~1	hn	4	-706.57	1421.1	1421.5	113.99	0.00	26.7(3.4)
50T & 50R		LC_Mk D~1 g0~k sigma~1	hn	4	-797.58	1603.1	1603.5	296.02	0.00	28.9(3.4)
		LC_MT D~1 g0~T sigma~1	hn	4	-805.88	1619.7	1620.1	312.61	0.00	21.6(2.2)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-803.55	1621.1	1622.2	313.96	0.00	24.2(3.0)
		LC_Mt D~1 g0~t sigma~1	hn	6	-805.65	1623.3	1624.1	316.17	0.00	21.6(2.2)
		LC_Mb D~1 g0~b sigma~1	hn	4	-818.92	1645.8	1646.2	338.69	0.00	20(2.17)
		LC_MB D~1 g0~B sigma~1	hn	4	-820.74	1649.4	1649.8	342.34	0.00	21.1(2.0)
	Model _Sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-699.67	1411.3	1412.2	0.00	1.00	22.4(2.3)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-711.61	1433.2	1433.8	21.88	0.00	22.9(2.4)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-717.73	1445.4	1446.0	34.13	0.00	21.8(2.3)
		LC_M0 D~1 g0~1 sigma~1	hn	3	-385.29	776.59	776.90	0.00	0.60	25.0(3.2)
		LC_MK D~1 g0~K sigma~1	hn	4	-385.29	778.59	779.11	2.00	0.22	25.0(3.2)
		LC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-384.47	778.93	779.73	2.34	0.18	26.4(3.7)
		LC_Mbk D~1 g0~bk sigma~1	hn	4	-427.21	862.42	862.95	85.83	0.00	41.5(8.8)
	No_sex	LC_MBk D~1 g0~Bk sigma~1	hn	4	-427.71	863.42	863.94	86.83	0.00	39.2(7.8)
100T & 0R		LC_Mk D~1 g0~k sigma~1	hn	4	-429.62	867.24	867.76	90.65	0.00	143.9(83)
		LC_MT D~1 g0~T sigma~1	hn	4	-475.13	958.27	958.79	181.68	0.00	24.1(3.0)
		LC_Mbt D~1 g0~b + t sigma~1	hn	7	-473.76	961.53	963.06	184.94	0.00	30.0(6.1)
		LC_Mt D~1 g0~t sigma~1	hn	6	-475.01	962.03	963.17	185.44	0.00	24.1(3.0)
		LC_Mb D~1 g0~b sigma~1	hn	4	-481.60	971.20	971.72	194.61	0.00	21.6(3.0)
		LC_MB D~1 g0~B sigma~1	hn	4	-482.34	972.68	973.21	196.09	0.00	24.6(3.9)
		LC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-426.92	863.85	864.65	0.00	0.48	25.5(3.4)
	Model _Sex	LC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-426.26	864.51	865.65	0.66	0.35	25.0(3.2)
		LC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-427.96	865.92	866.72	2.08	0.17	25.0(3.2)

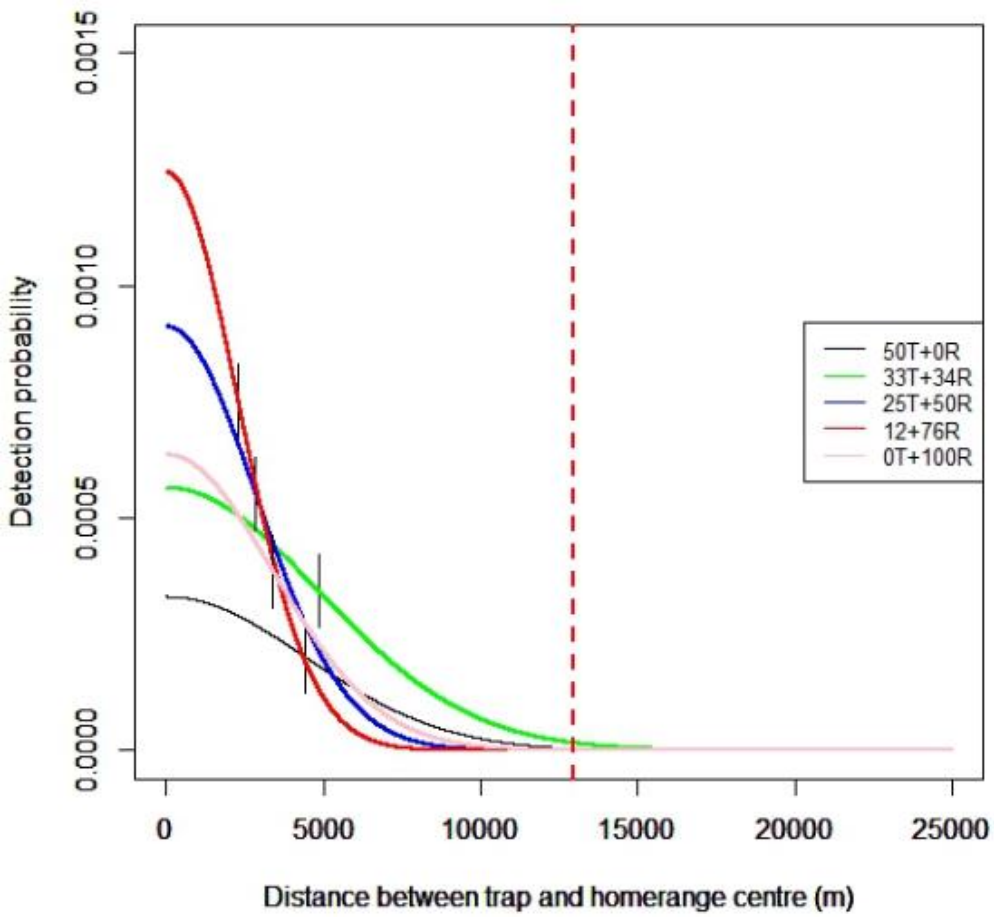
Table S10. Density estimates of marbled cat from different combination of trail (T) and random (R) cameras, given a total availability of 100 stations. The T & R combination identifies numbers of trail stations with paired cameras and random stations with single cameras. Parameters as for Table S1.

Camera Combination	**Model**	**model specification**	**df**	**np**	**logLik**	**AIC**	**AICc**	**dAIC**	**AICwt**	**Density**
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-328.89	667.78	669.60	0.00	1.00	8.01(1.6)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-339.60	685.20	685.89	17.42	0.00	6.56(1.1)
		MC_MK D~1 g0~K sigma~1	hn	4	-339.60	687.20	688.38	19.42	0.00	6.56(1.1)
		MC_Mk D~1 g0~k sigma~1	hn	4	-361.49	730.98	732.16	63.21	0.00	10.2(2.3)
	No_sex	MC_MBk D~1 g0~Bk sigma~1	hn	4	-366.12	740.25	741.42	72.47	0.00	6.96(1.3)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-368.94	745.88	747.05	78.10	0.00	6.94(1.3)
75 T & 25 R		MC_Mt D~1 g0~t sigma~1	hn	6	-404.17	820.34	822.97	152.56	0.00	6.52(1.1)

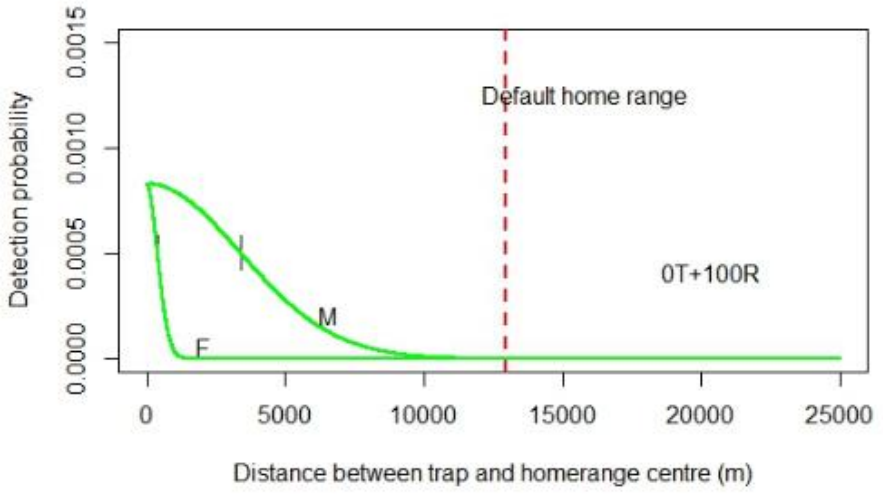
		MC_Mb D~1 g0~b sigma~1	hn	4	-406.68	821.35	822.53	153.57	0.00	6.24(1.0)
		MC_MT D~1 g0~T sigma~1	hn	4	-406.82	821.65	822.83	153.87	0.00	6.51(1.1)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-404.17	822.34	825.95	154.56	0.00	6.51(1.1)
		MC_MB D~1 g0~B sigma~1	hn	4	-407.48	822.97	824.14	155.19	0.00	6.46(1.1)
	Model_sex	MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-357.99	727.97	730.60	0.00	0.52	6.68(1.1)
		MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-359.14	728.28	730.10	0.31	0.44	6.74(1.1)
		MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-361.52	733.05	734.87	5.08	0.04	6.56(1.1)
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-352.09	714.18	716.12	0.00	1.00	6.25(1.1)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-359.66	725.33	726.06	11.15	0.00	5.95(1.0)
		MC_MK D~1 g0~K sigma~1	hn	4	-359.66	727.33	728.58	13.15	0.00	5.95(1.0)
	No_sex	MC_Mk D~1 g0~k sigma~1	hn	4	-380.89	769.78	771.03	55.60	0.00	10.0(2.4)
		MC_Mbk D~1 g0~bk sigma~1	hn	4	-402.83	813.65	814.90	99.47	0.00	6.21(1.1)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-402.88	813.76	815.01	99.58	0.00	6.19(1.1)
		MC_MB D~1 g0~B sigma~1	hn	4	-435.35	878.70	879.95	164.52	0.00	6.35(1.1)
25T & 75R		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-432.46	878.93	882.79	164.75	0.00	6.83(1.3)
		MC_Mb D~1 g0~b sigma~1	hn	4	-435.91	879.83	881.08	165.65	0.00	6.23(1.1)
		MC_MT D~1 g0~T sigma~1	hn	4	-436.24	880.48	881.73	166.30	0.00	5.94(1.0)
		MC_Mt D~1 g0~t sigma~1	hn	6	-434.84	881.69	884.49	167.51	0.00	5.93(1.0)
	Model_Sex	MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-380.31	770.62	772.56	0.00	0.53	5.9(1.05)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-379.98	771.96	774.76	1.34	0.27	5.9(1.05)
		MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-381.25	772.50	774.44	1.88	0.21	5.9(1.05)
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-303.88	617.76	619.83	0.00	1.00	7.27(1.6)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-311.41	628.81	629.59	11.05	0.00	6.0(1.08)
		MC_MK D~1 g0~K sigma~1	hn	4	-311.41	630.81	632.15	13.05	0.00	6.0(1.08)
	No_sex	MC_Mk D~1 g0~k sigma~1	hn	4	-327.99	663.97	665.31	46.21	0.00	8.72(2.0)
		MC_MBk D~1 g0~Bk sigma~1	hn	4	-338.62	685.25	686.58	67.48	0.00	6.34(1.2)
50T & 50R		MC_Mbk D~1 g0~bk sigma~1	hn	4	-340.21	688.42	689.75	70.65	0.00	6.33(1.2)
		MC_Mt D~1 g0~t sigma~1	hn	6	-365.97	743.94	746.94	126.18	0.00	5.99(1.0)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-365.93	745.86	750.01	128.09	0.00	6.07(1.1)
		MC_MT D~1 g0~T sigma~1	hn	4	-368.99	745.98	747.31	128.21	0.00	5.97(1.0)
		MC_Mb D~1 g0~b sigma~1	hn	4	-369.43	746.86	748.19	129.09	0.00	5.76(1.0)
		MC_MB D~1 g0~B sigma~1	hn	4	-369.89	747.79	749.12	130.02	0.00	5.87(1.0)
	Model_Sex	MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-331.87	673.75	675.81	0.00	0.43	6.08(1.1)
		MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-331.94	673.89	675.96	0.14	0.40	6.06(1.0)
		MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-331.86	675.71	678.71	1.97	0.16	6.08(1.1)
		MC_Mh2 D~1 g0~h2 sigma~1 pmix~h2	hn	5	-416.28	842.57	844.28	0.00	0.99	6.15(1.1)
		MC_M0 D~1 g0~1 sigma~1	hn	3	-422.80	851.60	852.25	9.03	0.01	6.08(1.0)
		MC_MK D~1 g0~K sigma~1	hn	4	-422.80	853.60	854.71	11.03	0.00	6.08(1.0)
		MC_Mk D~1 g0~k sigma~1	hn	4	-456.75	921.50	922.61	78.93	0.00	8.49(1.6)
	No_sex	MC_MBk D~1 g0~Bk sigma~1	hn	4	-459.29	926.58	927.69	84.01	0.00	6.31(1.1)
100T & 0R		MC_Mbk D~1 g0~bk sigma~1	hn	4	-460.17	928.34	929.45	85.77	0.00	6.33(1.1)
		MC_Mt D~1 g0~t sigma~1	hn	6	-505.75	1023.5	1025.9	180.93	0.00	6.08(1.0)
		MC_Mbt D~1 g0~b + t sigma~1	hn	7	-505.00	1024.0	1027.4	181.44	0.00	6.47(1.1)
		MC_MT D~1 g0~T sigma~1	hn	4	-508.39	1024.7	1025.8	182.20	0.00	6.09(1.0)
		MC_Mb D~1 g0~b sigma~1	hn	4	-509.10	1026.2	1027.3	183.64	0.00	6.01(1.0)
		MC_MB D~1 g0~B sigma~1	hn	4	-509.11	1026.2	1027.3	183.65	0.00	6.14(1.0)

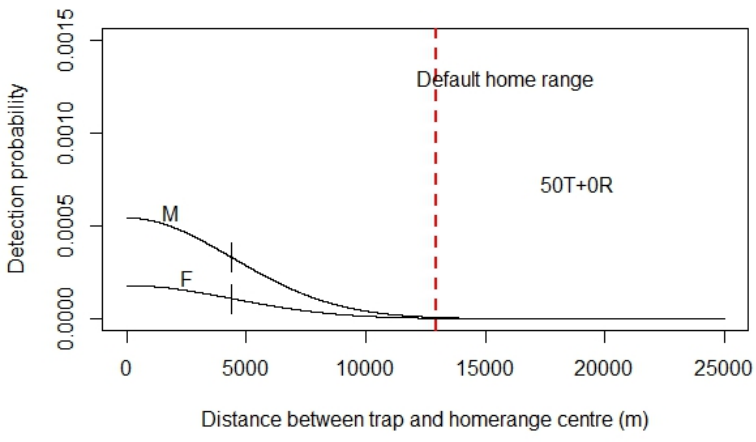
Model_Sex	MC_g0sex_sigma D~1 g0~h2 sigma~1 pmix~h2	hn	5	-444.57	899.13	900.85	0.00	0.41	6.11(1.0)
	MC_g0_sigmasex D~1 g0~1 sigma~h2 pmix~h2	hn	5	-444.81	899.61	901.32	0.48	0.33	6.08(1.0)
	MC_g0sex_sigmasex D~1 g0~h2 sigma~h2 pmix~h2	hn	6	-444.04	900.07	902.54	0.94	0.26	6.10(1.0)

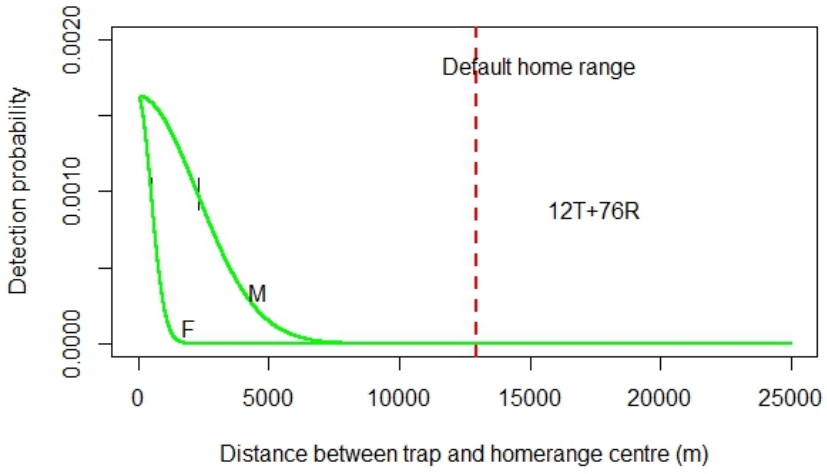
Figure S2: Detection probability of clouded leopard from different combination of trail and random stations for without sex and sex-based models with availability of 100 camera traps and 100 camera stations

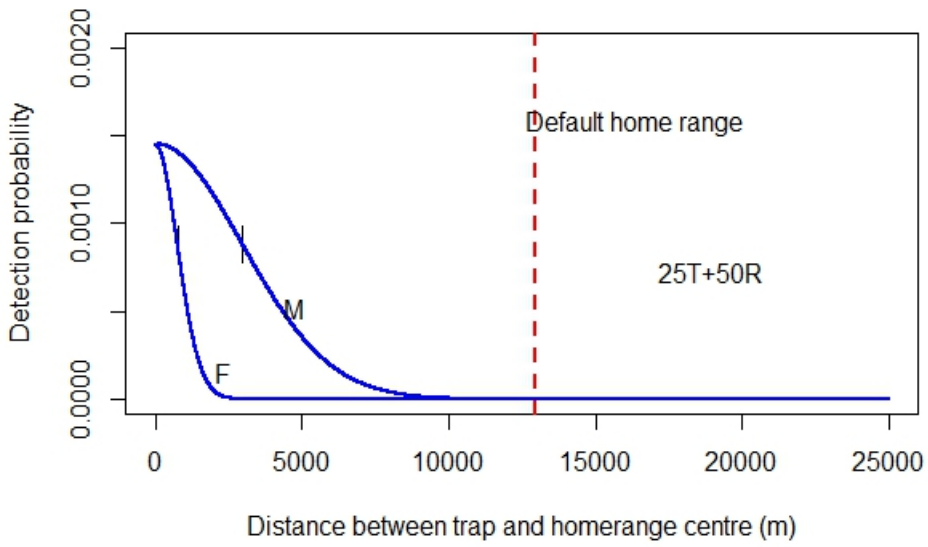


FigureS21. Detection probability and sigma from trail (T) and random (R) combination of stations with availability of 100 camera traps from model without sex specific detection. Vertical black lines on the detection probability curve represent sigma.









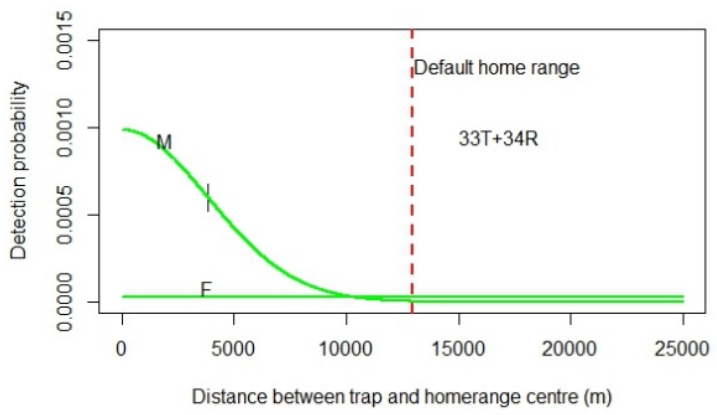


Figure S22. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

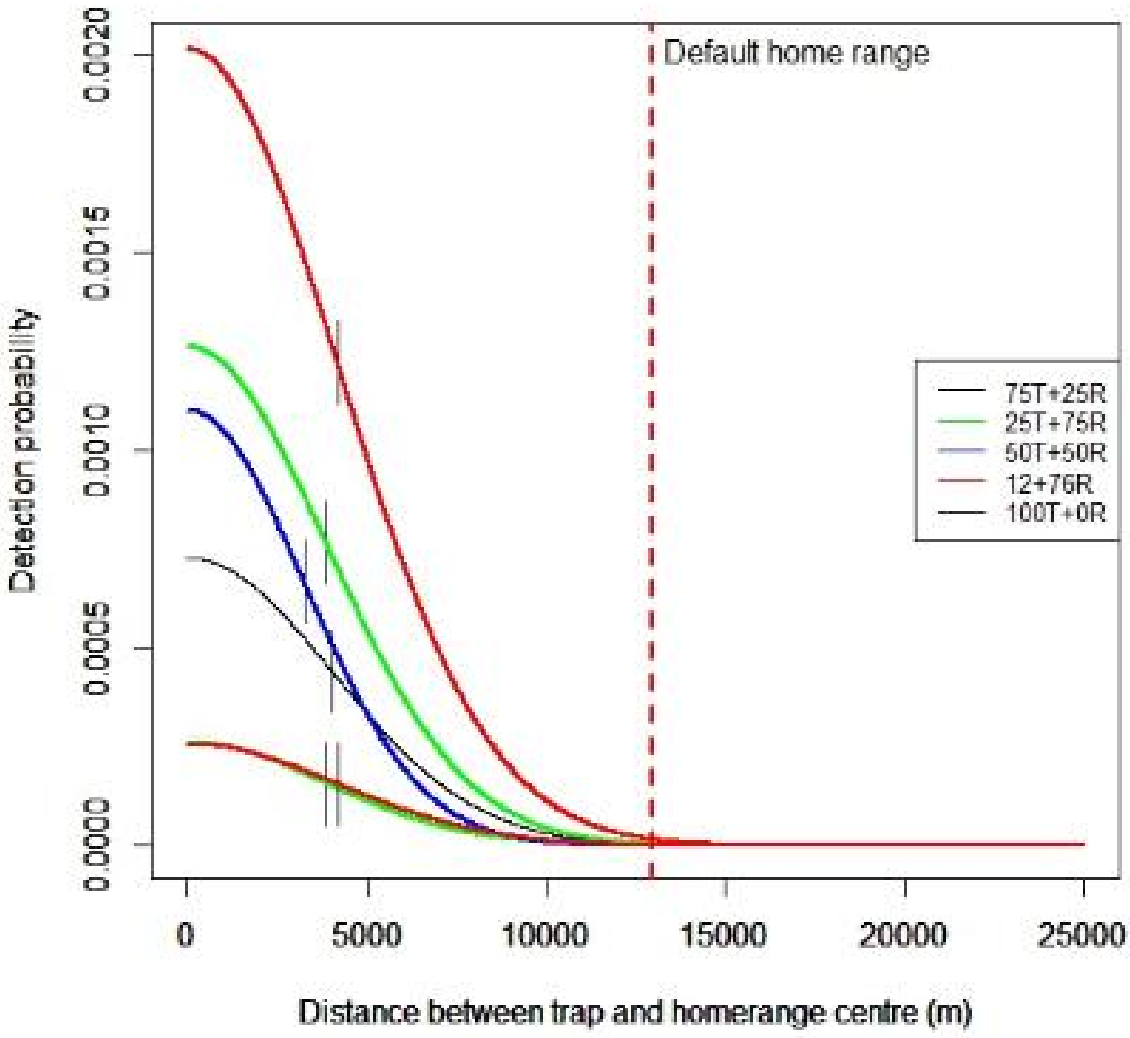
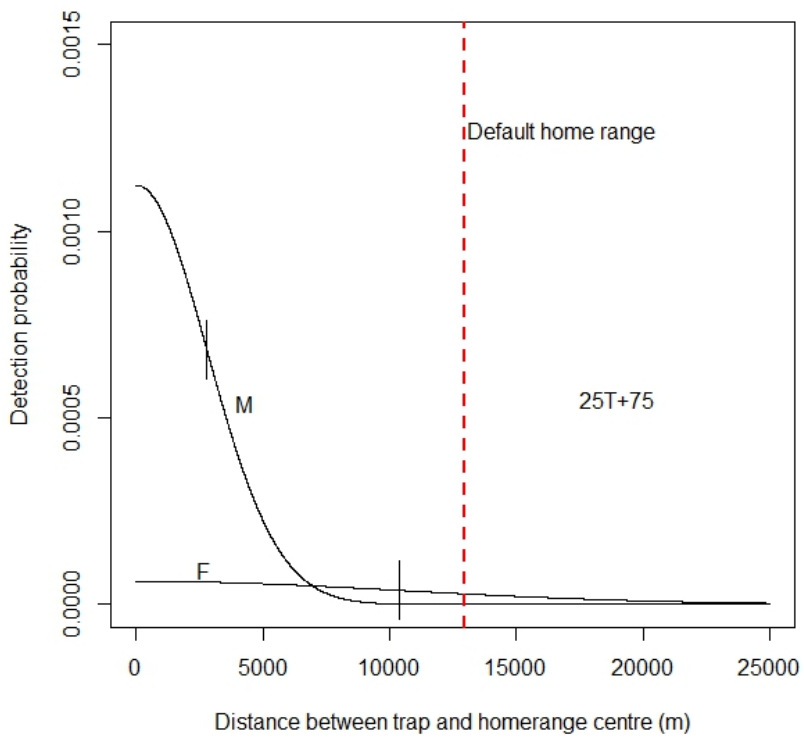
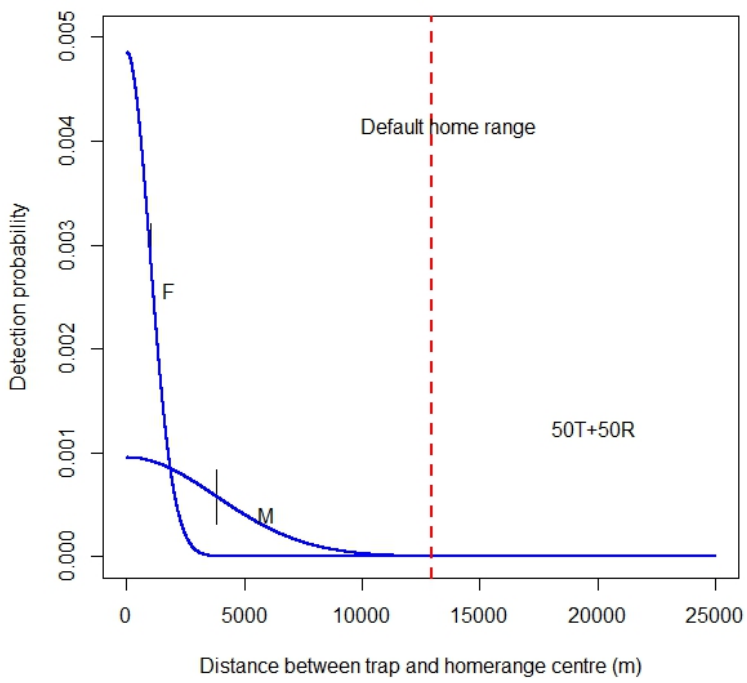
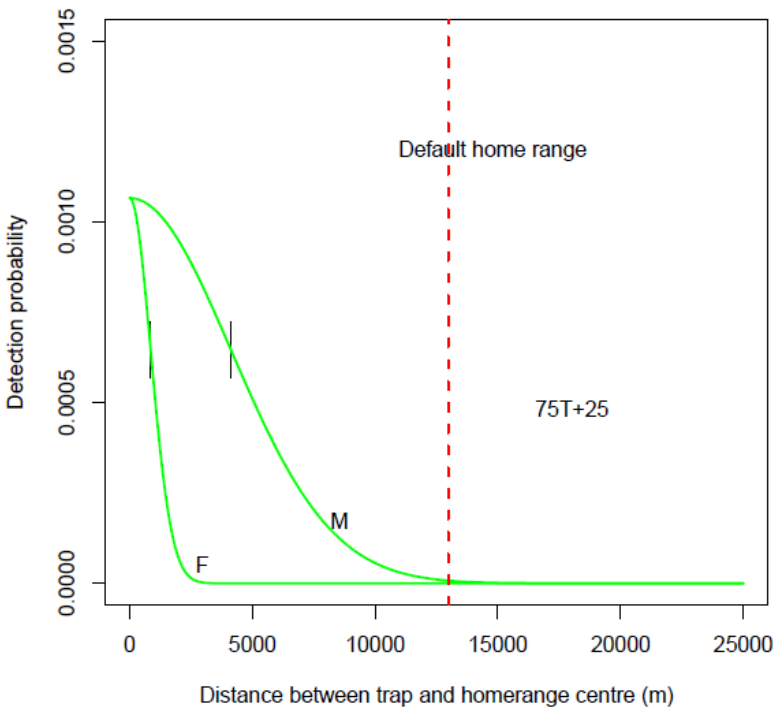


Figure S23. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera stations without sex-based detection. Vertical black lines on the detection probability cure represents sigma.







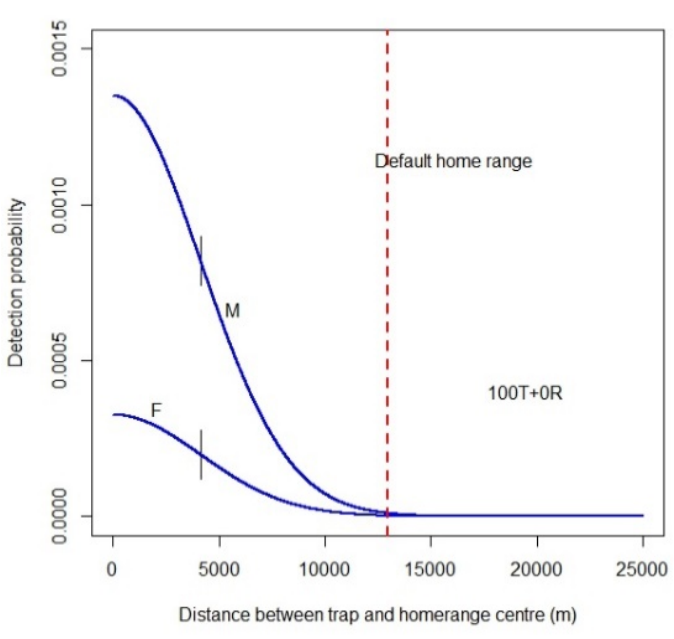
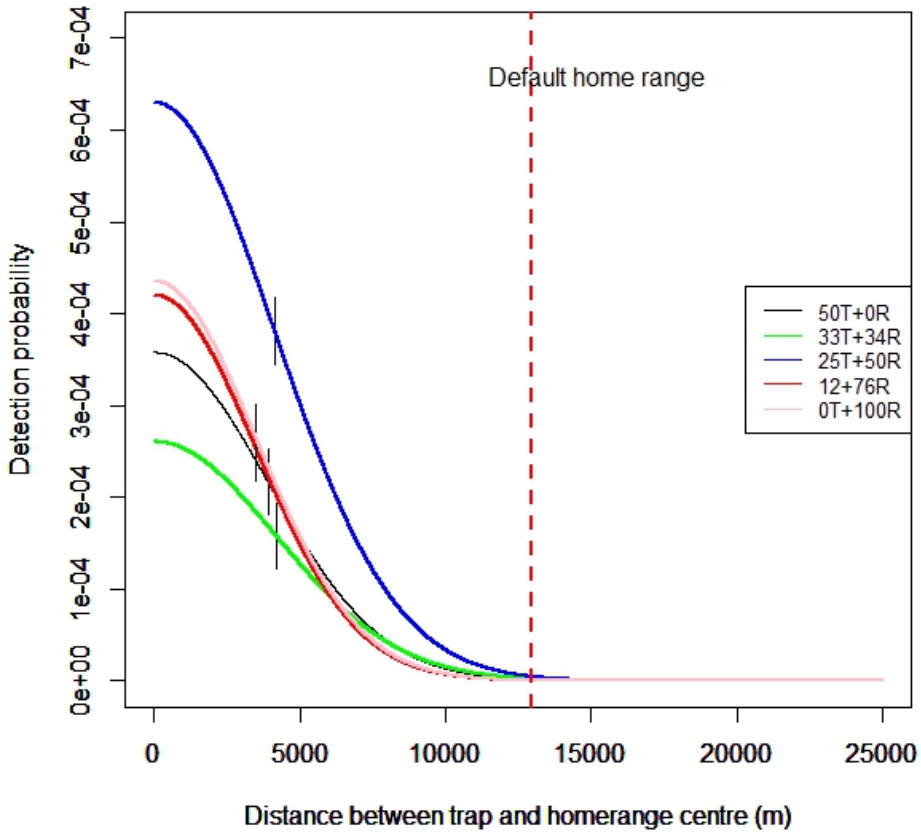
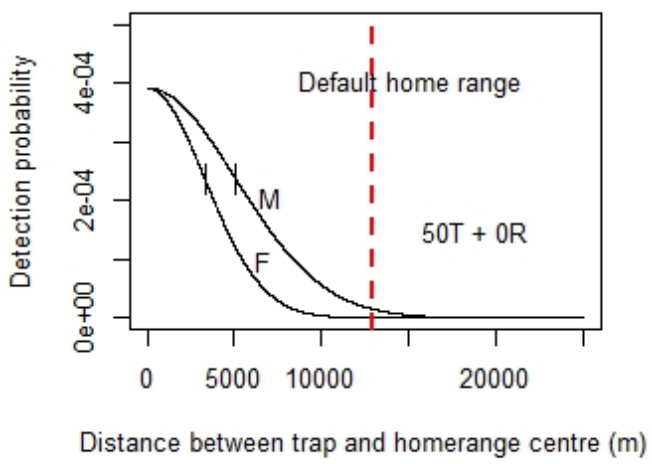


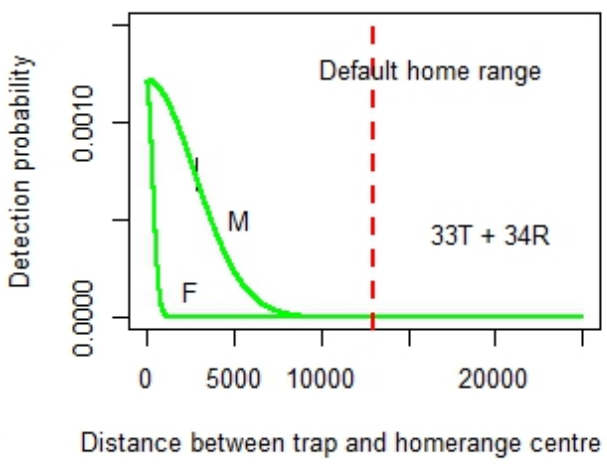
Figure S24. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 stations traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

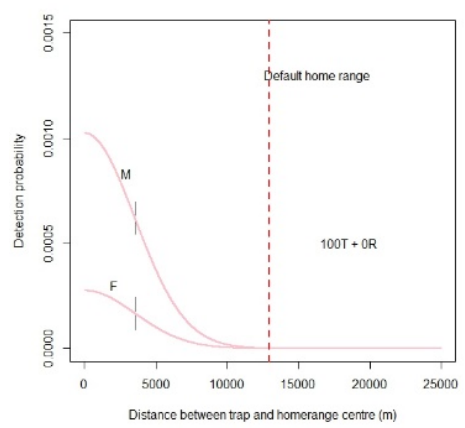
Figure S3: Detection probability of leopard from different combination of trail and random stations for without sex and sex-based models with availability of 100 camera traps and 100 camera stations

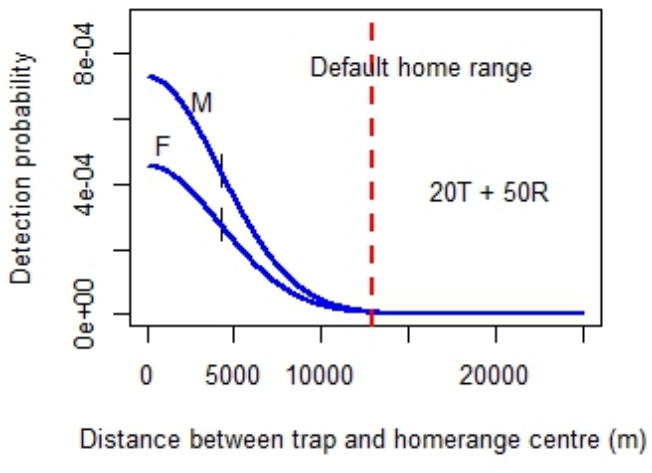


FigureS31. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera traps from model without sex specific detection. Vertical black lines on the detection probability cure represents sigma.









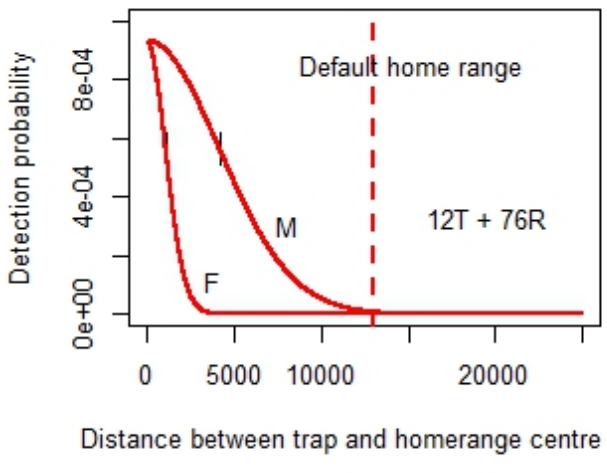


Figure S32. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

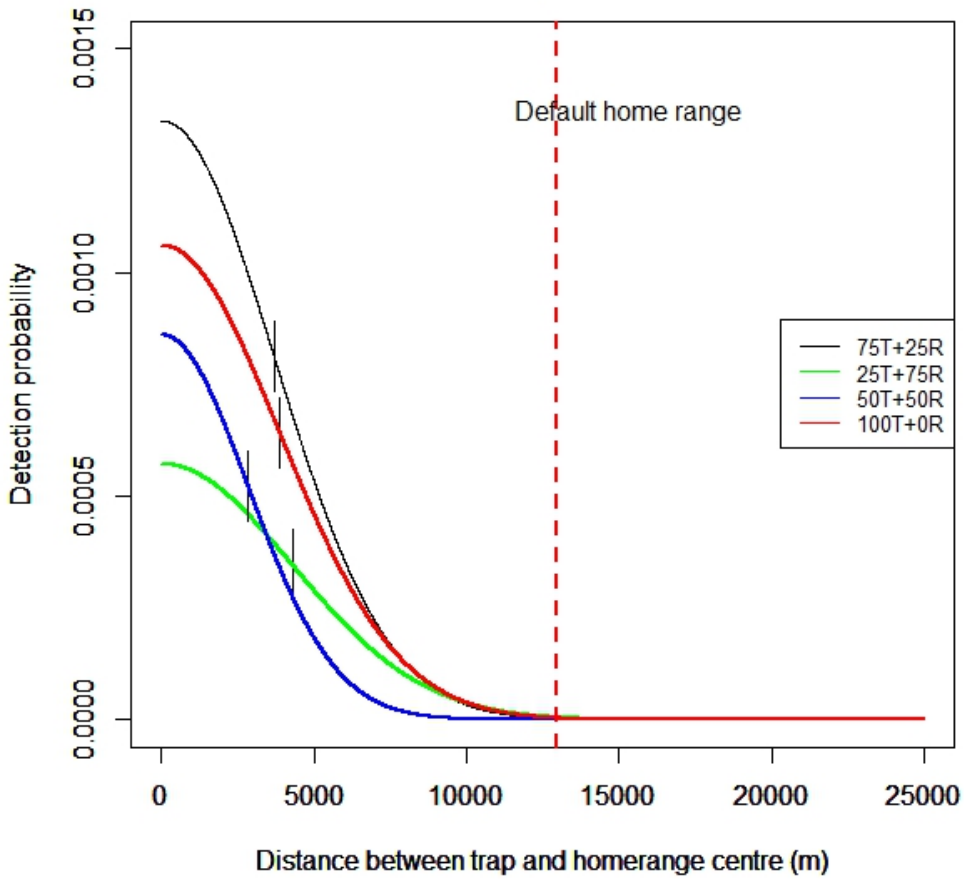


Figure S33. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera stations without sex-based detection. Vertical black lines on the detection probability cure represents sigma.

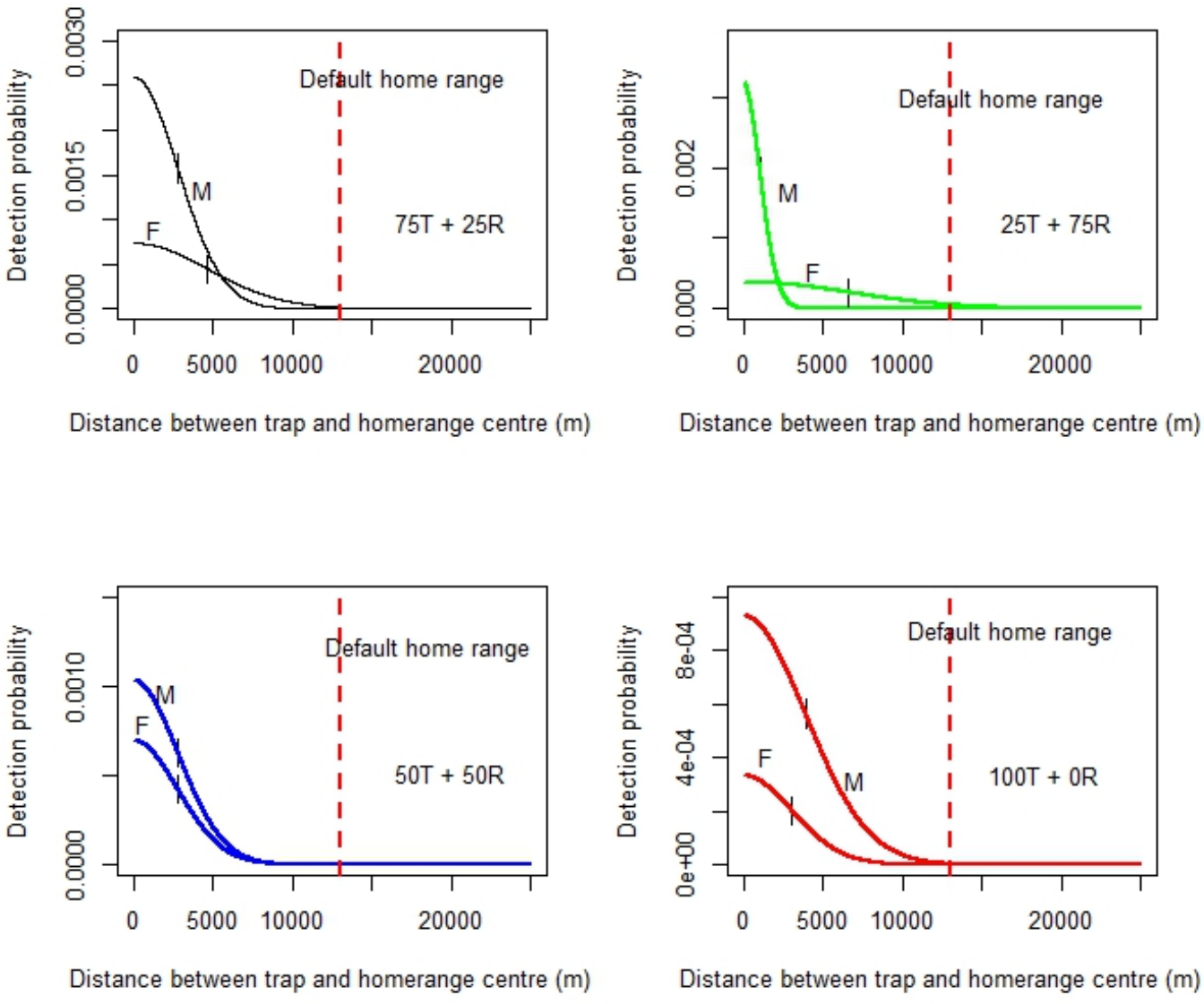


Figure S34. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 stations traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

Figure S4: Detection probability of leopard cat from different combination of trail and random stations for without sex and sex-based models with availability of 100 camera traps and 100 camera stations

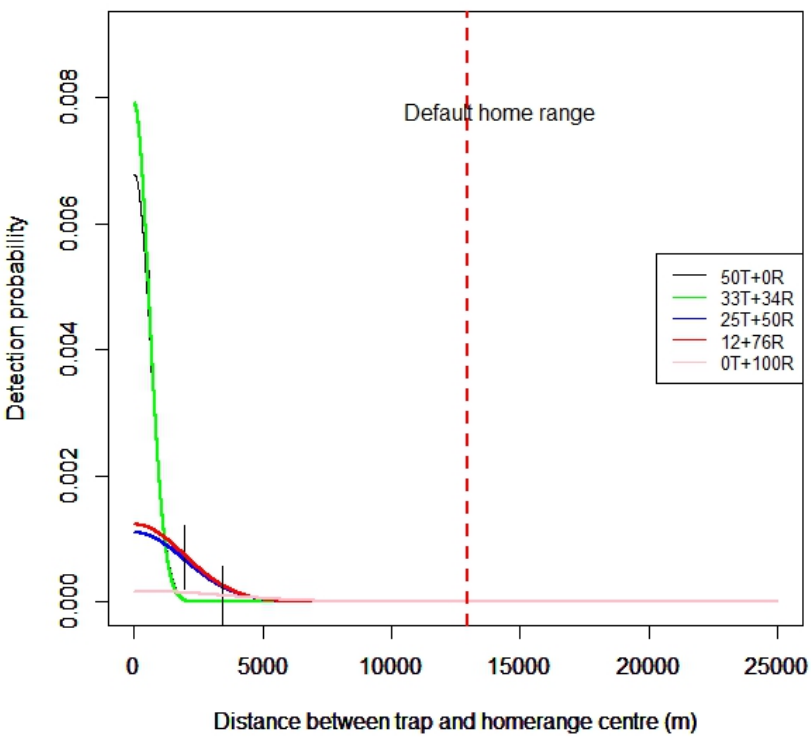


Figure S41. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera traps from model without sex specific detection. Vertical black lines on the detection probability curve represents sigma.

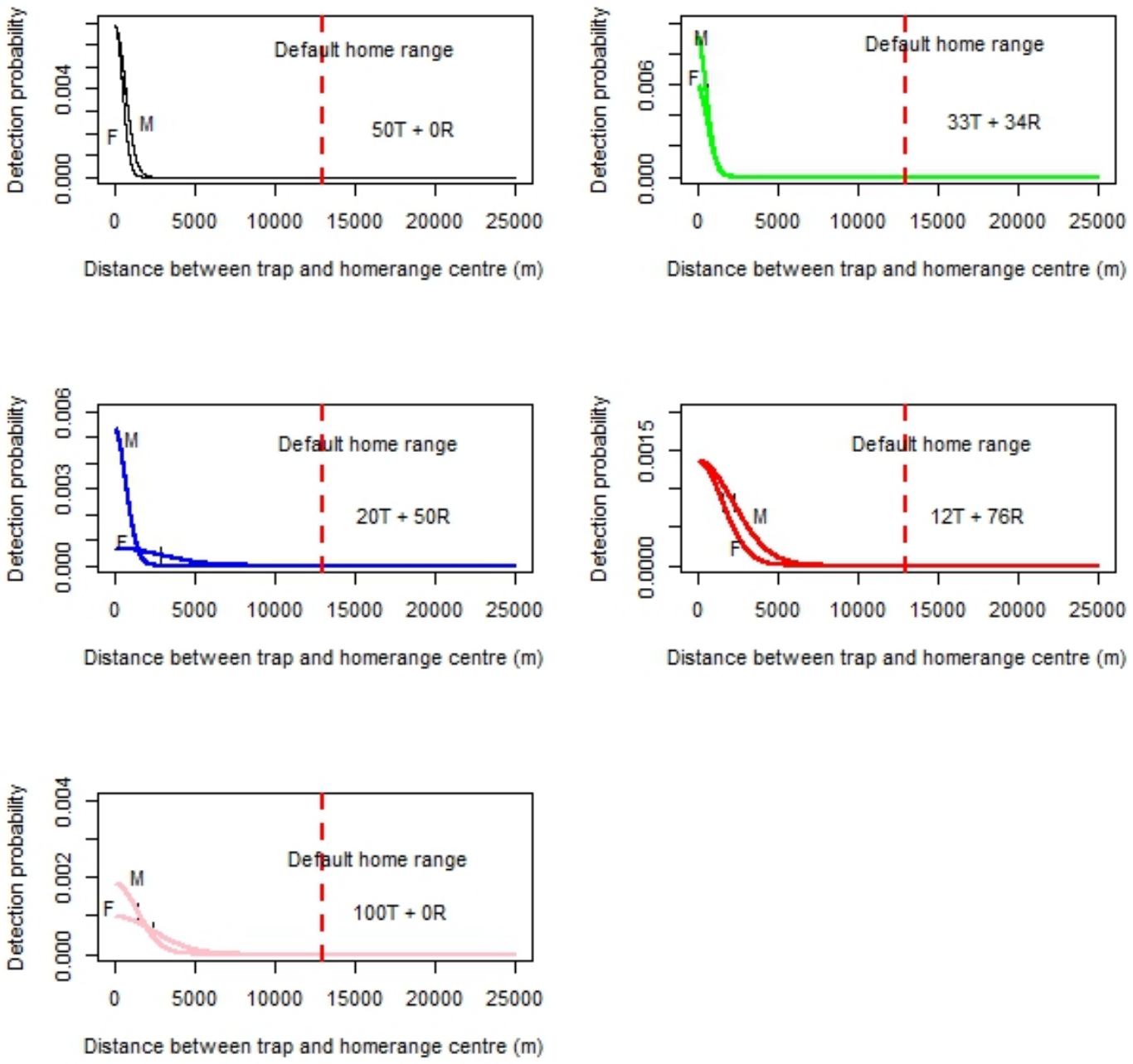


Figure S42. Detection probability and sigma from trail (T) and random (R) combination of stations with availability of 100 camera traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

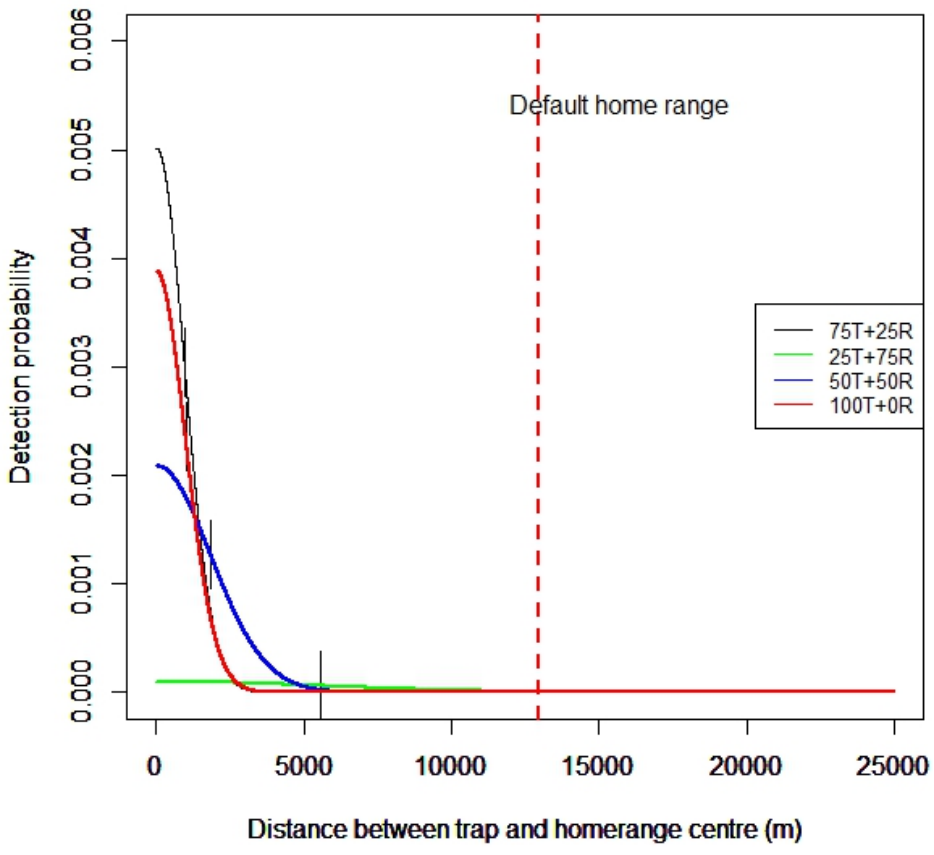


Figure S43. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera stations without sex-based detection. Vertical black lines on the detection probability cure represents sigma.

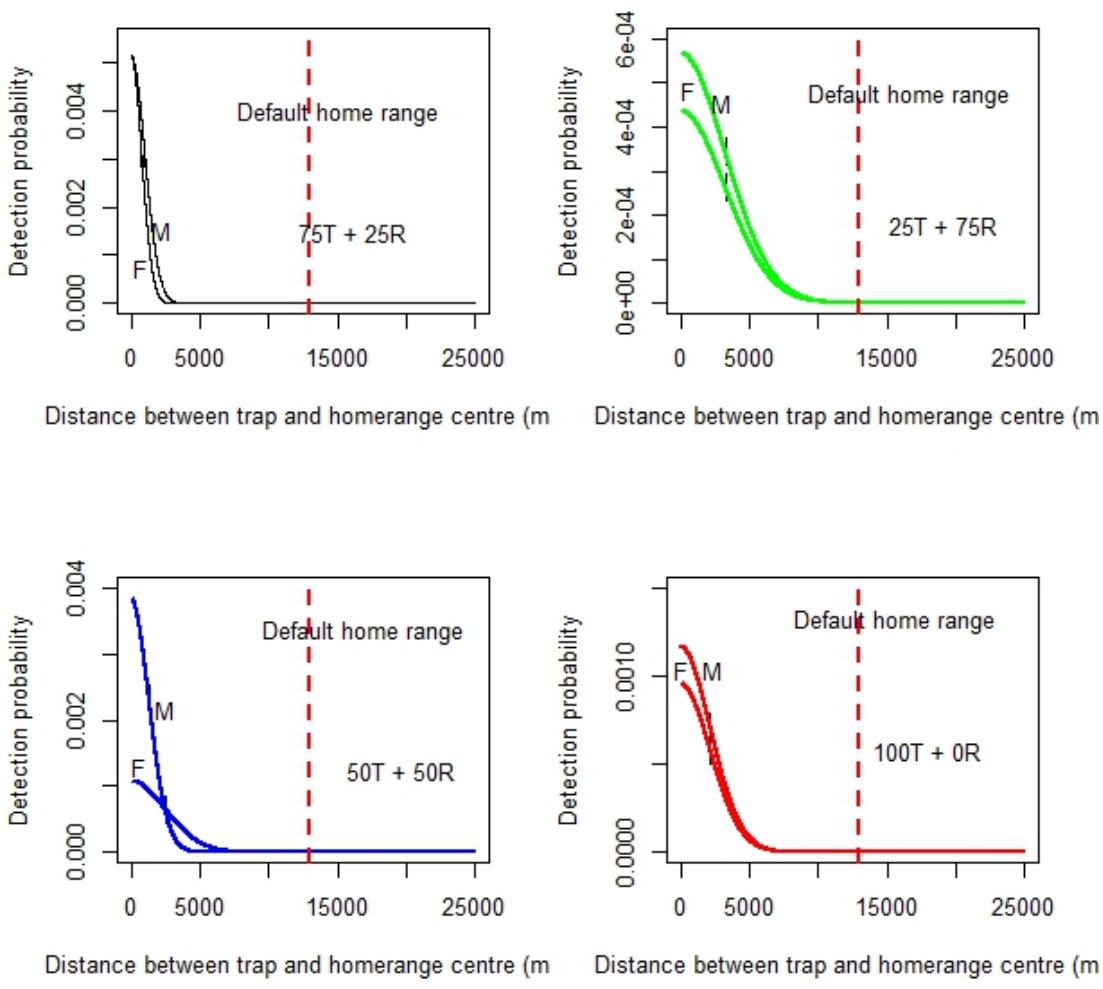
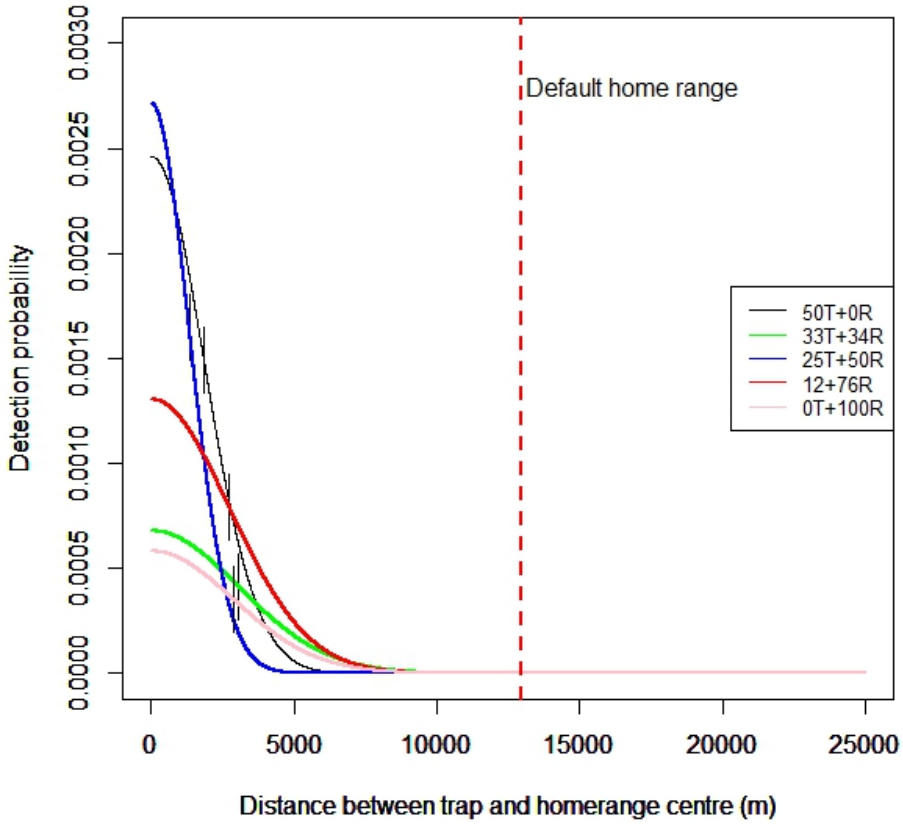
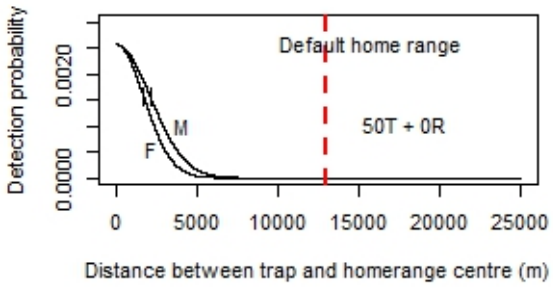


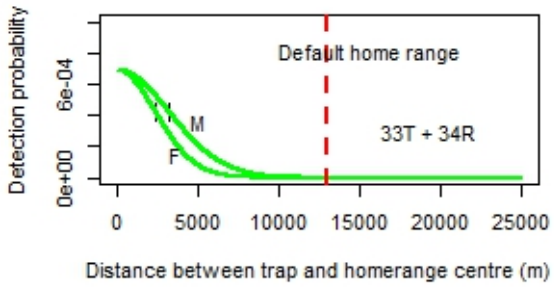
Figure S44. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 stations traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

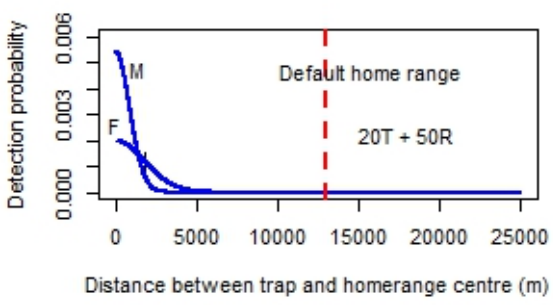
Figure S5: Detection probability of marbled cat from different combination of trail and random stations for without sex and sex-based models with availability of 100 camera traps and 100 camera stations

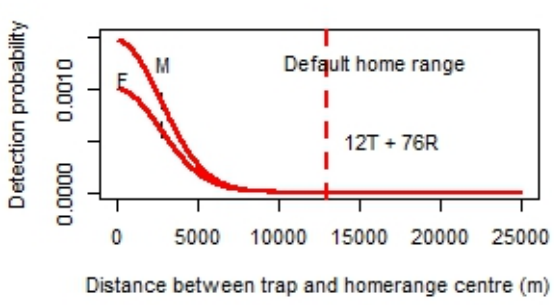


FigureS51. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera traps from model without sex specific detection. Vertical black lines on the detection probability curve represents sigma.









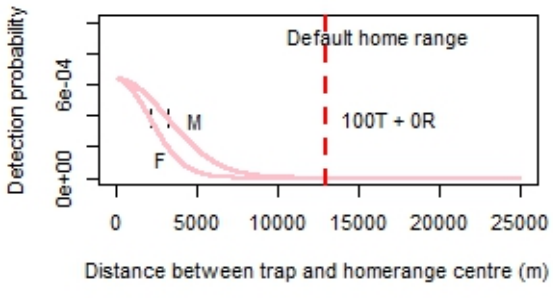


Figure S52. Detection probability and sigma from trail (T) and random (R) combination of stations with availability of 100 camera traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

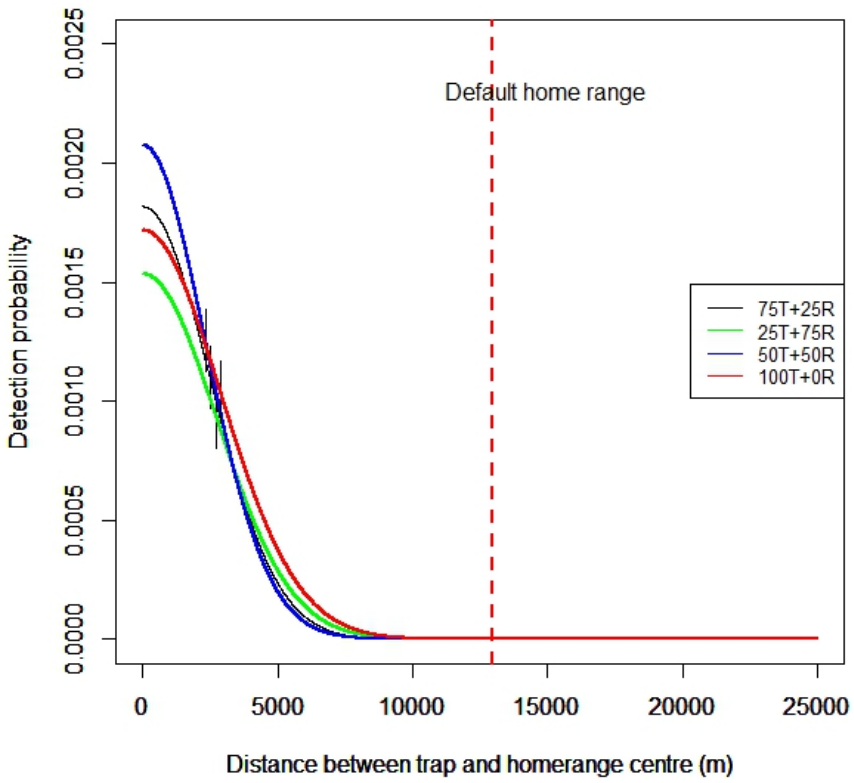
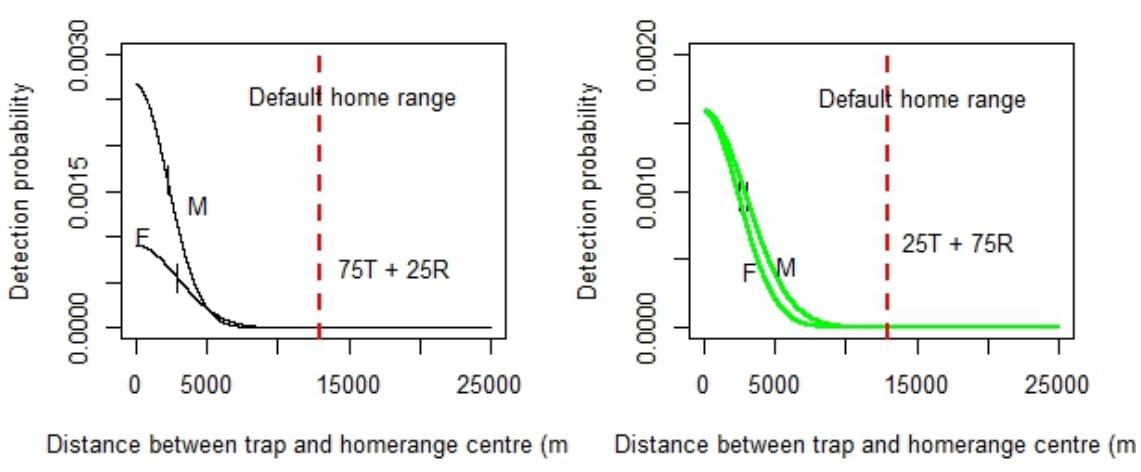


Figure S53. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 camera stations without sex-based detection. Vertical black lines on the detection probability cure represents sigma.



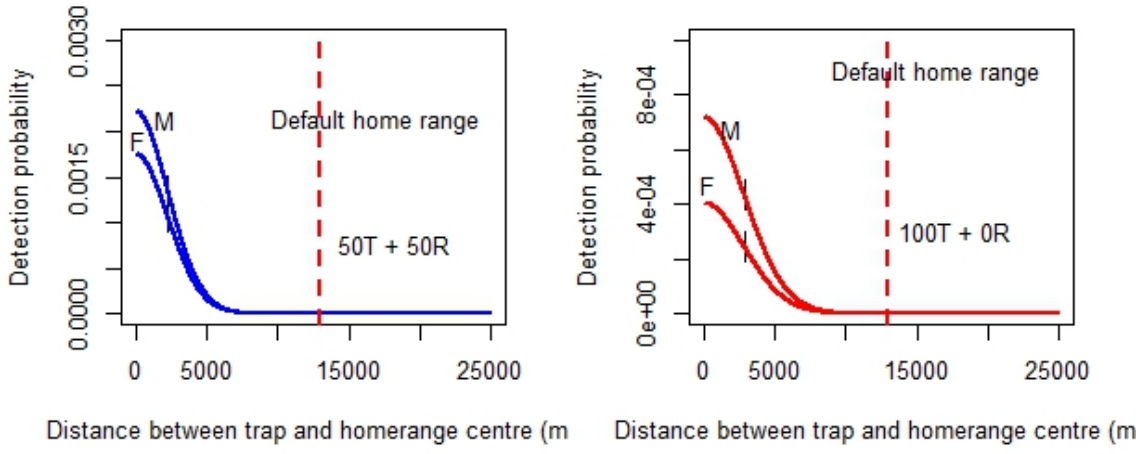


Figure S54. Detection probability and sigma from train (T) and random (R) combination of stations with availability of 100 stations traps for sex-based models. Vertical black lines on the detection probability cure represents sigma.

Appendix 2. Supplementary information for Chapter 3

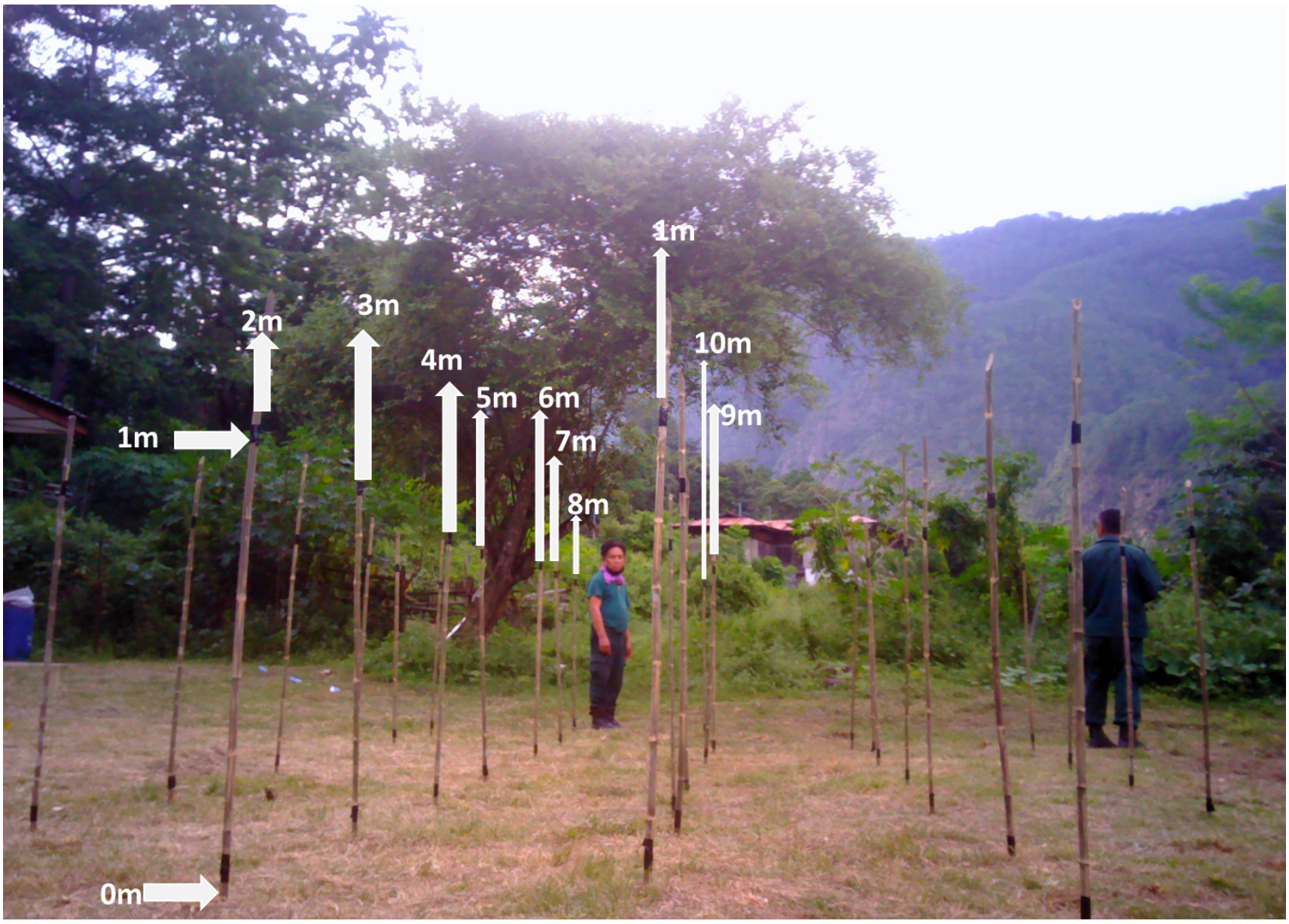


Figure S1: Shows the position of markers used for calibrating Panthera V.7 Xenon camera traps. Marker poles of one meter (horizontal white arrow depicts the height of the markers in black bands) was placed across the view of camera traps in 1…,10 meters. The 0 m was marked on the ground level and the 1m on the band at the upper position of the pole. The vertical arrows represent the distance from camera trap to the poles.

Appendix 2a: Protocol for deployment calibration

We followed CT-tracking guide available at https://github.com/MarcusRowcliffe/CTtracking/blob/master/CTtracking to estimate the detection distance of animals by the camera traps for Random Encounter Modelling (REM).

To evaluate the detection distances, we need to follow the following protocol:

1. Calibrate cameras with the 'pole dance'. It is super easy and quick to do once you get the hang of it. But basically, get someone to sit behind the camera and trigger it repeatedly while you dance about with the pole or set it in rapid-fire mode (aim for 15-20ish locations spread across the viewshed). Later, you can use these pole images to calibrate the camera location and then obtain automatic estimates of how far away animals are when you click on them in the image.
2. For pole dance, prepare a pole of known length (1 m works well) with contrasting 10 cm black and white bands and a visible mark (e.g., a coloured band) to indicate where the middle of the pole lies. Tape and bamboo are suggested materials.



Figure 1: Pole of length 1 m with 10 cm colour bands used for deployment calibration in the field.

3. Starting about 1m directly in front of the camera, hold the pole vertically with its base on the ground so that it is visible by the camera, and held still long enough to ensure a clear image
4. Repeat this for further pole placements across the field of view and away from the camera with placements spaced 1-2 m apart. Continue away from the camera to the maximum extent that any animals are likely to be captured or a bit beyond. Their distribution pattern should look like that shown in the figure below.

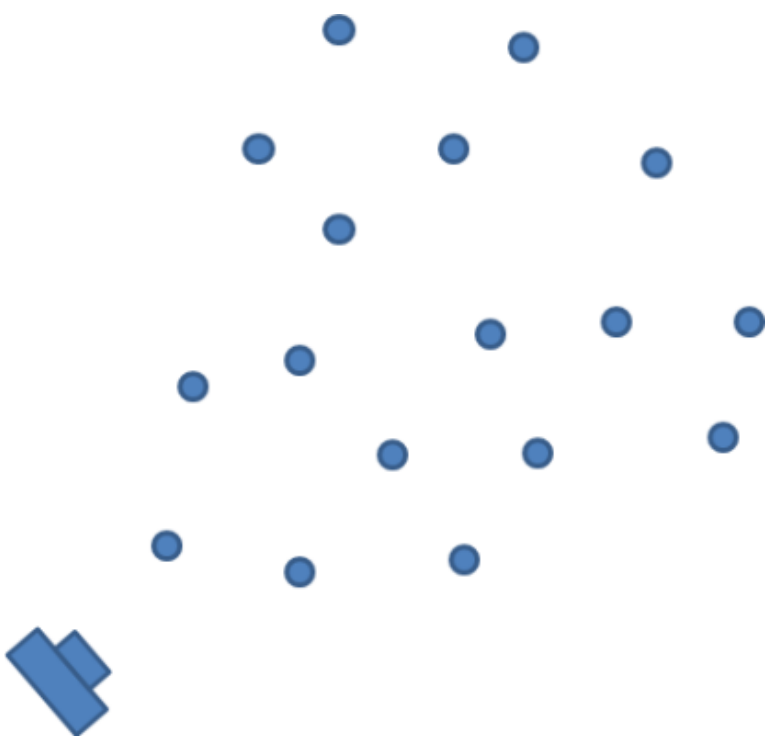


Figure2: Pattern of pole dance in the field (photo:

https://github.com/MarcusRowcliffe/CTtracking/blob/master/CTtracking)



Figure 3: Example of camera calibration in the field, walked in front of the camera's view as per the point depicted in figure 2 of this appendix in the camera detection zone.

Appendix 2b: Protocol for digitizing camera calibration and deployment calibration data

Measurement of animal position and speed

We need to digitize the poles of known dimension for every camera station to calculate the radial and angular distance of animal in the photographs.

Protocols to digitize camera trap images (deployment calibration)

We need descent connection of internet for the calibration of camera trap images and can be done with this online image digitization tools (the html tool animal tracker to digitise images, see https://lauravzarco.github.io/animaltracker). Need to refresh this tool for every station and station subfolders).

- Open the station folders containing camera (deployment) calibration images (images of pole dance)



Figure 1. Add camera calibration images and adding measurement point to the pole.

- Can add the measurement point on the pole by choosing add sequence option and need to choose for every new point (as shown in figure 1)
- Add additional field name height to add the measurement (your pole is 1m in height and every section is equivalent to 10 cm) as shown in figure 2
- Always put measurement in cm as decimal digits (0, 0.1, 0.2……..1m) as shown in figure 3

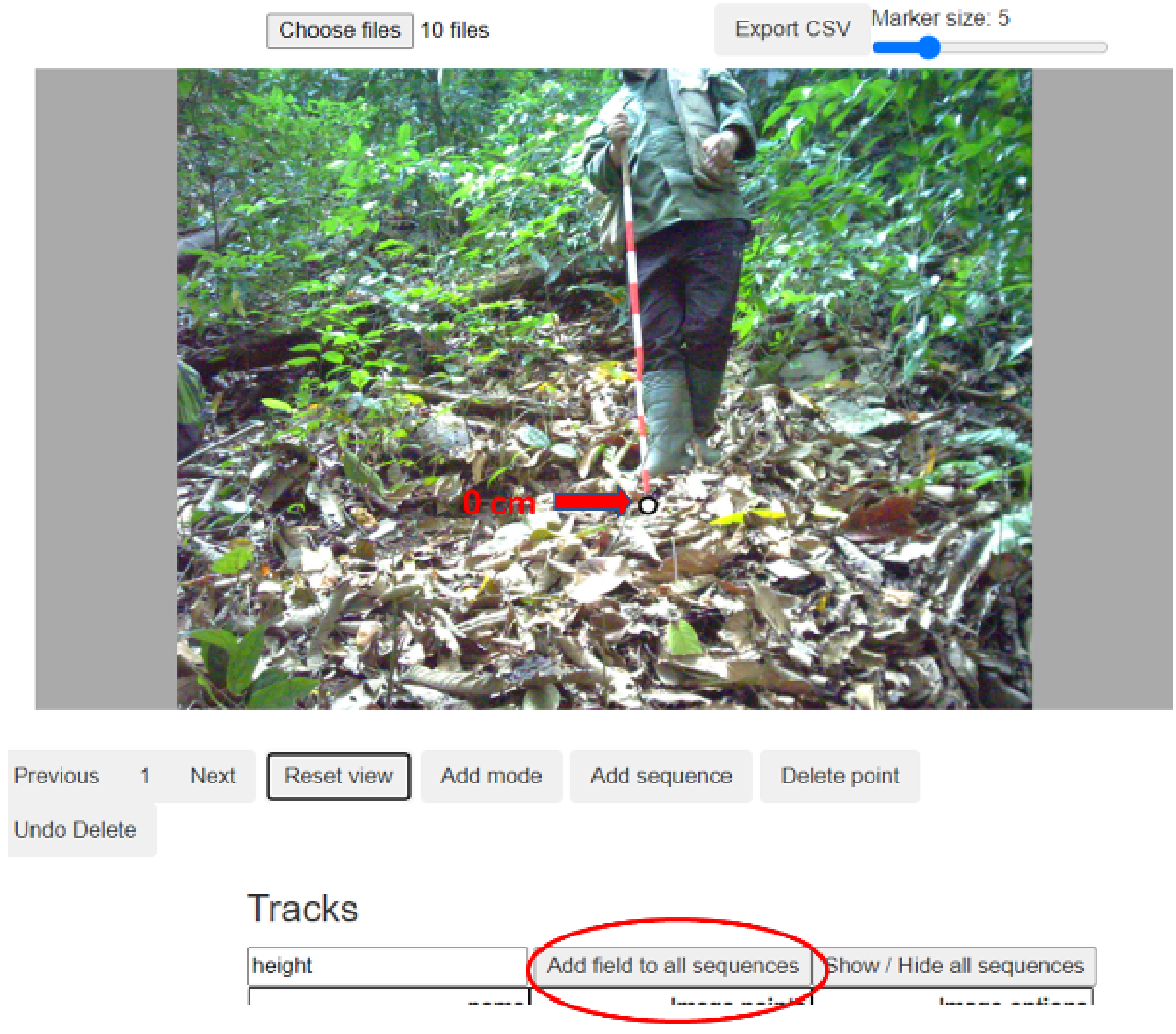


Figure 2. adding additional field name height to create a field where height measurement can be entered

- We can delete the points that are mistakenly digitized.

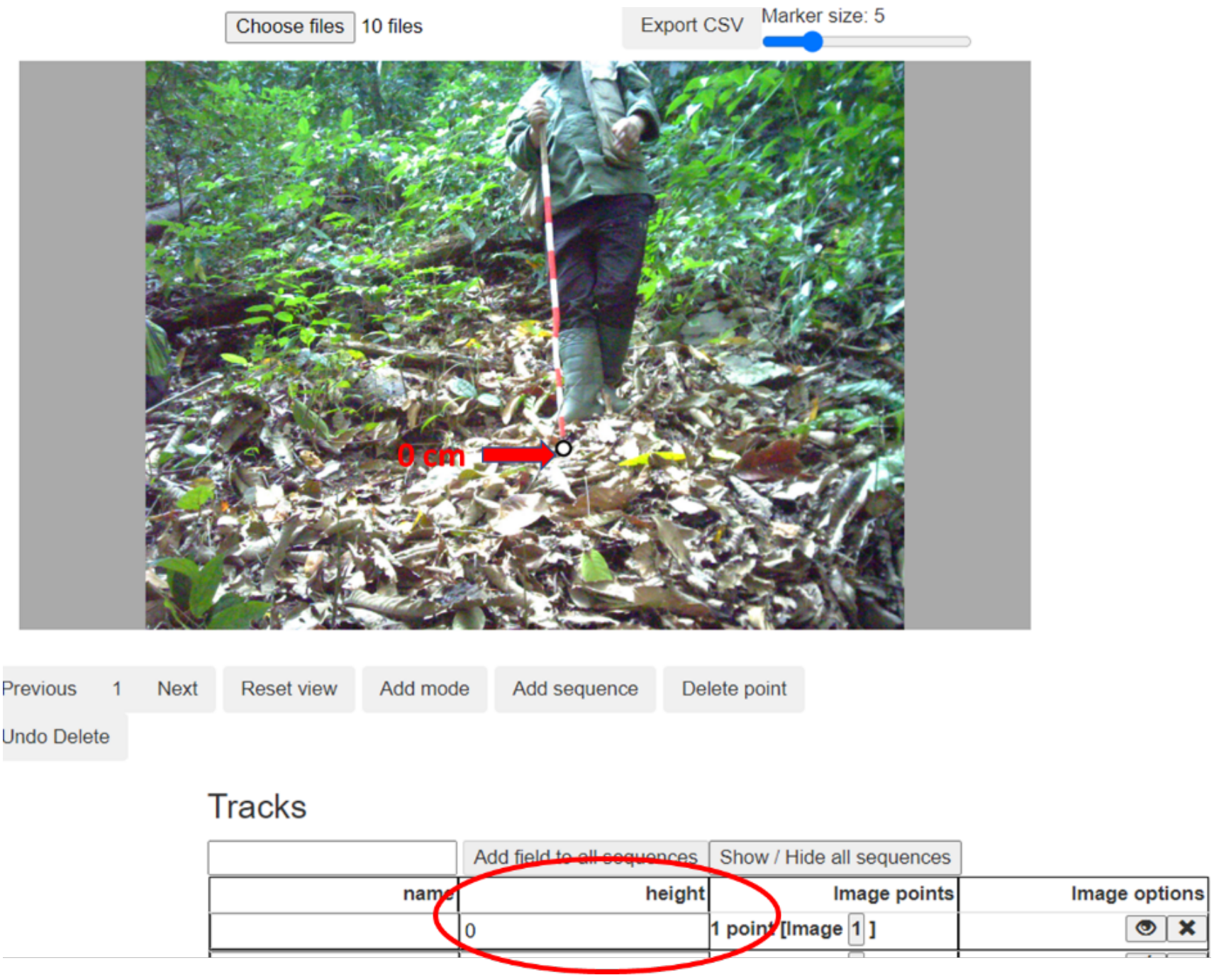


Figure 3. adding measurement to the new field height and entering the value of measurement. Here 0 for the ground position of the pole.

- After completing digitization of all the images in a station folder, export the measurement in the form of csv from export csv option and save the file in their respective folder. Rename the file as “digidat”.
- **Always avoid addition of more or less than 2 points on one image, and double digitization of one image**



Figure 4. Digitization sequence of animal position, the first point is added at midpoint on the ground between the forelegs and followed in subsequent images. The number 1-4 shows the sequences of tagging on the photographs. The measurement data is stored in same "digidat" file.

Table S1. Comparative density estimates of felids from REM with REM parameter values measured in the survey and REM parameter values after manipulation. Parameters are manipulated by doubling (e.g., speed x 2) in first situation and by reducing to half (e.g., speed x 0.5) in another situation. REM densities are calculated from 100 random-only deployment (0T +100R) deployment of camera traps. REM parameters in table represents the manipulation of REM parameter values, $Density_1$: density after manipulation of REM parameter values, LCL & UCL: lower and upper confidence limit. of 95% confidence interval, $Density_2$: density from REM parameters derived from survey, Reference density from full deployment (100T + 100R) with SECR null model and ΔREM density: $Density_1 - Density_2$.

Species	**REM parameters**	**$Density_1$**	**LCL**	**UCL**	**$Density_2$**	**Reference density**	**ΔREM density**
Clouded leopard	speed x 2	17.29 (6.53)	14.81	19.78	35.4 (13.48)	3.50(0.96)	18.11
	activity x 2	17.29 (6.38)	14.87	19.72			18.11
	radius x 2	17.29 (6.25)	14.91	19.67			18.11
	angle x 2	27.37 (10.43)	23.40	31.34			8.03
	speed x 0.5	69.17(25.83)	59.35	79.00			-33.77

	activity x 0.5	69.17 (26.63)	59.04	79.30			-33.77
	radius x 0.5	69.17 (31.96)	57.02	81.33			-33.77
	angle x 0.5	39.84 (14.82)	34.20	45.47			-4.44
Common leopard	speed x 2	2.75 (0.79)	2.45	3.05	5.49(1.61)	1.80(0.48)	2.74
	activity x 2	2.75 (0.80)	2.45	3.05			2.74
	radius x 2	2.75(0.78)	2.45	3.05			2.74
	angle x 2	4.75(1.35)	4.24	5.26			0.74
	speed x 0.5	11.00(3.10)	9.82	12.18			-5.51
	activity x 0.5	11.00(3.20)	9.78	12.22			-5.51
	radius x 0.5	11.00(3.20)	9.78	12.22			-5.51
	angle x 0.5	5.97(1.69)	5.33	6.61			-0.48
Leopard cat	speed x 2	42.27(9.71)	38.58	45.96	18.04(5.40)	26.40(2.60)	-24.23
	activity x 2	42.27(9.89)	38.51	46.03			-24.23
	radius x 2	42.27(9.80)	38.54	46.00			-24.23
	angle x 2	72.88(16.76)	66.51	79.26			-54.84
	speed x 0.5	169.07(39.56)	154.03	184.12			-151.03
	activity x 0.5	169.07(39.56)	154.03	184.12			-151.03
	radius x 0.5	169.07(39.56)	154.03	184.12			-151.03
	angle x 0.5	91.88(21.41)	83.74	100.02			-73.84
Marbled cat	speed x 2	2.48(1.11)	2.22	2.74	4.9(2.21)	7.70(1.20)	2.42
	activity x 2	2.48(1.11)	2.22	2.74			2.42
	radius x 2	2.48(1.11)	2.22	2.74			2.42
	angle x 2	4.12(1.85)	3.69	4.55			0.78
							4.90

speed x 0.5	9.91(4.62)	8.84	10.98	-5.01
activity x 0.5	9.91(4.62)	8.84	10.98	-5.01
radius x 0.5	9.91(4.62)	8.84	10.98	-5.01
angle x 0.5	5.52(2.47)	4.95	6.09	-0.62

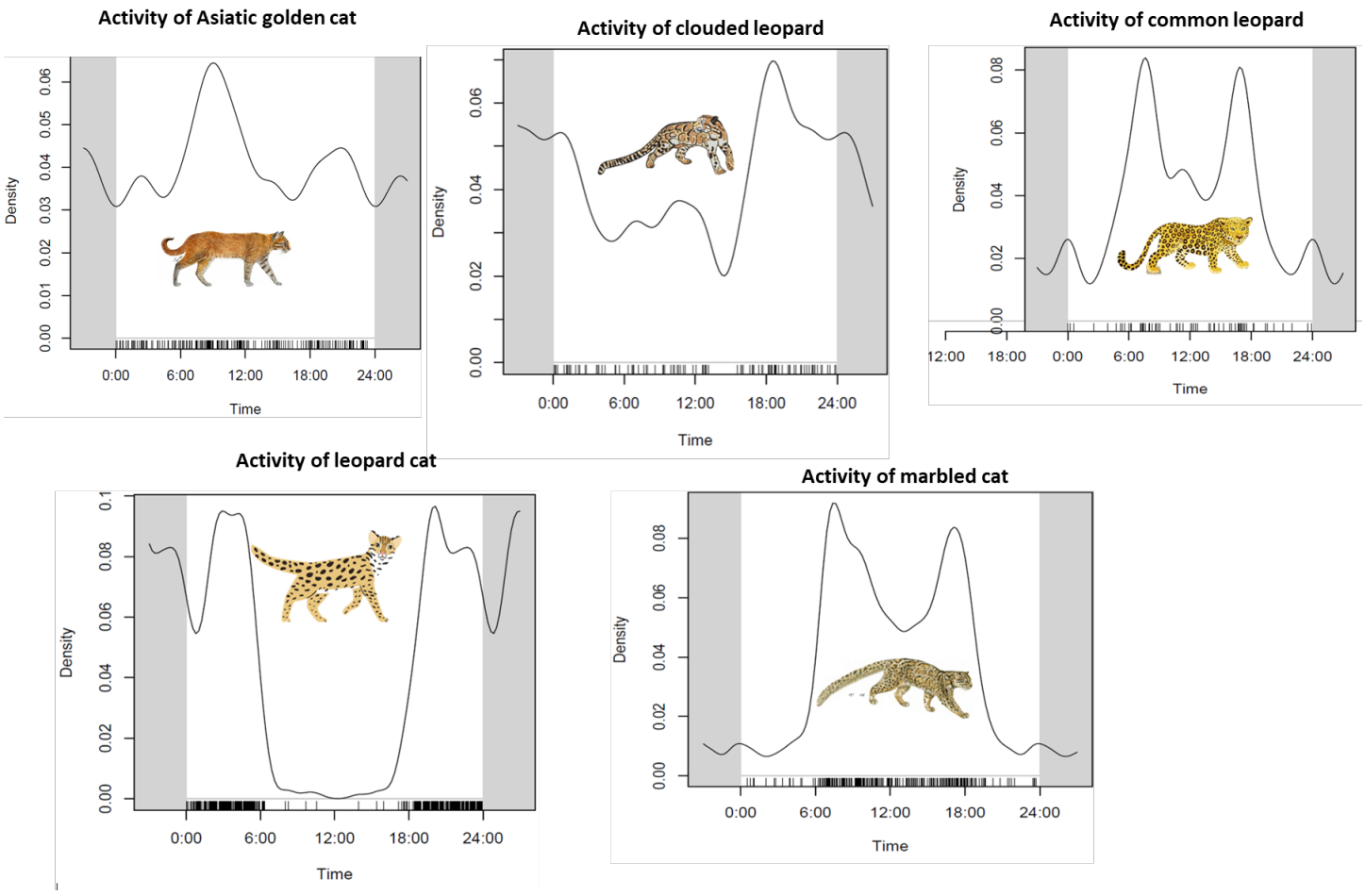


Figure S2. Activity pattern of wild felids calculated as per number of encounters with the camera traps and time of encounter. Y-axis depicts the density of encounter in the time represented by black shading in x-axis.

Appendix 2

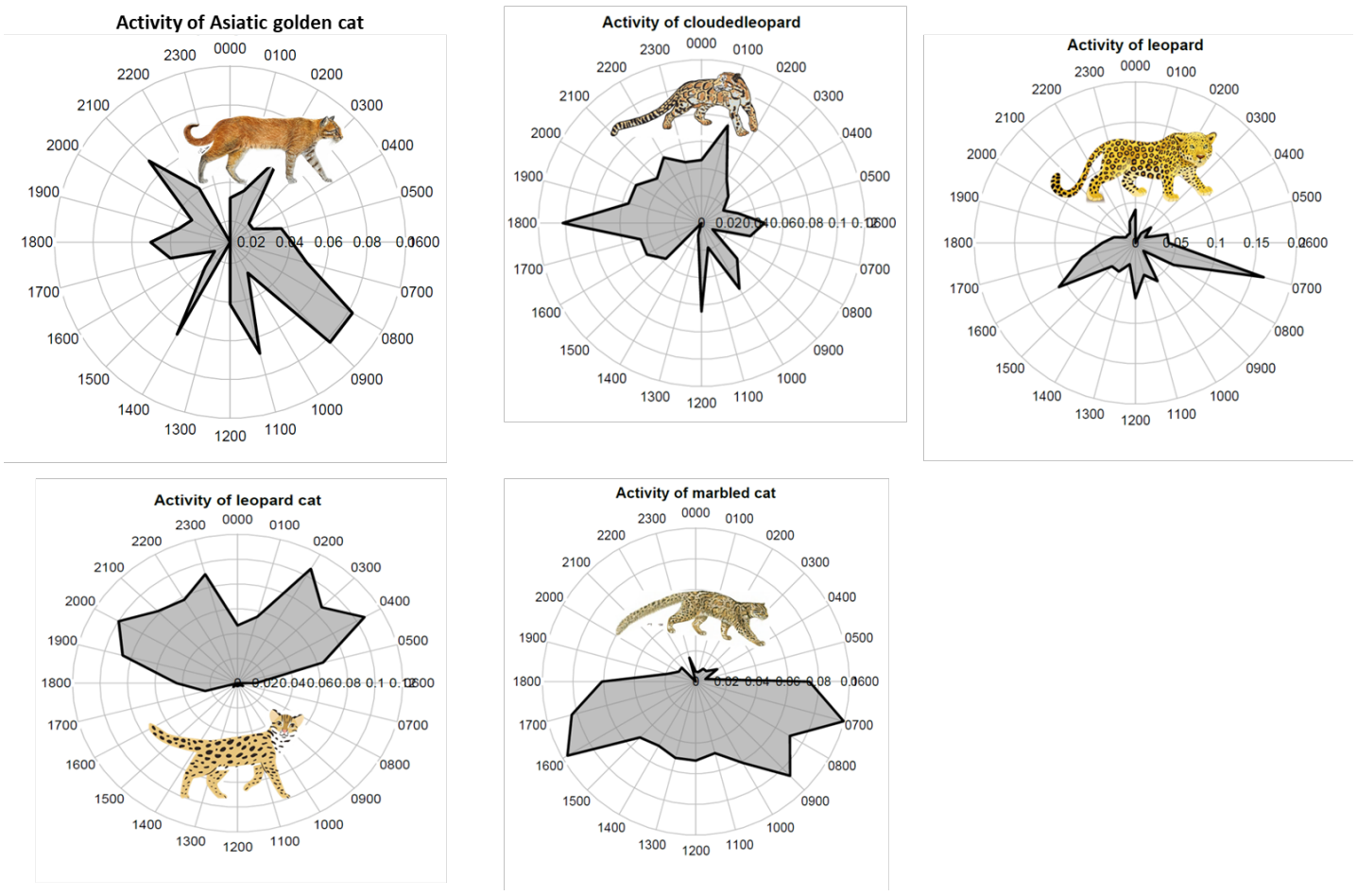


Figure S3. Radial activity pattern of wild felids calculated as per number of encounters with the camera traps and time of encounter. Area in the black shading represents the density of activity in 24hr timeframe.

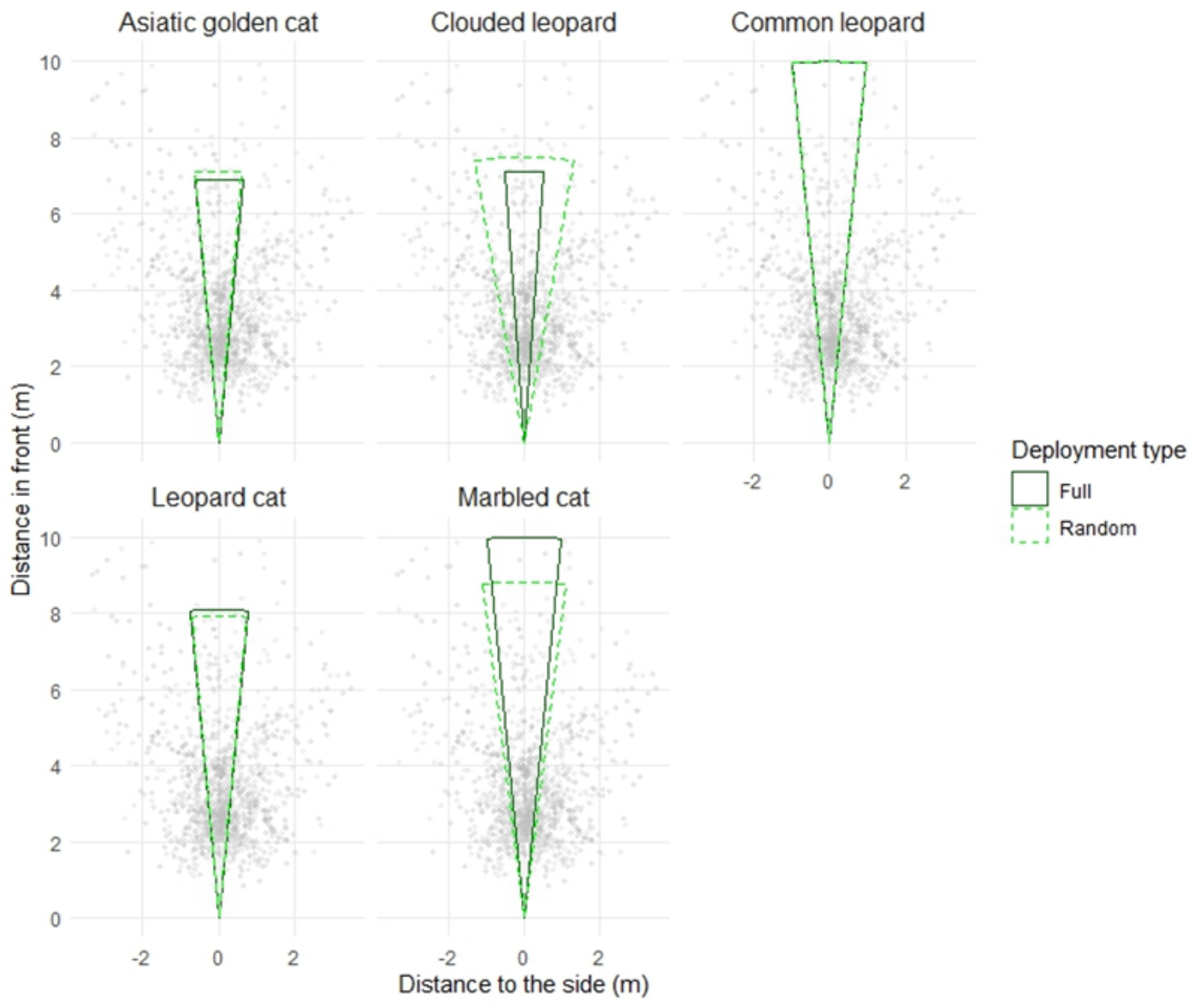
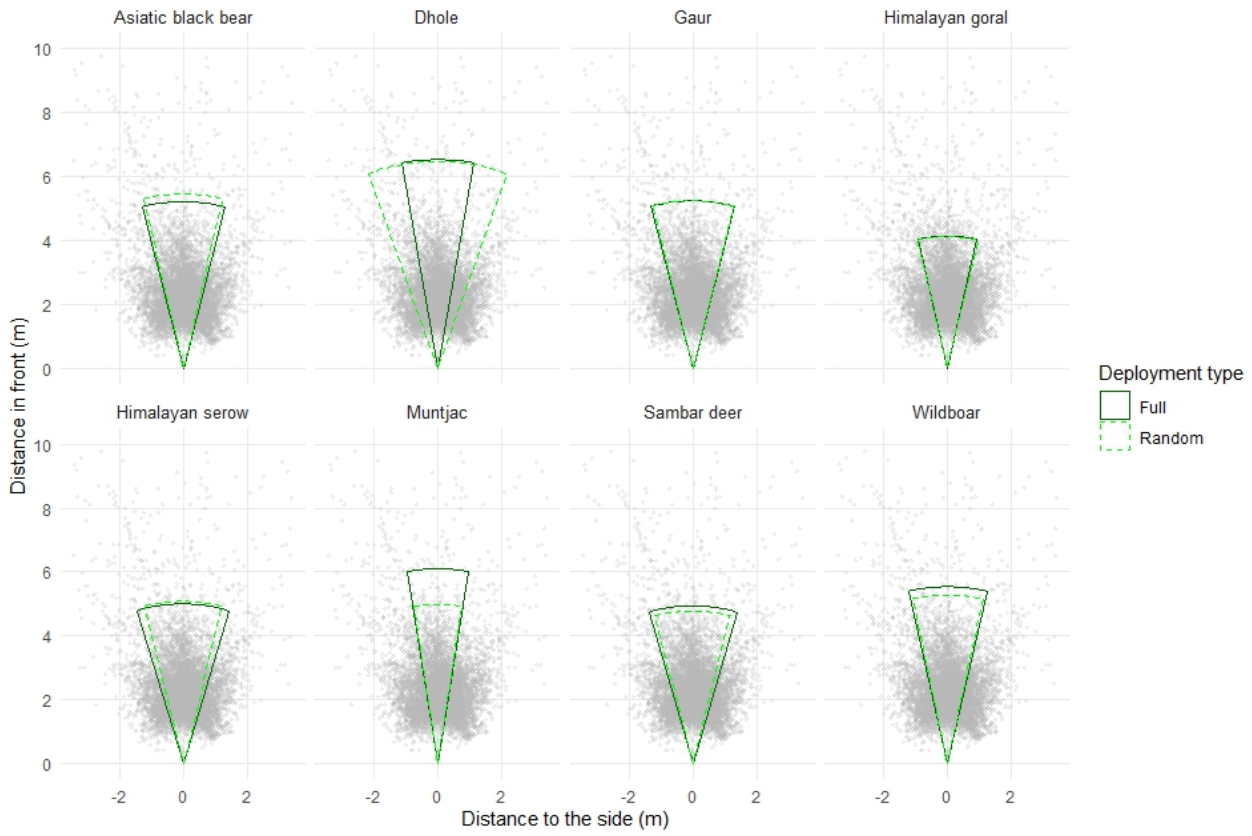


Figure S4. The detection zone of wild felids estimated of Panthera V7 Xenon camera deployed in the trail stations (black) and the random station (green). Detection zones are derived from angle of

detection and the radius of detection. The grey points represent the position of animal in front of the camera traps.



FigureS5. Detection zone of prey species detected in trail and random stations derived from angle and radius of detection. Rest of the figure legends are same as for Figure 3.

Table S2. Coefficient of variance of mean density estimates from SECR and REM for different combination of camera stations. The numbers in bold represent the most precise estimates for each species.

Species	**Station combinations**	**$CV_{meanREM}$(%)**	**$CV_{meanSECR}$(%)**
Common leopard	100T & 100R	58.95	**26.67**
	100T&0R	30.65	30.67
	0T&100R	**29.33**	42.65
Clouded leopard	100T & 100R	39.42	27.43
	100T&0R	32.69	**25.79**
	0T&100R	**28.03**	49.75
Marbled cat	100T & 100R	**0.30**	15.58
	100T&0R	35.20	17.89
	0T&100R	45.10	**12.55**
Leopard cat	100T & 100R	33.57	**9.85**
	100T&0R	37.36	12.80
	0T&100R	**28.23**	34.22

Table S3. Species, day range, encounter rate and detection zone were applied as fixed factor effecting bias (response variable), and station combination is used as random factor. MC (Marbled cat), CL (Clouded leopard), L (Leopard), and LC (Leopard cat).

Station combination	Species	Day range	Encounter rate	Detection zone	Bias
100T & 100R	MC	Adequate	Adequate	Adequate	22.6
100T & 0R	MC	Adequate	Conservative	Adequate	18.6
0T & 100R	MC	Adequate	Adequate	Adequate	-3.9
25T & 75 R	MC	Adequate	Adequate	Adequate	12.32
75T & 25R	MC	Adequate	Conservative	Adequate	13.87
12T & 76R	MC	Conservative	Adequate	Conservative	11.12
50T	MC	Conservative	Conservative	Conservative	10.52
50T & 50R	MC	Adequate	Adequate	Adequate	16.73
33T &34R	MC	Conservative	Adequate	Conservative	-9.69
25T &50R	MC	Conservative	Adequate	Conservative	11.17
100T & 100R	CL	Adequate	Adequate	Adequate	20.76
100T & 0R	CL	Adequate	Conservative	Adequate	39.65
0T & 100R	CL	Conservative	Adequate	Adequate	36.99
25T & 75 R	CL	Conservative	Adequate	Adequate	10.89
75T & 25R	CL	Conservative	Conservative	Adequate	13.66
12T & 76R	CL	Conservative	Adequate	Adequate	23.49
50T	CL	Conservative	Adequate	Conservative	10.61
50T & 50R	CL	Adequate	Adequate	Adequate	11.17
33T &34R	CL	Conservative	Adequate	Conservative	12.02
25T &50R	CL	Conservative	Adequate	Conservative	10.14
100T & 100R	L	Adequate	Adequate	Adequate	4.49
100T & 0R	L	Adequate	Conservative	Adequate	6.75
0T & 100R	L	Conservative	Adequate	Adequate	6.6
25T & 75 R	L	Conservative	Adequate	Adequate	2.64
75T & 25R	L	Conservative	Conservative	Adequate	1.82
12T & 76R	L	Conservative	Adequate	Adequate	2.71
50T	L	Conservative	Conservative	Conservative	0.99
50T & 50R	L	Adequate	Adequate	Adequate	2.8
33T &34R	L	Conservative	Adequate	Conservative	-0.74
25T &50R	L	Conservative	Adequate	Conservative	0.4
100T & 100R	LC	Conservative	Conservative	Adequate	68.23
100T & 0R	LC	Conservative	Adequate	Adequate	60.24
0T & 100R	LC	Conservative	Adequate	Adequate	-13.88
25T & 75 R	LC	Conservative	Adequate	Adequate	31.08
75T & 25R	LC	Conservative	Conservative	Adequate	46.78
12T & 76R	LC	Conservative	Adequate	Adequate	24.75
50T	LC	Conservative	Conservative	Conservative	22.53
50T & 50R	LC	Conservative	Conservative	Conservative	76.72
33T &34R	LC	Conservative	Adequate	Conservative	39.29

25T &50R	LC	Conservative	Adequate	Conservative	40.18

Table S4: Results of LLM showing the factors that determines the reliability of REM.

Predictors	**Estimates**	**CI**	**p**
(Intercept)	1.32	-12.19 – 14.83	0.844
Detection zone Conservative	-1.23	-13.99 – 11.53	0.845
Encounter rate Conservative	10.52	-0.56 – 21.60	0.062
Day range Conservative	-1.79	-16.23 – 12.64	0.802
Species [Leopard cat]	36.36	22.68 – 50.03	**<0.001**
Species [Marbled cat]	7.07	-6.96 – 21.10	0.312
Species [Clouded leopard]	17.14	4.04 – 30.25	**0.012**
Observations	40		
Marginal R^2 / Conditional R^2	0.499 / 0.533		

Appendix 3. Supplementary information for Chapter 4

Appendix 3a. Standard Operating Procedure for live trapping

STANDARD OPERATING PROCEDURES FOR LIVE-TRAPPING AND CHEMICAL IMMOBILIZATION OF CLOUDED LEOPARD (*NEOFELIS NEBULOSA*)



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UNIVERSITY OF Southampton
School of Biological Sciences

19 November, 2021

To whom it may concern,

APPROVAL OF STANDARD OPERATING PROCEDURE

Title: Standard Operating Procedure for Live-trapping and Chemical Immobilization of Clouded Leopard (*Neofelis nebulosa*)

In my role as Academic Supervisor of Mr Lungten Dorji's PhD at the University of Southampton, I hereby approve the Standard Operating Procedure (SoP) for Live-trapping and Chemical Immobilization of Clouded Leopard (*Neofelis nebulosa*) for his PhD project "Resolving bias in population density estimates of big cats."

This SoP has been reviewed by Dr Lon Grassman, who has over 30 years of experience in live-trapping small and large Asian felids, including clouded leopards. The SoP will guide Mr Lungten and his field assistant in carrying out live-trapping fieldwork for his field study of the movement ecology of clouded leopards in Bhutan, which is an essential component of his PhD project.

Yours faithfully,

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Introduction

The purpose of this Standard Operating Procedure (SOP) is to guide the live trapping of clouded leopard (*Neofelis nebulosa*), its chemical immobilization, and fitting of GPS collars for studying its movement ecology. The guidelines in this SOP are based upon a review of scientific papers, technical guides for animal capture and immobilization, expert guidance, and legal documents. The SOP guides the entire process of live-trapping clouded leopards for the project "Resolving bias in population density estimates of big cats" and "Mitigating human-felid conflict with the knowledge of cats movement ecology." The stepwise live-trapping techniques, chemical immobilization techniques, and collaring procedures will guide the principal investigator and the team in the field.

This SOP has three chapters: the first chapter covers detailed techniques for trapping clouded leopards, types of traps, use of bait, safety, and trap monitoring. The second chapter discusses chemical immobilization techniques, including handling trapped animals, assessing health before delivering anaesthetic drugs, recommended sedation and reversal drug dosages, and monitoring animal health during recovery. The third chapter outlines protocols for fitting GPS-collars and subsequent field telemetry. The SOP appendices include a checklist for drug administration kits, trap monitoring form, drug administration chart, animal health, and biology.

This SOP is specifically for the live trapping of clouded leopards for the project mentioned in the first paragraph of this section. The University of Southampton, Dr. Lon Grassman, and the Department of Forests and Park Services of Bhutan developed this SOP. The authors will not be responsible for any injury, death, or damage to animals or humans due to applying the techniques presented in this text except for the project mentioned above.

"THERE ARE NO SAFE DRUG COMBINATIONS AND NO SAFE ANESTHETIC PROCEDURES; ONLY SAFER ANESTHETISTS MAKING BETTER CHOICES!" (ZSSD 2021)

CHAPTER 1: STANDARD OPERATING PROCEDURES FOR LIVE-TRAPPING CLOUDED LEOPARDS

For live-trapping clouded leopards, the survey team, consisting of foresters and veterinarians, will deploy guillotine door box-traps at predetermined locations in the field (Appendix 1). Each trap will have separate bait boxes secured to the rear of the trap with live chickens as the bait. Bait chickens will be protected from physical harm. The project will utilize eleven box traps with bait boxes built on the recommendation of Dr. Lon Grassman (Grassman, Tewes et al. 2005).

- ### Construction of guillotine door box-trap

The trap is a guillotine door box-trap (50H X 40W X 160L cm) with a door drop mechanism, and foot treadle located about 100 cm within the trap (Fig. 1.1). A strong mesh/fencing material covers the trap with an opening large enough to allow easy access for a pole syringe during chemical immobilization. The traps are designed with smooth interior surfaces to minimize injuries to animals from the door closure or efforts to escape the trap.

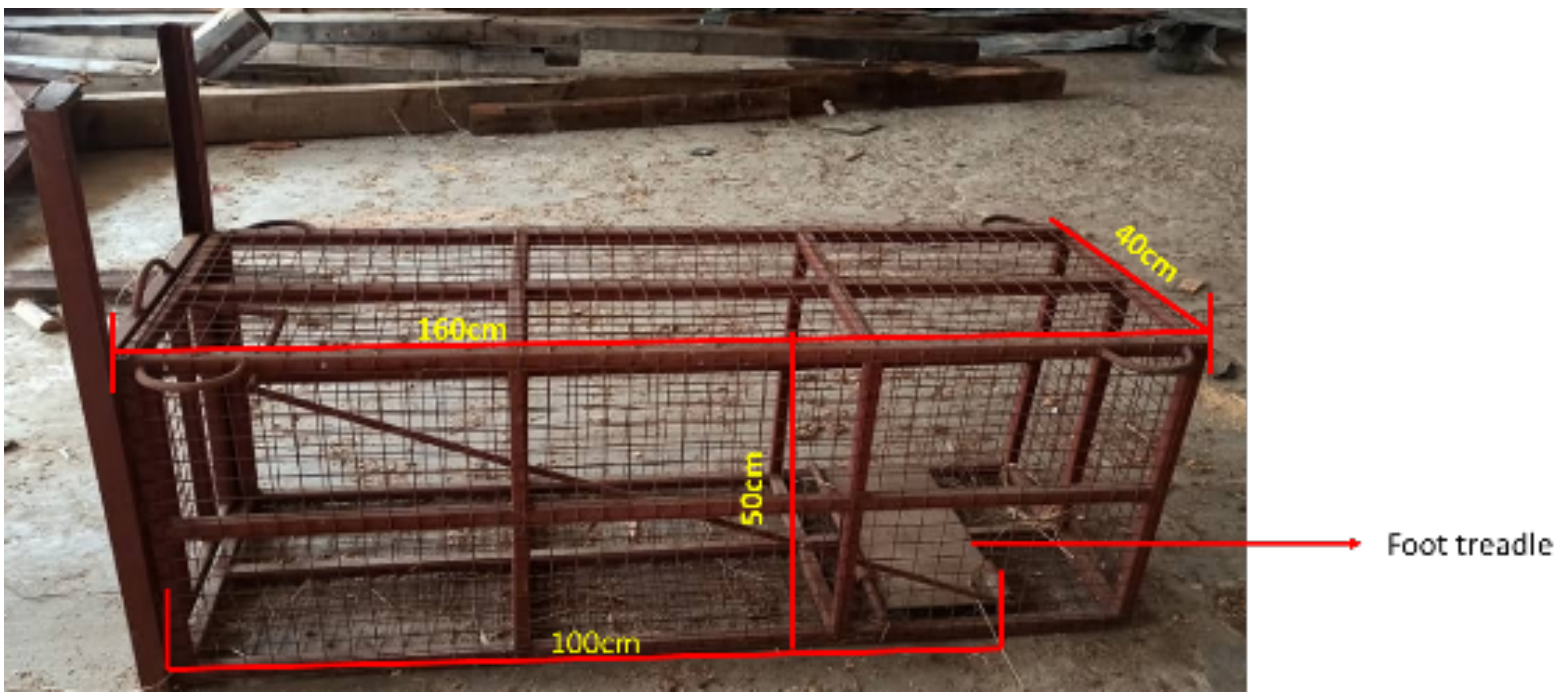


Fig 1.1: Dimensions of the guillotine door box-trap

The trap has a sliding door trip mechanism that is triggered when an animal steps on the 12 x 45 cm foot treadle (Fig. 1.2). Average foot treadle trip weight is about two kilograms.



Fig 1.2: Guillotine door box-trap showing door trip mechanism.

- Fabrication of bait-boxes and choice of bait

Bait boxes for live chickens have a dimension of 46 wide x 30 length x 51 height cm and have a robust and secure lid on top for access to the chickens (Fig.1.3). These boxes are wired to the back of the trap when completed. We used the strongest materials possible to avoid injury or loss of chickens from carnivores ripping the lid off. Plastic cups for water and food will be wired inside the boxes, and a perch stick will be installed prior to adding the chickens.



Fig 1.3: Bait box for live chickens

We will use live domestic chickens as bait for clouded leopards with one chicken per bait box. Chickens will be quarantined for one week before taking them to the field. The veterinarian will determine chicken fitness for use as bait.

- Selection of trap site

We will place traps in locations having a high probability of clouded leopard presence based on the occupancy rate and capture rate of clouded leopards from a camera trap study of this project. Eleven locations were chosen spread across the northern side of Royal Manas National Park (RMNP) and the central part of Jigme Singye Wangchuck National Park (JSWNP), based on the camera-trap results (Appendix 1). Traps will be run for sixty days in these areas, and then we will shift traps to other locations in the central portion of RMNP and southern parts of JSWNP (Appendix 2) for an additional sixty days. Trap movement may also occur based on real-time information such as pug marks, indicating clouded leoard presence in a particular area.

- Setting traps in the field

Micrositing within the potential trap site locations will be based upon clouded leopard sign (i.e., scats and pug marks); in addition to positive camera trap locations. We will cover both the traps and bait boxes with vegetation for shade and camouflage (Fig. 1.4).



Fig 1.4: Example of Tomahawk™ style mesh trap with vegetation covering the top of the trap from clouded leopard study in Thailand (photo: L. Grassman).

- Monitoring traps

After placing traps at the designated locations, we will monitor each trap on a varying schedule based on the presence or absence of electronic door monitoring devices. Traps that are close to roads and are not equipped with a door closure monitoring devices (Catch Alive™) will be checked every twenty-four hours for captures. Traps that are located further away from roads equipped with Catch Alive™ monitoring devices will be checked at least once every

two days, unless a door closure alert is received in which case these traps will be checked as soon as possible. The Catch Alive™ monitors will send SMS alerts upon the closing the trap doors (Fig.1.5). The monitoring team will update the trap monitoring form (Appendix 3 using the Epi collect data collection software (Epicollect5).



Fig 1.5: Example of Tomahawk™ trap fitted with Catch Alive™ remote trap monitor, and schematic of monitor placement on the guillotine door box-trap to be used in this study.

- Protocol for fitting trap monitor

We will weld a thin metal plate to the sliding door edge (RED 15cm x width), and one to the outside rail, from which the monitor will be attached (YELLOW 10 x 14cm). A 10-20 mm thick plastic backing (GREEN) will be glued to the red plate and a magnet glued to this backing (BLUE) at a position that is in the correct location to the monitor (Fig. 1.6). The magnet will be located <20 mm from the monitor, close to the yellow cross in the below photo.

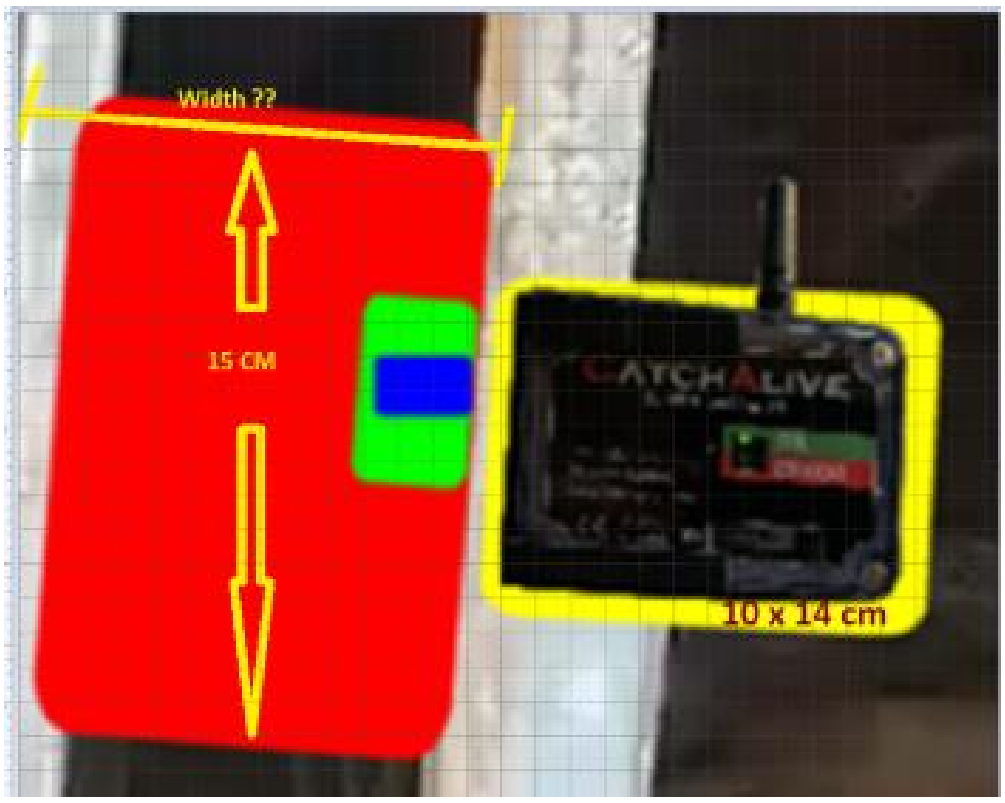




Fig 1.6: Schematic for fitting the trap monitor

- Animal handling

Live-trapping will result in either no captures, non-target species captures, or clouded leopard captures. Each monitoring team will check the traps for animal captures, and will also trip each empty trap and reset to ensure that trap functionality is adequate. All non-target captured animals will be released after visual observation by the veterinarian for any health issues. If the trapped animal is an adult or young adult, healthy clouded leopard then the veterinarian will administer the sedation drugs and fit a GPS collar to the clouded leopard following prescribed protocols in the following chapters (Chapter 2). All juvenile or unhealthy clouded leopards will not be collared and will be released immediately after veterinarian observation (Fig. 1.7).

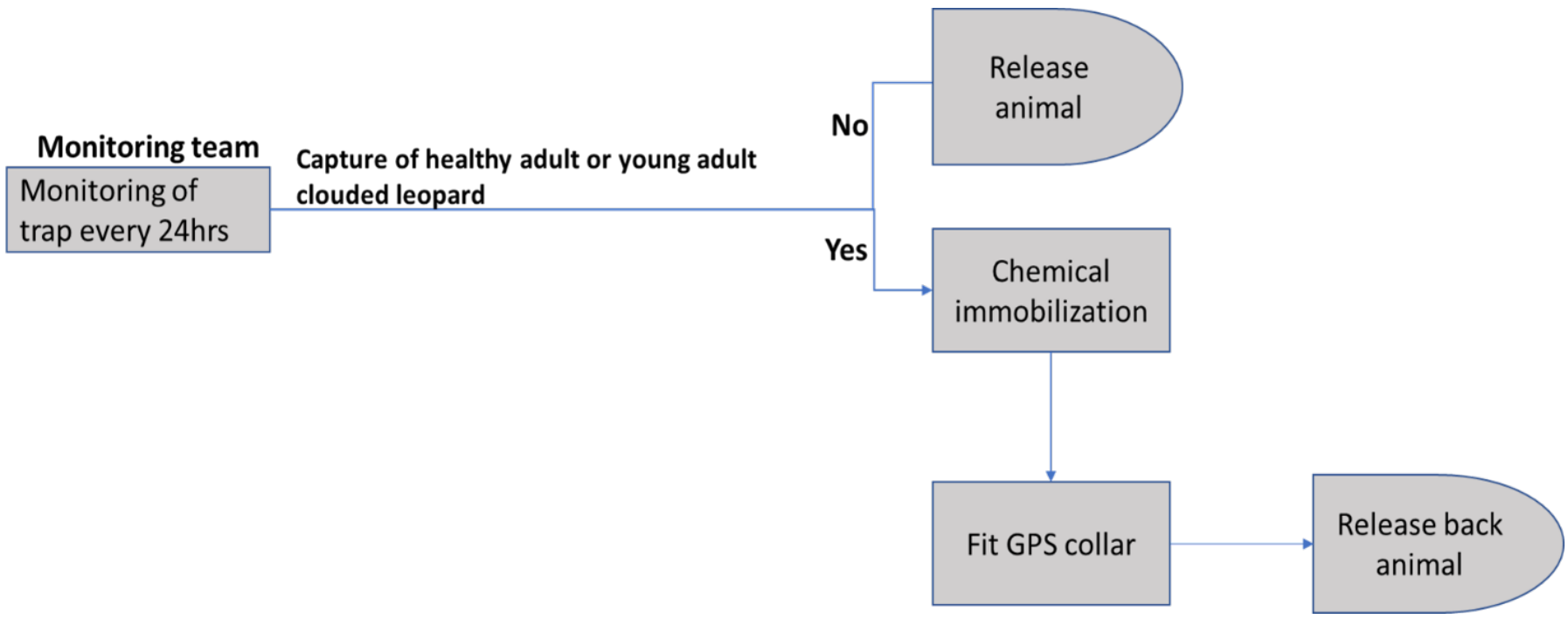


Fig 1.7: Decision tree during live trap monitoring.

- Operation plan for live trapping

We will set live traps in eleven different locations spread across the Gomphu Range of Royal Manas National Park, the Tingtibee Range, and the Nabji Range of Jigme Singye Wangchuck National Park. We will have three monitoring teams for the monitoring of live traps. Each monitoring team will check the traps for animal captures and will also trip each trap and reset to ensure that trap functionality is adequate. Bait chickens will be providing water and feed *ad libitum* during each visit, and a general health assessment of the chicken will be made. Bait chickens that appear to be unhealthy or unduly stressed, will be replaced with healthy birds. The monitoring team shall complete a trap monitoring form daily (on epi collect) and send to the principal investigator.

In the event that non-target small mammals are captured, they will be immediately released to reduce capture stress. If a large, non-target carnivore is captured, the animal will be anesthetized by a veterinarian and released remotely for the safety of the animal and humans. If the trapped animal is a clouded leopard or a common leopard, the monitoring team will alert the on-call veterinarian and follow the immobilization process. The principal investigator will assist the monitoring team and veterinarian and update the progress weekly to Patrick Doncaster and Lon Grassman.

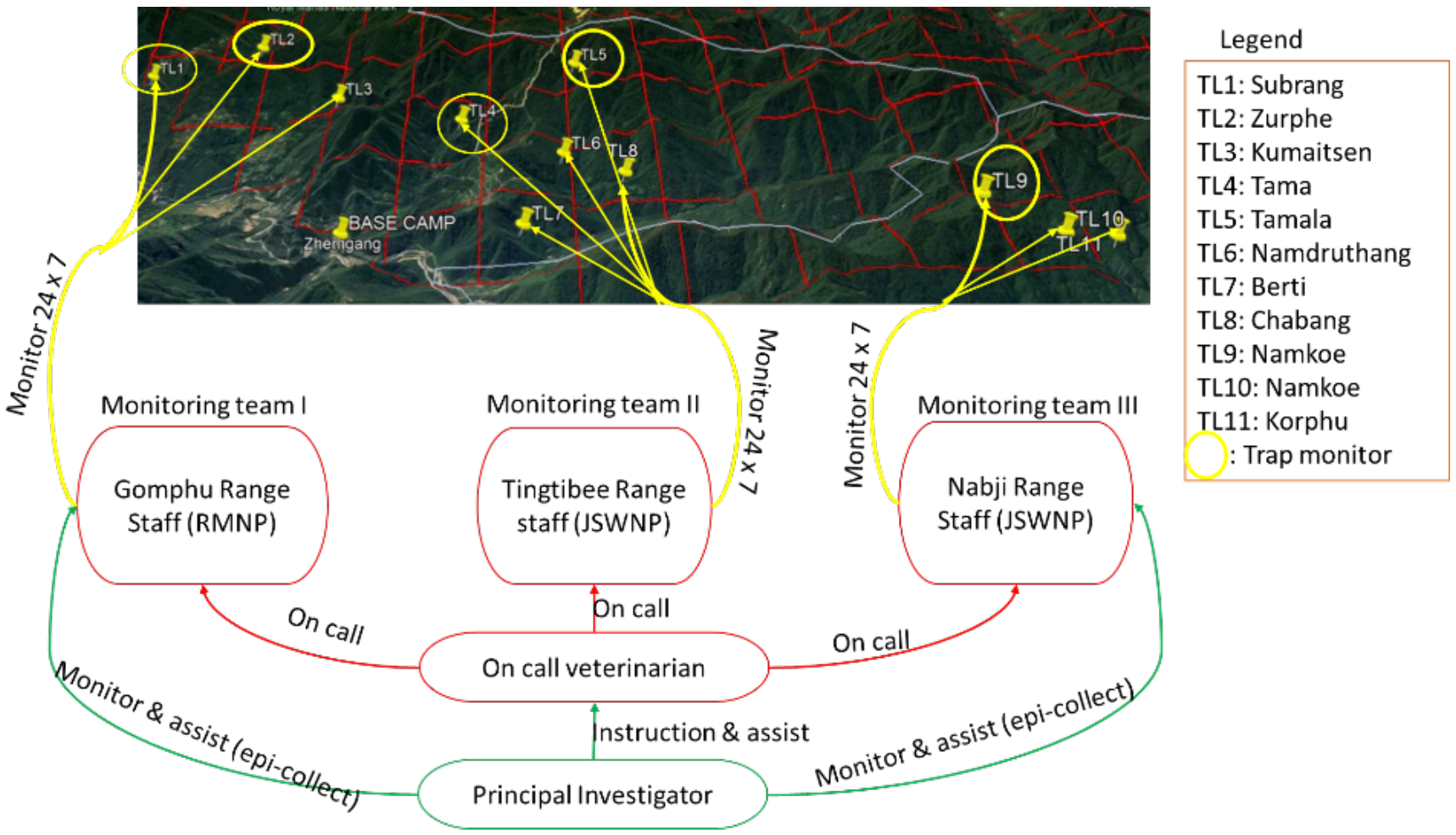


Fig 1.8: Schematic workflow plan for live-trapping.

CHAPTER 2: STANDARD OPERATING PROCEDURES FOR CHEMICAL IMMOBILIZATION AND HANDLING OF ANIMALS

This chapter describes the guidelines for handling trapped animals and the administration of drugs for anaesthesia.

2.1. Trapping procedures

Trapped animals are subjected to physical and mental stress from unfamiliar or unnatural conditions. Every monitoring team will assess the condition of the trapped animals (whether stressed or calm) and endeavour to minimize stress and induce a relaxed state to administer the anaesthesia. Minimizing stress before capture has been shown to bring about more positive sedation results. The team shall ensure a minimal presence of team members are near the trapped animal before anaesthesia to reduce stress.

2.2. Chemical immobilization of clouded leopard

Clouded leopards will be immobilized by intramuscular injection of medetomidine-ketamine, which has been previously demonstrated as safe for the congeneric (*Neofelis diardi*) in Borneo (Nájera, Hearn et al. 2017). We may also use ketamine hydrochloride and xylazine hydrochloride (KH-XH), which was successfully used on wild-caught clouded leopards in Thailand and has an excellent safety record (Grassman, Austin et al. 2004). Intramuscular injections will be administered using a pole syringe jabbed into the hindquarters of captured felids.

The immobilization of each animal will follow strict compliance with protocols prescribed by the National Animal Health Center of Bhutan and with the Manual on Chemical Immobilization of Wild Animals of the Central Zoo Authority of India (CZA 2017), following national guidelines in Bhutan. These procedures comply with the ethics policy and guidelines of the University of Southampton (Ethics and Research Governance Online number 53715). The team will strictly follow the following detailed Protocols for administering drugs for chemical immobilization:

2.2.1. Preparation before proceeding to the field

Before proceeding to the field, each team shall carry the following Equipment and the checklists of documents:

1. Drug kits (pole syringe, anesthetic drugs [medetomidine-ketamine or ketamine hydrochloride/xylazine hydrochloride (KH-XH)], and a reversal drug).
2. Forms (drug administration chart, animal biometrics form, and health checklist)
3. Equipment (tarpaulin sheet, hanging scale, measuring tape, canine and mouth protection, cornea protection gel, non-latex gloves, face mask, etc.).

2.2.2. Choice of drug delivery method

To administer chemical immobilization drugs to clouded leopards, we will use a pole syringe for the direct injection into trapped animals, transport containers, or handling facilities. Pole syringes, sometimes known as push poles or jab sticks, come in various types, each with

varying mechanisms of action. As a basic description, a pole syringe is a syringe mechanism contained within or mounted on the end of an extendable pole. Pole syringes are an essential piece of equipment for all capture kits.

We will use a mechanical pole syringe (Dan-Inject™ Jabstick) that discharges its contents automatically using mechanical pressure from a spring-loaded or gas (air or butane) discharge mechanism. The Dan-Inject™ Jabstick is a 3 ft (0.9 m), stainless steel pole with a removable 3 ft (0.9 m) extension handle (Fig. 2.1-2). It has a multi-use, nylon, friction tip 10 ml syringe. This pole syringe is pressurized by hand cocking. Once cocked, rotation of the safety mechanism below the syringe prevents accidental discharge. With the safety mechanism in the fire position the medication is discharged when the head of the syringe contacts against the animal.



Fig 2.1: Dan-Inject™ Jabstick and stainless pole syringe

2.2.3. Procedure for drug loading

The veterinarian will follow the Protocol for loading the drugs with care to avoid human exposure.

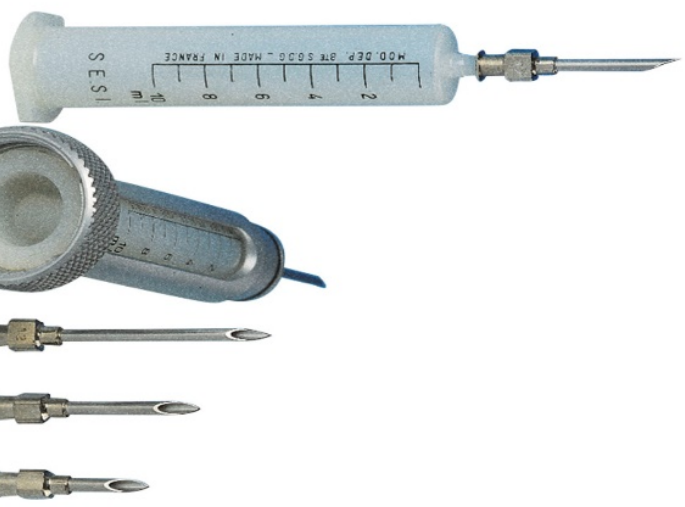


Fig 2.2: Syringe of Dan-inject Jabstick

2.2.4. Choice of anesthetic and reversal drugs

Chemical restraint is a form of animal restraint technique in which a drug or a chemical is used to restrict an animal's movement (walking, running, aggression) or to sedate or calm an animal. Chemical restraint is a safe and effective capture method when applied correctly and with due precaution. Chemical restraint is advantageous over physical capture because it allows examining and treating sick and injured animals or animals caught in snares or traps in the wild by poachers. There are different types of chemical immobilization:

Anaesthesia: (from Greek and-"without" and aesthesis- "sensation"), a state of total loss of sensation in a body, induced by a drug that depresses the activity of nervous tissue peripherally (local and regional anesthesia) or centrally (general anesthesia).

Analgesia: The loss of sensibility to pain (relief pain) without loss of consciousness.

Narcosis: State of sleep accompanied by analgesia.

Hypnosis: Artificially-induced sleep-like state from which stimuli can arouse the animal.

Sedation: Calming due to mild degree of depression of central nervous system; most sedatives cause drowsiness.

Tranquilization: A state of behavioural changes in which the animal is relaxed and unconcerned by its surroundings.

Local analgesia (anaesthesia): A loss of sensation in a defined area of the body.

Regional analgesia: Loss of sensation in a larger but limited body area.

Balanced anesthesia: General anaesthesia produced by a combination of two or more anaesthetic drugs or techniques to achieve optimum hypnosis, analgesia and muscular relaxation.

General anesthesia: Complete unconsciousness produced by a controlled, reversible intoxication of the central nervous system in which there is muscle relaxation and diminished response to external stimuli.

A variety of drugs have been used for the chemical restraint of zoo and wild animals. As such, there is no perfect drug or an anaesthetic that will suit a variety of animal species. We will use one or more of the following drugs for chemical immobilization:

3. Medetomidine-ketamine 3-4.4 mg/kg, which has been previously demonstrated as safe for the congeneric (*Neofelis diardi*) in Borneo (Nájera, Hearn et al. 2017) to induce anesthesia in clouded leopards.
4. Ketamine hydrochloride and xylazine hydrochloride (KH-XH) at 15.00±1.00 mg/kg, which was successfully used on wild-caught clouded leopards in Thailand, and on other felid species worldwide, and has an excellent safety record (Grassman, Austin et al. 2004). For the ketamine-xylazine combination, we will use Yohimbine 0.125 mg/kg (intravenously) or 0.25mg/kg (intramuscularly), which is recommended for xylazine reversal in carnivores.

5. Tiletamine and zolazepam may be used at 5.0 mg/kg as it also has been used in the chemical immobilization of multiple wild felids, including clouded leopards.

We will use these prescribed dosages to immobilize clouded leopards for this project (Table 2.1). We will also follow the standard drug dose calculation formula to calculate the correct drug dosage for the animal (Fig. 2.3).

How to calculate drug doses

$$\text{Volume of drug} = \frac{\text{Body weight x Dose}}{\text{Concentration of Drug}}$$

For example, if a leopard weighs 100 Kg and the recommended dose of Drug 'Ketamine for this animal is 3 mg/kg. Ketamine is available in a 100 mg/ml solution. So, first calculate the total mg of ketamine required for leopard.

mg of Ketamine needed = 100 kg x 3 mg/kg = 300 mg

Then calculate the total volume of Ketamine solution

$$\text{ml of Ketamine needed} = \frac{300\ \text{mg}}{100\ \text{mg/ml}} = 3\ \text{ml of Ketamine solution}$$

Fig 2.3: Example of drug dosage calculation.

Sl.No	Drug combination	Dosage	Reversal
1	ketamine hydrochloride and xylazine hydrochloride (KH-XH)	15.00±1.00 mg/kg	Yohimbine 0.125 mg/kg (intravenously) or 0.25mg/kg (intramuscularly)
2	medetomidine-ketamine	3-4.39 mg/kg	
3	Tiletamine and zolazepam (Zoletil©)(Fernando, Andrew et al. 2013)	2.6±0.33 mg/kg	Does not require reversal agent

Table 2.1: Chemical immobilization drug and its concentration

2.2.5. Procedure to follow before initiating chemical immobilization

Before initiating the immobilization protocols, the monitoring team will consider the following:

1. **Are all aspects of the biology of the animal and the safest anesthetic techniques for the species known?** How is the animal likely to respond to capture and restraint? How susceptible is the animal to stress or self-injury? What is the safest and least traumatic technique for the species? How will these species respond to darting? Will it tend to attack? The more that is understood about the species' biology, the better versed on techniques that have historically been used in the species at hand, the better an anesthetist can be for that animal.

2. **What is the physical condition of the animal?** Can the weight of the animal be accurately estimated for safe dosage calculation? Is the animal emaciated, old, injured, sick, highly stressed, pregnant, or lactating with associated young?

3. **What is the mental condition of the animal?** Has the animal been pursued prior to capture? Is it scared or highly stressed? The calmer the animal is at the time of dart placement and medication injection, the more consistent the response to the drugs.

The monitoring team will consider these conditions with the veterinarian before proceeding with administration of the anesthetic drugs.

2.2.6. Protocol for the administration of anesthesia

The veterinarian will administer the anesthesia with an intramuscular injection using the Dan-Inject™ jab stick preloaded with the drug. The injection site will be the animal's posterior thigh muscle, which is typically the most muscular part of a cat and has a heavy network of blood vessels (Fig. 2.4).



Fig 2.4: Hindquarter location on a clouded leopard for the drug injection.

2.2.7. Approaching the immobilized animal

We will approach trapped animals slowly, quietly, and from outside of the visual range of the animal upon recommendation of the accompanying veterinarian. We will observe the animal's eyes and ears for any sign of conscious perception (awareness) of the approach. We will break a stick or make a low clicking noise and look for the animal to cock an ear or raise its head. It is essential for animal and human safety that an incompletely immobilized animal is not approached until it is taken to a proper depth of anesthesia. Any sign of awareness by the animal indicates an inadequately immobilized animal and warrants more medication before a full approach. Approaching an inadequately immobilized animal will initiate a flight response by the animal, increase the chance of stress-related mortality, and decrease the effectiveness of any subsequent medication administered. As such, we will allow adequate time for the full effects of sedation to occur.

2.2.8. Animal handling after administration of anesthesia

After administering anesthesia, the animal will be held in the recommended position to avoid complications from sedation. Every team will follow the post-capture Protocol after the administration of anesthetic drugs.

2.2.9. Post-capture care

The team will protect the animal as feasible to reduce injury and stress by following the veterinarian's advice. Sedated carnivores will be placed in either sternal recumbency or lateral recumbency, but ideally will be in the left lateral recumbency (Fig. 2.5). The esophagus is located on the left side of the neck and enters the pharynx in the upper left hand side of the mouth. If an animal is placed in left lateral recumbency with the head in a neutral position or nose downward, and regurgitates while under anesthesia, the vomitus will run along the left side of the throat and out of the mouth. If the animal is placed in right lateral recumbency, the vomitus must first cross the airway and then proceed along the right side of the throat exiting the mouth. Left lateral recumbency adds a safety factor to reduce possible aspiration should regurgitation occur.



Fig 2.5: Captured clouded leopard in lateral recumbency position (Photo: L. Grassman).

2.2.10. Anesthetic monitoring

There are three major purposes for monitoring an animal under anesthesia. When a state of anesthesia is produced in an animal, the anesthesia may partially or fully incapacitate the animal's ability to perform normal physiologic and homeostatic functions. Physiologic disruptions may include an increase or decrease in blood pressure, decreased tissue perfusion and circulation, alterations in the ability to regulate blood vessel diameter (vasodilation, vasoconstriction), loss of muscle tone, or the ability to maintain body temperature (thermoregulation), increases or decreases in the depth or rate of respiration and alterations in gastrointestinal motility. The person administering anesthetic medications to an animal assumes moral and legal responsibility for that animal's safety until complete recovery, including physiologic stability. As such, observation of the animal for signs of any physiologic malfunction caused by the anesthetic medications or the procedures performed will be done.

We will perform anesthetic monitoring mainly with the following goals:

1. **Ensure adequate gaseous exchange**: The first goal is to ensure that the animal has adequate gas exchange during respiration. Is the animal achieving unimpeded airflow into the lungs with inspiration, and unimpeded gas flow out of the lungs with expiration?
2. **Ensure adequate tissue perfusion:** The second goal in anesthetic monitoring is to ensure good tissue perfusion. Is the oxygen taken into the lungs being circulated to the tissues of the body? Air is taken into the lungs with inspiration, but air is only 20% oxygen. This inspired oxygen diffuses through the alveolar membrane of the lung and dissolves into the blood. When blood is circulating

well, the oxygenated blood is carried to the tissues to replenish the tissue oxygen required for metabolism. Metabolism produces waste products, which must be removed from the tissue for continued proper function. Carbon dioxide, the by-product or waste product of aerobic cellular metabolism, must be removed from the tissues and carried back to the lungs. As the blood passes into the lung tissue, the carbon dioxide diffuses through the alveolar membrane and is exhaled. As blood passes through the lungs, it is replenished with oxygen, and the by-products of metabolism, carbon dioxide, are removed.

3. **Assess the depth of the anesthetic plane:**

The third goal of anesthetic monitoring is to determine the quality of the anesthetic depth. How well anesthetized is the animal? What is the depth of central nervous system depression? How well have the drugs depressed consciousness and the animal's awareness of the environment? An animal under an appropriate plane or depth of anesthesia has no conscious awareness of the environment and no response to stimuli. If an animal is aware of its surroundings, it will incur stress with handling. To minimize stress, ensure that the animal has little or no conscious perception of visual, auditory, or tactile stimulation like sight, noise or touch. A cumulative decision based on the results of many "indicator" observations or reflexes is made to assess anesthetic depth.

Protocols to assess the depth of anesthesia:

1. **Blink reflex:** Touch the medial canthus of the eye, where the two eyelids come together on the side of the nose and observe for a blink response. In a well-anesthetized animal, this reflex with be absent, or with some anesthetic drugs like cyclohexamines may be a slow or weak.
2. **Pinnal (ear flap) reflex:** Sensation on the inside of the ear is one of the last sensations to be depressed during anesthesia. Place a finger inside the ear and observe for movement of the earflap by the animal or arousal (awakening from anesthesia). An animal that is well anesthetized will have no pinnal response or a very weak response. An animal which is not at an appropriate depth of anesthesia may move the ear. Regaining pinnal sensation and the ability to move the earflap is also one of the first reflexes observed during recovery and thus a good initial indicator of arousal from anesthesia.
3. **Tail tone:** In species that have tails, gently feel for muscle tone in the tail. A well anesthetized animal will have little to no tail tone. An animal not well anesthetized may move the tail, fight against tail manipulation, or arouse as the tail is handled.
4. **Toe pinch (withdrawal) reflex:** Pinch a toe and observe the animal for any signs of arousal, conscious perception of the pinch, or withdrawal of the limb. An

animal that is well anesthetized will show no response. An animal that is recovering from anesthesia may lift its head or withdraw the limb. This is a sign of near impending recovery or the "two-minute warning".

5. **Jaw tone:** Manipulate the lower jaw and assess the amount of muscle tone present. A well anesthetized animal will show a lack of jaw tone, but jaw tome increases as recovery occurs.
6. **Heart rate and respiration rate:** Assess initial heart rate and respiratory rate values and look for trends in these values as the anesthetic period progresses. Over time, these values will generally increase as the animal recovers from anesthesia. Often times it helps to assess heart rate and respiratory rate while performing a toe pinch or testing the pinnal reflex. The animal may not be arousable enough to move an ear or withdraw a limb, but there may be an increase in heart rate or respiratory rate that more subtly indicates the beginning of the recovery process.

2.2.11. Fitting of GPS-Collars

The team shall fit GPS-Collars to clouded leopards as per standard procedures mentioned in Chapter 3 of this document.

2.3. Animal release

After collecting biometric data and fitting the GPS-Collar to the animal, the veterinarian will administer the reversal drug, if indicated. The animal will be placed back into the trap to recover. After recovery, the trap door will be raised with a rope from a safe distance to release the animal.

Chapter 3: Standard Operating Procedure for GPS-Collaring and Data Management

We will use Advanced Telemetry System's (ATS) G5™ series Iridium GPS collars to study clouded leopard movement ecology. The collar is easily programable, and the location data (fixes) are stored on the ATS website, which the users can download. Collars will be fitted with ATS SureDrop™ release system, which we will program for the collars to drop off the animal on a specific date.

This chapter has three sections covering protocols before taking GPS collars to the field, protocols to follow with GPS collars in the field, and protocols after deployment of GPS collars in the field.

3.1. Protocols before taking GPS collar to the field

This section describes the Protocol for programming collars to fit the field situation and the study's objectives. It also covers the Protocol for programming the SureDrop™ mechanism to release the collar at the designated time.

3.1.1. Equipment required

For programming the GPS collar we will use the ATS PC/GPS Wildlink module (Fig. 3.1), ATSFixes software, a personal computer, and ATS-GPS collar.



Fig 3.1: ATS PC/GPS Wildlink module (photo: ATS G-5 Series manual).

For programming the SureDrop™ we will use the ATS SureDrop collar break-off mechanism hardware, ATS SureDrop break-off mechanism software, ATS WS100 Radio Link Dongle, and a personal computer.

3.1.2. Brief Description of ATS-GPS Collar and its construction

The ATS Iridium/GPS collar has the following different assemblies (Fig. 3.2):

1. The collar belting or attachment mechanism
2. An electronic assembly attached to the collar belting
3. Antennas for VHF, GPS, and Iridium systems
4. Battery supply
5. The collar has a magnetic on/off switch indicated by two dots.

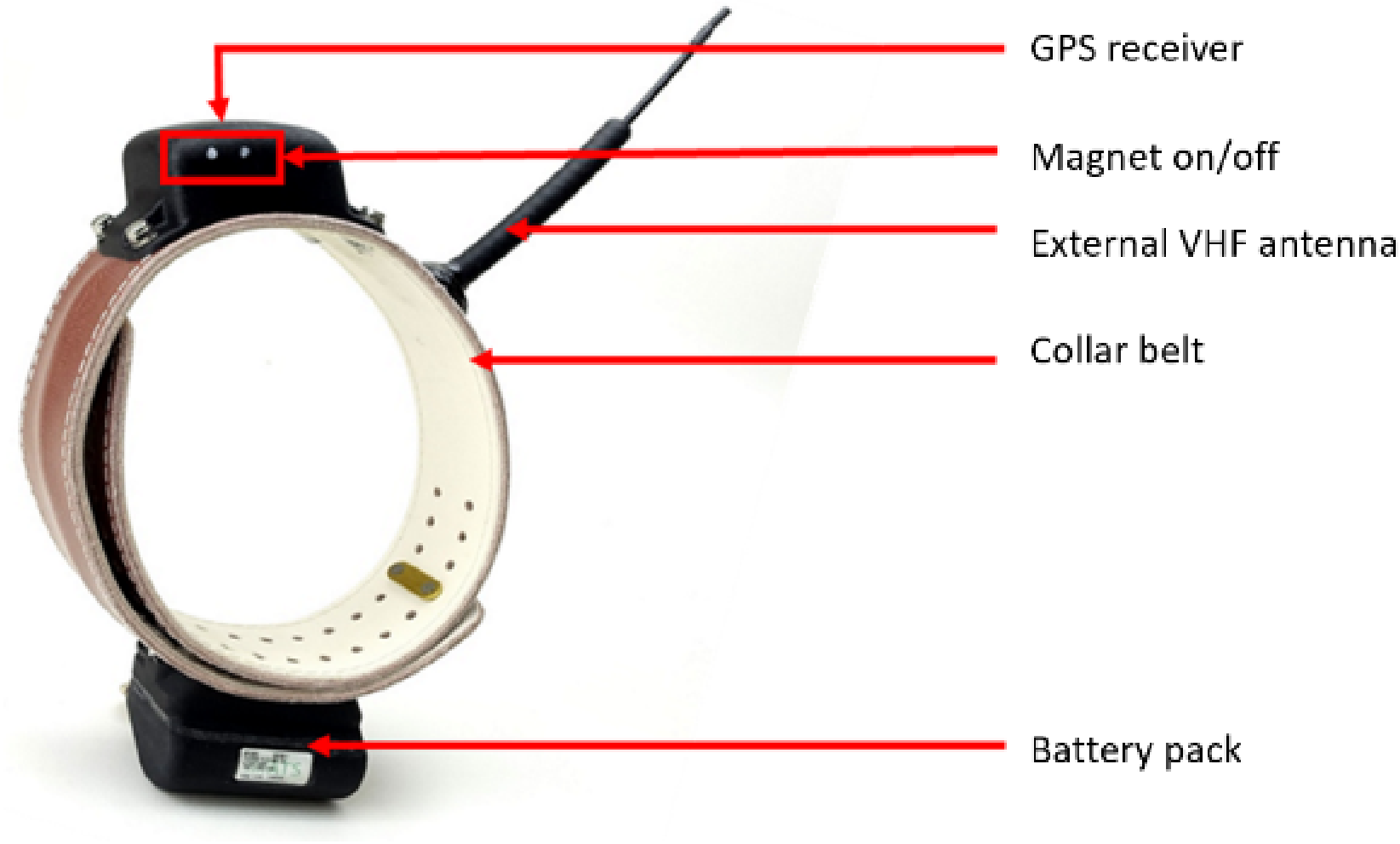


Fig 3.2: ATS Iridium GPS collar and its parts

The collar has the following specifications for the project:

Collar specs :

Mean neck circumference: 35 cm +/- 8 cm (14 +/- 3 inches). The VHF antenna will be imbedded within the collar material to protect it.

VHF frequency range: 148 MHz upwards, at 40 KHz spacing (suitable for a TRX-10S receiver).

Initial program settings:

VHF on/off times: on 10:00 – 14:00 (local time).

Time zone: GMT + 6 hrs (Bhutan)

GPS fix times: 6 fixes per day, at 18:00, 20:00, 24:00, 02:00, 04:00 (local time). Program the collar with the longest fix-rate possible (180 secs/fix) due to the thick forest canopy.

Data transmission interval: 48-hr download schedule.

Mortality hours delay: 12 hrs.

Release date/time:

The collar release date will be programmed one year after collaring animals in the field.

3.1.3. Protocol for programming GPS Collar

The "SureDrop" and "G5-D GPS" manuals will be read completely before using the collars.

We will use the Wildlink module to connect the GPS collar with the personal computer for programming GPS collars. The Wildlink module driver must be installed prior to using ATS Fixes for Satellite Collars to program the collar.

3.1.3.1 Protocol for connecting Wildlink module to Personal Computer

For connecting the GPS collar, pull the magnet off from the GPS collar and hook the Wildlink dongle to PC via USB port and keep the collar at around 200mm from the GPS collar. Follow the programming protocol mentioned on pages 6-8 of the manual.

3.1.4. Pre-testing of GPS collars

- Pull the magnets off all the GPS collars 1 week before you start trapping to make sure they are activated. Check the VHF signal between 10:00-14:00 (Bhutan time) and let the GPS signals upload throughout the day.
- Tape the magnets back on the GPS sensor.
- Check the results by logging in to the ATS data download website one day after you test the collars: https://www.atsidaq.net/login.aspx
- The manufacturer has already preset the GPS upload and VHF activation schedules.
- In the event of a mortality or collar drop-off, you will receive an email from iridium@atsidaq.net. Make sure this does not go to junk mail or spam. This info can also be found on the ATS download website when you log in.

3.1.5. Fitting of GPS collar to animal

The collar weight with the SureDrop mechanism of 415 grams will require that clouded leopards weighing >14 kg be collared to stay within <3% of animal body weight. However, clouded leopards weighing between 11.5-13.9 kg may be collared by reducing the collar weight to 350 grams by replacing the SureDrop mechanism with plastic ties as has been done in other wild cat studies (L. Grassman, pers. Com). Use of plastic ties results in the collar releasing from the animal after normal wear of around 1 year. The size of the collar can be adjusted by aligning bolts or plastic ties through collar holes, as depicted in figure 3.3.



Fig 3.3: Collar attachment options showing bolts with the Sure Drop, and plastic ties (photo: L. Grassman)

- First, remove the collar adjustment bracket nuts and plate from the collar adjustment bracket and remove the collar adjustment bracket from the main collar.
- Wrap the collar around the animal's neck so that the extra length (if any) of the main collar is tucked inside the main collar end with the VHF antenna.
- Observe where the set of holes on the VHF antenna end of the main collar line up with the holes on the other end of the main collar such as to maintain a desired tension level on the animal's neck.
- Place the collar attachment bracket through both sets of holes and through the brass bracket and tighten the collar adjustment bracket nuts using the provided nut driver. Do not over-tighten as this may damage the collar adjustment bracket.
- Finally, ensure that the case nuts have been tightened before releasing the animal.

3.1.6. Programming SureDrop

To program the SureDrop mechanism, we will follow the following protocols:

1. Download "ATS SureDrop" and "ATS fixes for Satellite Collars" software.

2. Read the "SureDrop" and "G5-D GPS" manuals completely before doing anything with the collars.
3. Pull the magnet off the the SureDrop release unit on one collar.
4. Hook up cord to SureDrop WS 100 radio link dongle and USB on your computer.
5. Follow the prompts to set the release date and update the date/time for the drop-off in the "PC Communication via Radio" mode (see p. 3 of manual). It should be set about 12 months from the estimated date that you will capture a cat, as this is about 60 days before the estimated battery life of the GPS unit. It can also be set for a shorter duration if you don't need as much data.

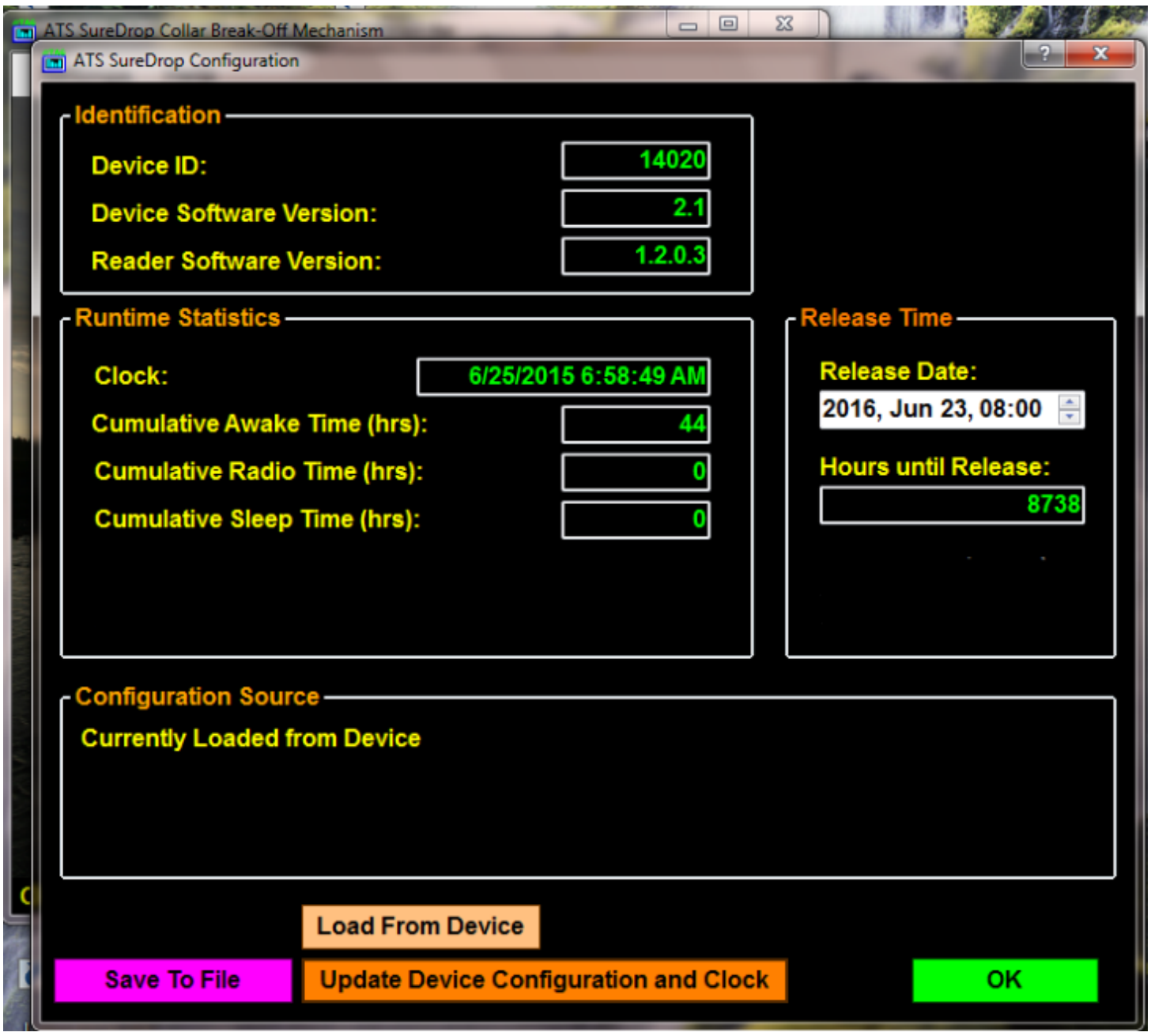


Fig 3.4: SureDrop configuration window

6. Keep in mind that if the SureDrop release is programmed too far ahead and releases after the GPS batteries are depleted, it will be impossible to retrieve the collar in the field via VHF. So, make sure that you take into account the GPS battery life before deciding on a collar release date.

7. Note that you have to be patient for the computer to communicate with the radio link dongle. It takes time for the COM port to be recognized. Also, when a release date is set it take several minutes for the drop-off unit to cycle through the commands.
8. If needed, program one collar before the first day of trapping and wait to program the others later in the trapping season so that they are not programmed too early. They are currently set to release on Dec 31, 2022.
9. When you are finished, tape the SureDrop magnet back on.

References

CZA (2017). "A Manual on Chemical Immobilization of Wild Animal."

Epicollect5. https://five.epicollect.net/.

Fernando, N., et al. (2013). "Chemical immobilization of Bornean leopard cats (Prionailurus bengalensis borneoensis) with tiletamine and zolazepam under field conditions in Borneo." The Thai Journal of Veterinary Medicine **43**(3): 445.

Grassman, L. I., et al. (2004). "Comparative Immobilization of Wild Felids in Thailand." Journal of Wildlife Diseases **40**(3): 575-578.

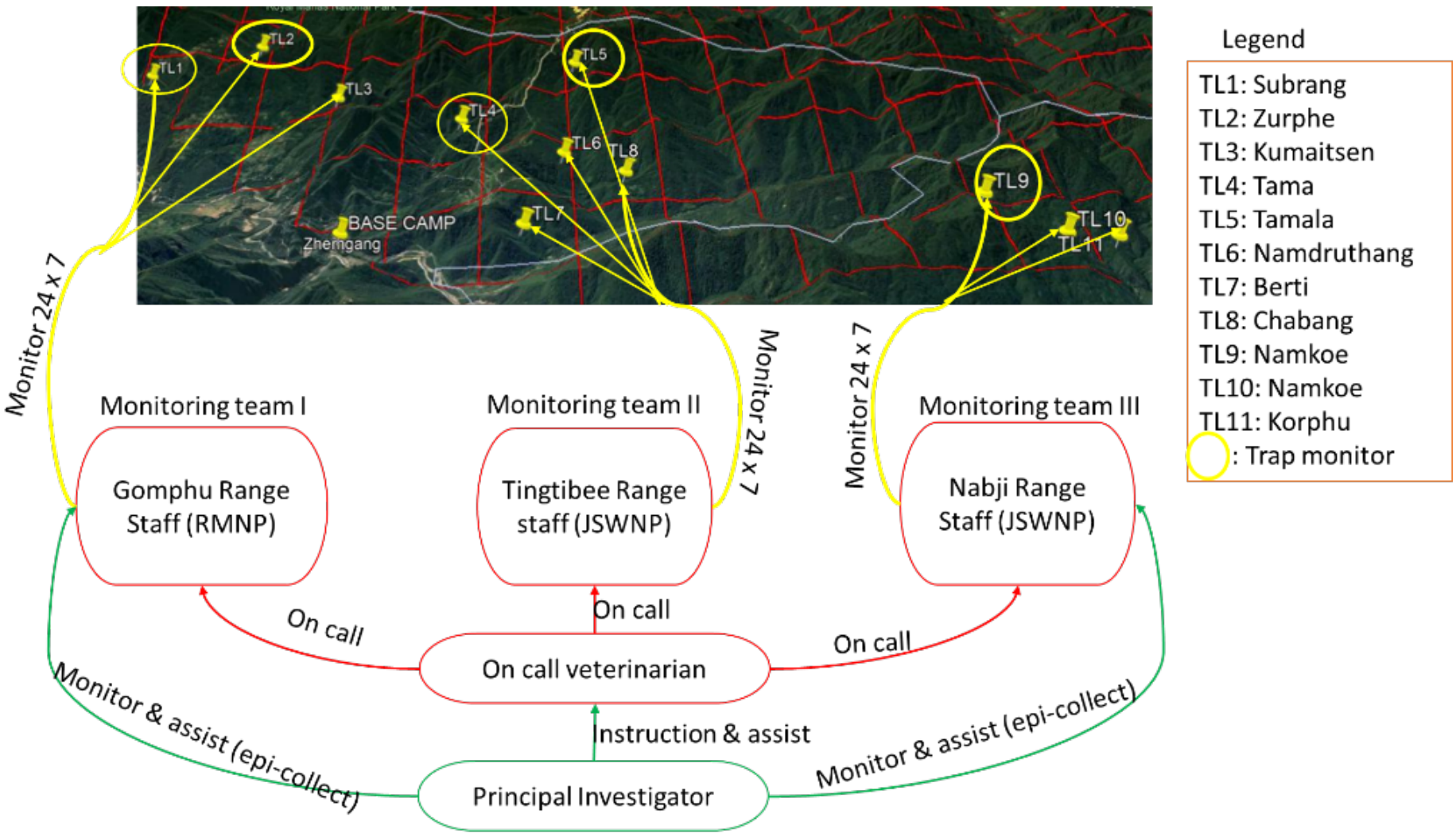
Grassman, L. I., et al. (2005). "ECOLOGY OF THREE SYMPATRIC FELIDS IN A MIXED EVERGREEN FOREST IN NORTH-CENTRAL THAILAND." Journal of Mammalogy **86**(1): 29-38.

Nájera, F., et al. (2017). "Chemical immobilization of free-ranging and captive Sunda clouded leopards (Neofelis diardi) with two anesthetic protocols: medetomidine-ketamine and tiletamine-zolazepam." Journal of Veterinary Medical Science: 17-0259.

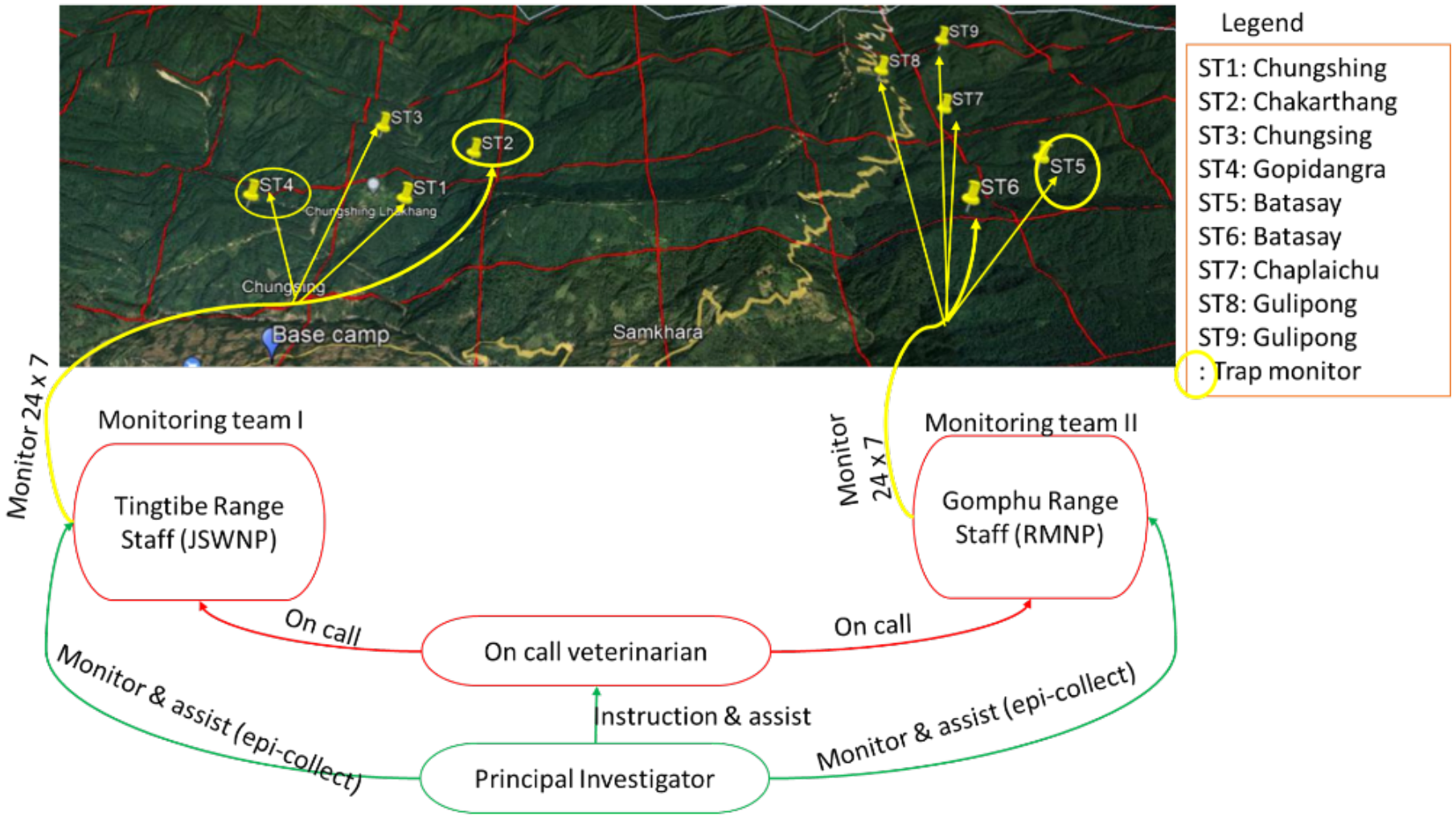
ZSSD (2021). Chemical Immobilization of Animals Technical Field Notes: 2021. San Diego, California 92112, U.S.A, SAN DIEGO ZOO WILDLIFE ALLIANCE ACADEMY SAFE CAPTURE.

Appendices

Appendix 1. Map indicating live-trap locations (Northern Block)



Appendix 2. Map indicating live-trap locations (Southern Block)



Appendix 3. Trap monitoring form

Trap Monitoring Form

1. Region
a. Southern Region ☐
b. Northern Region
c. Trap No_____

	D	M	S
2. Trap Location			

3. Place Name_____

4. Date and Time of Monitoring

DD	MM	YYYY

H	M	S

5.Name of person _____

6. Photo of Trap
7. Status of trap door
a. Open
b. Closed ☐

8. If closed
a. Presence of animal
b. No presence of animal ☐

9. Species _____
10. Photo of animal

11. Status of animal
a. Injured & stressed
b. Calm ☐
c. Stressed

12. Estimated size
a. Length_____
b. height_____
c. weight_____

	H	M	S
13. Time of release			

14. Photo

15. Status of bait
a. Heathly
b. Weak ☐
16. Photo

17. Status of food and water of bait
a. Adequate
b. Low and replinished ☐

18. Photo

Appendix 4. Clouded leopard capture and chemical immobilization form

I.ANIMAL DESCRIPTION
1. Species_____
2. Sex_____
3. Estimated Age_____
4. Estimated Weight_____
5. Estimated Dimension L____H_____
6. Animal health
a. Fit for chemical immobilization & GPS collaring ☐
b. Not fit for chemical immobilization & GPS collaring
7. Resons for not collaring

a. Pregnancy
b. Juvenile ☐
c.Diseased
8. Photo

II. GENERAL INFORMATION
1. Time H M S

2. Weather_____
3. Temperature_____

III. Drug delivery
1. Projector used_____
2. Needle length_____
3. Start time_____
4. Drug delivered
a. ketamine hydrochloride and xylazine hydrochloride (KH-XH) at 15.00±2.00 mg/kg
b. medetomidine-ketamine 3-4.39 mg/kg
c. Zoletil 2.6±0.33 mg/kg
5. Additional dose _____

V.POST CAPTURE CARE
1. Initial post capture care (tick)
a.Open airways ☐
b. laterl recumbancy ☐ Photo
2. Capilary Refil Time (CRT)_____ Photo
3. Mucus Membrane(MM) color_____ Photo
4. Temperature_____Pulse_____Respiration_____

5. Post-capture monitoring

Time	Open airways	CRT/MM color	Temp	Pulse	Respiration	Photo

VI. ANIMAL BIOLOGY
1. Weight_____ 3. Height_____ 5. Neck circumference_____
2. Length_____ 4.Tail Length_____

VII. RECOVERY
1. Time of first recovery sign_____
2. Sign observed_____
3. Reversal Agent_____
4. Time of administration_____
5. Time of head up_____sternal_____standup_____full recovery_____

Name of Vetenarian_____
Signature_____
Signature of PI_____

APPENDIX 5. NOTES ON LIVE TRAPPING OF CLOUDED LEOPARD BY DR. LON GRASSMAN

Clouded Leopard Live-trapping and Sedation Checklist

Lon Grassman

Below are various notes and suggestions on live-trapping and anesthetizing clouded leopards. This information is based on my 30 years of field research capturing over 100 carnivores. Please read these suggestions carefully and let me know if you have any questions.

3. File down any sharp edges within every box trap to avoid abrasive injuries to a captured cat.

4. Test every trap for adequate pressure on the foot treadle when armed. If the treadle requires too much pressure, or sticks, fine tune the mechanism by filing and oiling the relevant parts for smooth closing.

5. Wire the bait box to the back of every trap once you are in the field. Use ONLY live bait! If chickens, put a perch stick in the trap of adequate size so the bird can comfortably perch when it wants to. This was a concern of the UK Animal Use Committee when I was publishing my papers. Also, have wired plastic cups inside the box to hold 3 days' food and water for the bird.

6. Traps should be placed on an animal trail (good) or near trail intersections (better), on level ground so that the trap does not rock/move when pushed. A better option would be to wire the trap to a tree on level ground. Often, cats will go to the rear of the trap to try to get the chicken and will move the trap, causing the door to trip prematurely. If you cover the bait box/rear of the trap with vegetation so that the cat can only see the chicken from the front, you will have a better chance of capture and less false door trips.

7. Every time that you check the traps, trip the foot treadle to ensure that the door closes smoothly. If you don't close the trap very often the door can snag and not close properly. Be careful when you camouflage traps with vegetation that the sticks do not interfere with the door closing.

8. Sedation should only be done with a pole syringe and not a blow gun dart, since you have better control with a pole syringe and can avoid dart ricochet if it hits the trap mesh.

9. Once an animal is captured, move everyone away from the trap and only speak in soft whispers to avoid stressing the animal. Once you have determined the appropriate dosage for the sedation (based on the estimated cat's weight) and have loaded the pole syringe, one person only should walk to the trap and kneel on their knees on one side. The animal may thrash about for a few moments, but eventually calm down. Slowly aim the pole syringe to the meaty portion of the cat's hindquarters and when the cat is completely still jab the syringe with a strong push (not light!) into the hindquarters to ensure that all of the drug is administered. Make sure that the syringe tip is already through the trap mesh about 2 cm and resting on the wire *before* you jab so that it doesn't hit the mesh and discharge the drug into the air when you try to aim it

through the mesh hole. Do not hesitate once you have decided that your aim is clear and push hard!

10. Sometimes, when the cat is too focused on the pole syringe and will not stay still, I would rub a small stick gently near the front of the trap with my left hand to attract the cat's attention, and then with my right hand jab the hindquarters.
11. IMPORTANT: make sure that the needle is of a large enough gauge and at the correct length when sticking out of the syringe sleeve. If too long and thin, the needle may hit bone and bend causing tissue damage. I normally like to have 1.5-2.0 cm off needle length from a 16-18 gauge needle. If the needle sticks out too far from the pole syringe sleeve, add paper to the bottom of the sleeve as a spacer so that not all of the needle sticks out, and you have about 1.5-2.0 cm sticking out.

12. Always wear latex gloves when handling anesthetized cats to avoid spread of zoonotic disease transmission, including rabies from animal saliva to minor cuts on human hands/arms.

13. **DO NOT ANESTHETIZE YOUNG, VERY THIN, OR SICKLY-LOOKING ANIMALS.** Release these animals immediately. Although you will be anxious to radio-collar clouded leopards, it is too risky for young or sick animals to be collared, as they may die shortly after release. Professional judgement and restraint must be practised when considering whether to radio collar a captured cat. Only anesthetize healthy young adult or adult cats.

14. Once a healthy cat has been anesthetized and weighed, determine which collar to attach. Remember that we do not want to radio-collar any cat under 14 kg because of the collar weight of 415 grams, and the need to stay under 3% body weight. However, if you remove the sure drop mechanism (50 grams) from the collar (and close with plastic ties so that the collar would eventually break off), then you could collar female clouded leopards that weigh at least 11.5 kg.

15. When collaring a cat, your index finger should slide easily under the collar at the neck; not too tight or too loose. Use the hole punch tool if you want to attach the bolts in-between the factory set holes for a better fit.

16. Put sedated cats back into the traps to recover, and only release them after they have fully recovered from the sedation. IMPORTANT: do not release big cats or binturongs by opening the trap door by hand, as they may attack you when they are released. Set up a rope over a tree to pull the trap open from a safe distance (or use some other, similar techniques).

UNIVERSITY OF Southampton
School of Biological Sciences

Appendix 3b. Certificate on wildlife handling and chemical immobilization



San Diego Zoo Wildlife Alliance Academy

CERTIFICATE OF COMPLETION

This certifies that

Lungten Dorji

has completed 16 hours of training in

Safe Capture - Chemical Immobilization of Animals

on

July 24, 2021

Presented by: San Diego Zoo Wildlife Alliance Academy

Instructor: Dr. Mark Drew, DVM, DACZM

Authorized by: _____

Nadine Lamberski, DVM, DACZM, DECZM (ZHM)
Chief Conservation & Wildlife Health Officer

www. sdzwaacademy.org/safecapture/

RACE

Appendix 3c. VHF telemetry form

VHF Radio Telemetry Data Form

Receiver Loc

Animal ID	Time	X	Y	Compass Bear (deg)	Activity (A/I)

Appendix 3d. MCPs for random data generation for RSF modelling

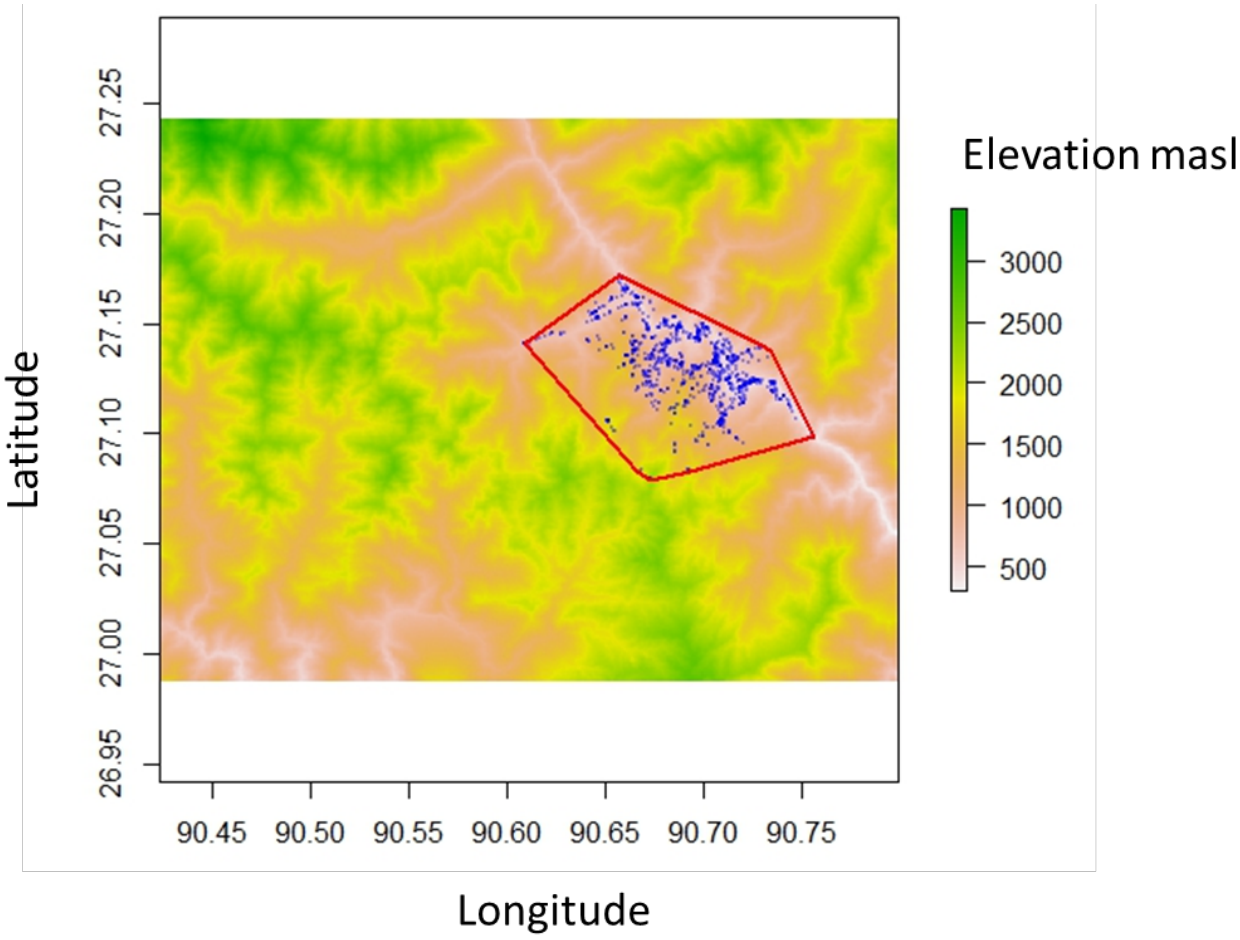


Figure S1. Maximum Convex Polygon (MCP) around the data points of leopard_1, which is used to generate random points of available site and site used by an animal. The background raster represents the elevation of the place in meters above sea level.

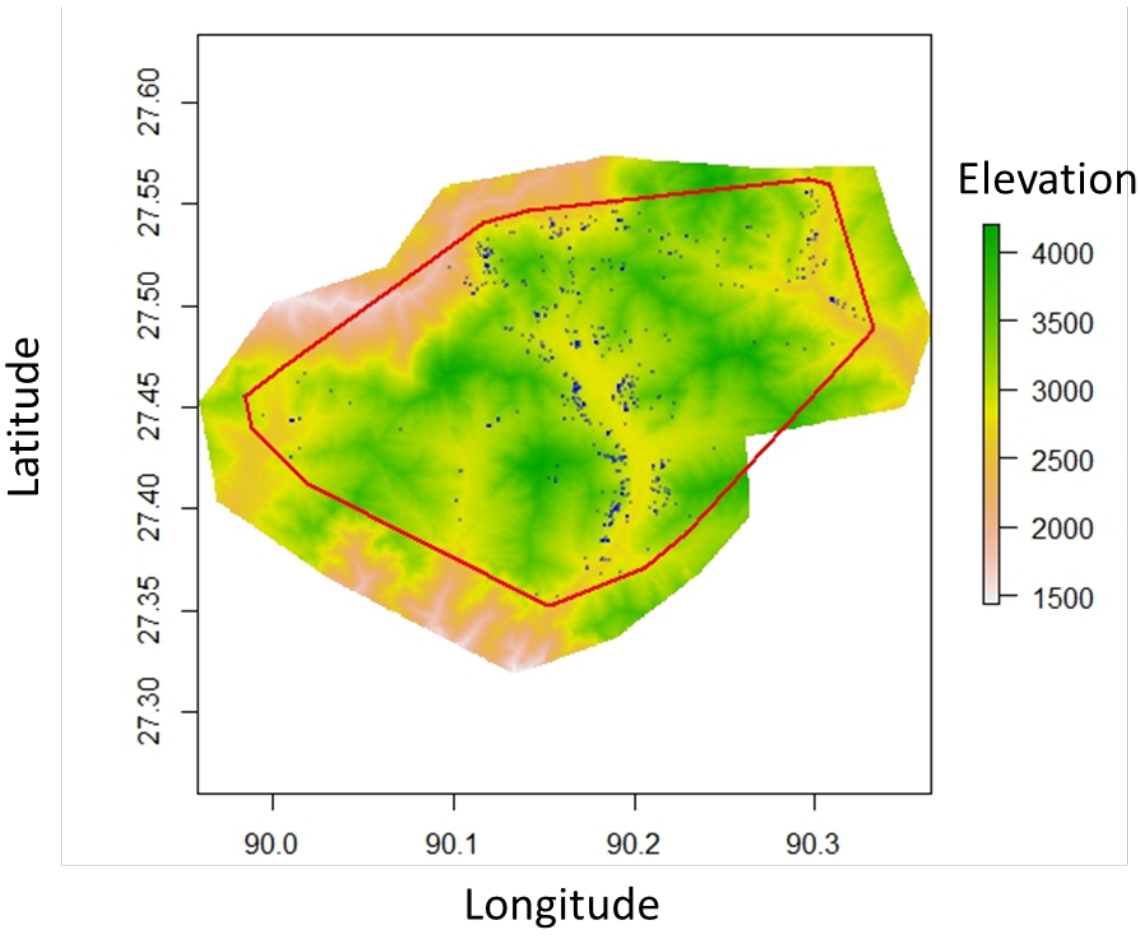


Figure S2. Maximum Convex Polygon (MCP) around the data points of leopard_2, which is used to generate random points of available site and site used by an animal. The background raster represents the elevation of the place in meters above sea level.

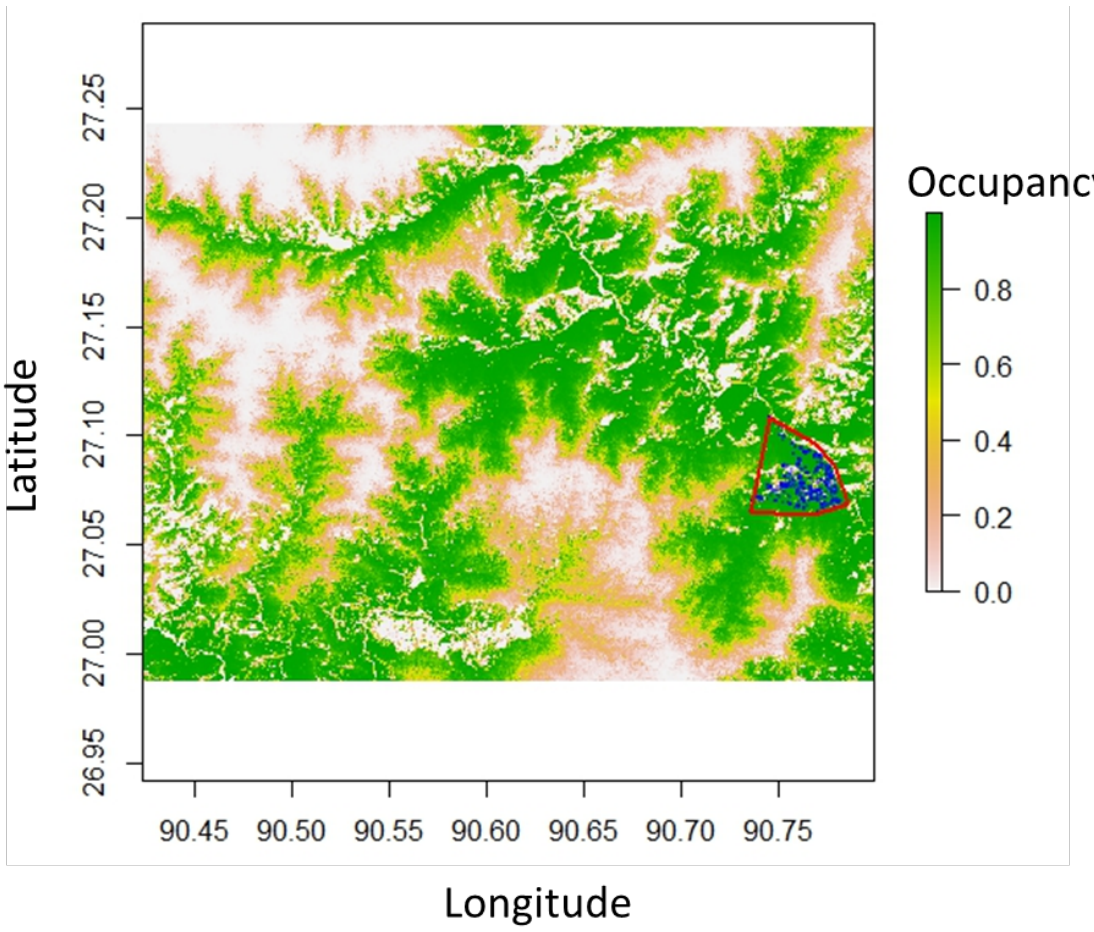


Figure S3. Maximum Convex Polygon (MCP) around the data points of leopard_3, which is used to generate random points of available site and site used by an animal. The background raster represents the occupancy of serow.

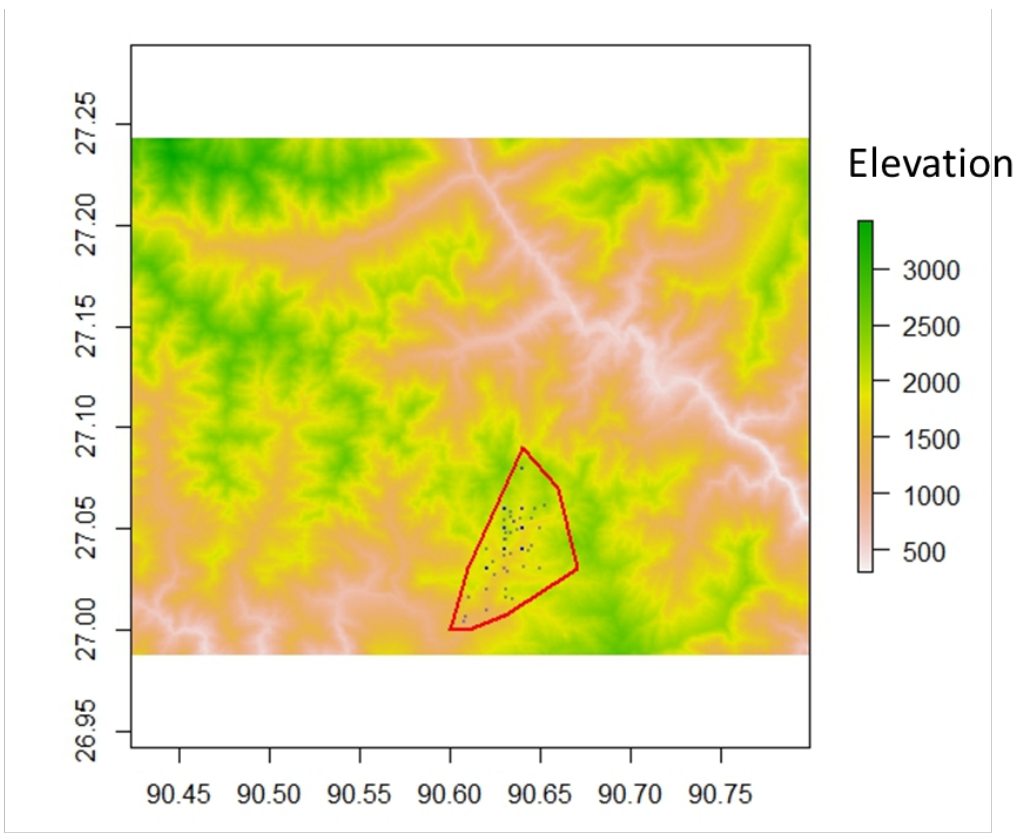


Figure S4. Maximum Convex Polygon (MCP) around the data points of Asiatic golden cat_1, which is used to generate random points of available site and site used by an animal. The background raster represents the elevation of the place in meters above sea level.

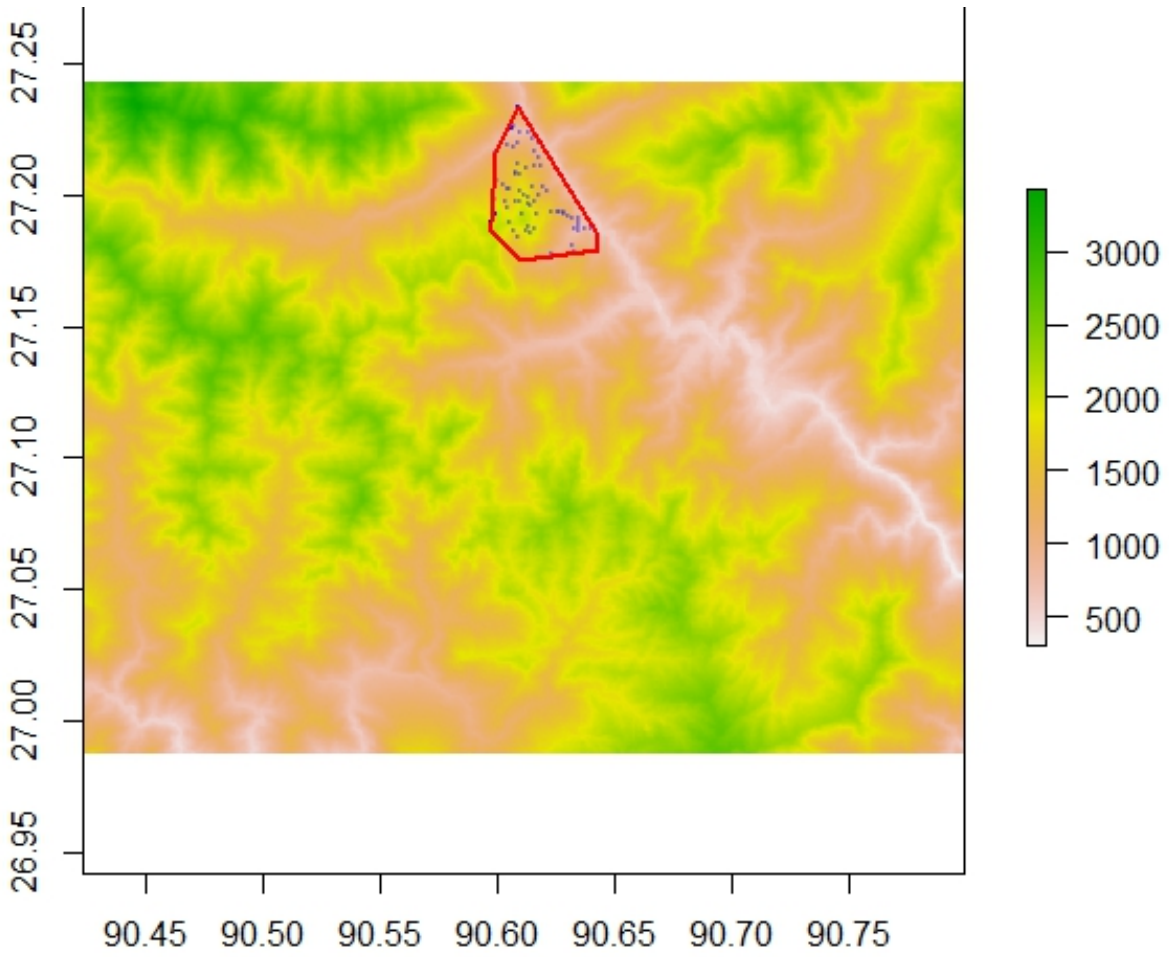


Figure S5. Maximum Convex Polygon (MCP) around the data points of leopard cat_1, which is used to generate random points of available site and site used by an animal. The background raster represents the elevation of the place in meters above sea level.

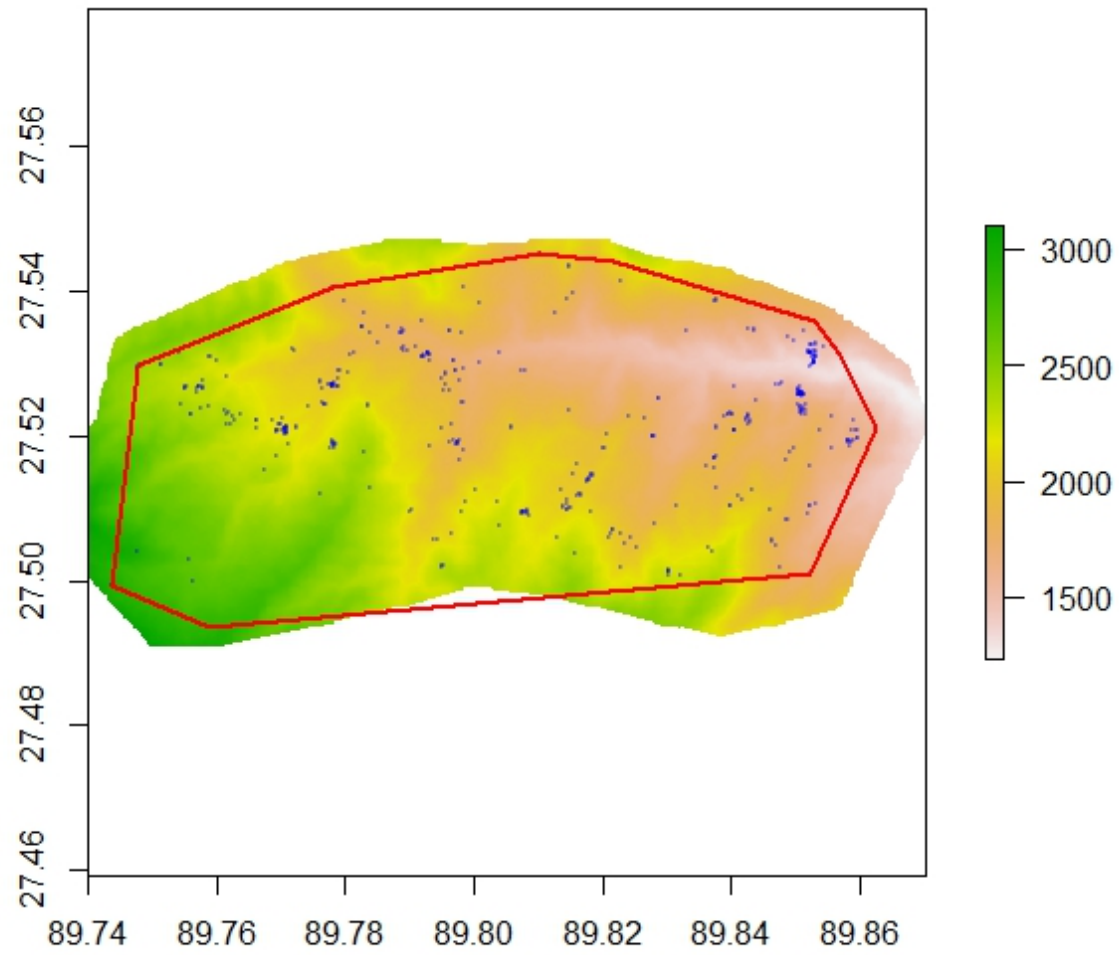


Figure S6. Maximum Convex Polygon (MCP) around the data points of dhole_1, which is used to generate random points of available site and site used by an animal. The background raster represents the elevation of the place in meters above sea level.

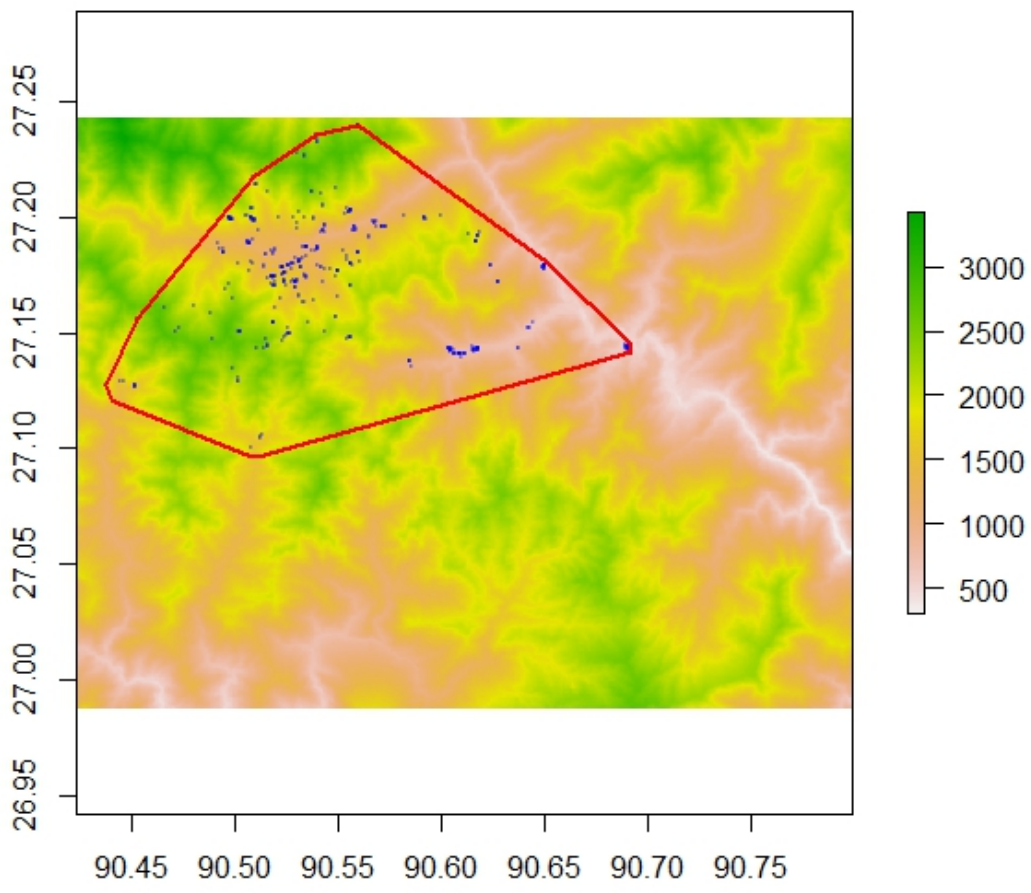


Figure S7. Maximum Convex Polygon (MCP) around the data points of dhole_2, which is used to generate random points of available site and site used by an animal. The background raster represents the elevation of the place in meters above sea level.

Appendix 3e. Random points generated for RSF

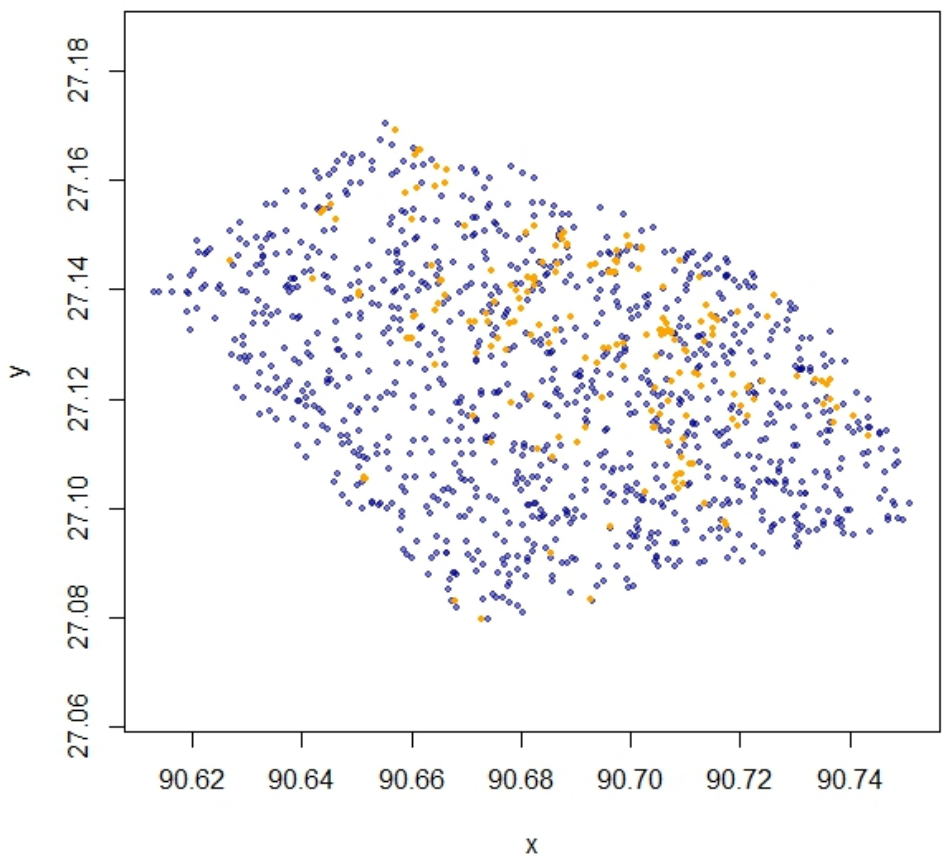


Figure S1. Random points generated for modelling resource use function for leopard_1, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

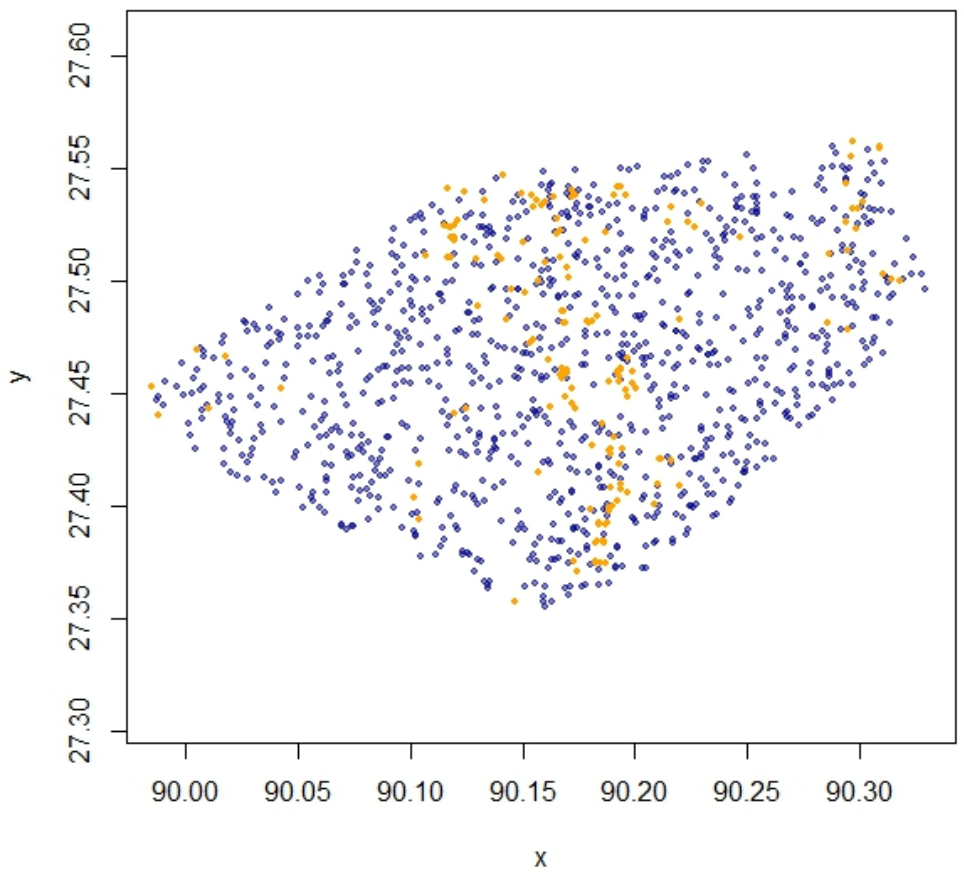


Figure S2. Random points generated for modelling resource use function for leopard_2, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

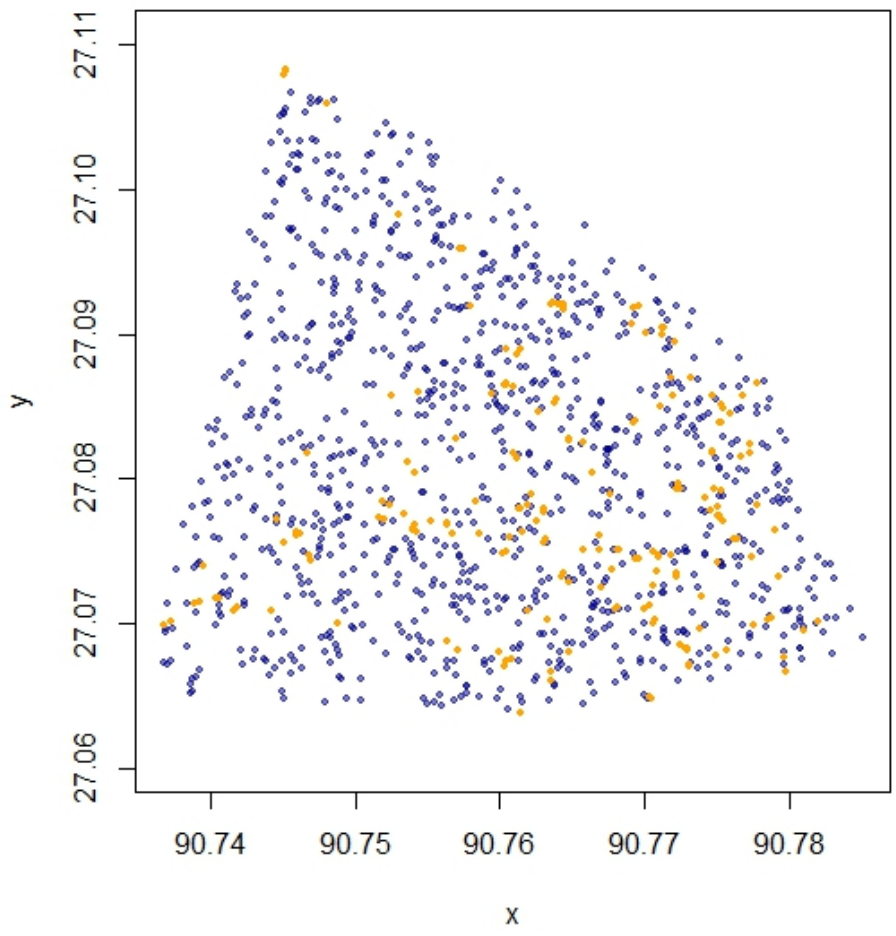


Figure S3. Random points generated for modelling resource use function for lepard_3, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

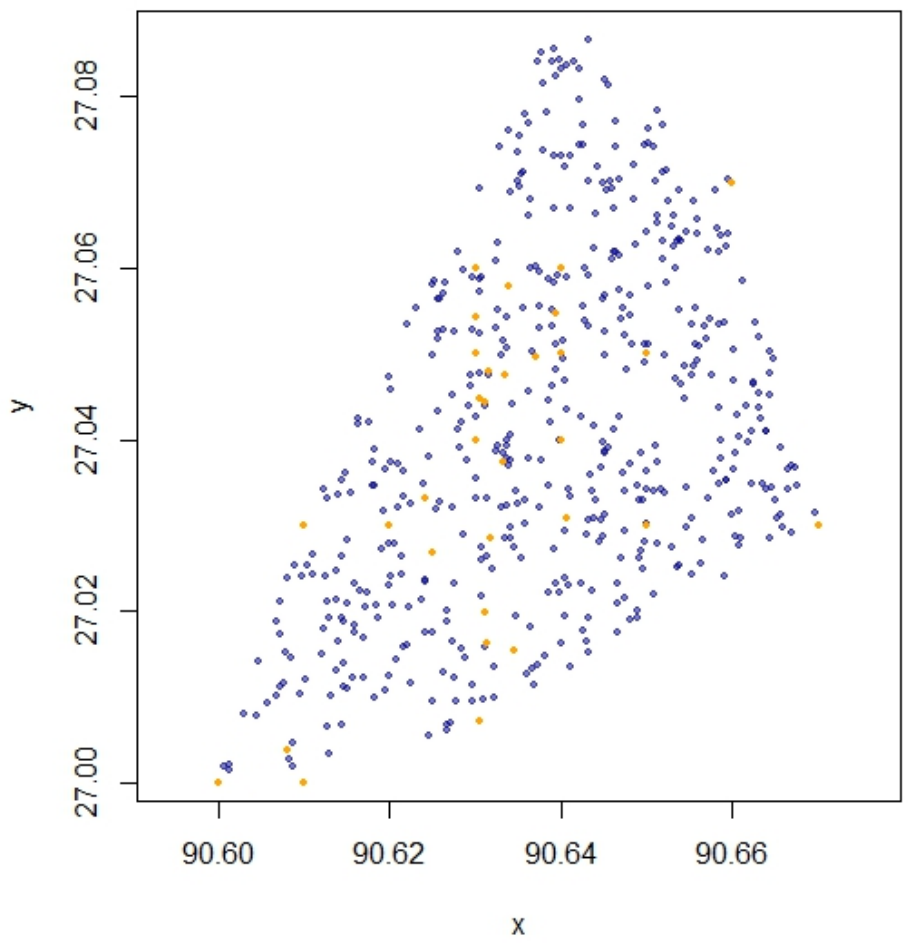


Figure S4. Random points generated for modelling resource use function for Asiatic golden cat_1, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

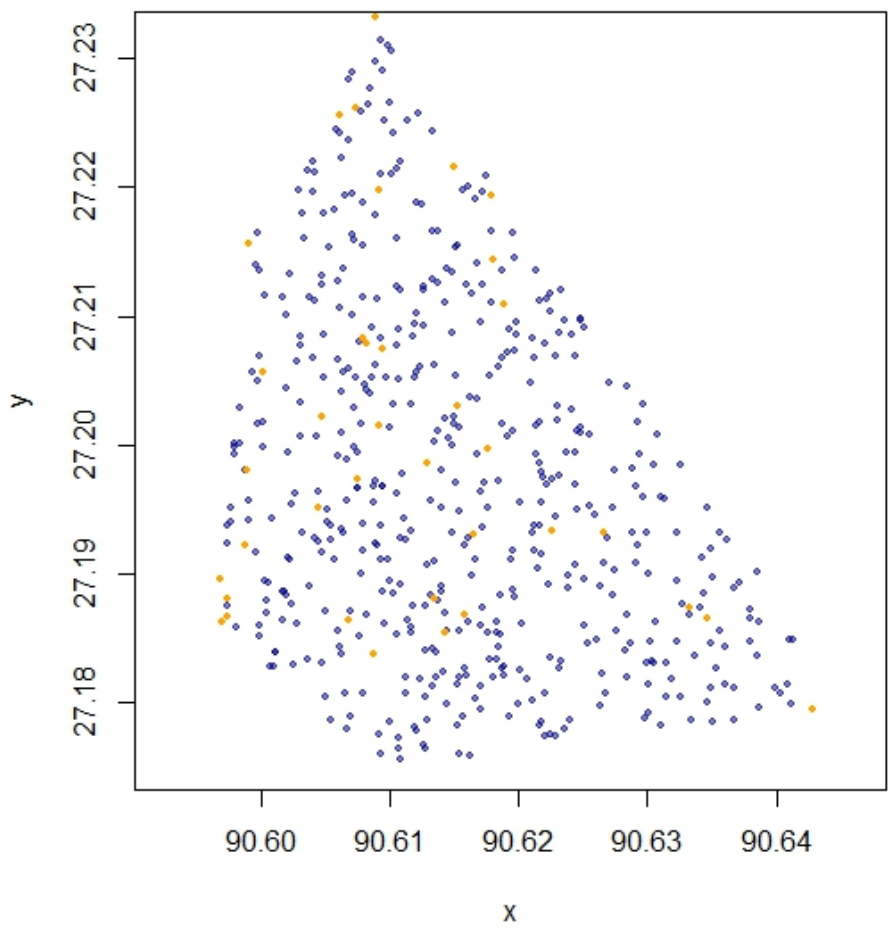


Figure S5. Random points generated for modelling resource use function leopard cat_1, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

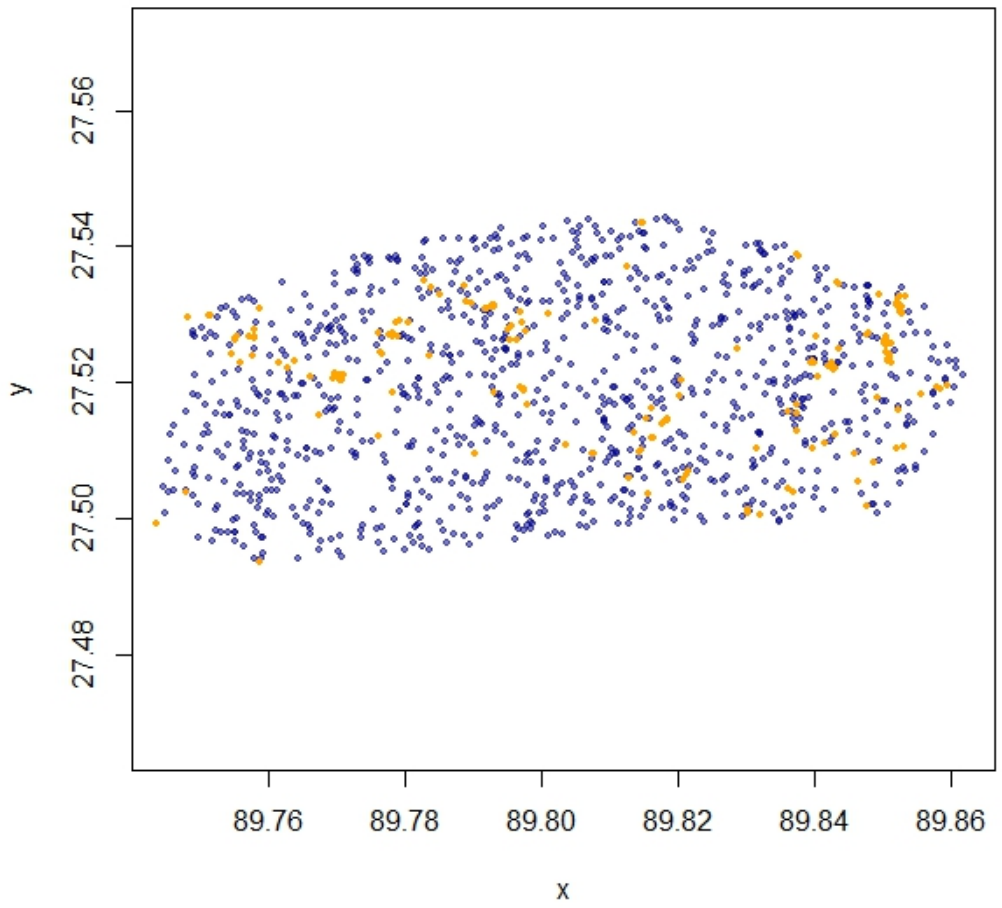


Figure S6. Random points generated for modelling resource use function of dhole_1, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

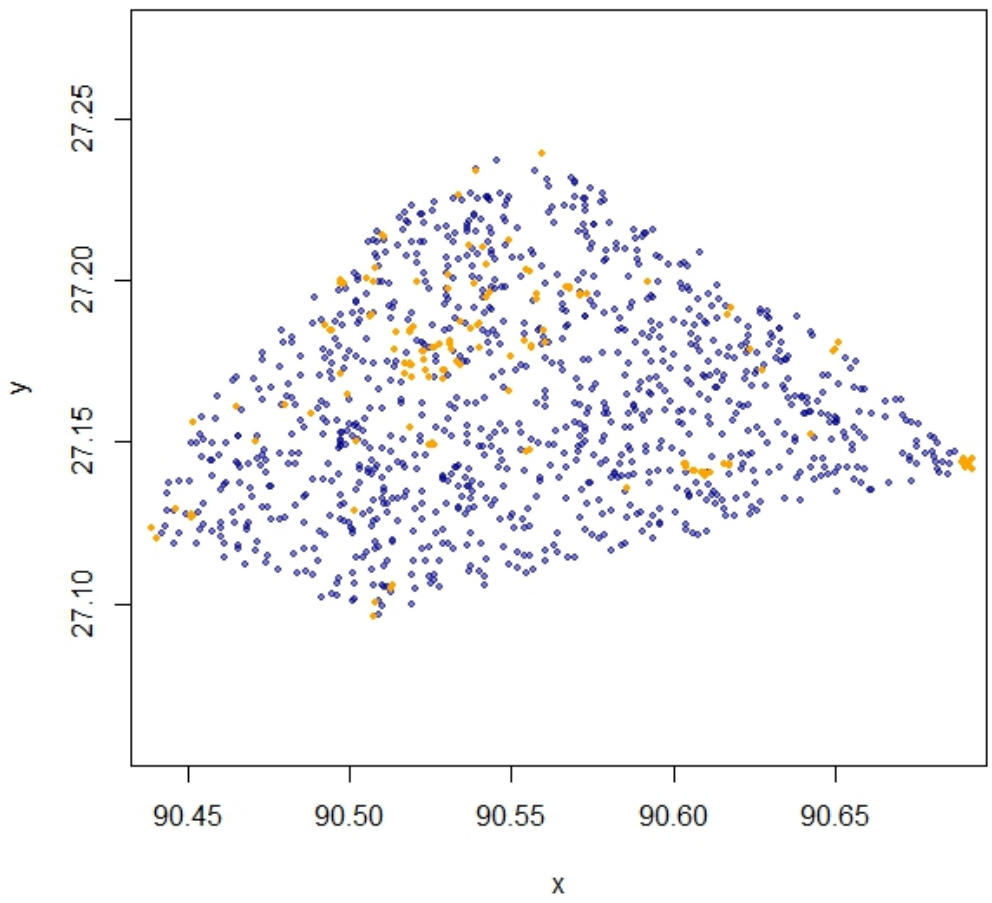


Figure S7. Random points generated for modelling resource use function dhole_2, where blue points represent random points available for resource exploitation by an animal and orange points are the site actually used by an animal.

Appendix 3f . Home range size of montane carnivores of Bhutan

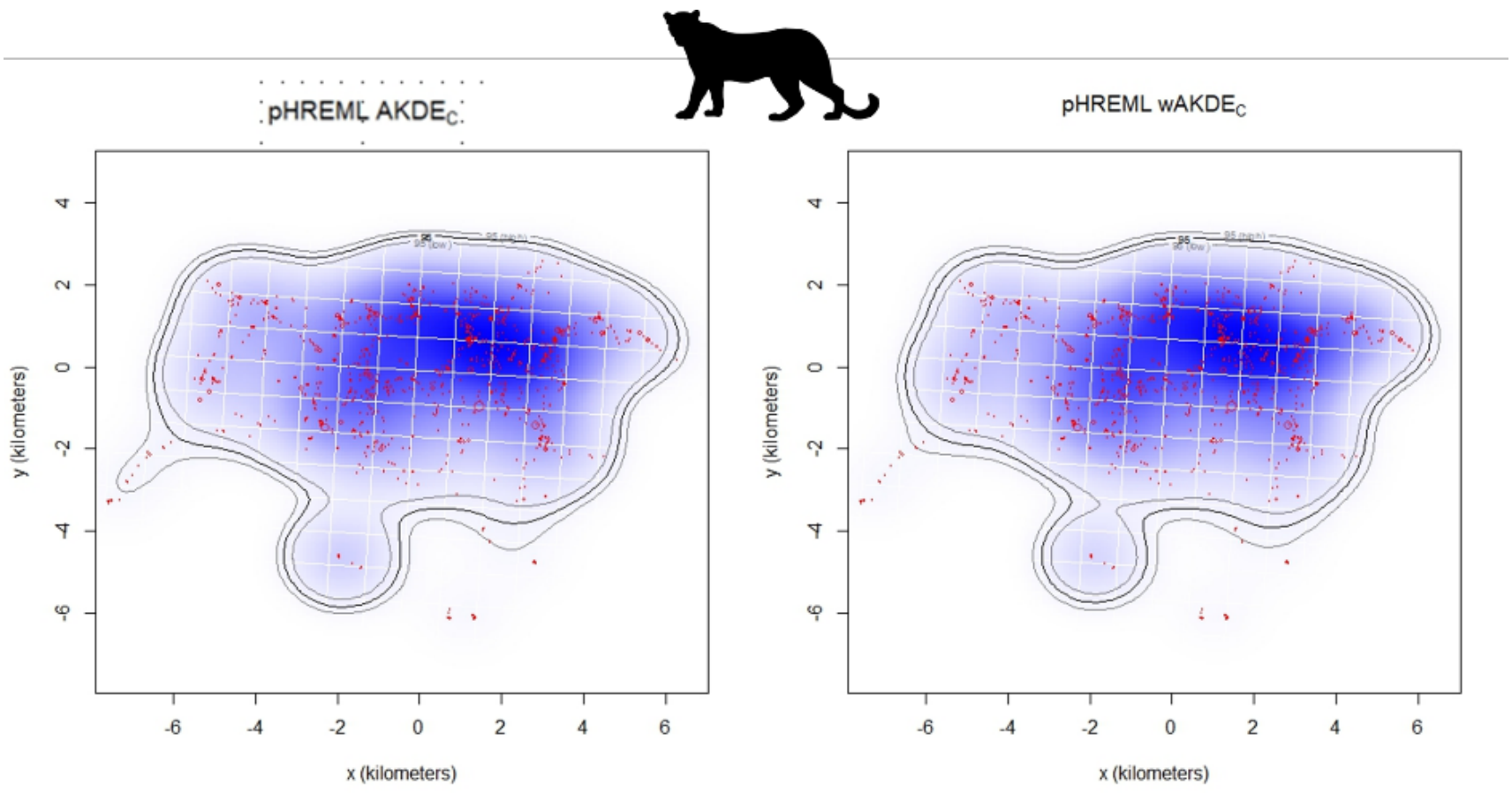


Figure S1. Autocorrelated kernel density estimates for common leopard_1 with area corrected AKDE ($AKDE_C$) left and weighted AKDE ($wAKDE_C$) right using perturbative Hybrid Residual Maximum Likelihood estimator (pREML). The thick black contour represents the 95% home range area estimate, the inner lighter one represents the lower confidence interval, and the outer lighter contour represents the upper confidence interval.

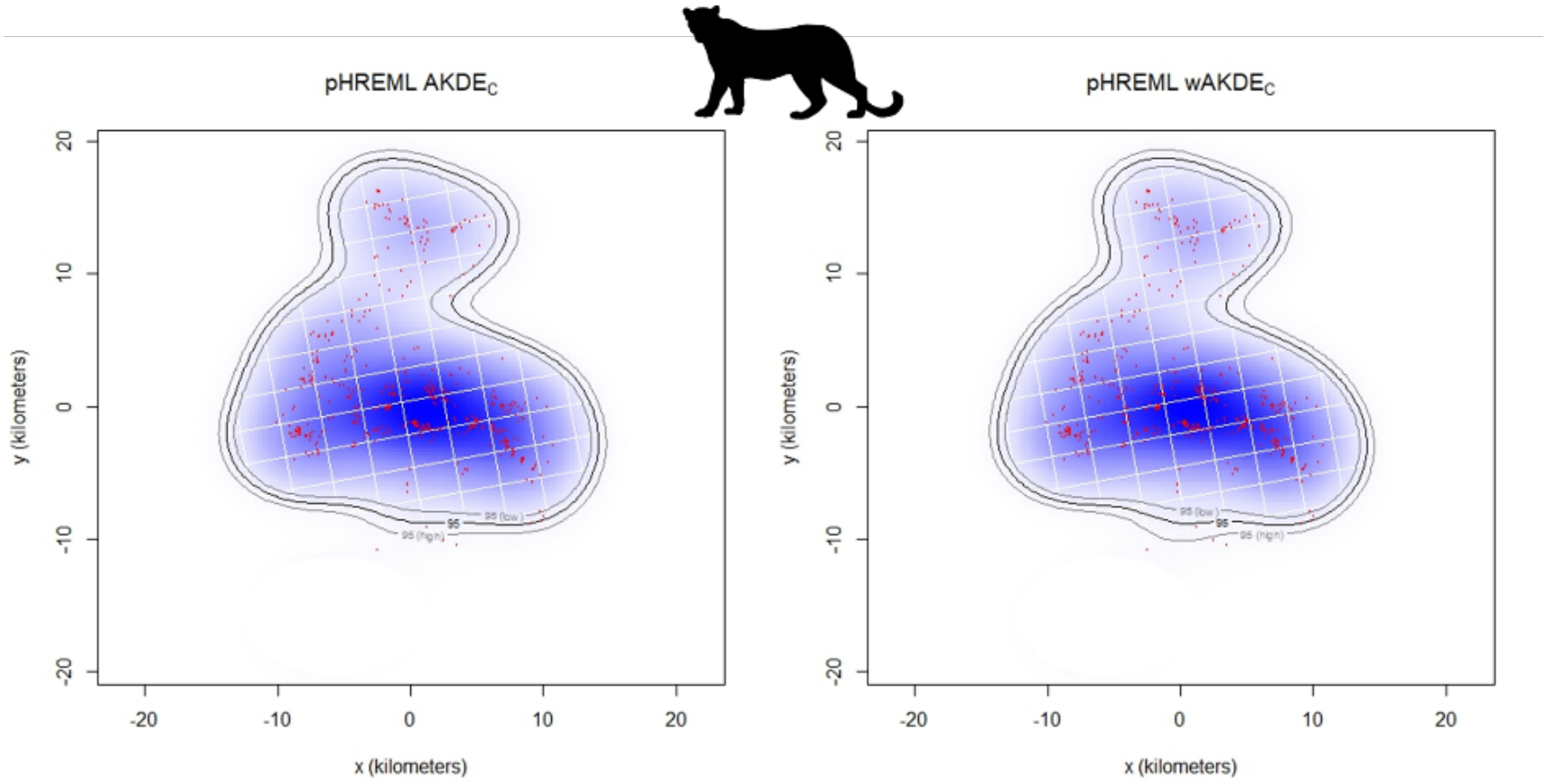


Figure S2. Autocorrelated kernel density estimates for common leopard_2. Figure legend are same for figure S1.

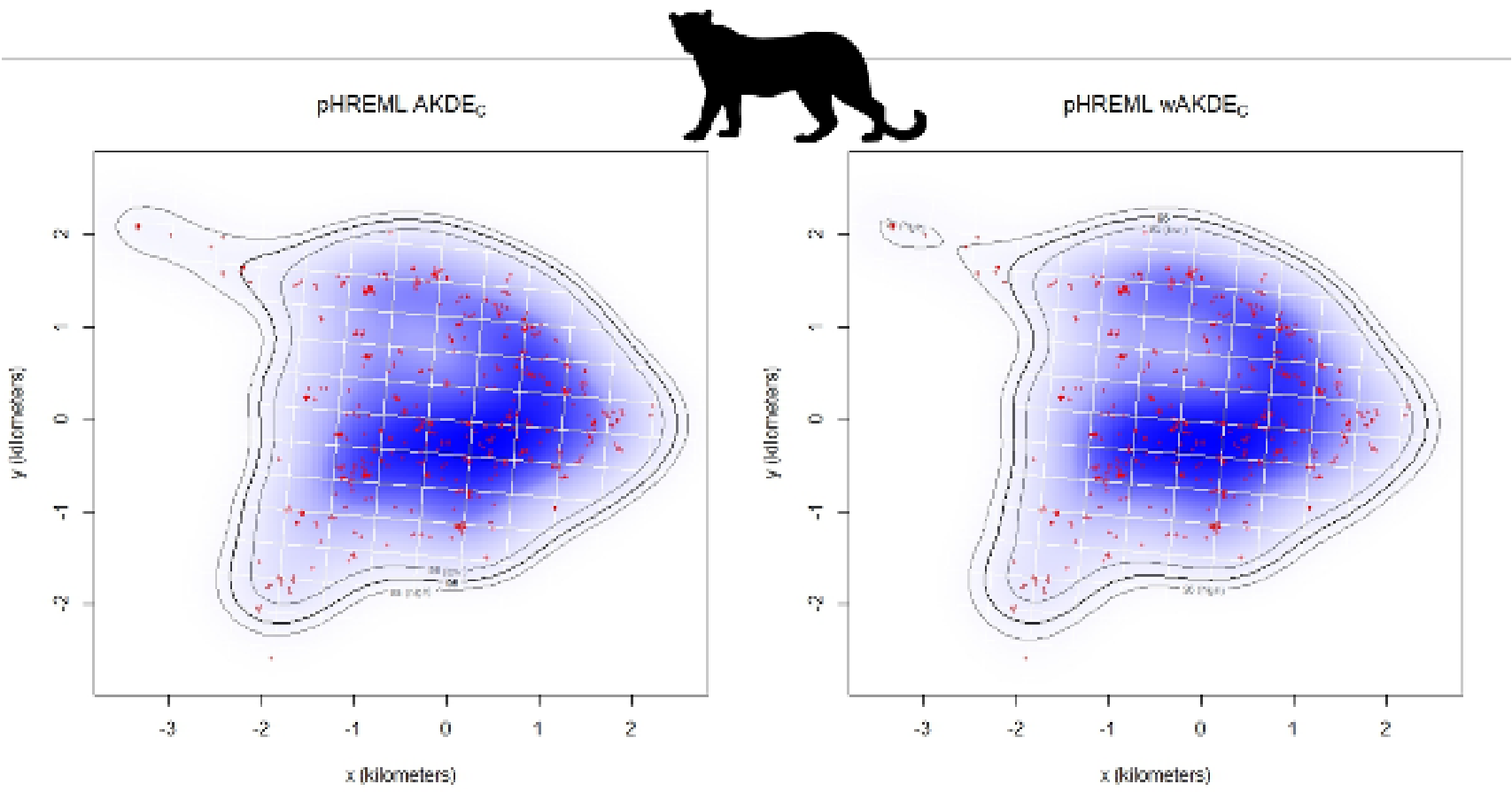


Figure S3. Autocorrelated kernel density estimates for common leopard_3. Figure legend are same for figure S1.

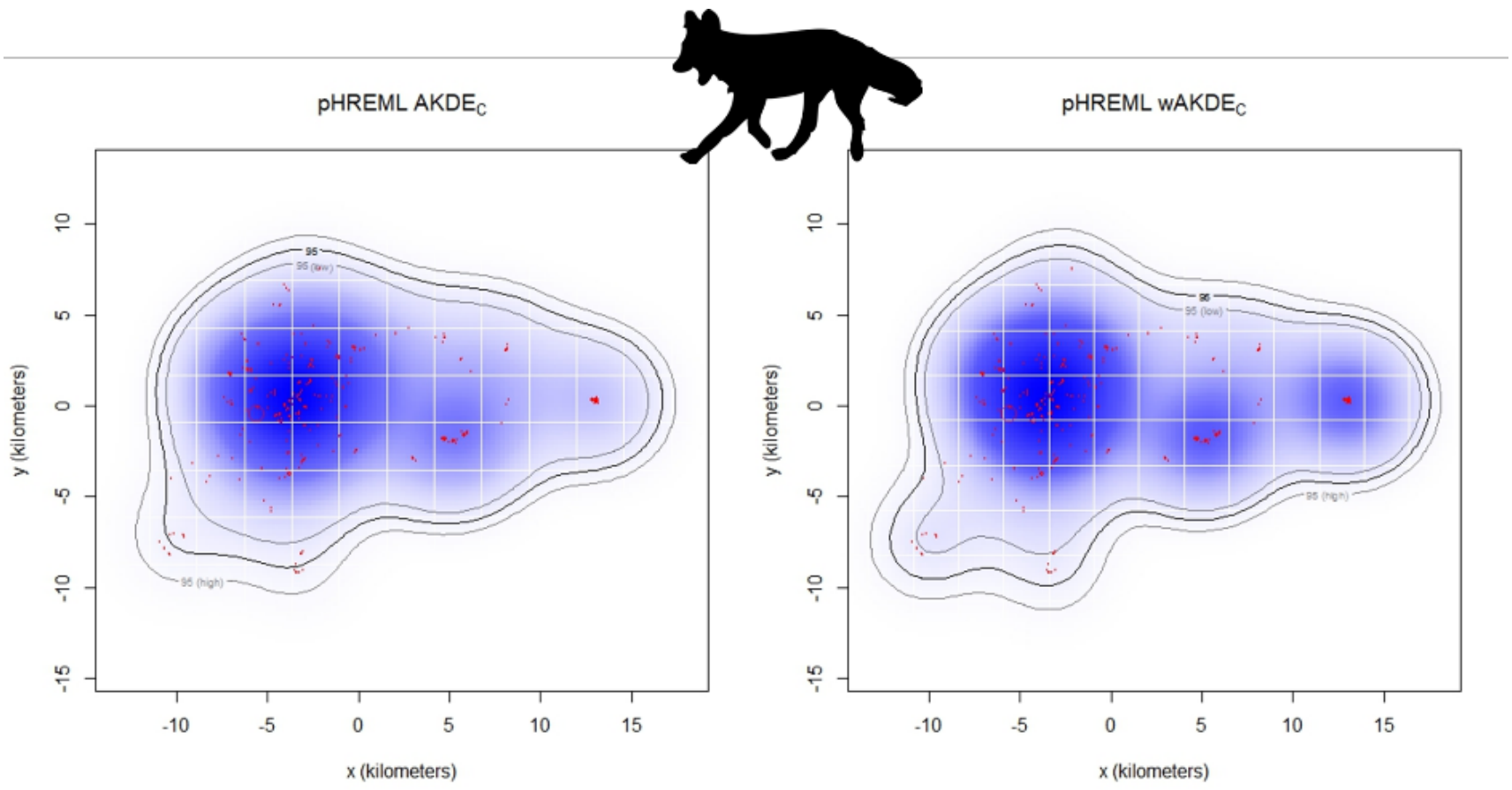


Figure S4. Autocorrelated kernel density estimates for common dhole_1. Figure legend are same for figure S1.

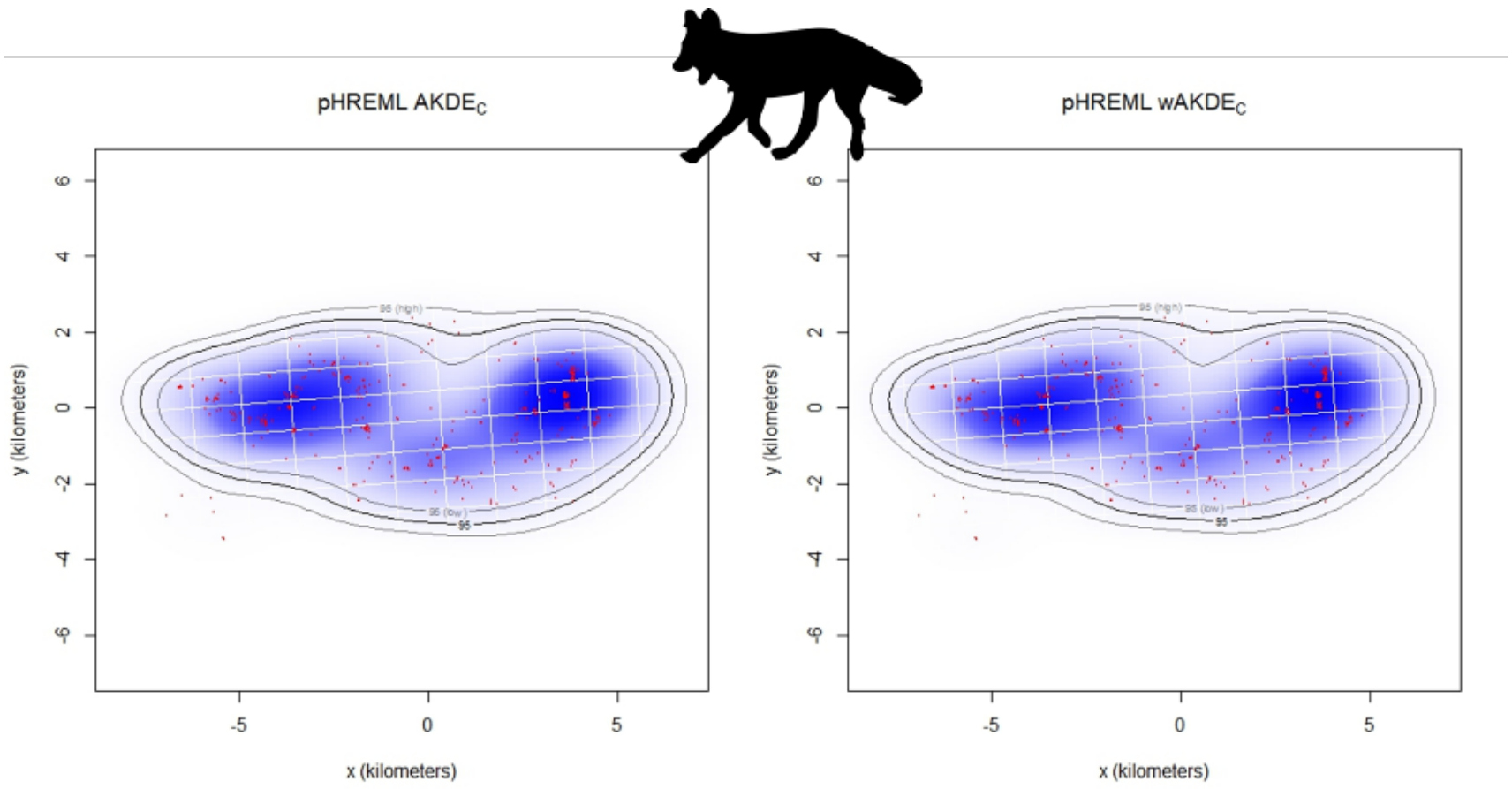


Figure S5. Autocorrelated kernel density estimates for common dhole_2. Figure legend are same for figure S1.

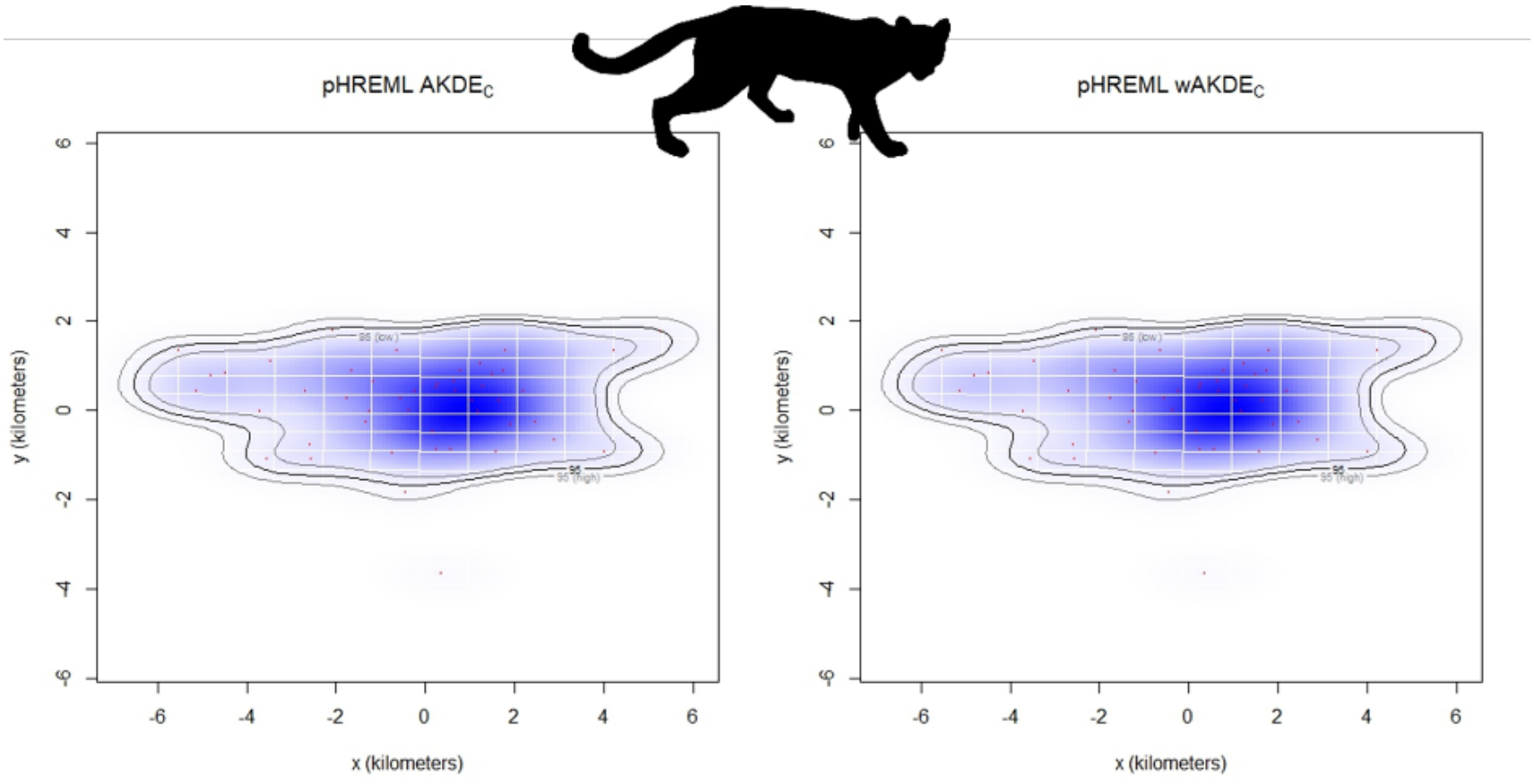


Figure S6. Autocorrelated kernel density estimates for common Asiatic golden cat_1. Figure legend are same for figure S1.

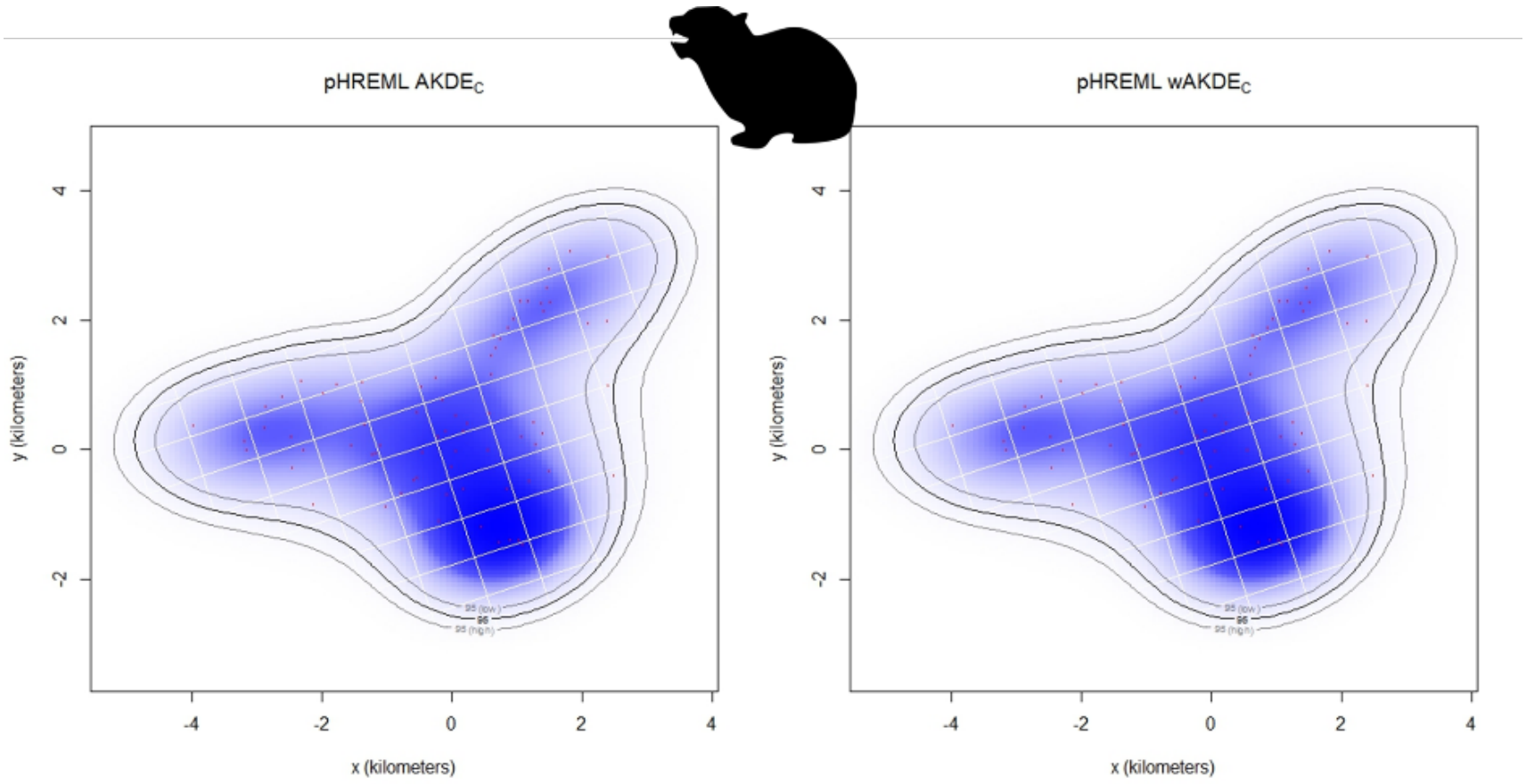


Figure S7. Autocorrelated kernel density estimates for common leopard cat_1. Figure legend are same for figure S1.

Appendix 3g. Home range size model selection

Table S1. Home range size model selection table for leopard _1. OU (Ornstein – Uhlenbeck), and OUF (Ornstein – Uhlenbeck Foraging) models. Anisotropic model assumes non-symmetric and can have an elongated or stretched shape where the influence or weight assigned to a data point varies in different direction from that point. Model are ranked based on dAICc.

Fitted models	**dAICc**
OUF anisotropic	0
OUF	18.25281
OU anisotropic	117.4893
OUf anisotropic	639.6385

Table S2. Home range size model selection table for leopard _2.

Fitted models	**dAICc**
OUF anisotropic	0
OUF	32.82361
OU anisotropic	62.06736
OUf anisotropic	274.017

Table S3. Home range size model selection table for leopard _3.

Fitted models	**dAICc**
OUF anisotropic	0
OU anisotropic	13.65677
OUF	34.96033
OUf anisotropic	155.4498

Table S4. Home range size model selection table for leopard cat. IID (Independent identically distributed), OU (Ornstein – Uhlenbeck), and OUF (Ornstein – Uhlenbeck Foraging) models. Anisotropic model assumes non-symmetric and can have an elongated or stretched shape where the influence or weight assigned to a data point varies in different direction from that point. Model are ranked based on dAICc.

Fitted models	**dAICc**

IID anisotropic	0
OU anisotropic	2.18
OUf anisotropic	4.41
IID	8.60
OU	10.70
OUf	10.70

Table S5. Home range size model selection table for leopard cat. Table legend are same for Table S1

Fitted models	**dAICc**
IID anisotropic	0
OU anisotropic	2.203663
Ouf anisotropic	69.04039
IID	71.14979
OU	73.30555
OUF	

Table S6. Home range size model selection table for dhole_1. Table legend are same for Table S1

Fitted models	**dAICc**
OUF anisotropic	0
OU anisotropic	2.779328
OUF	101.5099
OUf anisotropic	194.2127

Table S7. Home range size model selection table for dhole_2. Table legend are same for Table S1

Fitted models	**dAICc**
OUF	0
OUF anisotropic	0.482066
OU anisotropic	56.46954
OU	61.55718
OUf anisotropic	425.1874
OUf	430.7623

Appendix 3h. Resource selection model for carnivores

Table S1. Output of global model showing factors influencing resources selection by leopard_1. Columns show the variable coefficient β, its standard error, and the probability *p* of making an error in rejecting the null hypothesis of no influence. Emboldened variables have strongly evidenced influence.

Variable	**Estimate (β)**	**Std. Error**	***p***
(Intercept)	-2.09	0.12	< 2e-16***
Elevation	-2.27	0.38	0.00***
Distance to river	0.09	0.09	0.33
Tree cover	-0.10	0.29	0.73
Distance to HWC	0.36	0.11	0.00 ***
Occu_Bear	-0.29	0.21	0.17
Occu_dhole	0.09	0.30	0.77
Occu_wildboar	-0.90	0.31	0.00 **
Occu_sambar	-0.36	0.38	0.34
Occu_serow	-0.58	0.38	0.13
Occu_goral	-5.03	1.40	0.00 ***
Occu_muntjac	1.59	0.67	0.02 *
Occu_leopard Male	-0.37	0.26	0.15
Occu_leopard Female	4.22	1.29	0.00**
Distance to settlement	0.16	0.30	0.59
Interaction (Distance to HWC X Distance to settlement)	0.10	0.10	0.32

*** *p-value <0.001; ** p-value <0.05; * p-value <0.1*

Table S2. Output of global model showing factors influencing resources selection by leopard_2. Table legend are as for Table S1.

Variable	**Estimate (β)**	**Std. Error**	***p***
(Intercept)	-1.84	0.10	< 2e-16 ***
Elevation	-0.24	0.09	0.01
Distance to river	0.23	0.09	0.01 **
Distance to settlement	-0.80	0.13	0.001 ***
Treecover	0.16	0.11	0.13
Interaction (Distance to HWC X Distance to settlement)	-0.23	0.12	0.06

*** *p-value <0.001; ** p-value <0.05; * p-value <0.1*

Table S3. Output of global model showing factors influencing resources selection by leopard_3. Table legend are as for Table S1.

Variable	Estimate (β)	Std. Error	*p*
(Intercept)	-2.01	0.13	< 2e-16 ***
Elevation	0.03	0.37	0.94
Distance to river	0.26	0.10	0.001**
Tree cover	-0.40	0.22	0.07
Distance to human carnivore conflict	0.18	0.09	0.05 *
Occu.bear	1.21	0.39	0.002**
Occu.wildboar	0.27	0.34	0.43
Occu. sambar	-0.18	0.35	0.60
Occu.serow	-0.90	0.42	0.03 *
Occu.goral	0.57	0.61	0.34
Occu.dhole	1.68	1.65	0.31
Occu.muntjac	0.69	0.60	0.25
Occu.leopard male	-0.20	0.44	0.64
Occu.leopard female	-1.30	1.51	0.39
Distance to settlement	-0.51	0.31	0.10
Interaction (Distance to HWC X Distance to settlement)	0.04	0.09	0.68

**** p-value <0.001; ** p-value <0.05; * p-value <0.1*

Table S4. Output of global model showing factors influencing resources selection by Asiatic golden cat_1. Table legend are as for Table S1.

Variable	Estimate (β)	Std. Error	*p*
(Intercept)	-2.29	0.25	<2e-16 ***
Elevation	-0.56	0.41	0.17
Distance to river	0.47	0.25	0.05 *
Tree cover	-0.01	0.41	0.97
Distance to human carnivore conflict	-0.81	0.43	0.05 *
Occu.bear	-0.14	0.50	0.78
Occu.dhole	-0.46	0.56	0.41
Occu.muntjac	0.16	0.40	0.68
Occu.leopard	-0.19	0.25	0.46
Occu.clouded leopard	-0.91	0.85	0.28
Occu.marbled cat	-0.05	0.42	0.91
Distance to settlement	-0.33	0.79	0.68
Interaction (Distance to HWC X Distance to settlement)	-0.45	0.24	0.05 *

**** p-value <0.001; ** p-value <0.05; * p-value <0.1*

Table S4a. Output of global model showing factors influencing resources selection by leopard cat_1. Table legend are as for Table S1.

Variable	**Estimate (β)**	**Std. Error**	***p***
(Intercept)	-1.68	0.29	0.001 ***
Elevation	0.62	0.52	0.23
Distance to river	-0.14	0.19	0.46
Tree cover	-0.52	0.68	0.44
Distance to human carnivore conflict	-1.42	0.41	0.001 ***
Bear	0.02	0.47	0.97
Dhole	-0.04	0.55	0.94
Occu. Asiatic golden cat	-0.86	1.38	0.53
Occu. common leopard	0.17	0.28	0.55
Occu.clouded leopard	0.34	1.55	0.82
Occu. marbled cat	0.71	0.53	0.18
Distance from settlement	0.68	0.74	0.36
Interaction (Distance to HWC X Distance to settlement)	-1.33	0.41	0.01**

*** *p-value <0.001; ** p-value <0.05; * p-value <0.1*

Table S5. Output of global model showing factors influencing resources selection by dhole_1. Table legend are as for Table S1.

Variable	**Estimate (β)**	**Std. Error**	***p***
(Intercept)	-1.68	0.09	< 2e-16
Elevation	-0.56	0.10	0.001 ***
Distance to river	0.02	0.08	0.84
Distance to settlement	0.11	0.10	0.30
Tree cover	0.22	0.09	0.01**
Interaction (Distance to HWC X Distance to settlement)	-0.35	0.09	0,001 ***

*** *p-value <0.001; ** p-value <0.05; * p-value <0.1*

Table S6. Output of global model showing factors influencing resources selection by dhole_2. Table legend are as for Table S1.

Variable	**Estimate (β)**	**Std. Error**	***p***
(Intercept)	-2.05	0.15	< 2e-16 ***
Elevation	-1.24	0.33	0.001***
Distance to river	0.21	0.10	0.04 **

Tree cover	-0.50	0.24	0.04 **
Distance to human carnivore conflict	-0.66	0.23	0.001***
Occu.bear	0.63	0.26	0.02 *
Occu.wildboar	-0.12	0.21	0.55
Occu.sambar	0.00	0.26	0.99
Occu.serow	-0.04	0.37	0.92
Occu.goral	-0.54	0.21	0.01 **
Occu.gaur	-0.72	0.21	0.001 ***
Occu.muntjac	1.16	0.54	0.03 *
Presence of leopard male	-0.24	0.16	0.14
Presence of leopard female	-0.22	0.28	0.44
Distance to settlement	1.14	0.44	0.01 **
Interaction (Distance to HWC X Distance to settlement)	0.10	0.12	0.41

**** p-value <0.001; ** p-value <0.05; * p-value <0.1*

Appendix 3i. Resource selection map of carnivores

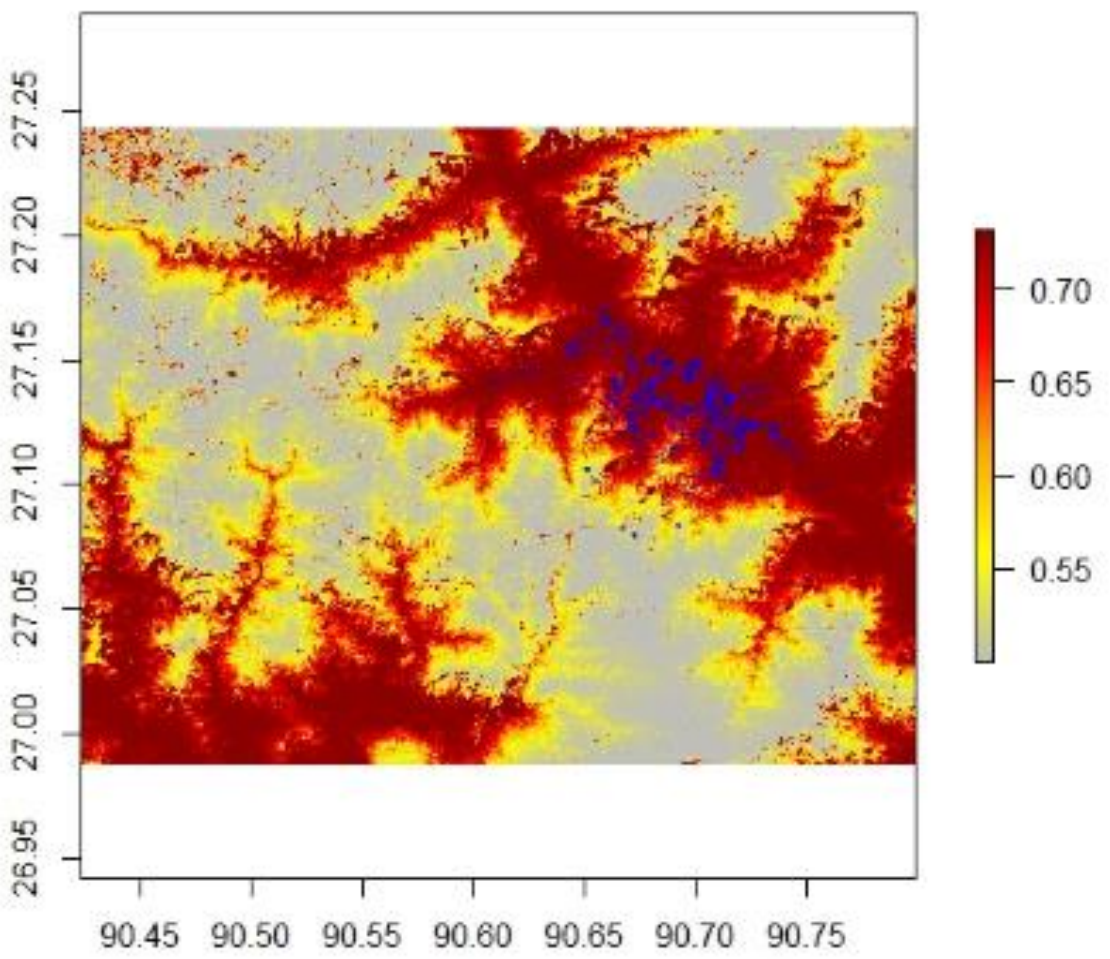


Figure S1. Resource selection function map of leopard_1. The colour scale from grey to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

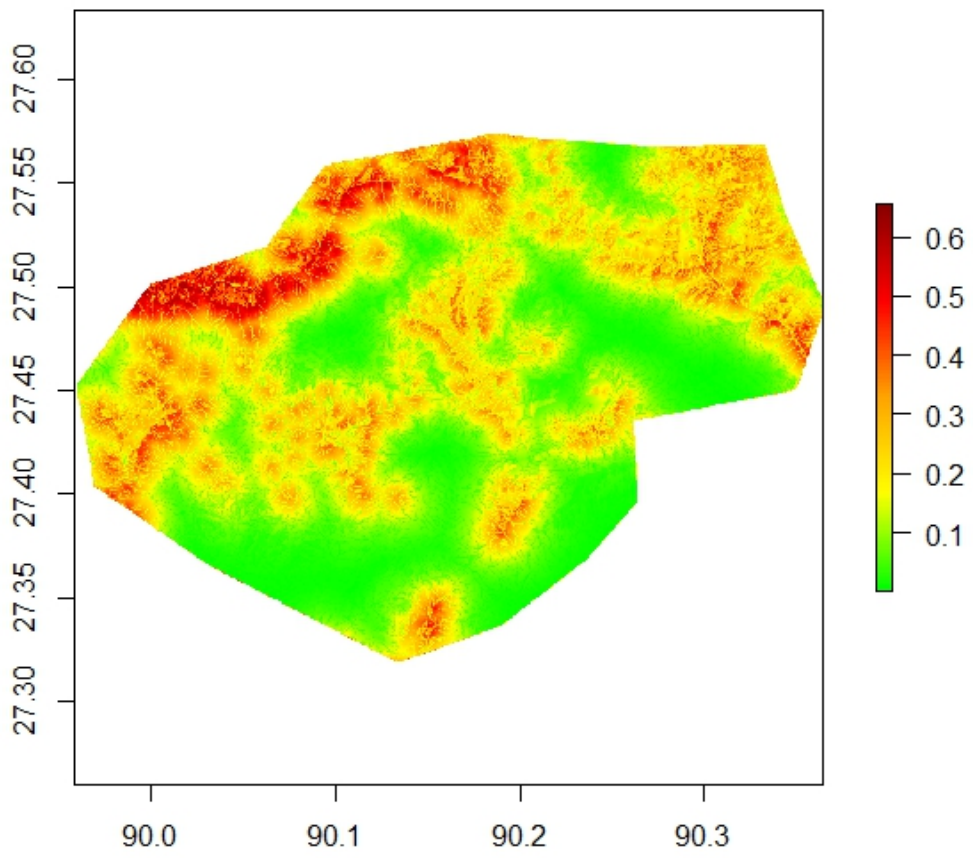


Figure S2. Resource selection function map of leopard_2. The colour scale from green to red represents the probability of resource use by an animal as shown in scale legend on right.

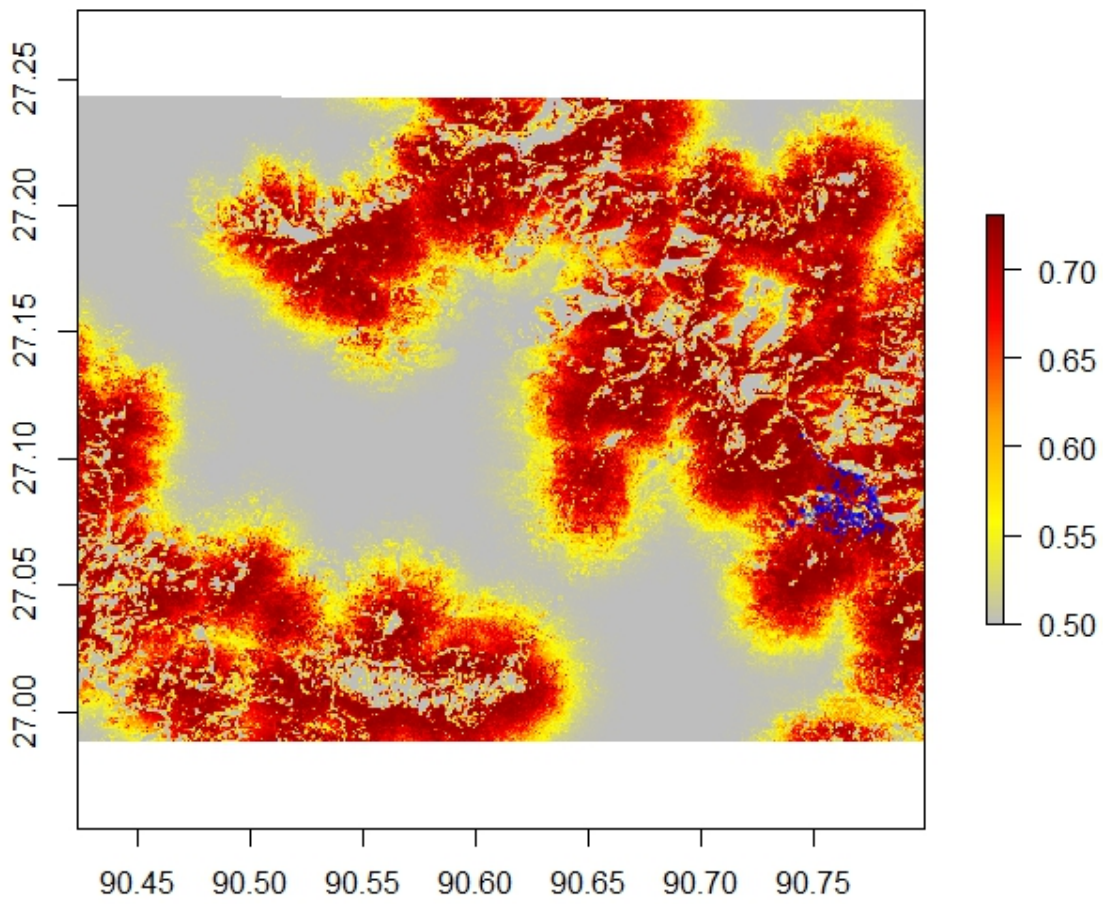


Figure S3. Resource selection function map of leopard_3. The colour scale from grey to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

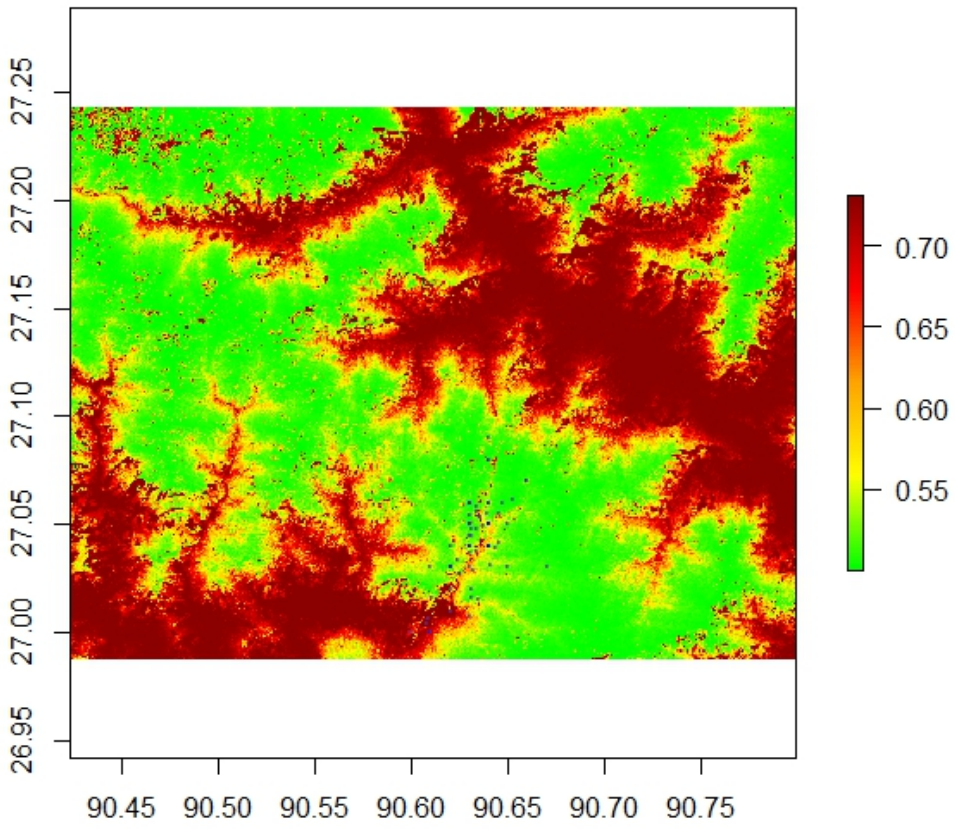


Figure S4. Resource selection function map of Asiatic golden cat_1. The colour scale from green to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

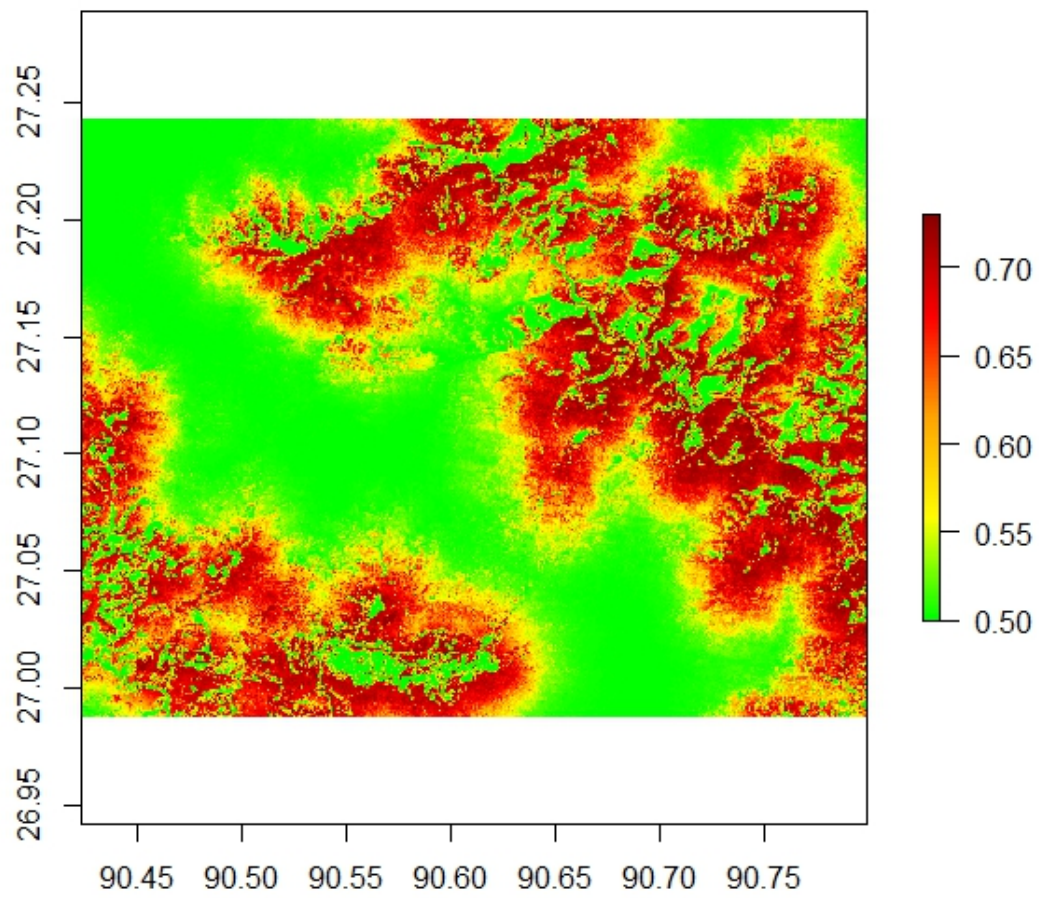


Figure S5. Resource selection function map of leopard cat_1. The colour scale from green to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

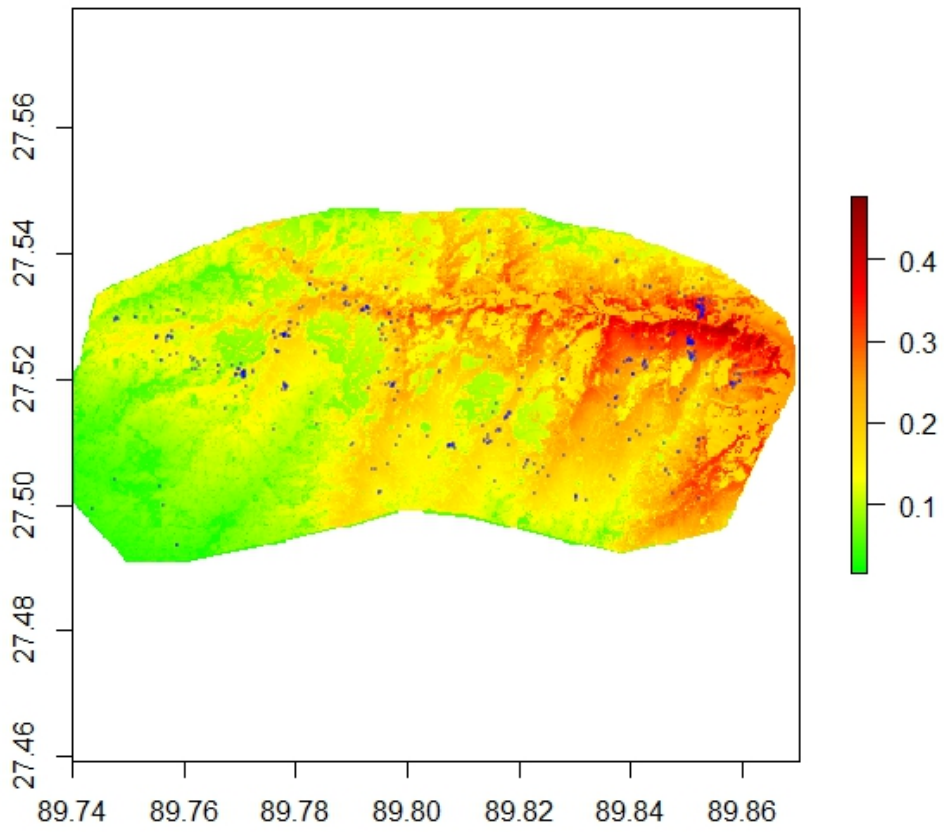


Figure S6. Resource selection function map of dhole_1. The colour scale from green to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

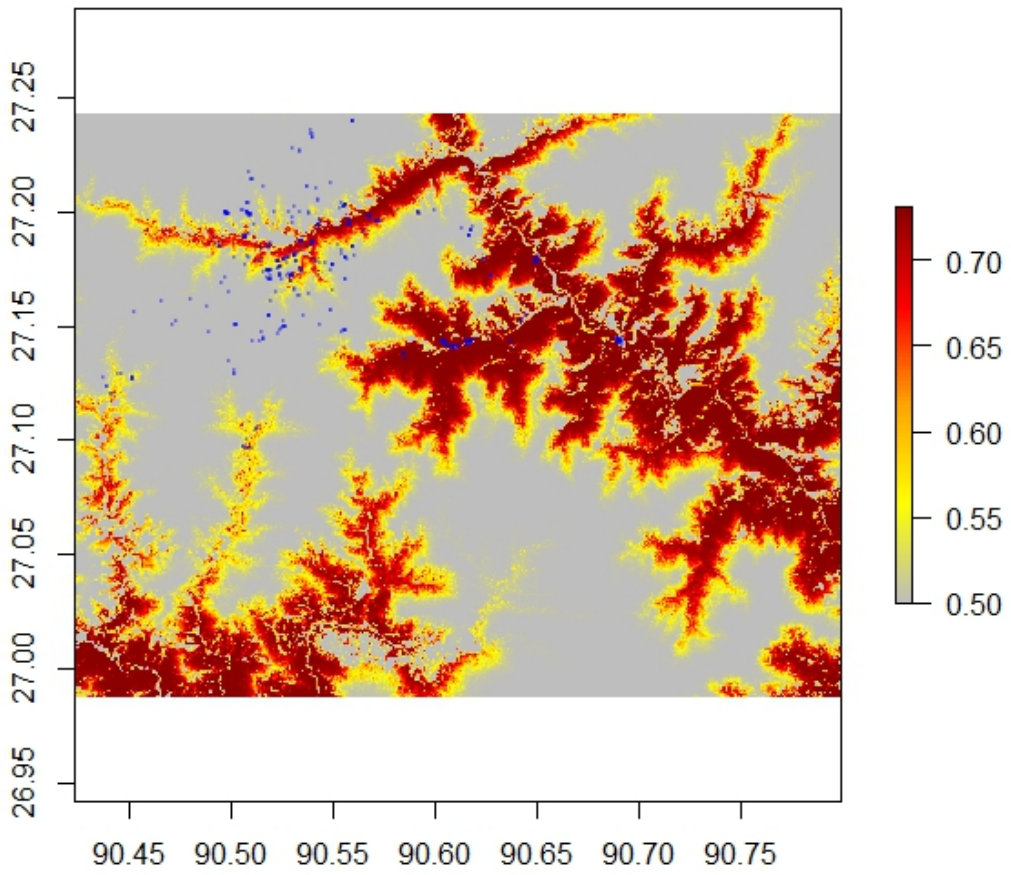


Figure S7. Resource selection function map of dhole_2. The colour scale from green to red represents the probability of resource use by an animal as shown in scale legend on right. The blue points are the position of animal from GPS collar data.

Appendix 3j. Interaction model of RSF

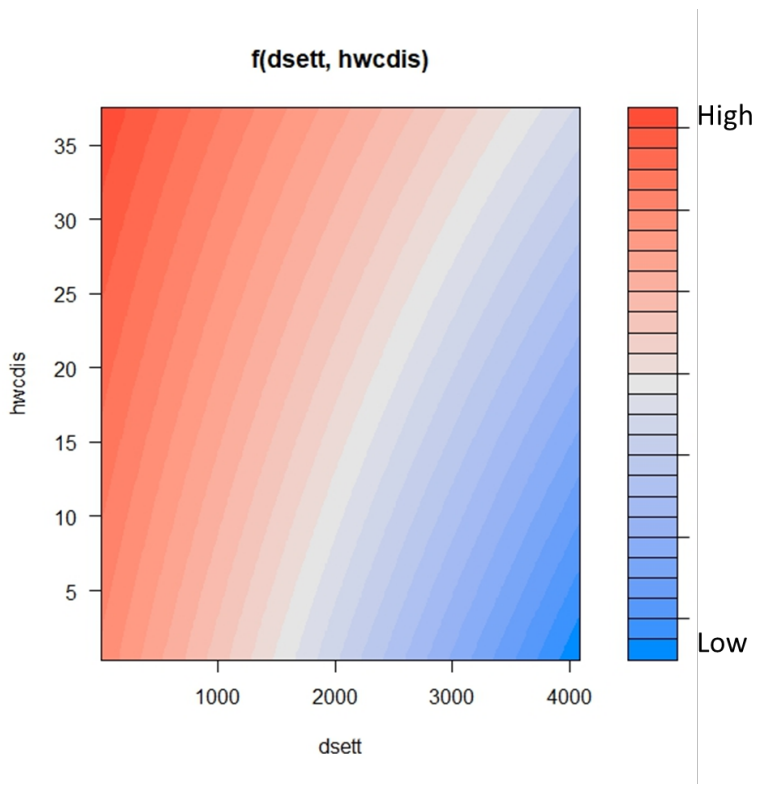


Figure S1. Interaction model of resource selection funciton for leopard_1. The plots depicts interaction between distance to incidences of human-carniovre conflicts (hwcdis) and distance to human settlment (dsett). The dark blue to dark red portion of plot shows resources selection by leopard_1 from low to high level of selection.

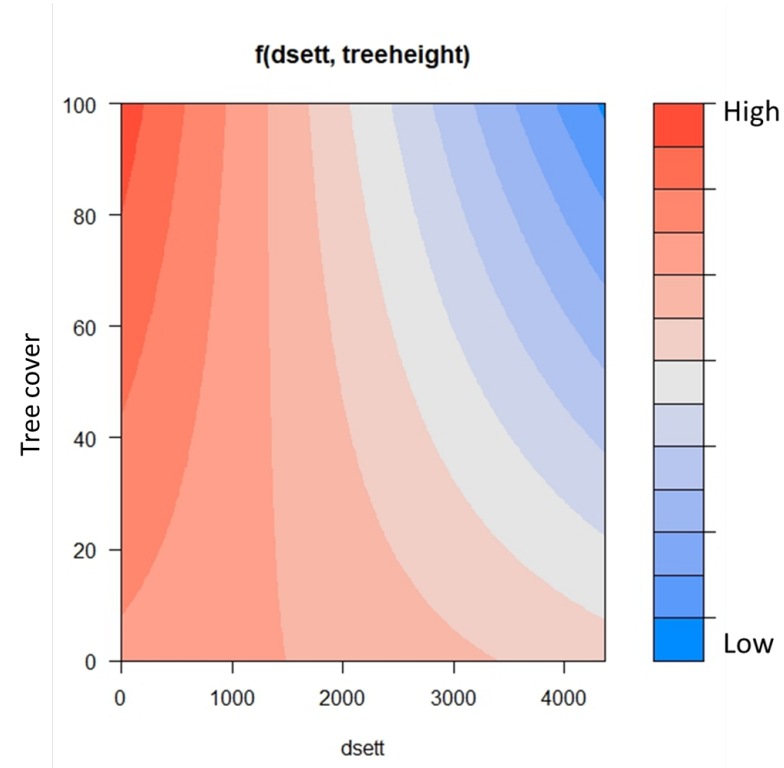


Figure S2. Interaction model of resource selection funciton for leopard_2. The plots depicts interaction between treecover and distance to settlment (dsett). The dark blue to dark red portion of plot shows resources selection by leopard_2 from low to high level of selection.

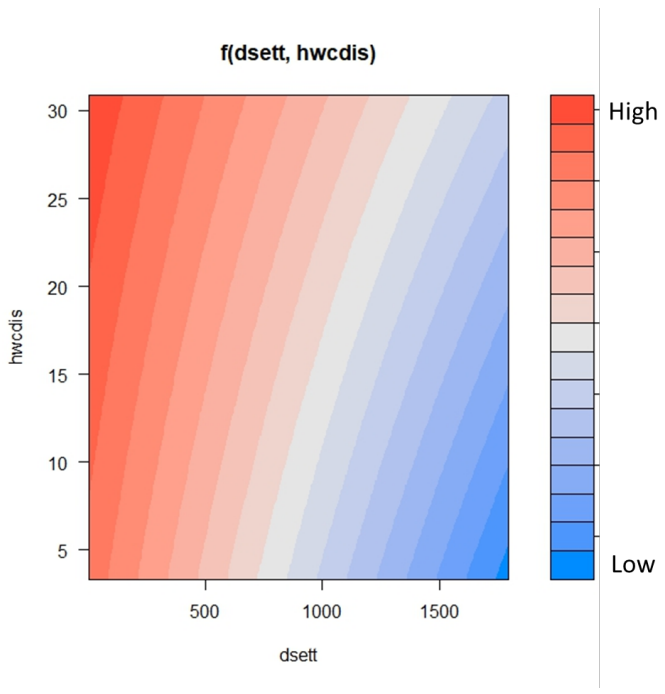


Figure S3. Interaction model of resource selection funciton for leopard_3. The figure legend as for Figure S1.

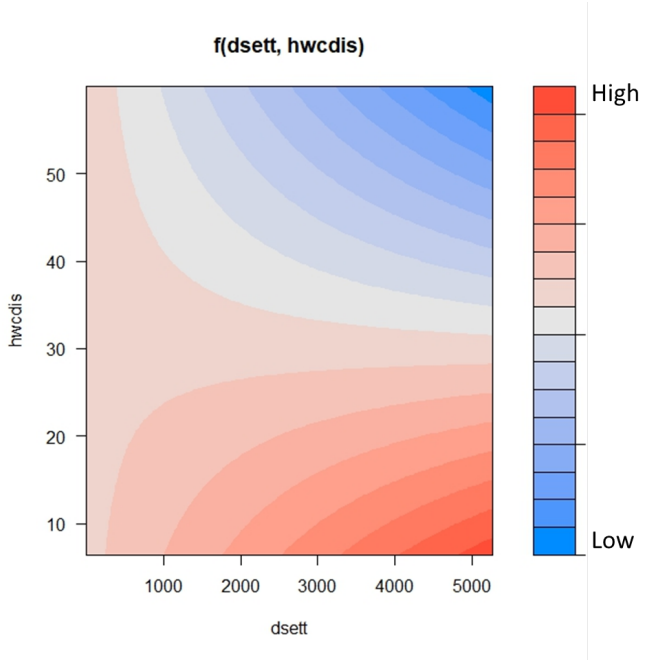


Figure S4. Interaction model of resource selection funciton for Asiatic golden cat_1. The figure legend as for Figure S1.

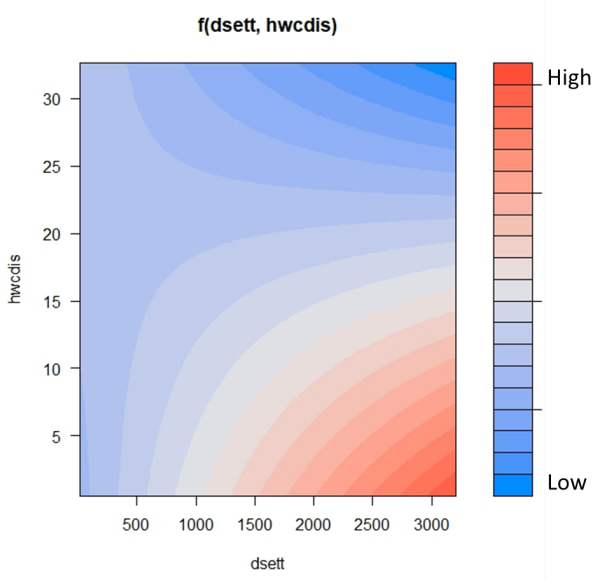


Figure S5. Interaction model of resource selection funciton for leoaprd cat_1. The figure legend as for Figure S1.

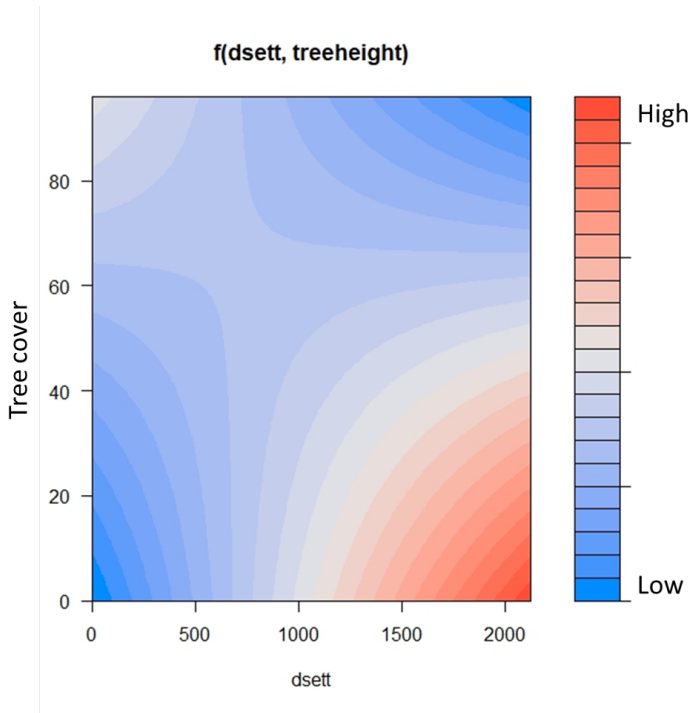


Figure S6. Interaction model of resource selection funciton for dhole_1. The figure legend as for Figure S2.

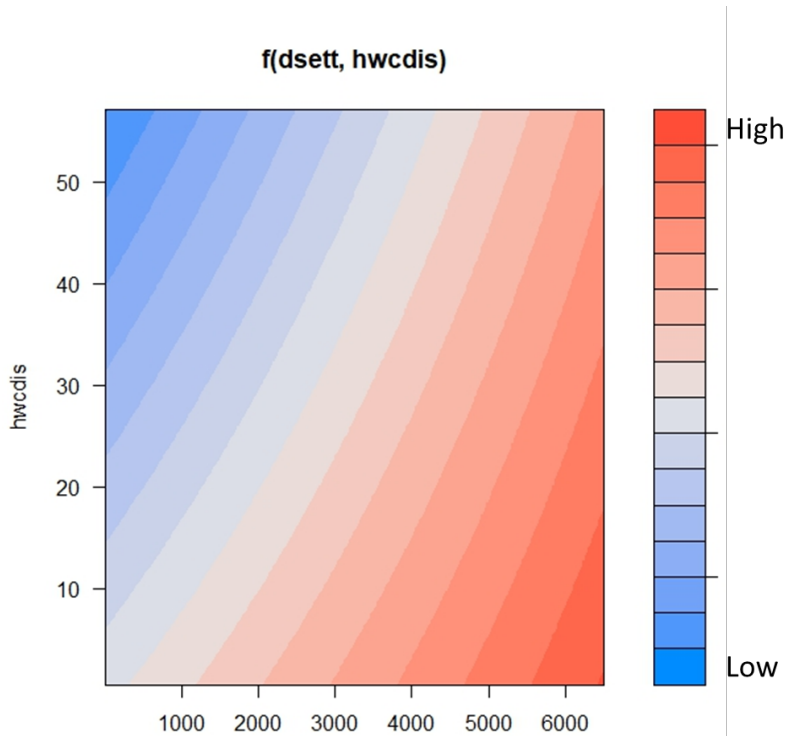


Figure S7. Interaction model of resource selection funciton for dhole_2. The figure legend as for Figure S1.

Appendix 3k. Influence of variables on RSF

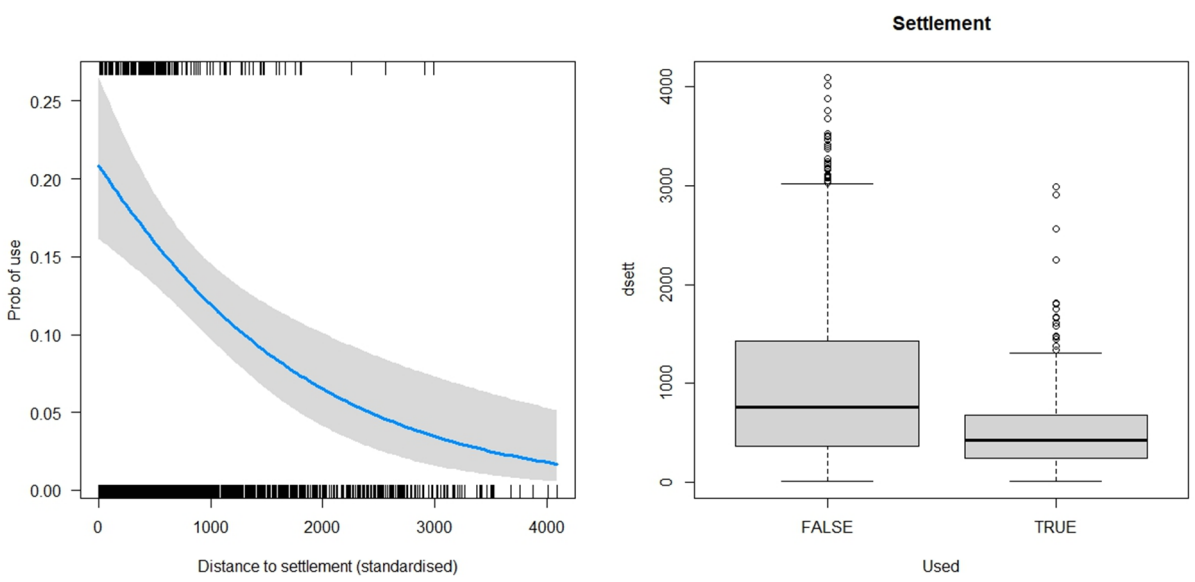


Figure S1. Probability of habitat use by leopard_1 in relation to distance from settlement left. The scale is standardized to 4km from the periphery of settlement. The box and whisker plot on right shows proportion of habitat use by leopard_1 with respect to the distance from settlement.

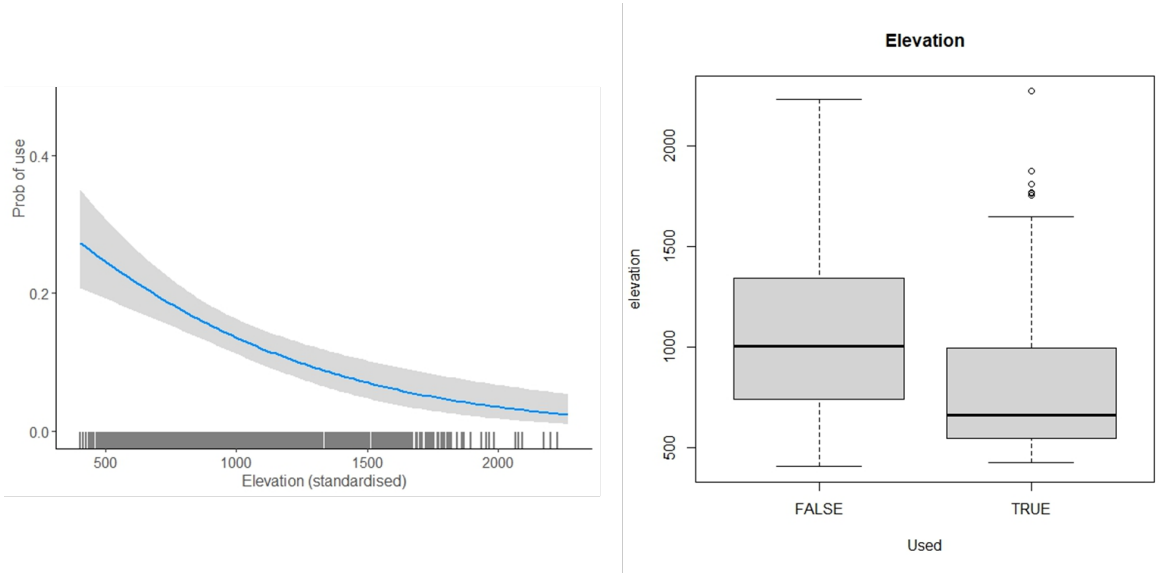


Figure S2. Probability of habitat use by leopard_1 in relation to elevation. Figure legends area same as Figure S1.

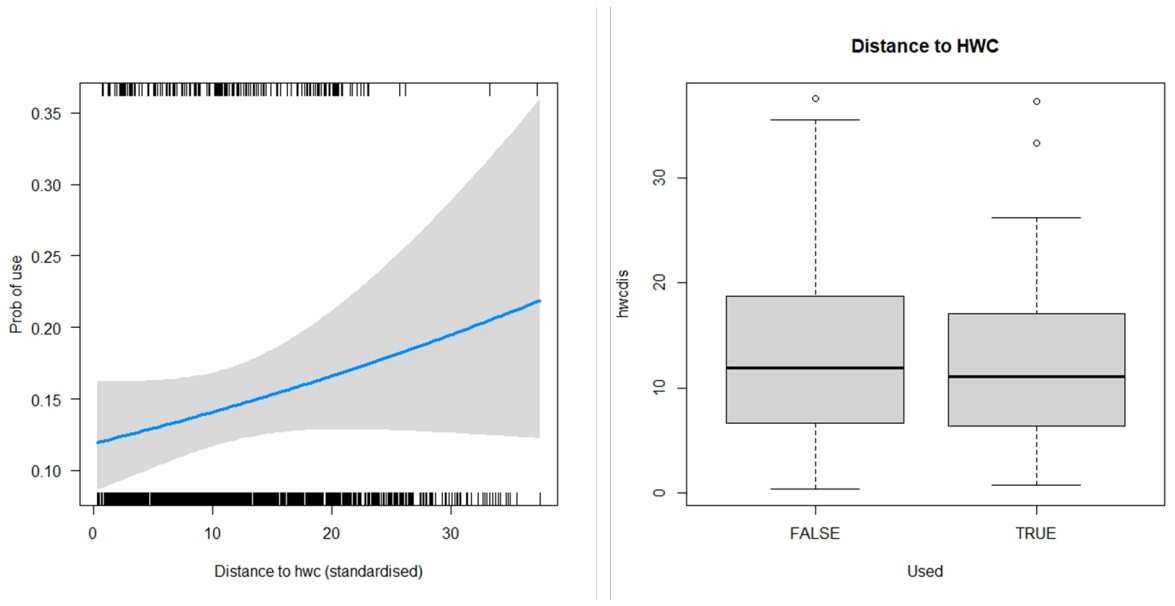


Figure S3. Probability of habitat use by leopard_1 in relation to human wildlife conflict (here carnivore) distance. Figure legends area same as Figure S1.

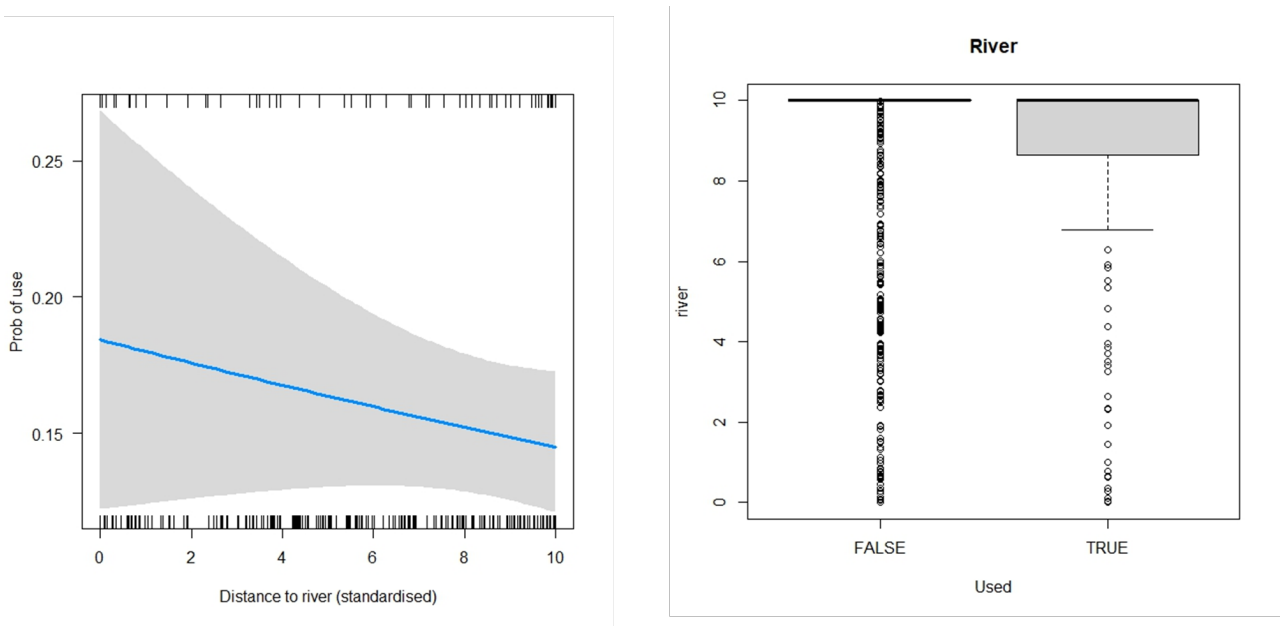


Figure S4. Probability of habitat use by leopard_1 in relation to distance from river. Figure legends area same as Figure S1.

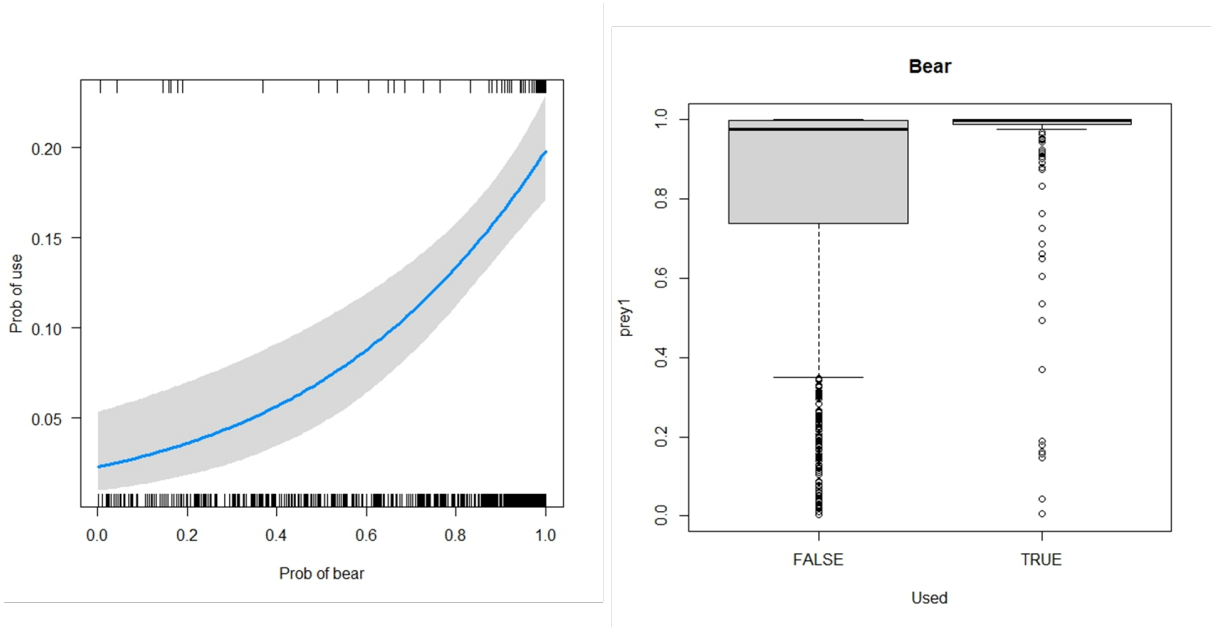


Figure S5. Probability of habitat use by leopard_1 in relation probability occupancy of bear.

Figure legends area same as Figure S1.

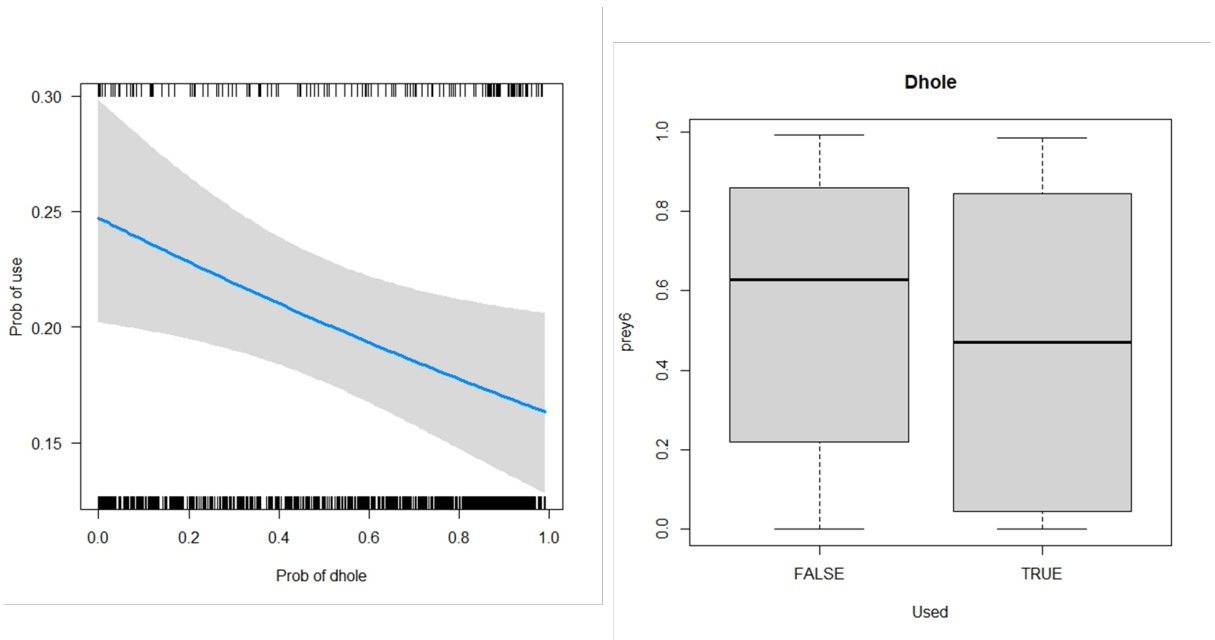


Figure S6. Probability of habitat use by leopard_1 in relation probability occupancy of dhole.

Figure legends area same as Figure S1.

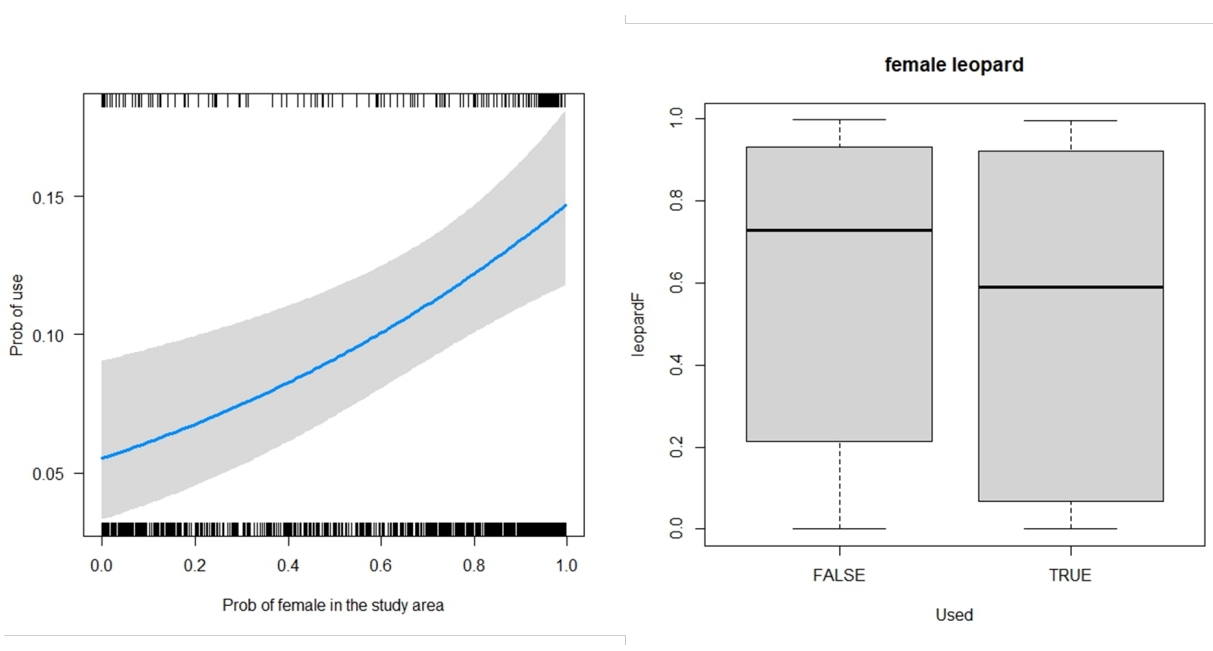


Figure S7. Probability of habitat use by leopard_1 in relation probability occupancy of female leopard. Figure legends area same as Figure S1.

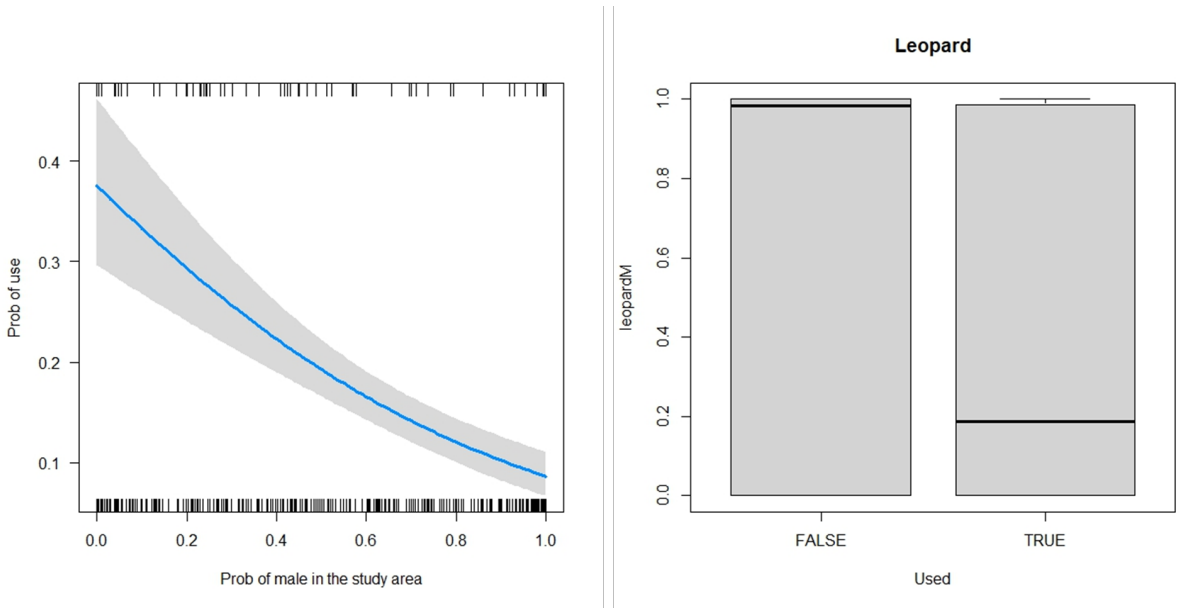


Figure S8. Probability of habitat use by leopard_1 in relation probability occupancy of male leopard. Figure legends area same as Figure S1.

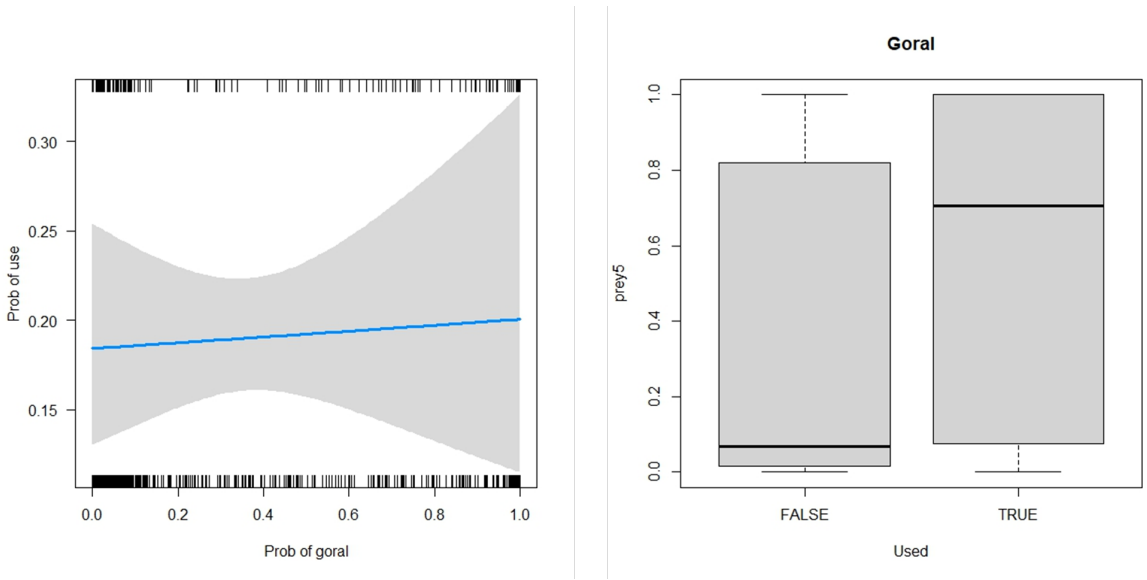


Figure S9. Probability of habitat use by leopard_1 in relation probability occupancy of goral. Figure legends area same as Figure S1.

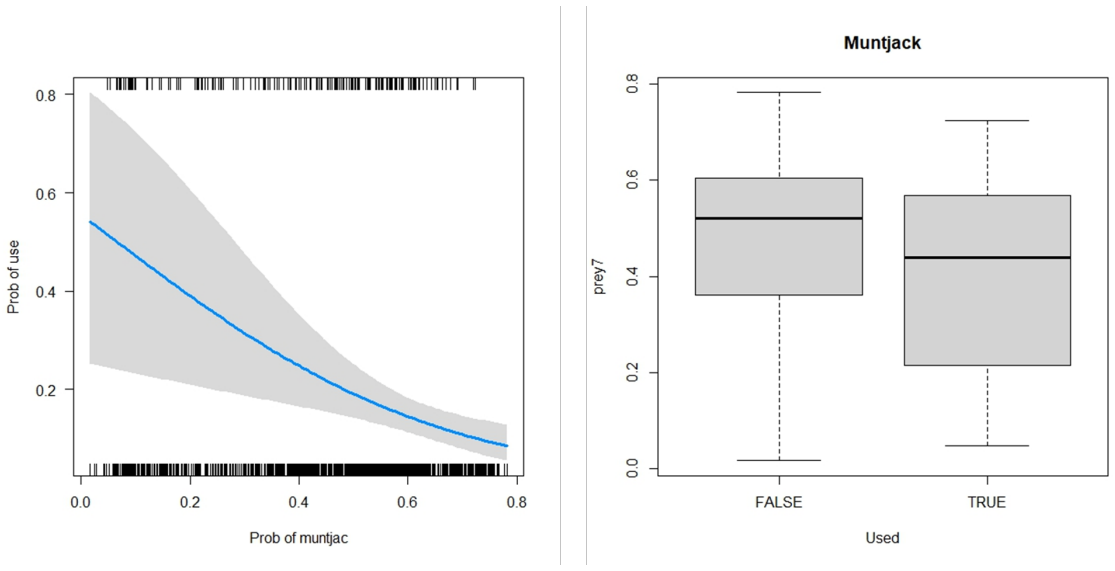


Figure S10. Probability of habitat use by leopard_1 in relation probability occupancy of muntjac. Figure legends area same as Figure S1.

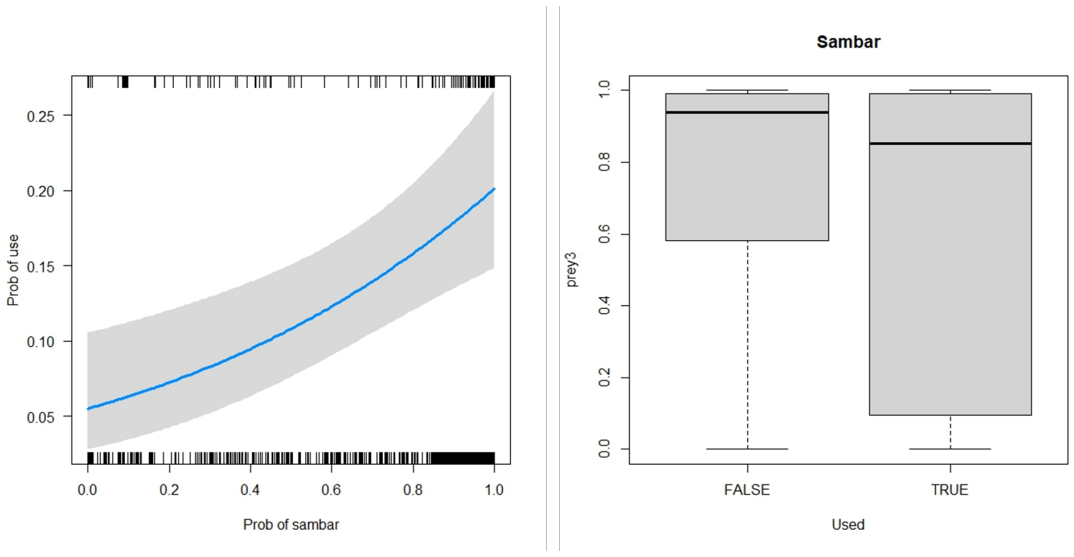


Figure S11. Probability of habitat use by leopard_1 in relation probability occupancy of sambar. Figure legends area same as Figure S.

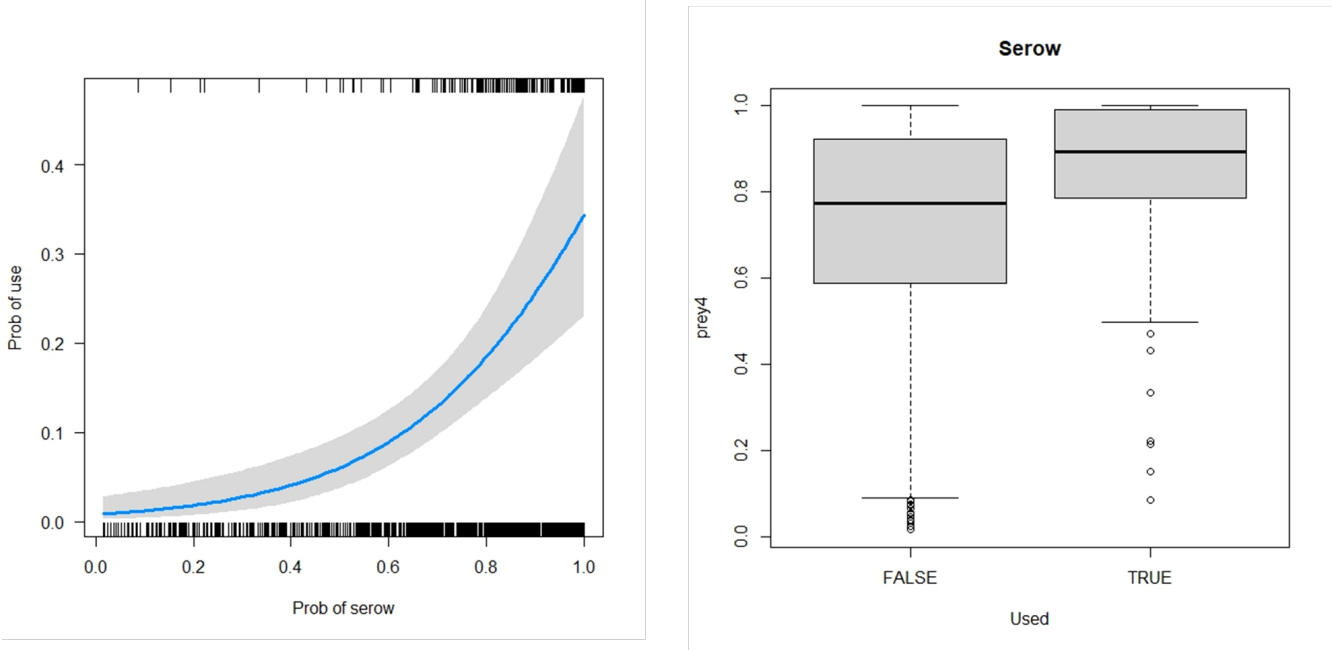


Figure S12. Probability of habitat use by leopard_1 in relation probability occupancy of serow. Figure legends area same as Figure S1.

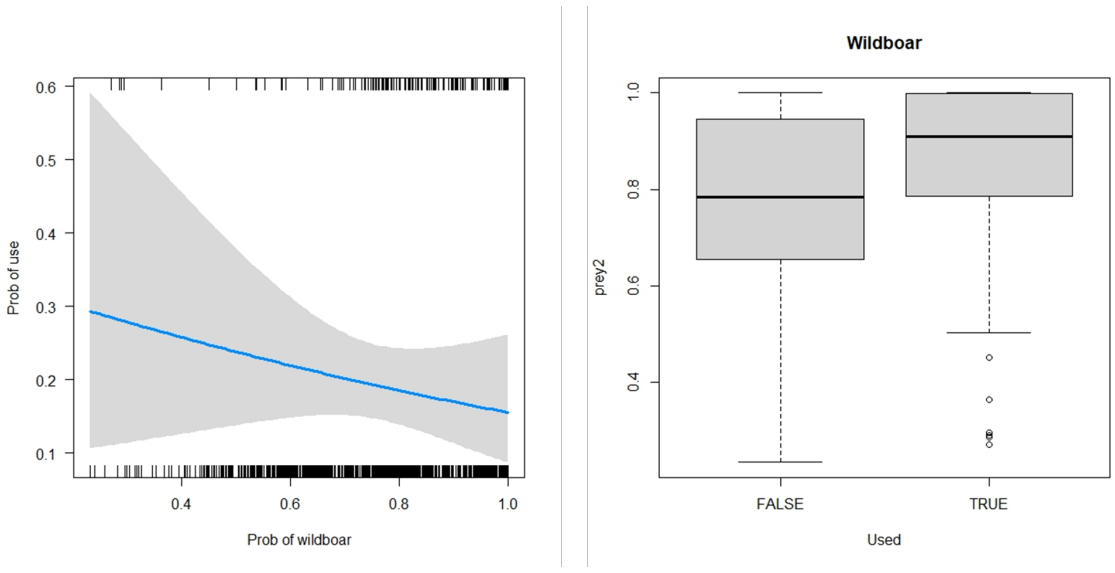


Figure S13. Probability of habitat use by leopard_1 in relation probability occupancy of wild boar. Figure legends area same as Figure S1.

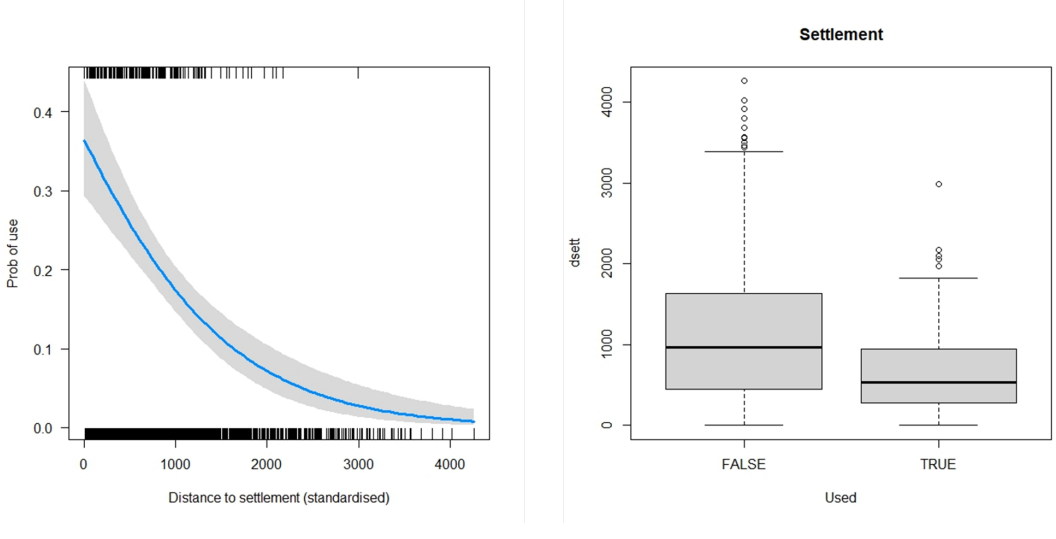


Figure S14. Probability of habitat use by leopard_2 in relation to distance from settlement. Figure legends area same as Figure S1.

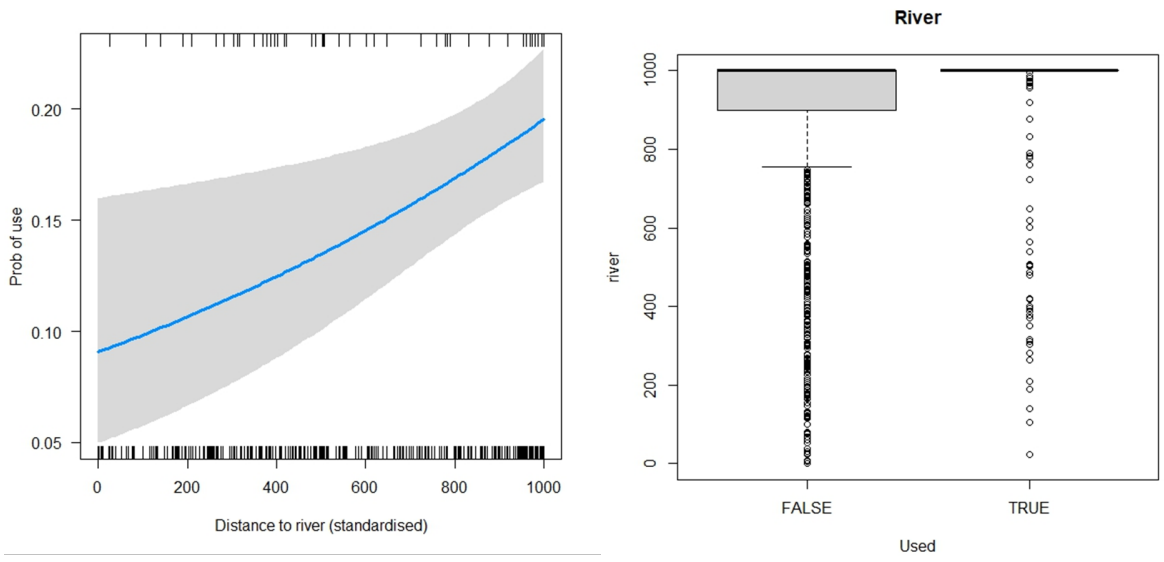


Figure S15. Probability of habitat use by leopard_2 in relation to distance from river. Figure legends area same as Figure S1.

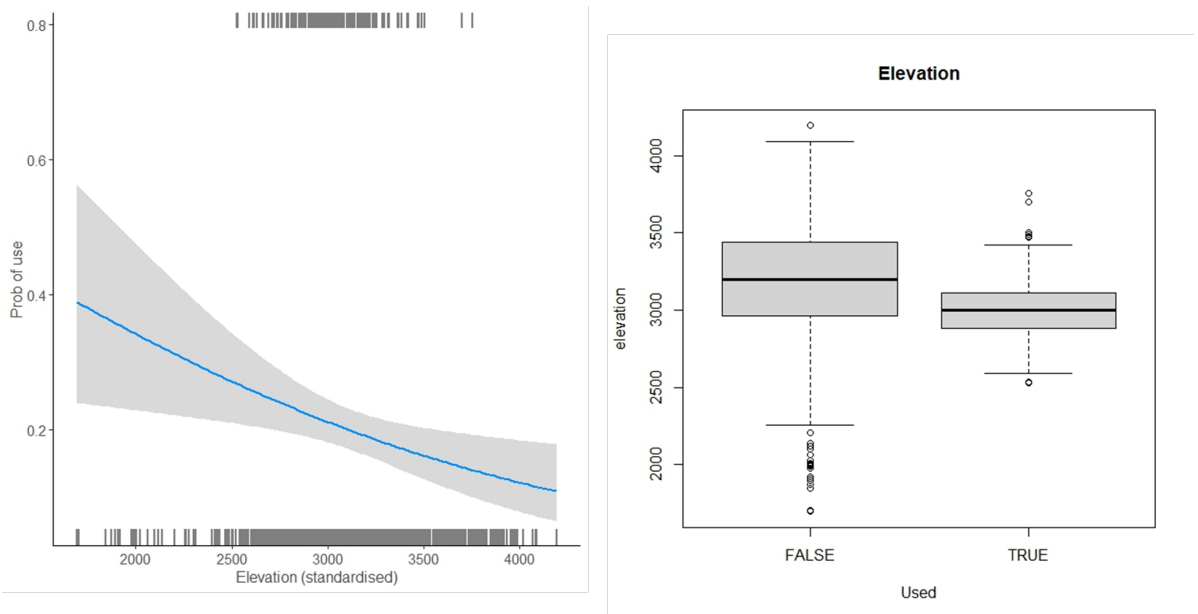


Figure S16. Probability of habitat use by leopard_2 in relation to elevation. Figure legends area same as Figure S1.

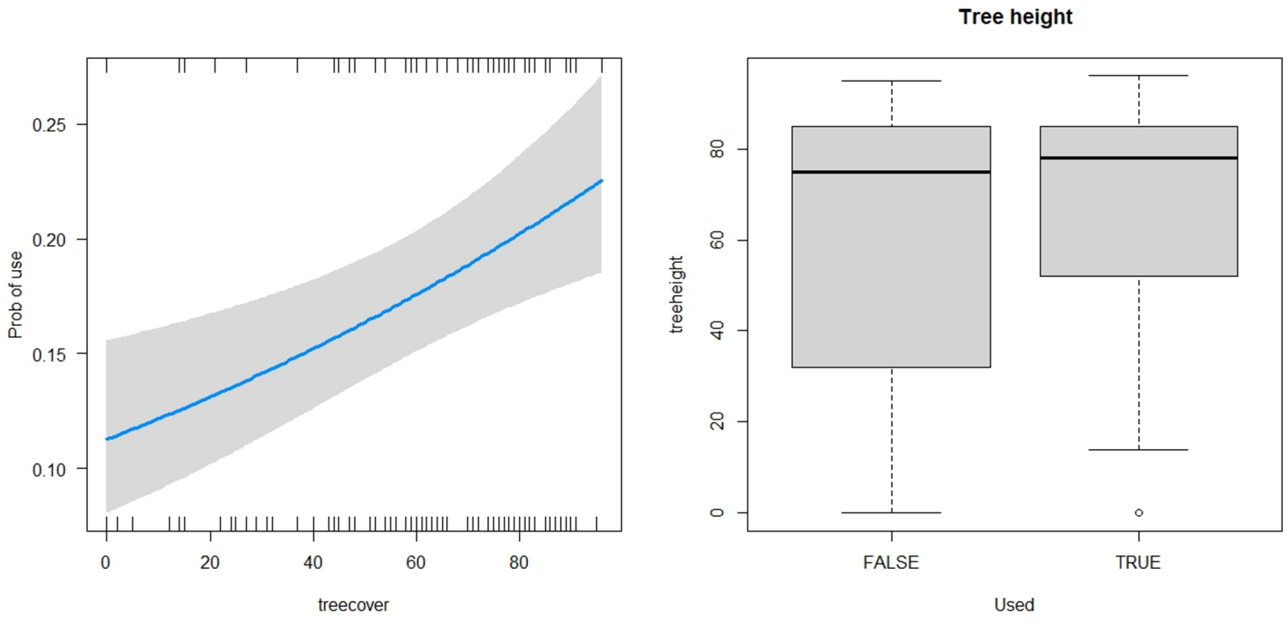


Figure S17. Probability of habitat use by leopard_2 in relation to tree cover. Figure legends area same as Figure S1.

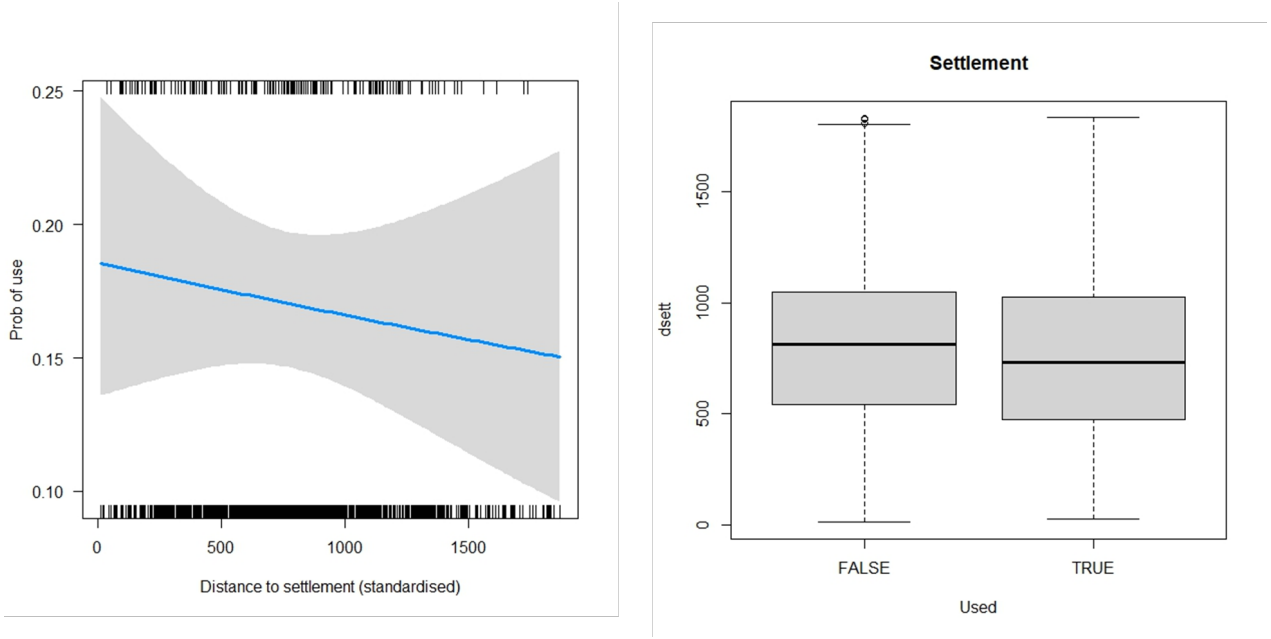


Figure S18. Probability of habitat use by leopard_3 in relation to distance from settlement. Figure legends area same as Figure S1.

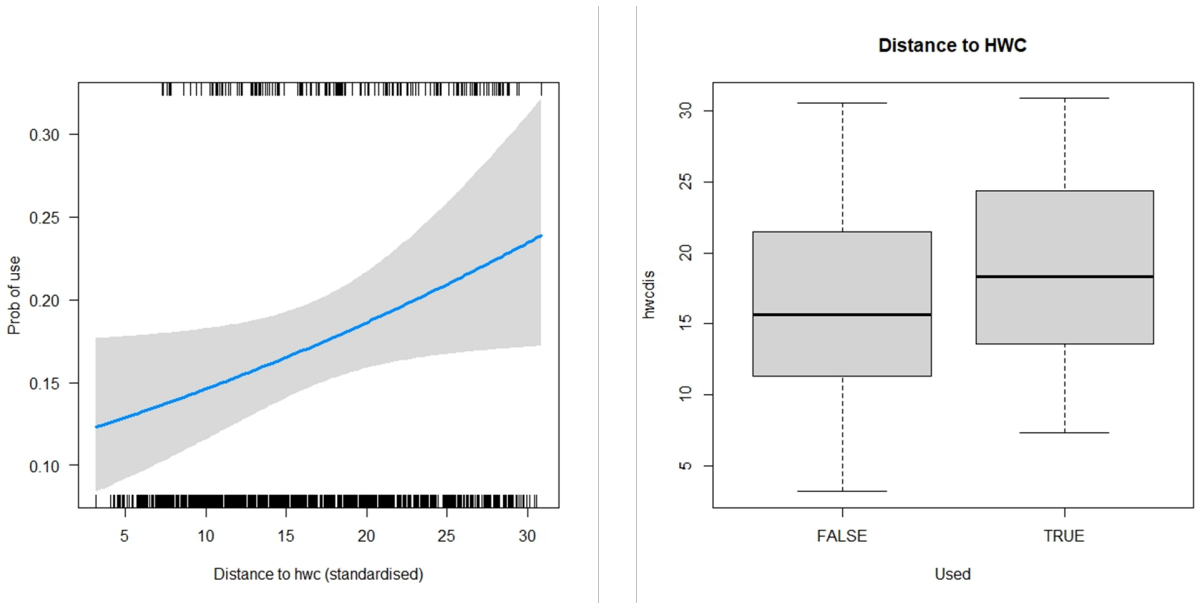


Figure S19. Probability of habitat use by leopard_3 in relation to distance from settlement. Figure legends area same as Figure S1.

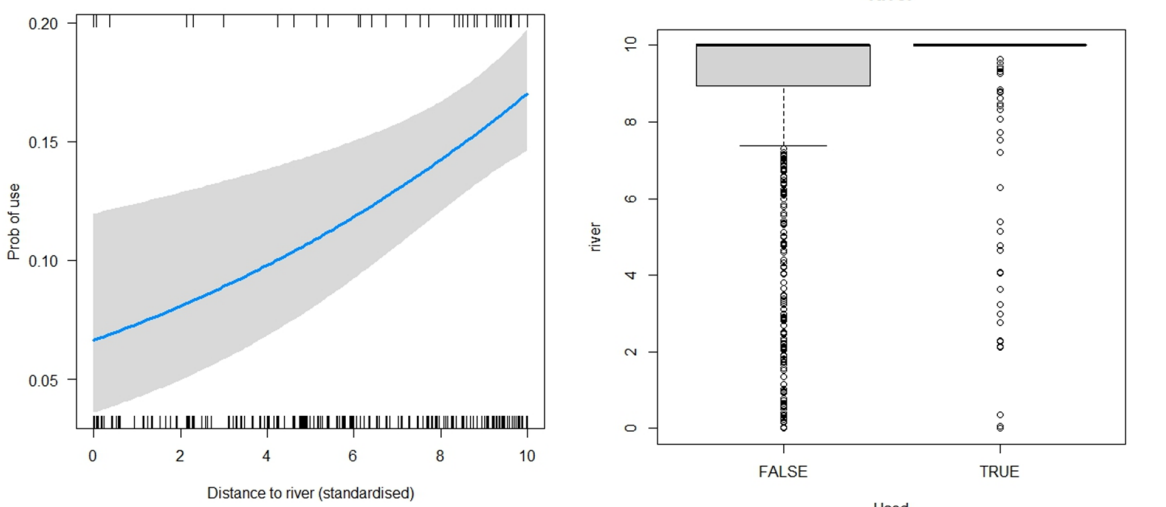


Figure S20. Probability of habitat use by leopard_3 in relation to distance from river. Figure legends area same as Figure S1.

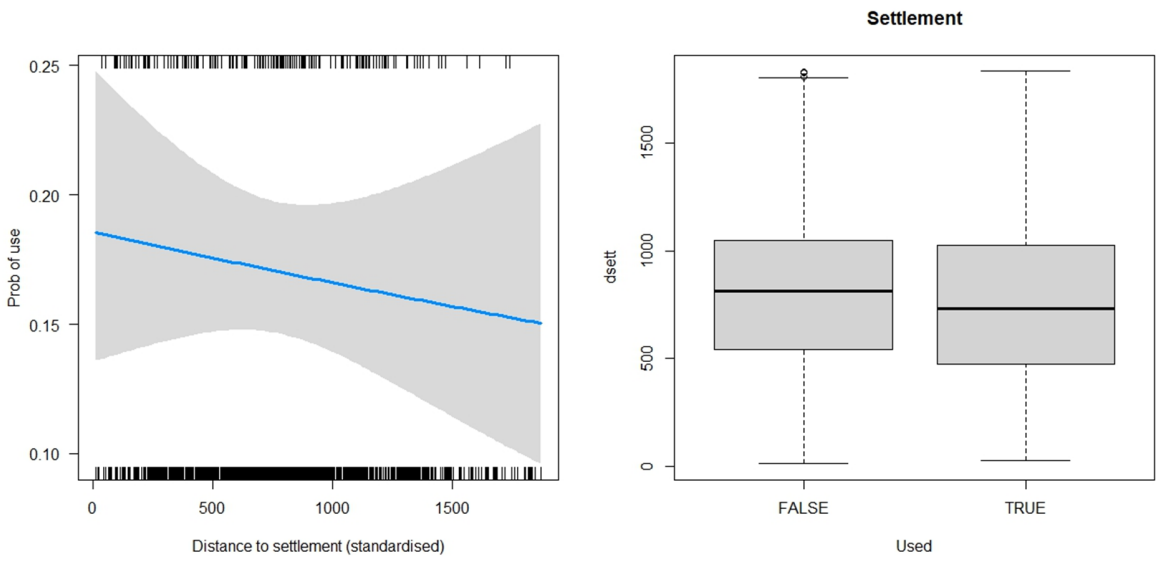


Figure S21. Probability of habitat use by leopard_3 in relation to distance from settlement. Figure legends area same as Figure S.

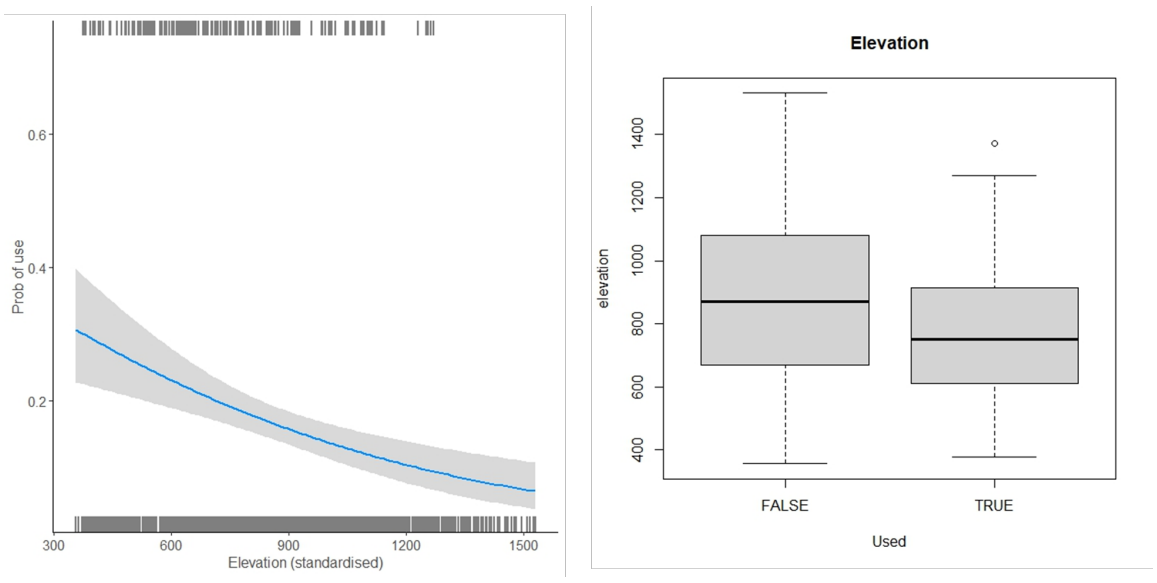


Figure S22. Probability of habitat use by leopard_3 in relation to elevation. Figure legends area same as Figure S1.

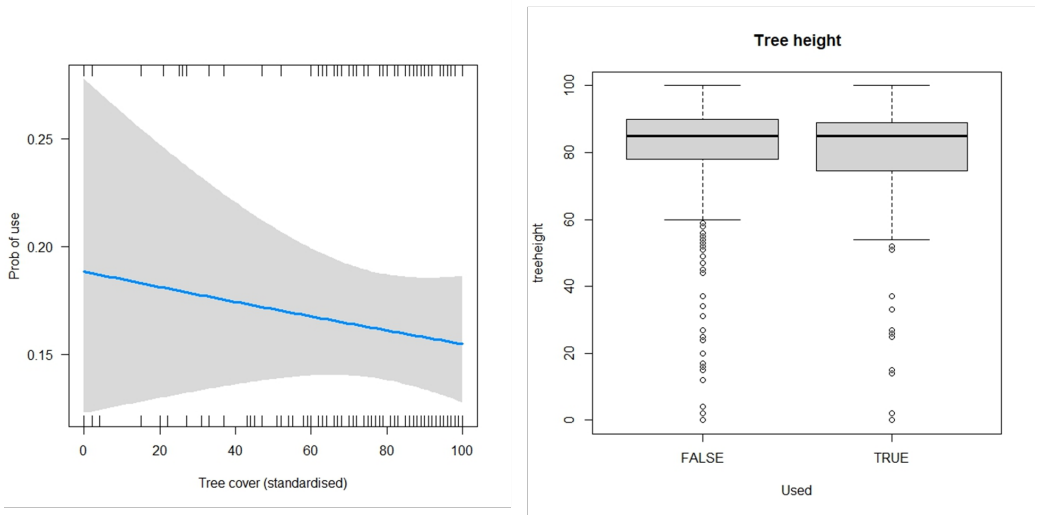


Figure S22a. Probability of habitat use by leopard_3 in relation to elevation. Figure legends area same as Figure S1.

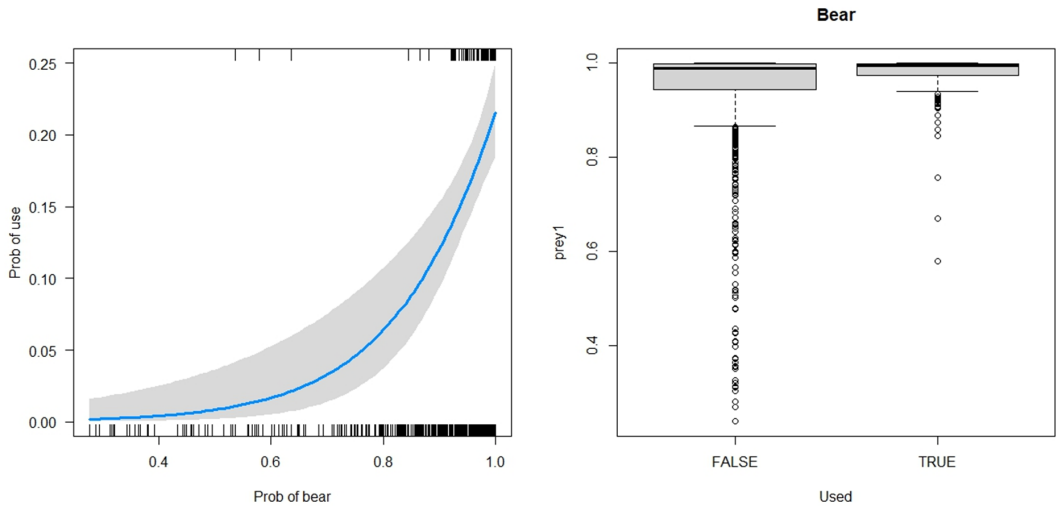


Figure S23. Probability of habitat use by leopard_3 in relation to occupancy of bear. Figure legends area same as Figure S1.

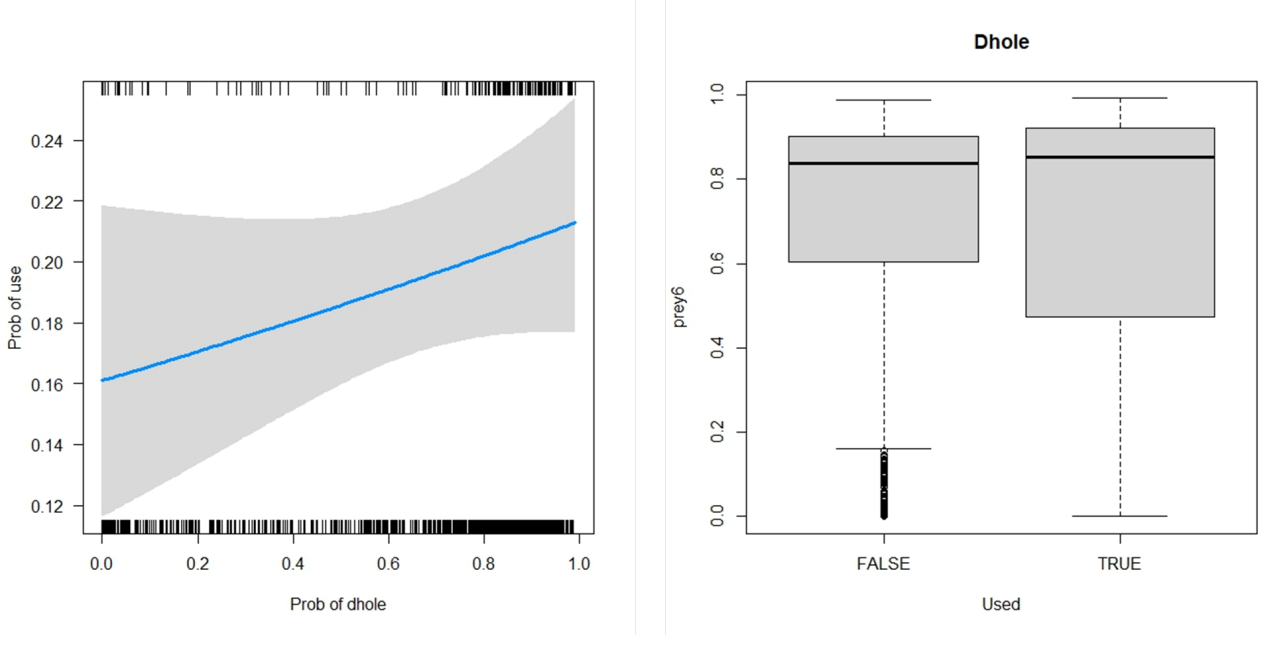


Figure S24. Probability of habitat use by leopard_3 in relation to occupancy of dhole. Figure legends area same as Figure S1.

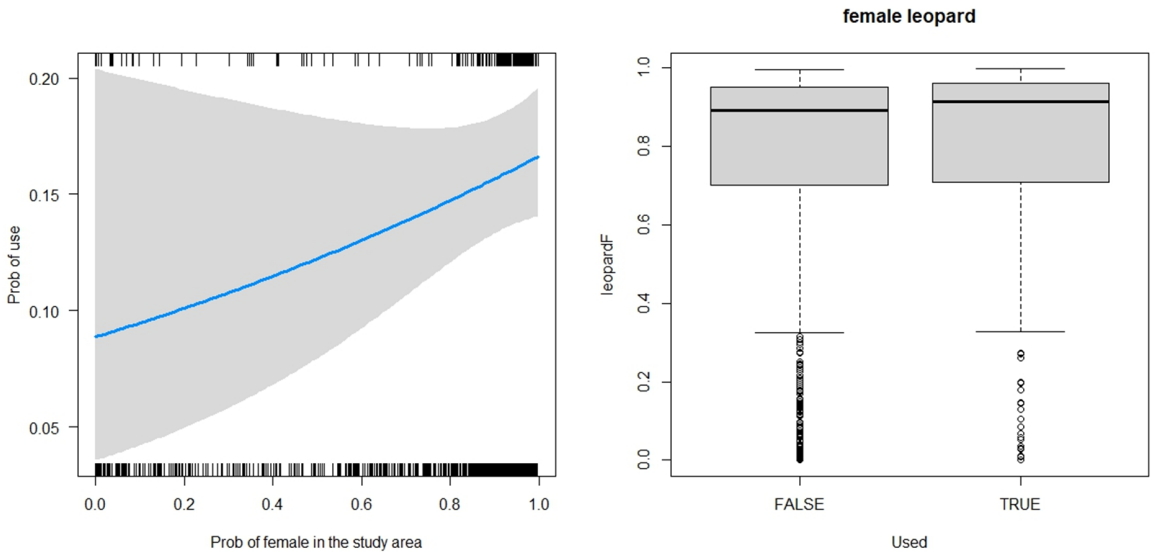


Figure S25. Probability of habitat use by leopard_3 in relation to occupancy of female leopards. Figure legends area same as Figure S1.

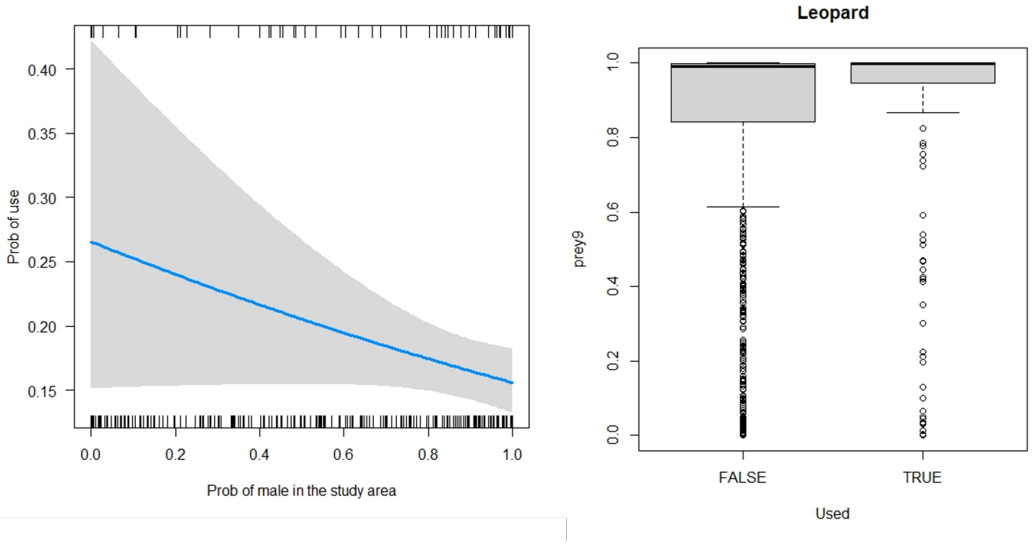


Figure S26. Probability of habitat use by leopard_3 in relation to occupancy of male leopards. Figure legends area same as Figure S1.

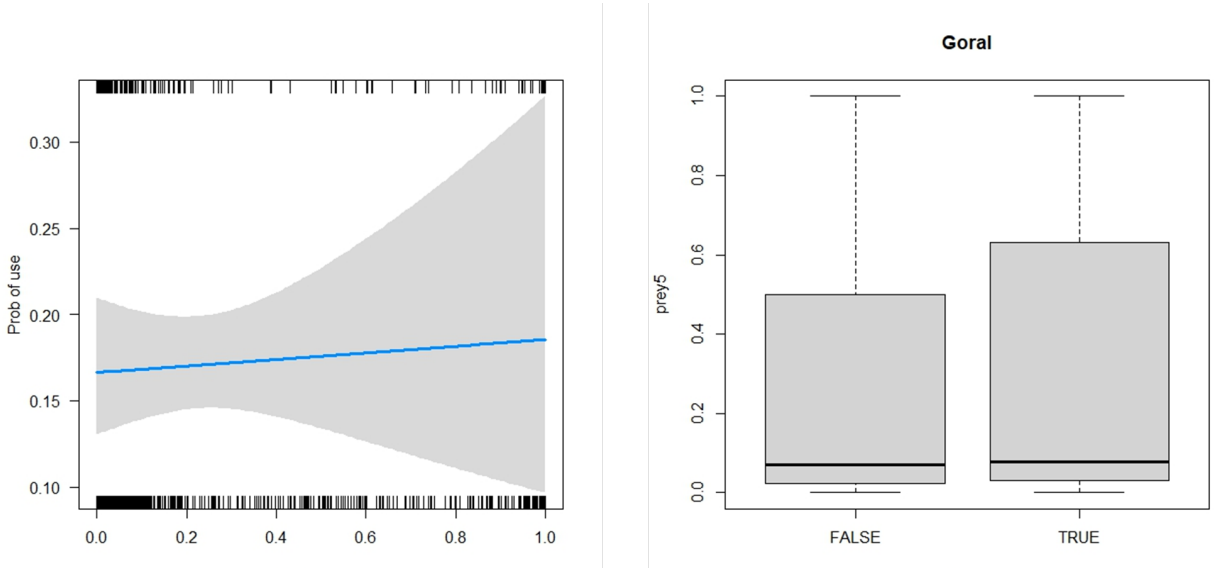


Figure S27. Probability of habitat use by leopard_3 in relation to occupancy of goral. Figure legends area same as Figure S1.

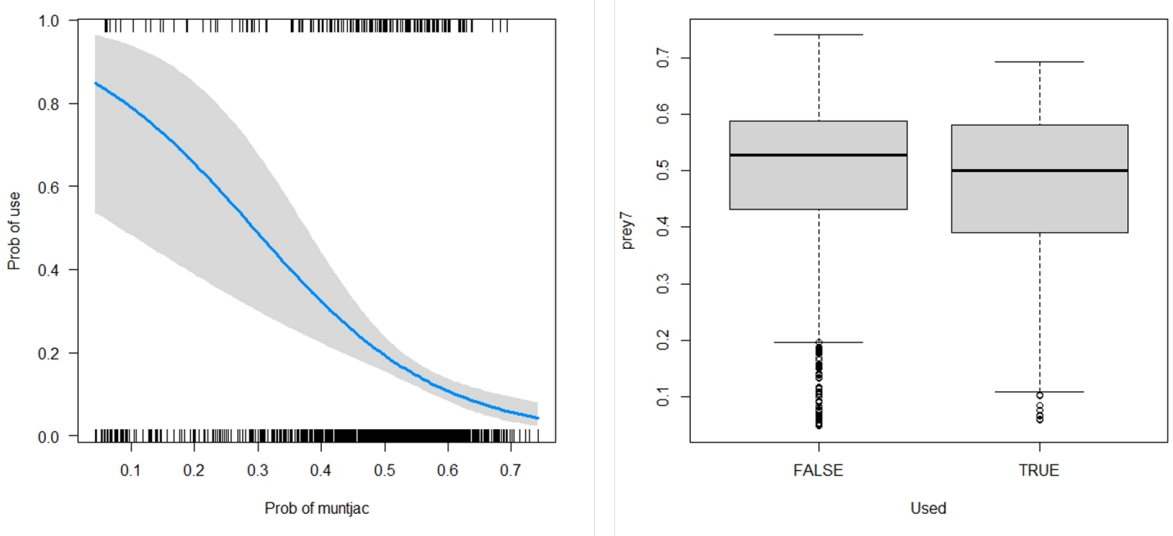


Figure S28. Probability of habitat use by leopard_3 in relation to occupancy of muntjac. Figure legends area same as Figure S1.

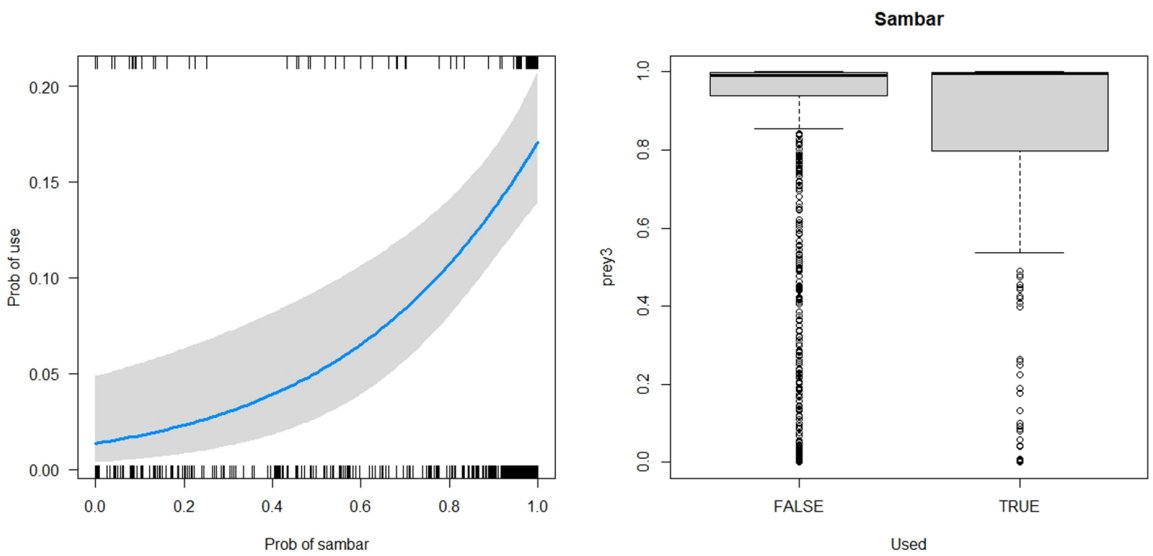


Figure S29. Probability of habitat use by leopard_3 in relation to occupancy of sambar. Figure legends area same as Figure S1.

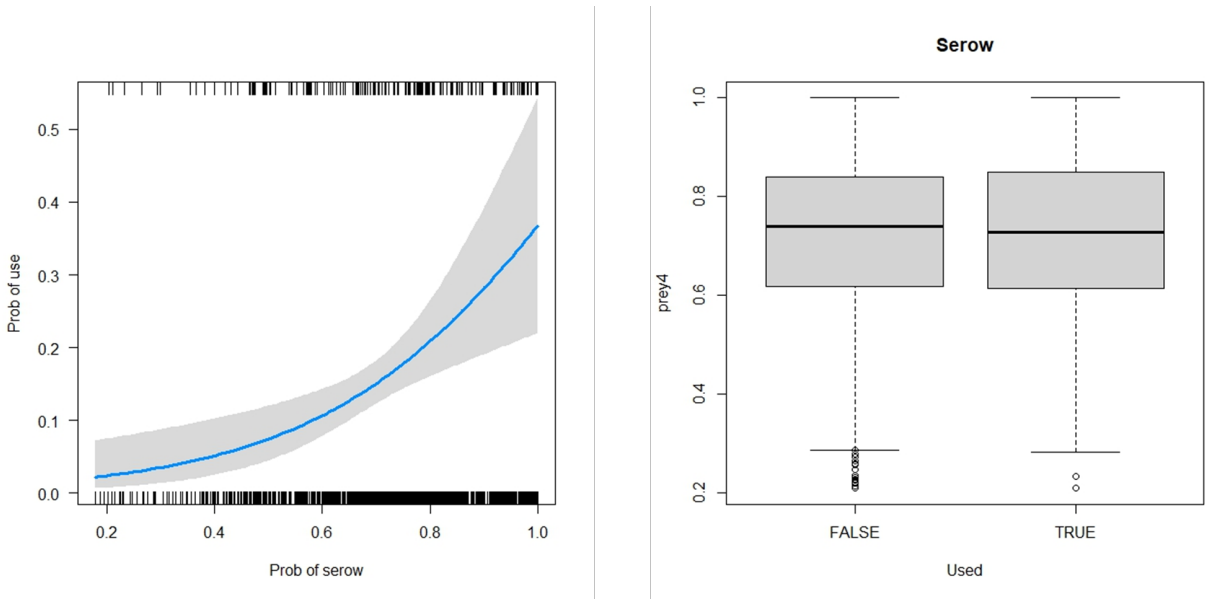


Figure S30. Probability of habitat use by leopard_3 in relation to occupancy of serow. Figure legends area same as Figure S1.

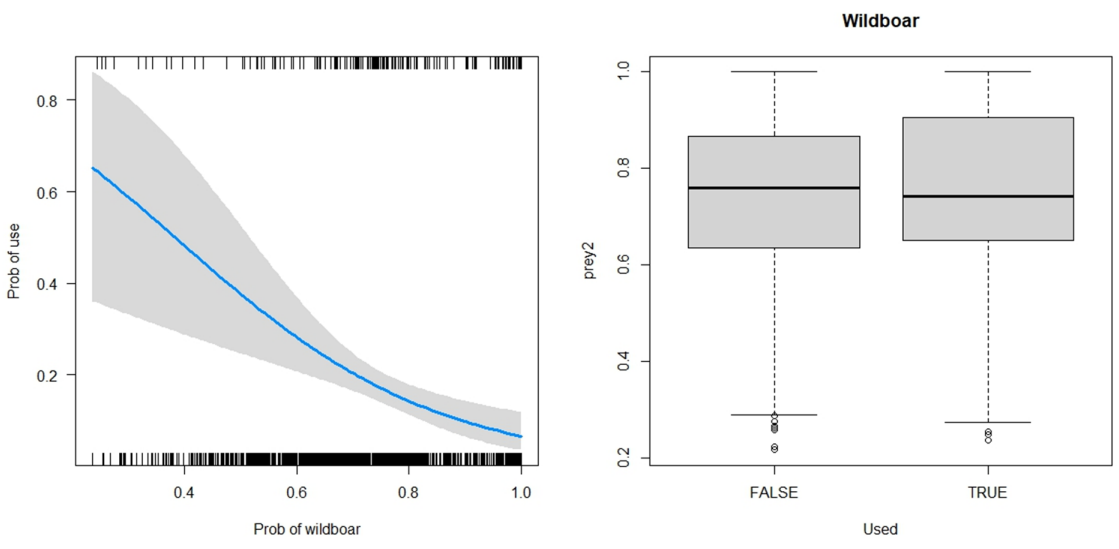


Figure S31. Probability of habitat use by leopard_3 in relation to occupancy of wild boar. Figure legends area same as Figure S.

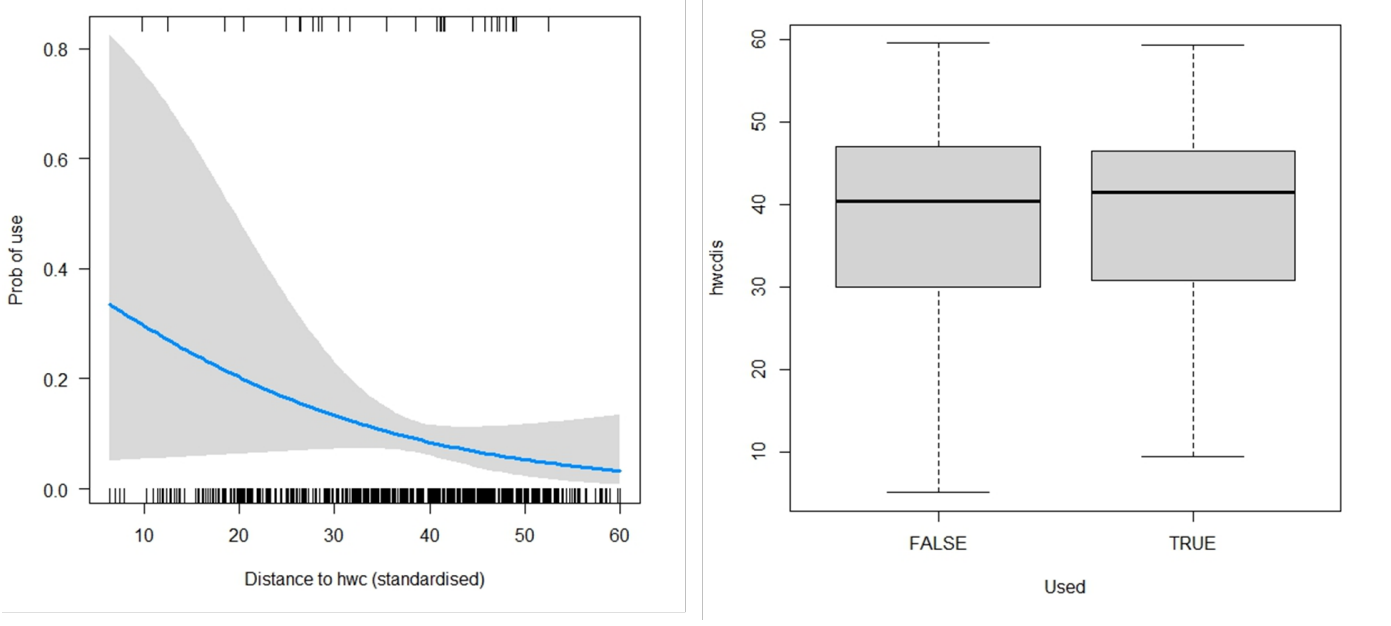


Figure S32. Probability of habitat use by Asiatic golden cat_1 in relation to distance from human-carnivore conflict. Figure legends area same as Figure S1.

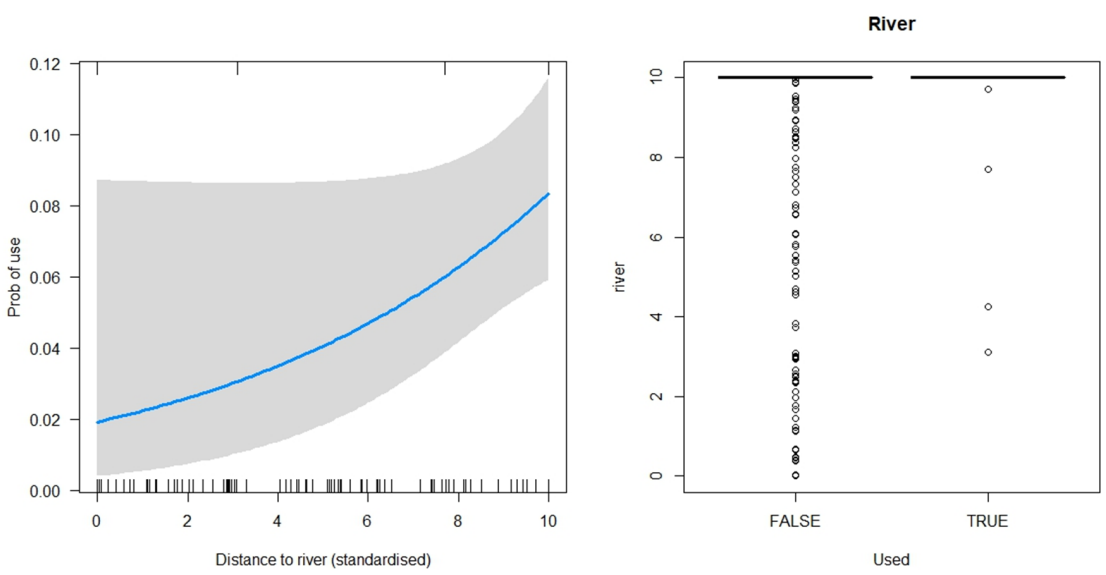


Figure S33. Probability of habitat use by Asiatic golden cat_1 in relation to distance from river. Figure legends area same as Figure S1.

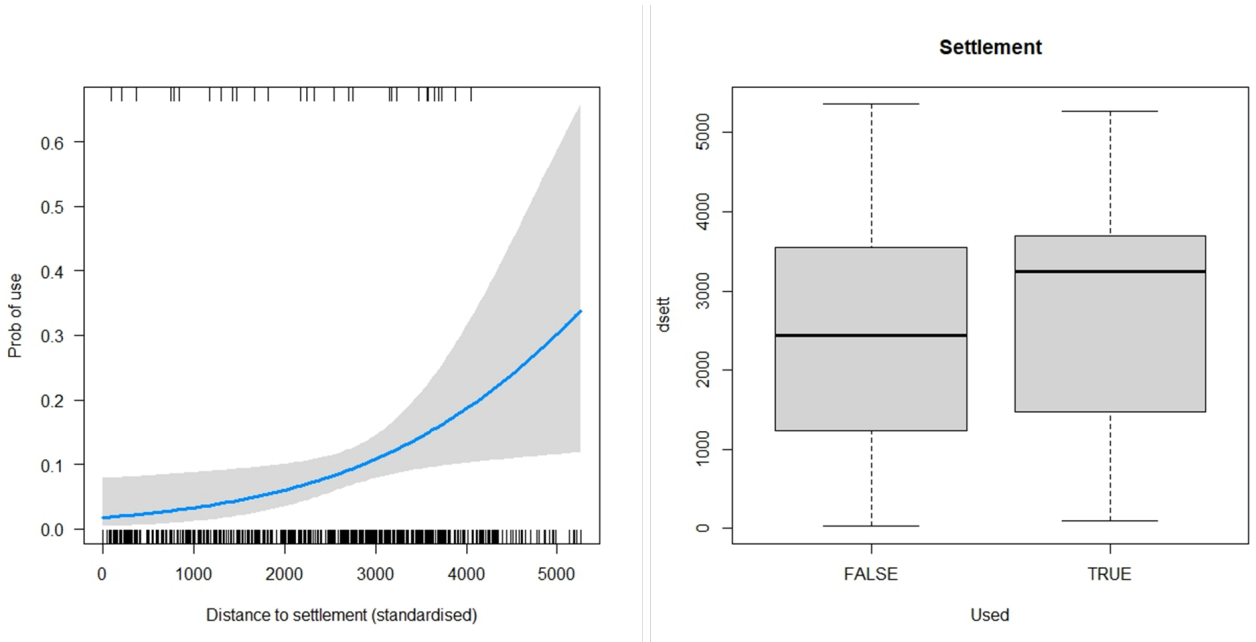


Figure S34. Probability of habitat use by Asiatic golden cat_1 in relation to distance from settlement.

Figure legends area same as Figure S1.

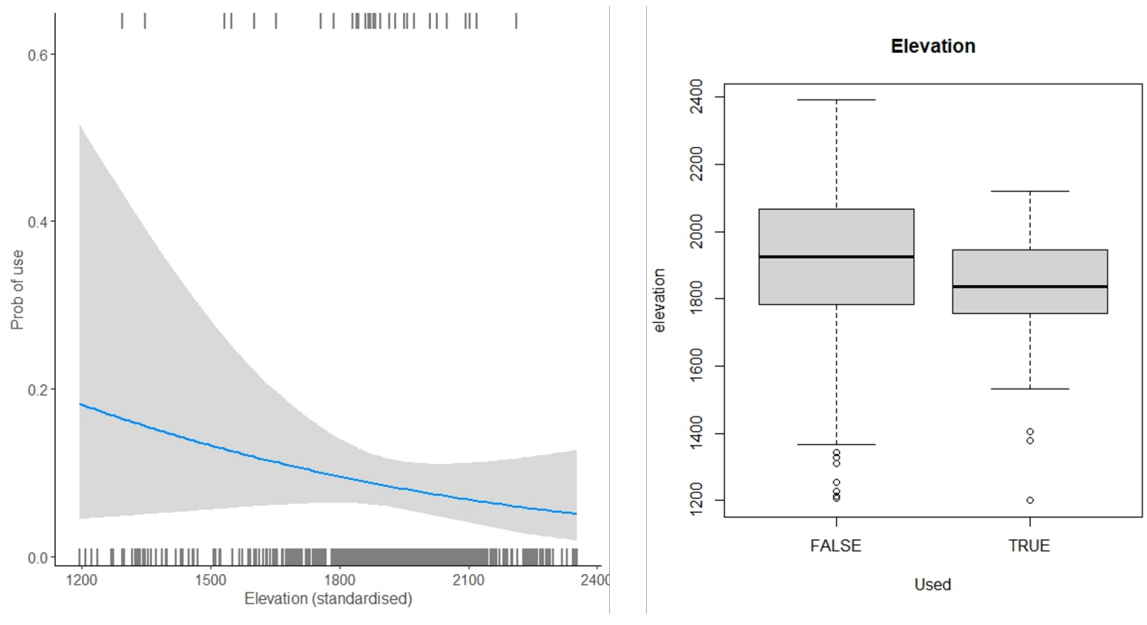


Figure S35. Probability of habitat use by Asiatic golden cat_1 in relation to elevation. Figure legends area same as Figure S1.

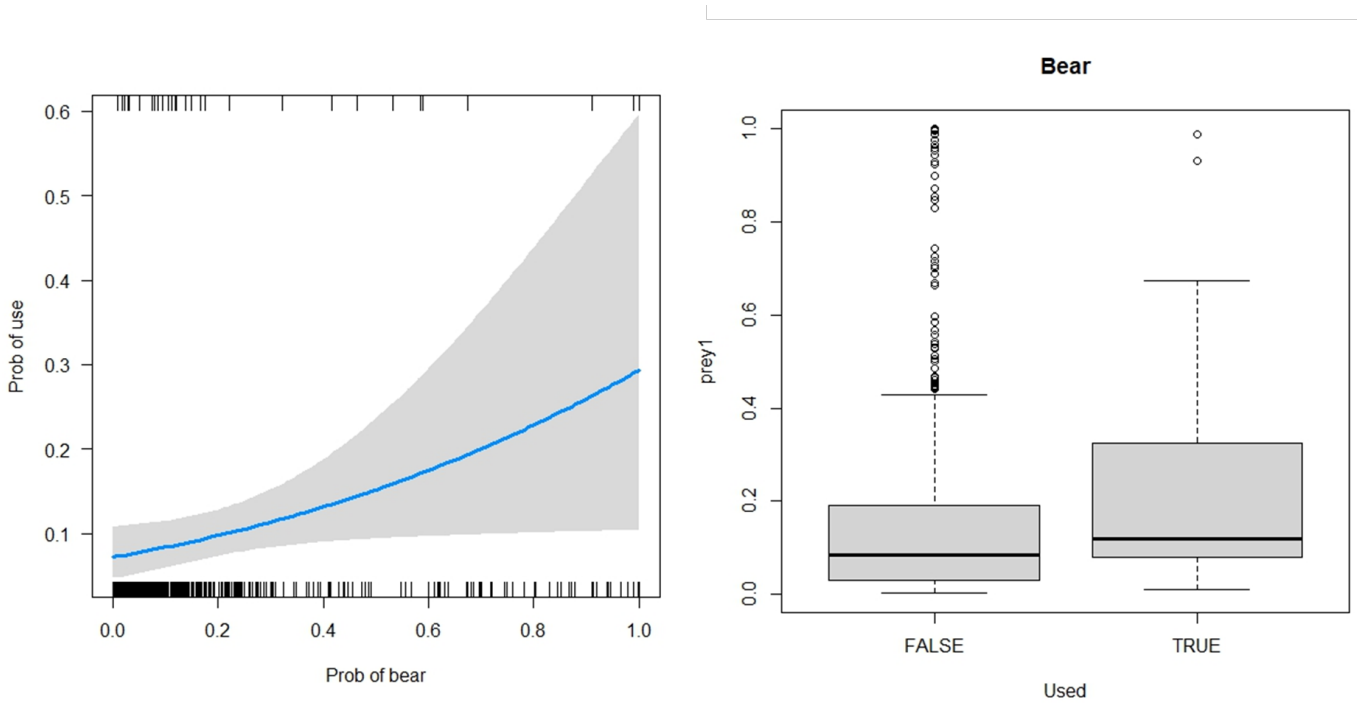


Figure S36. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of bear. Figure legends area same as Figure S1.

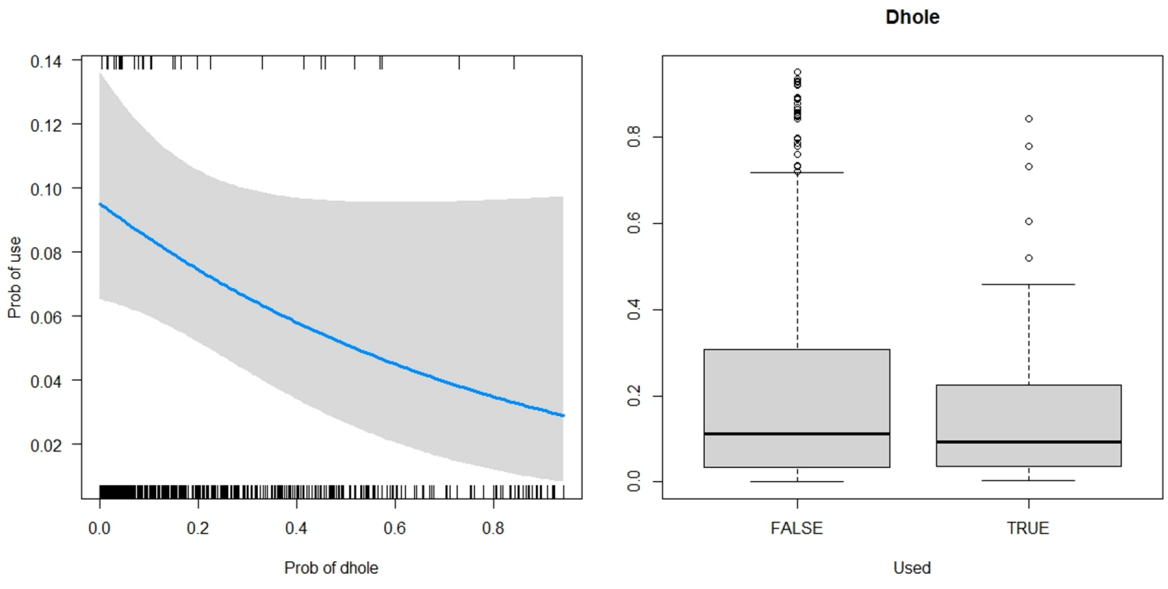


Figure S37. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of dhole. Figure legends area same as Figure S1.

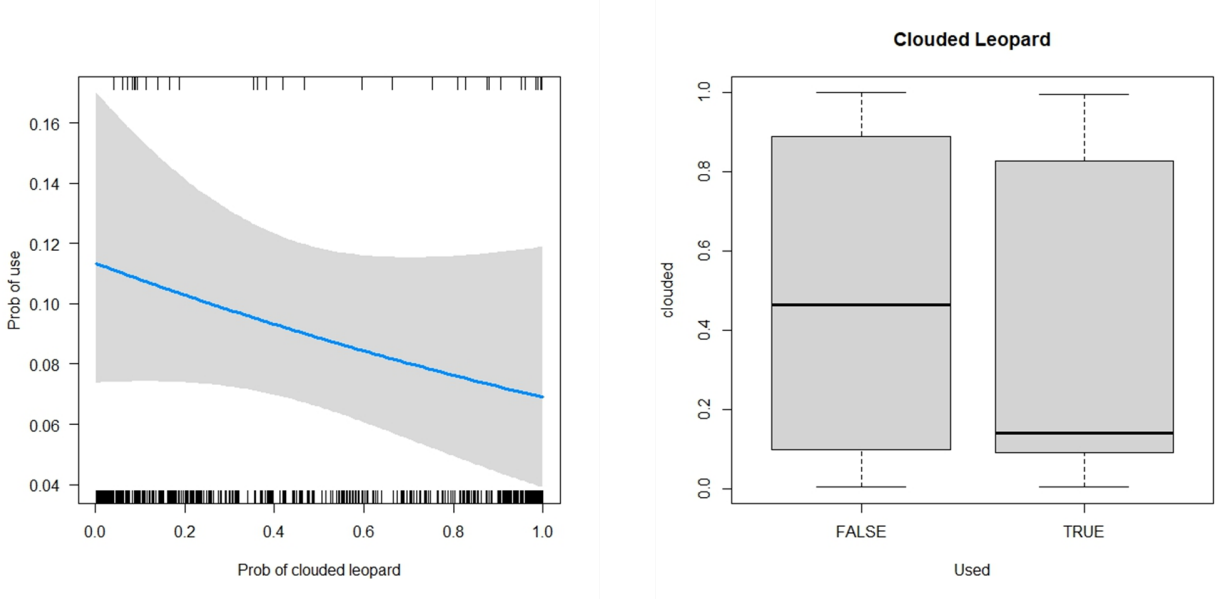


Figure S38. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of clouded leopard. Figure legends area same as Figure S1.

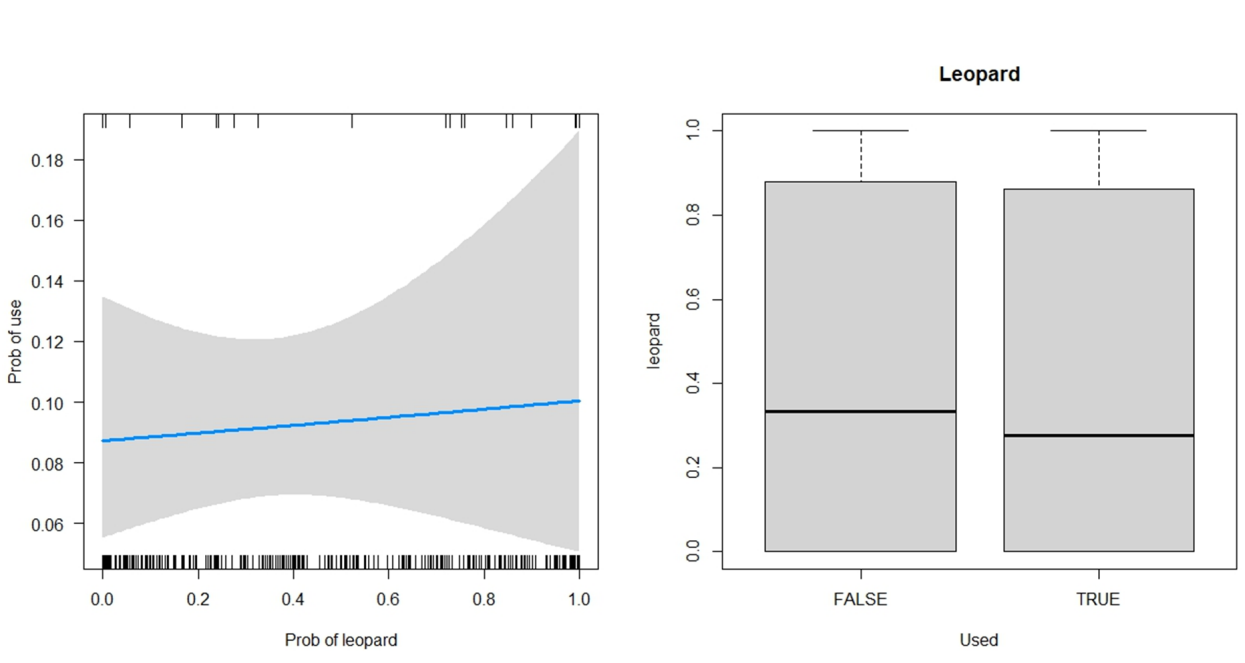


Figure S39. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of common leopard. Figure legends area same as Figure S.

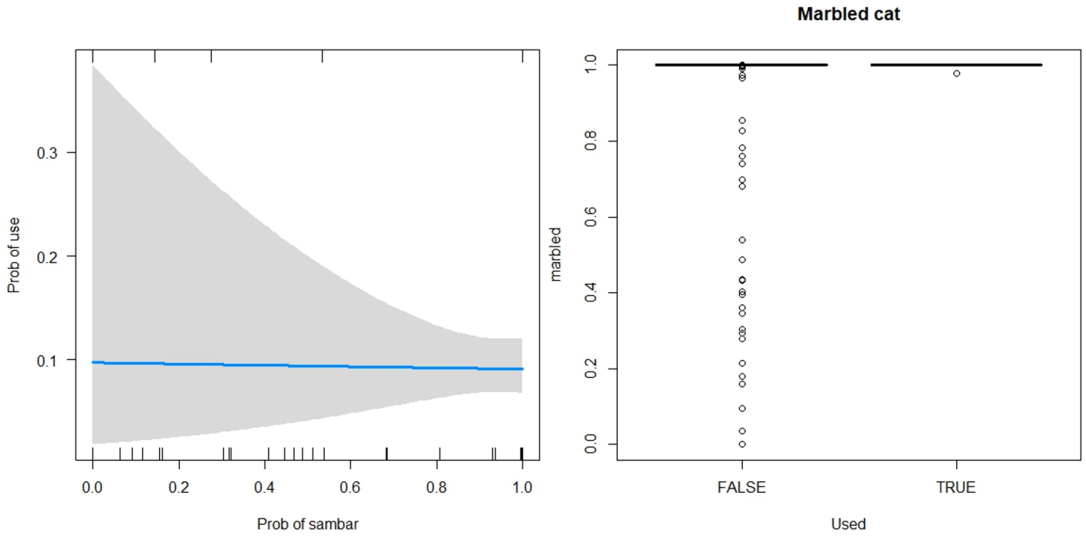


Figure S40. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of sambar. Figure legends area same as Figure S1.

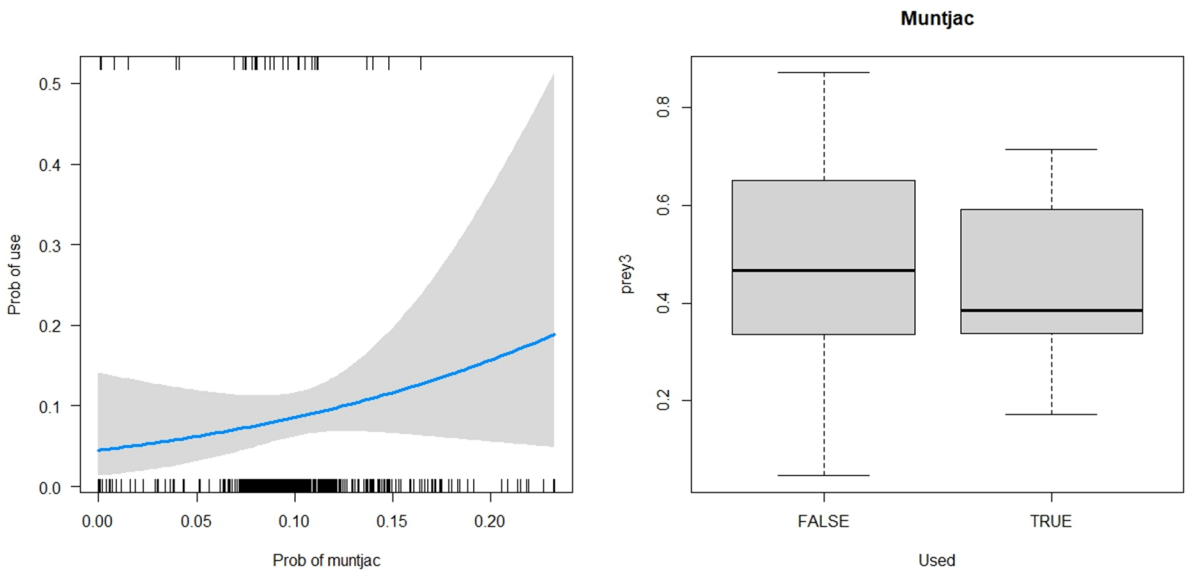


Figure S41. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of muntjac. Figure legends area same as Figure S1.

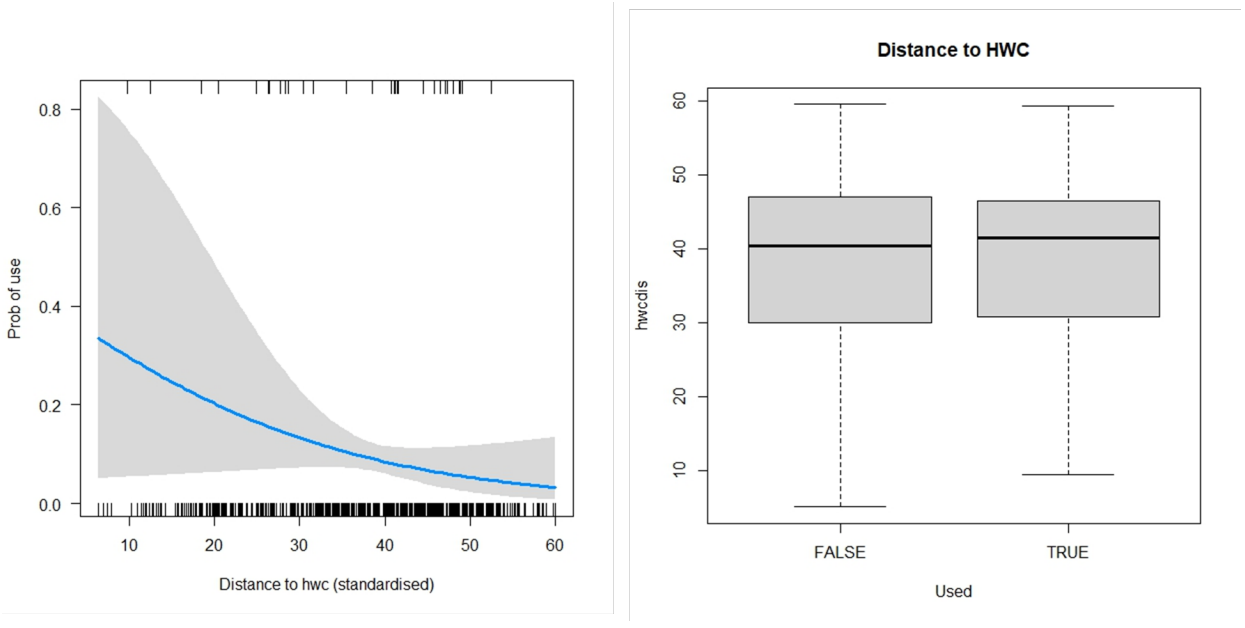


Figure S42. Probability of habitat use by Asiatic golden cat_1 in relation to distance from human-carnivore conflict. Figure legends area same as Figure S1.

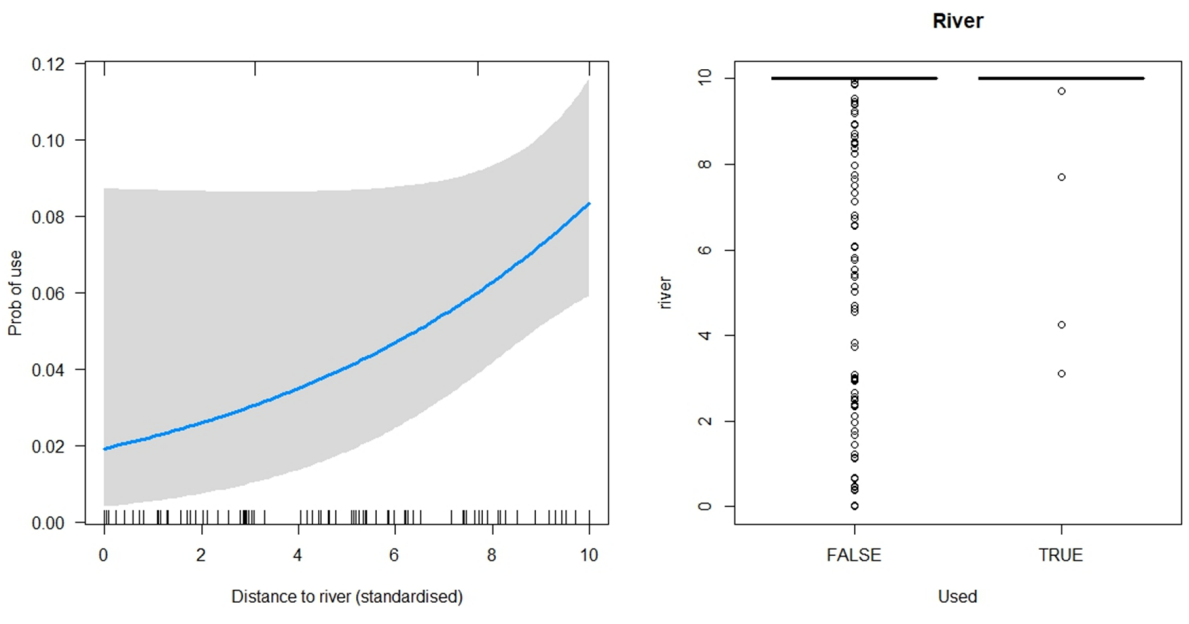


Figure S43. Probability of habitat use by Asiatic golden cat_1 in relation to distance from river. Figure legends area same as Figure S1.

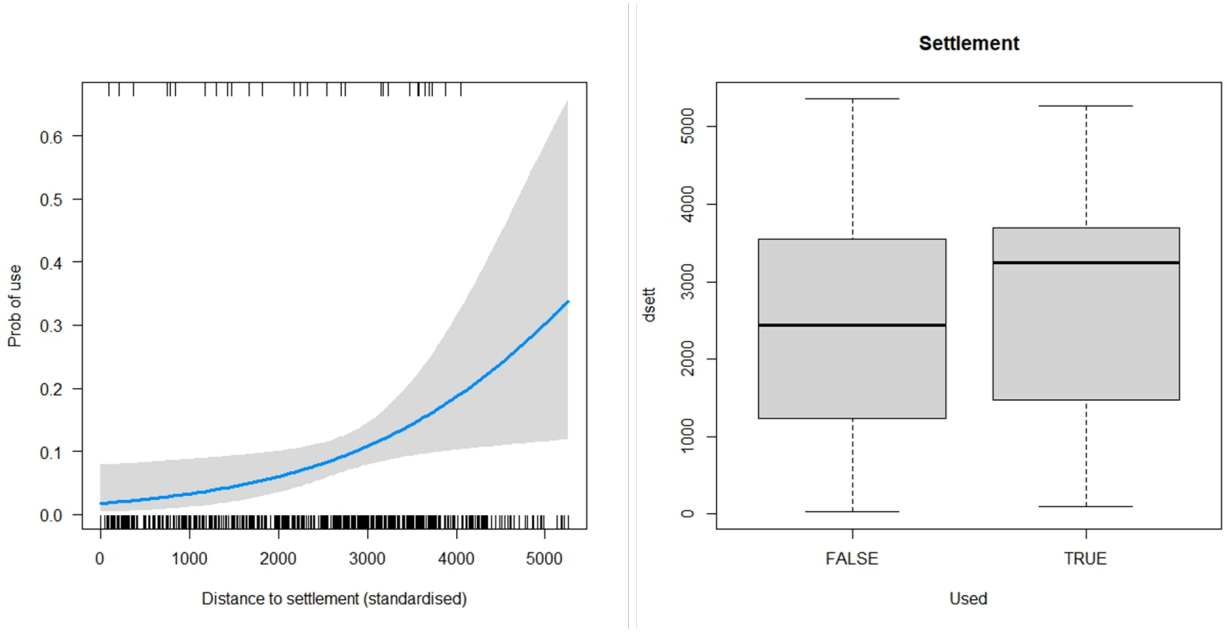


Figure S44. Probability of habitat use by Asiatic golden cat_1 in relation to distance from settlement. Figure legends area same as Figure S.

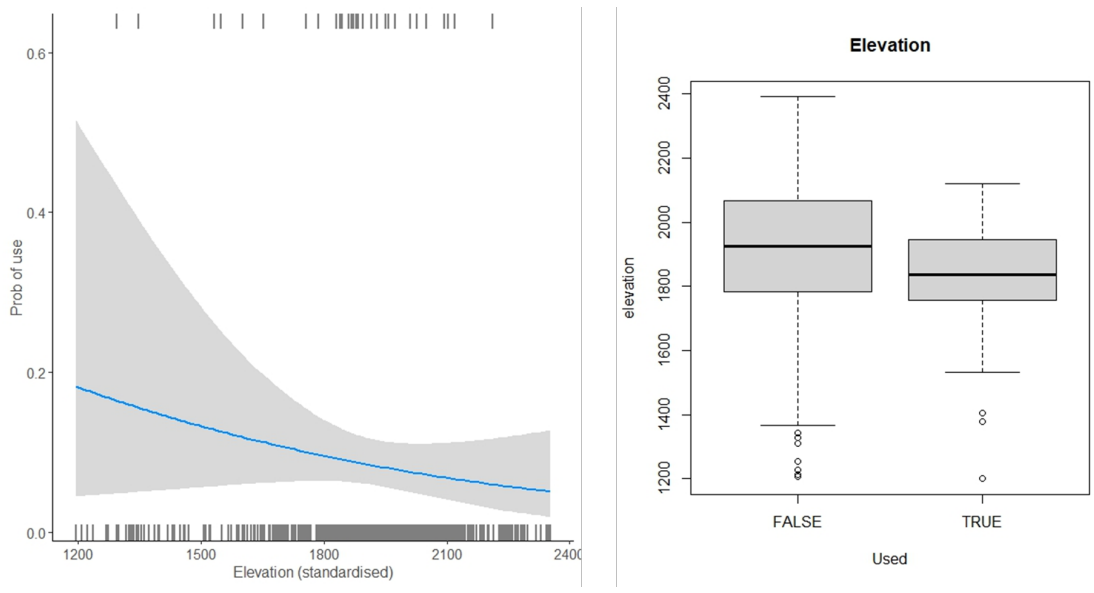


Figure S45. Probability of habitat use by Asiatic golden cat_1 in relation to elevation. Figure legends area same as Figure S.

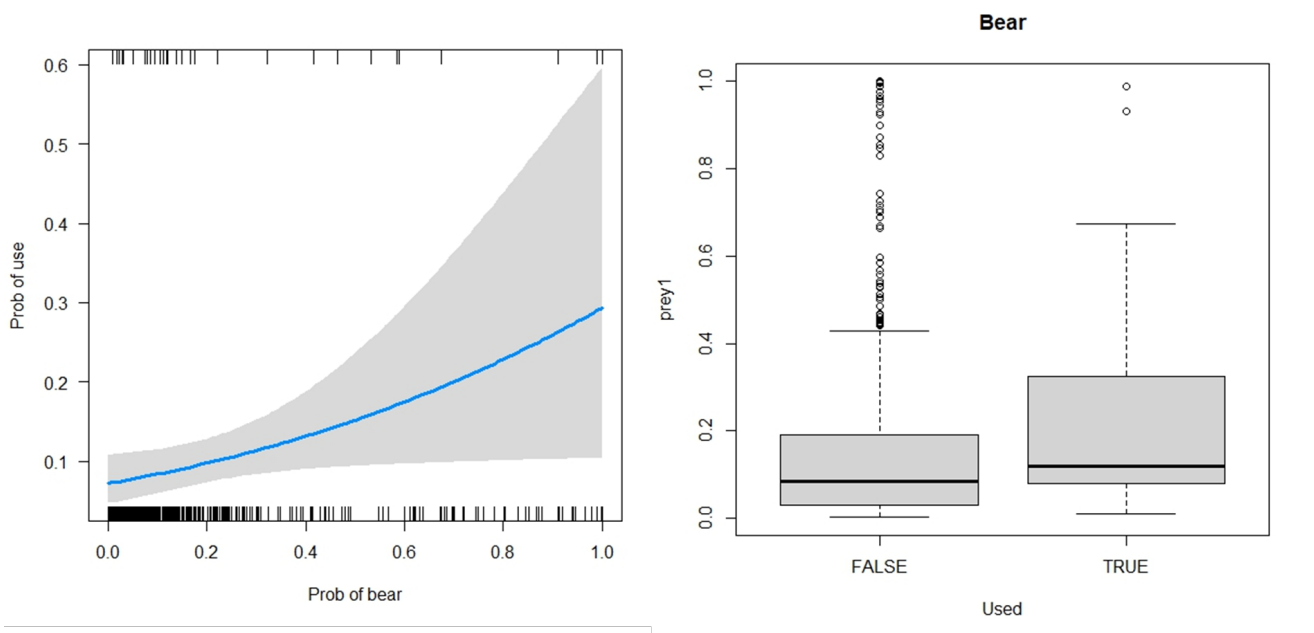


Figure S46. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of bear. Figure legends area same as Figure S1.

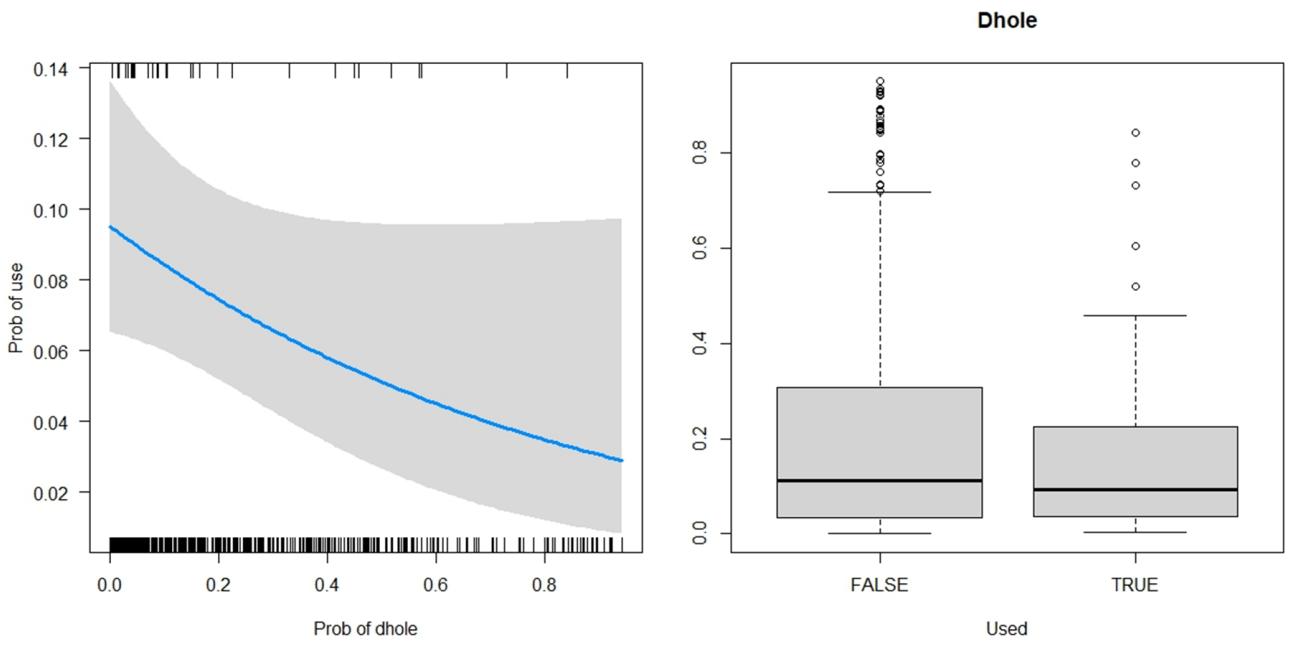


Figure S47. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of dhole. Figure legends area same as Figure S.

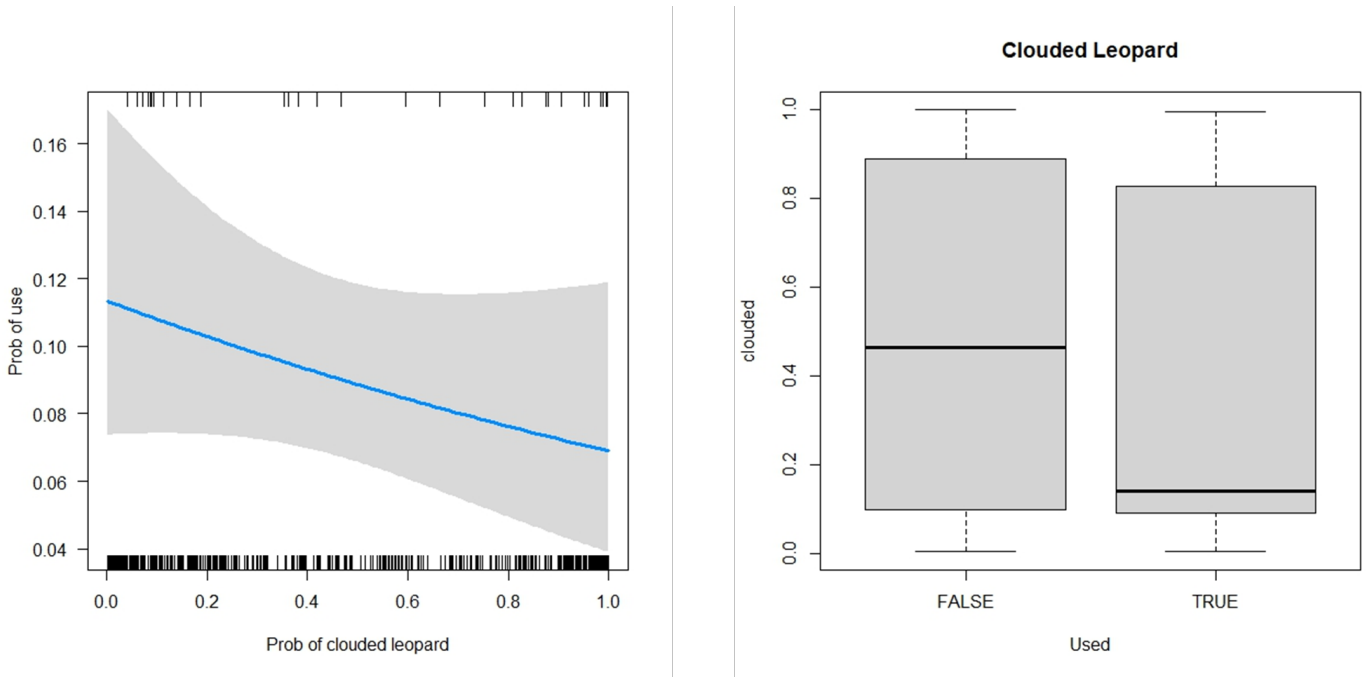


Figure S48. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of clouded leopard. Figure legends area same as Figure S.

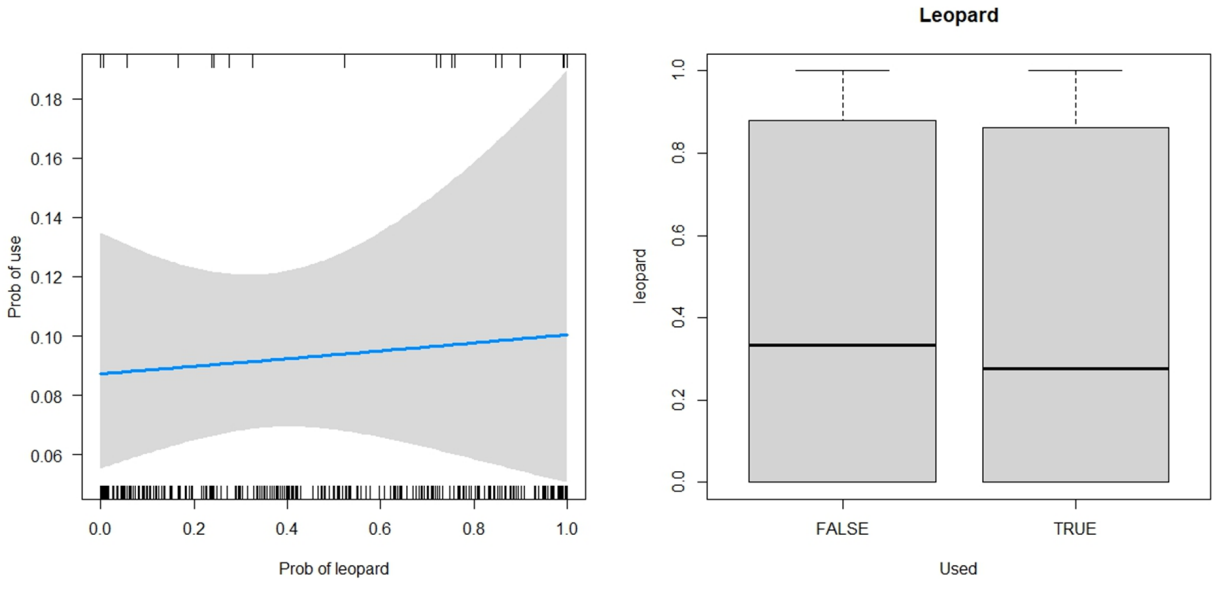


Figure S49. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of common leopard. Figure legends area same as Figure S1.

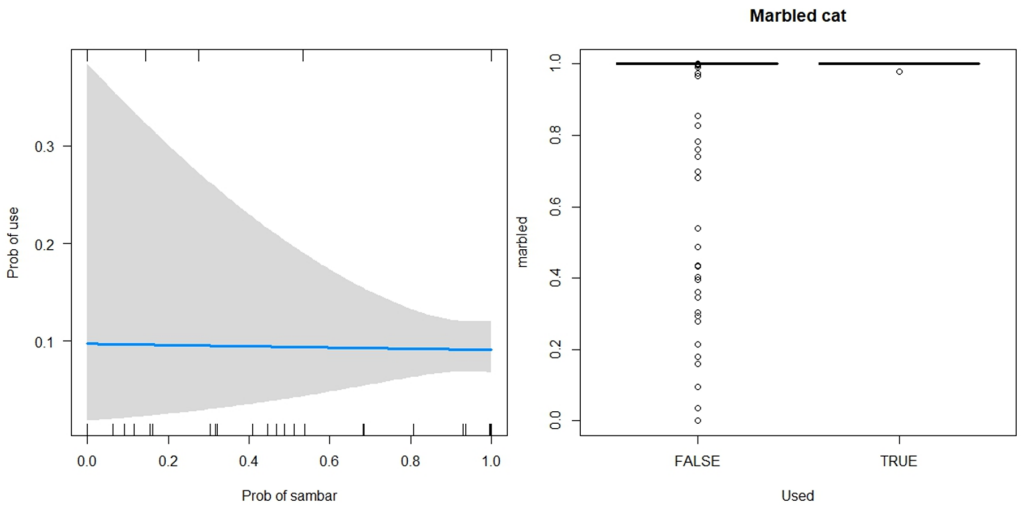


Figure S50. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of sambar. Figure legends area same as Figure S1.

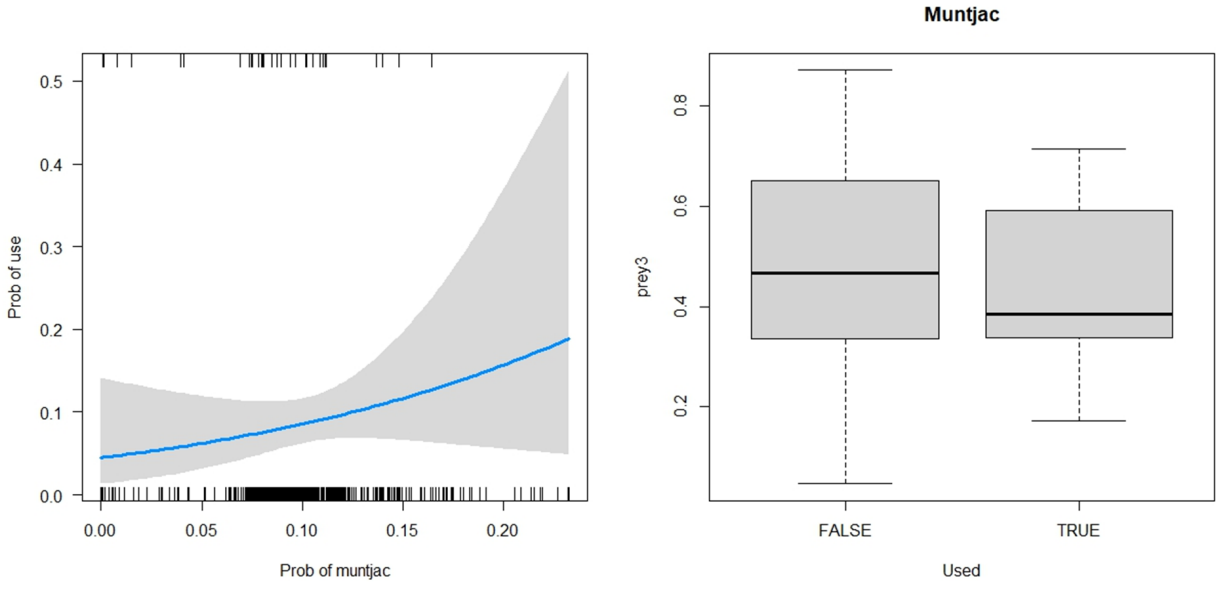


Figure S51. Probability of habitat use by Asiatic golden cat_1 in relation to the site occupancy of muntjac. Figure legends area same as Figure S.

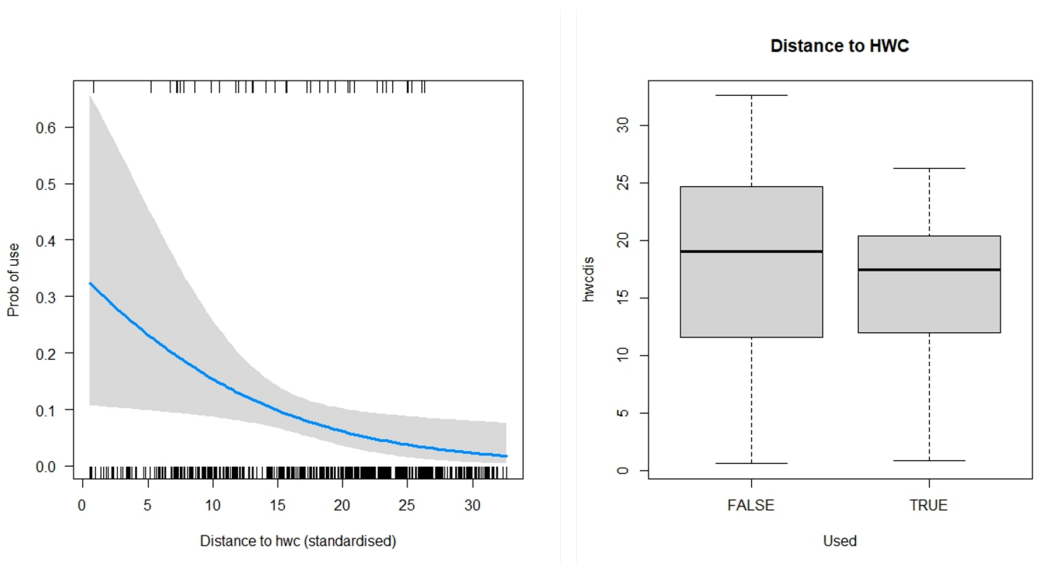


Figure S52. Probability of habitat use by leopard cat_1 in relation to the distance from human-carnivore conflict. Figure legends area same as Figure S1.

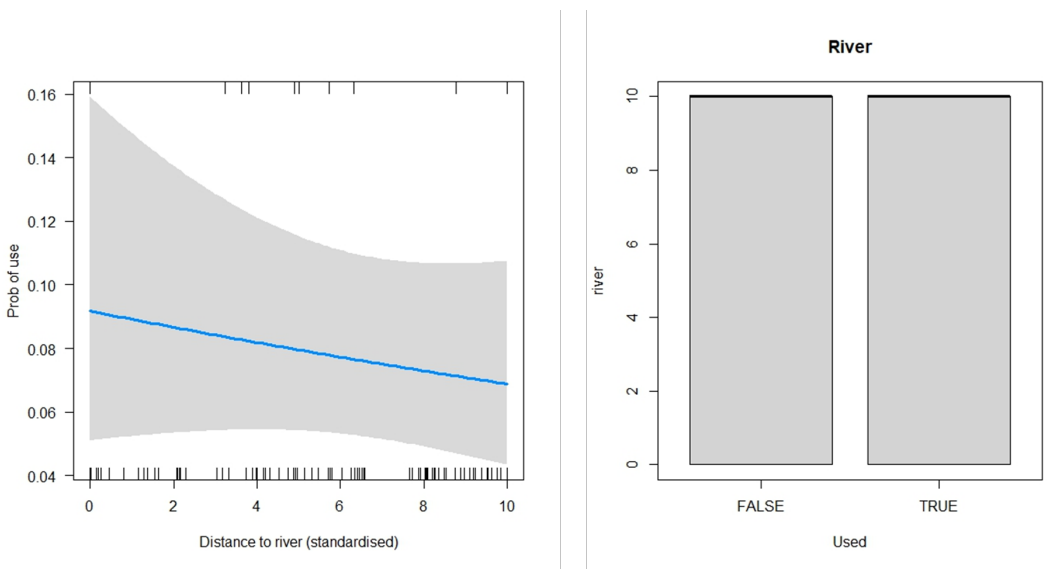


Figure S53. Probability of habitat use by leopard cat_1 in relation to the distance from river. Figure legends area same as Figure S1.

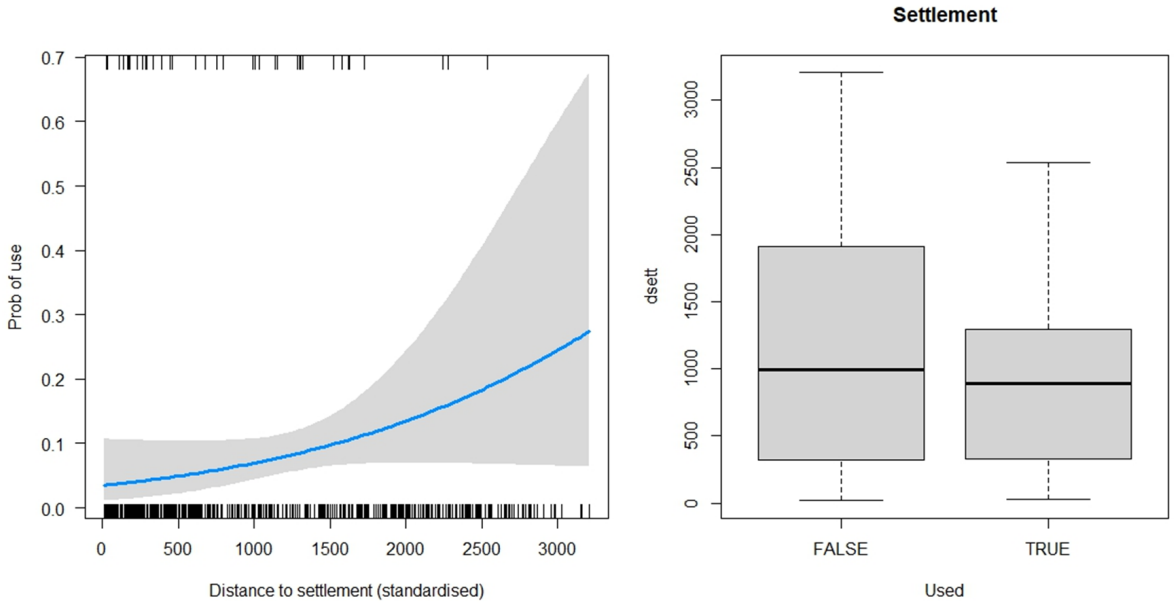


Figure S54. Probability of habitat use by leopard cat_1 in relation to the distance from settlement. Figure legends area same as Figure S1.

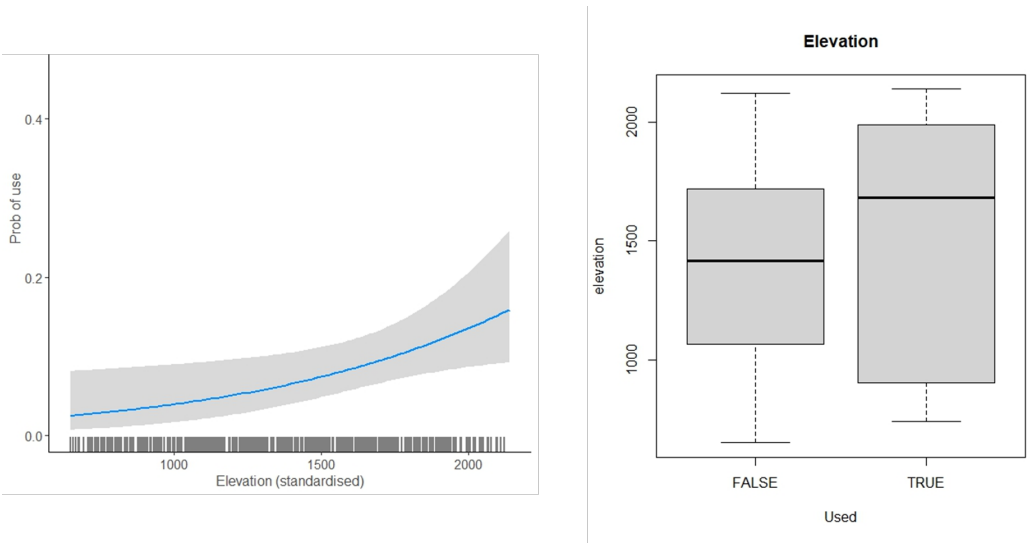


Figure S55. Probability of habitat use by leopard cat_1 in relation to the elevation. Figure legends area same as Figure S1.

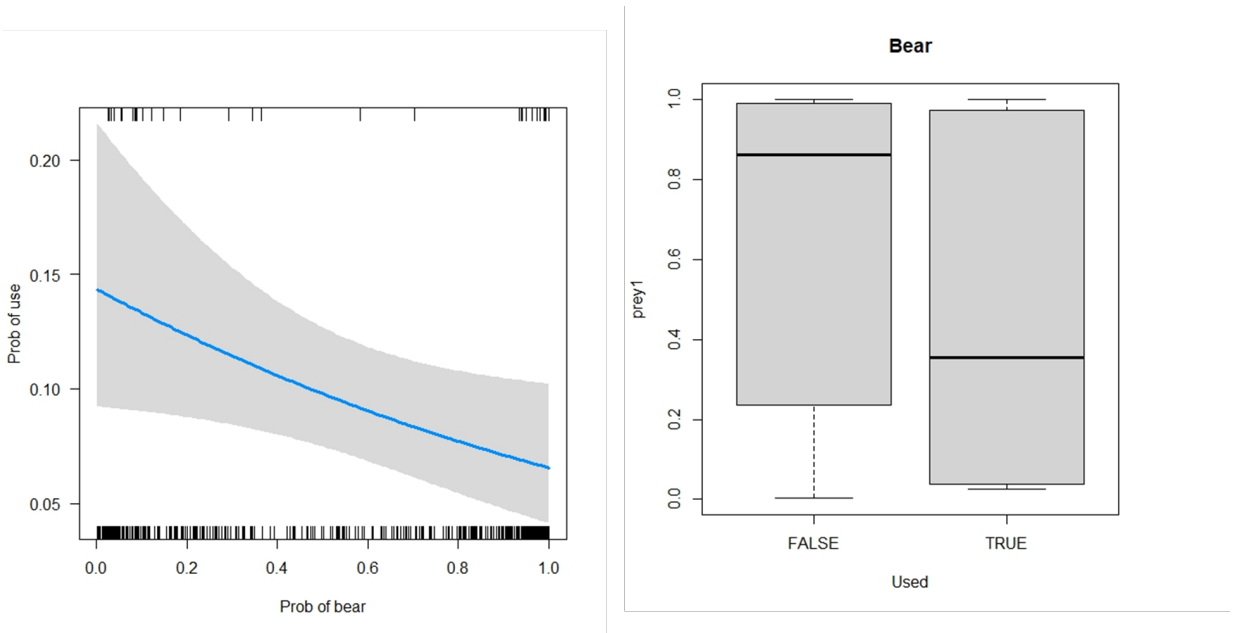


Figure S56. Probability of habitat use by leopard cat_1 in relation to the site occupancy of bear. Figure legends area same as Figure S1.

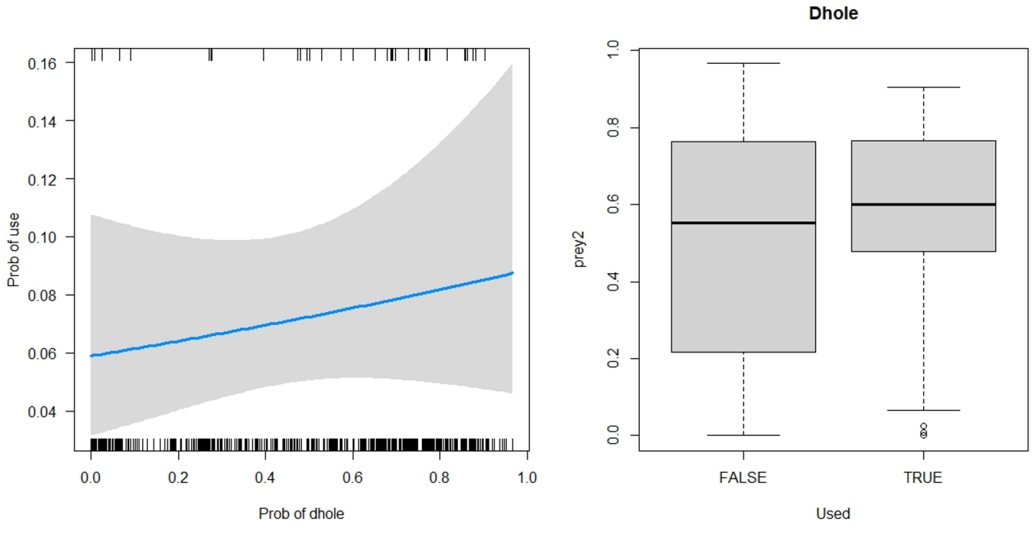


Figure S57. Probability of habitat use by leopard cat_1 in relation to the site occupancy of dhole. Figure legends area same as Figure S1.

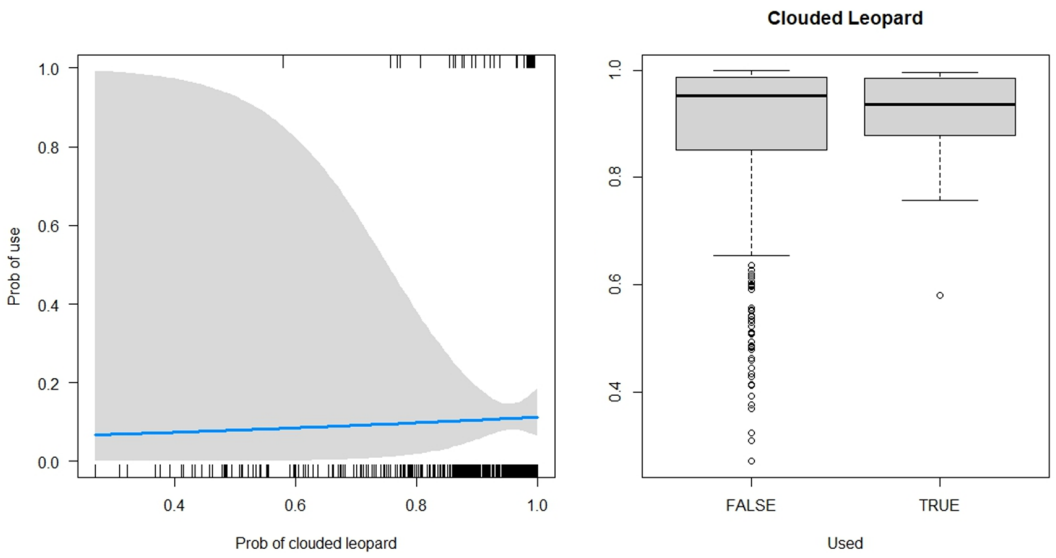


Figure S58. Probability of habitat use by leopard cat_1 in relation to the site occupancy of clouded leopard. Figure legends area same as Figure S1.

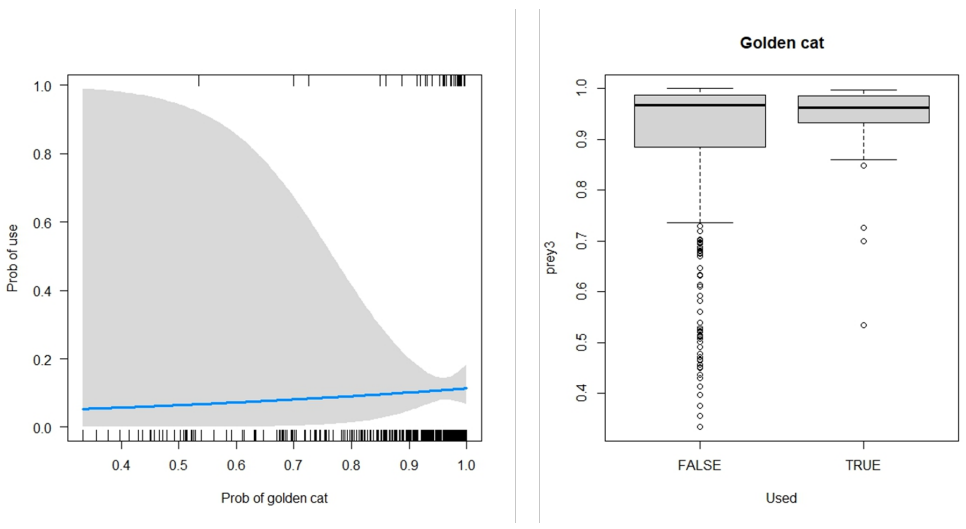


Figure S59. Probability of habitat use by leopard cat_1 in relation to the site occupancy of Asiatic golden cat. Figure legends area same as Figure S1.

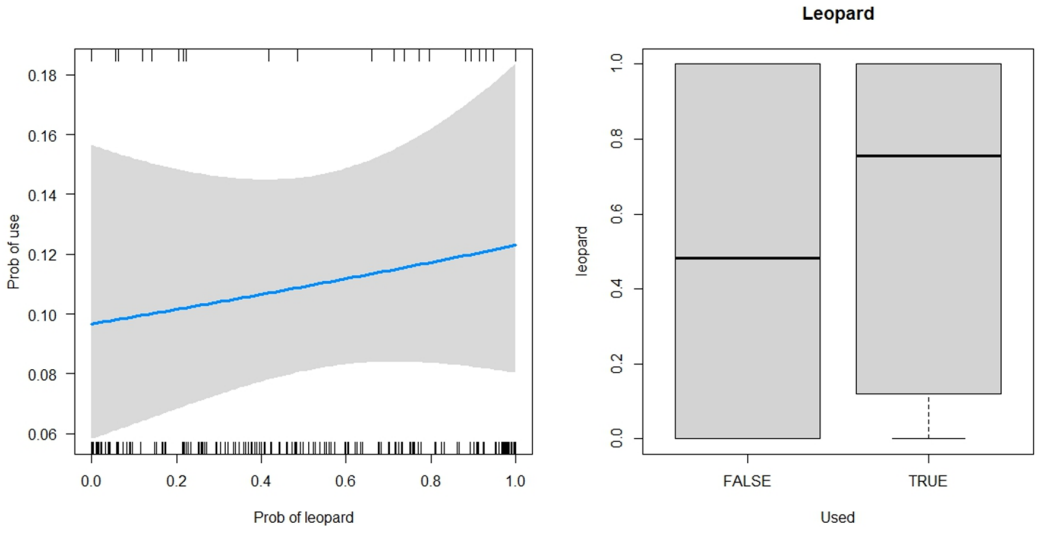


Figure S60. Probability of habitat use by leopard cat_1 in relation to the site occupancy of common leopard. Figure legends area same as Figure S1.

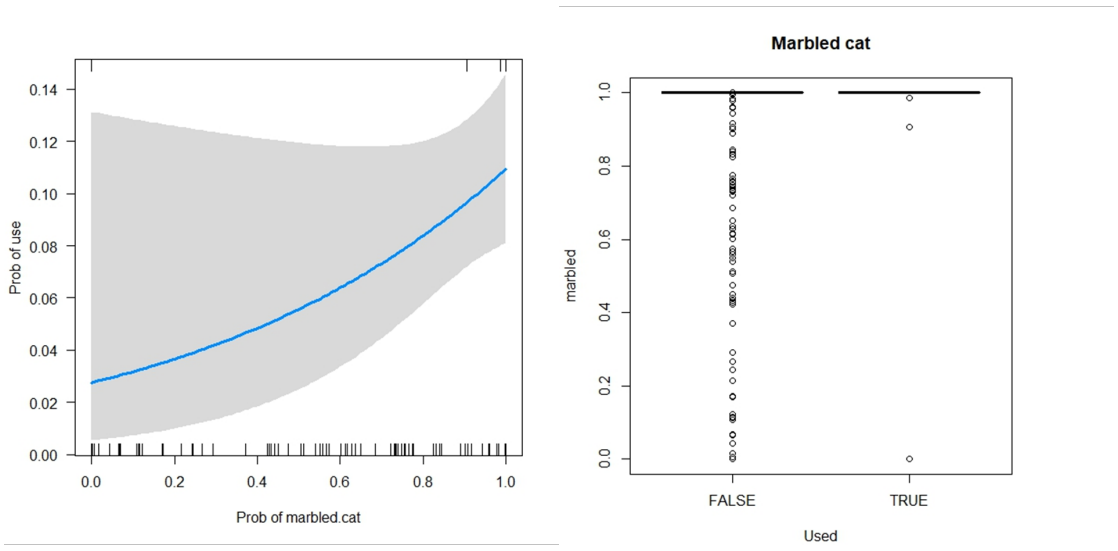


Figure S61. Probability of habitat use by leopard cat_1 in relation to the site occupancy of marbled cat. Figure legends area same as Figure S1.

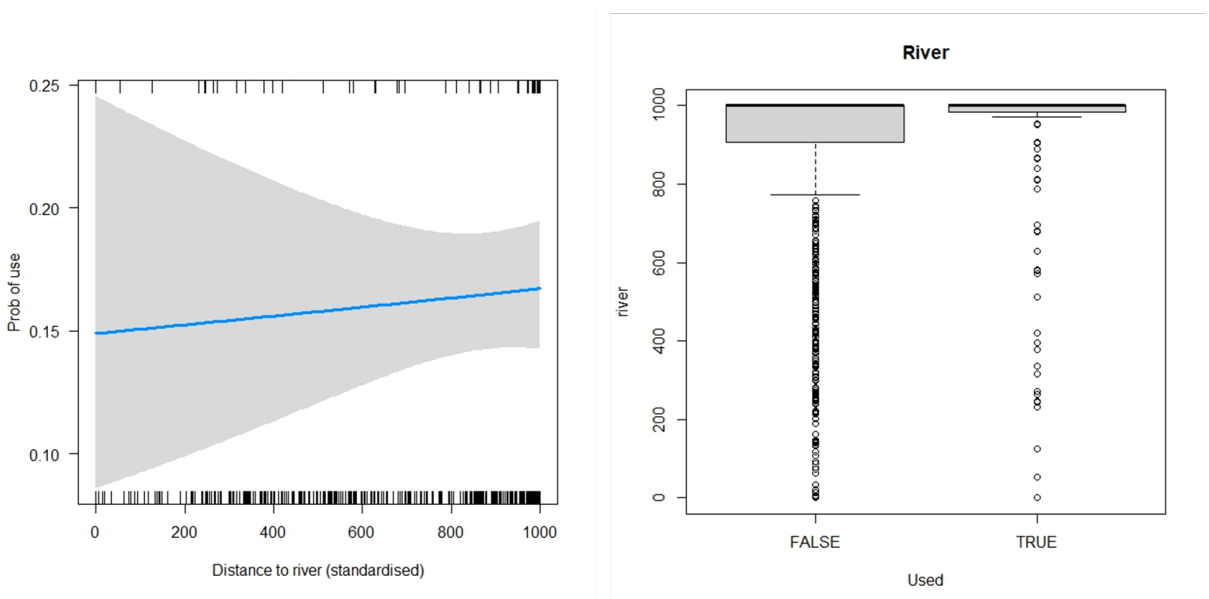


Figure S62. Probability of habitat use by dhole_1 in relation to the distance from river. Figure legends area same as Figure S1.

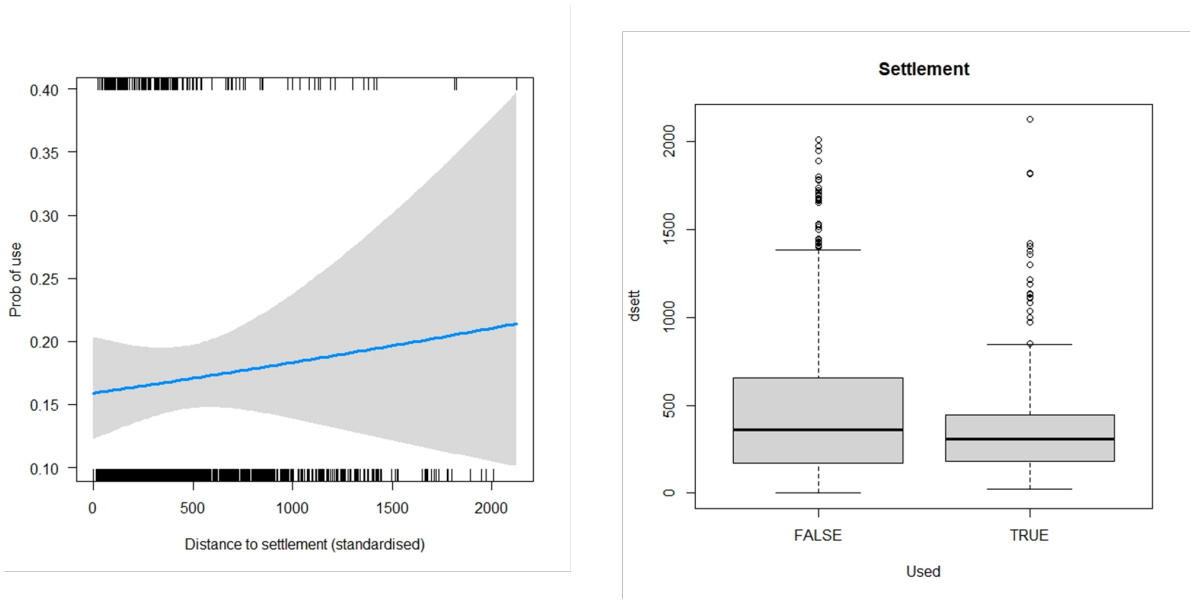


Figure S63. Probability of habitat use by dhole_1 in relation to the distance from settlement. Figure legends area same as Figure S1.

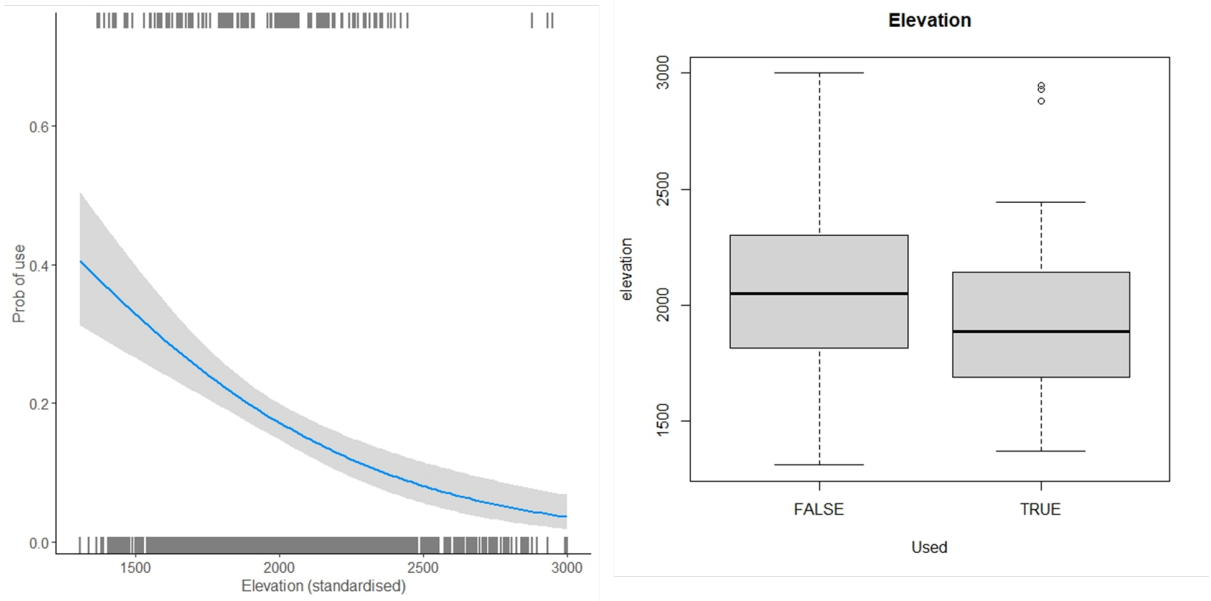


Figure S64. Probability of habitat use by dhole_1 in relation to the distance from settlement. Figure legends area same as Figure S1.

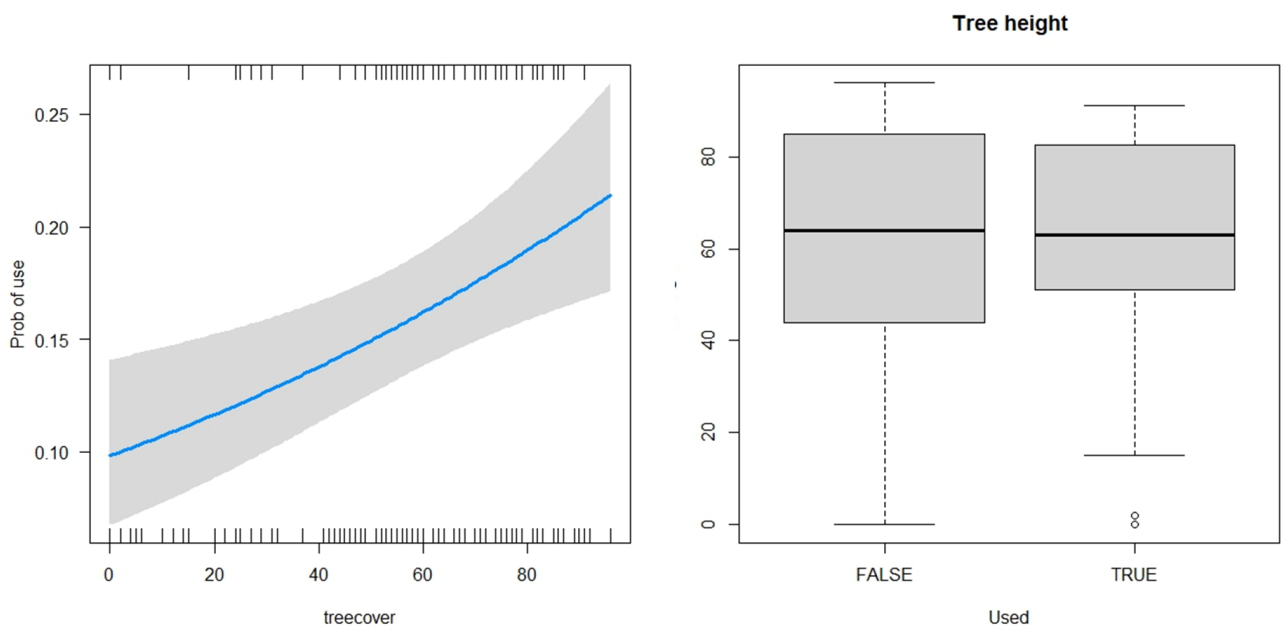


Figure S65. Probability of habitat use by dhole_1 in relation to tree cover. Figure legends area same as Figure S1.

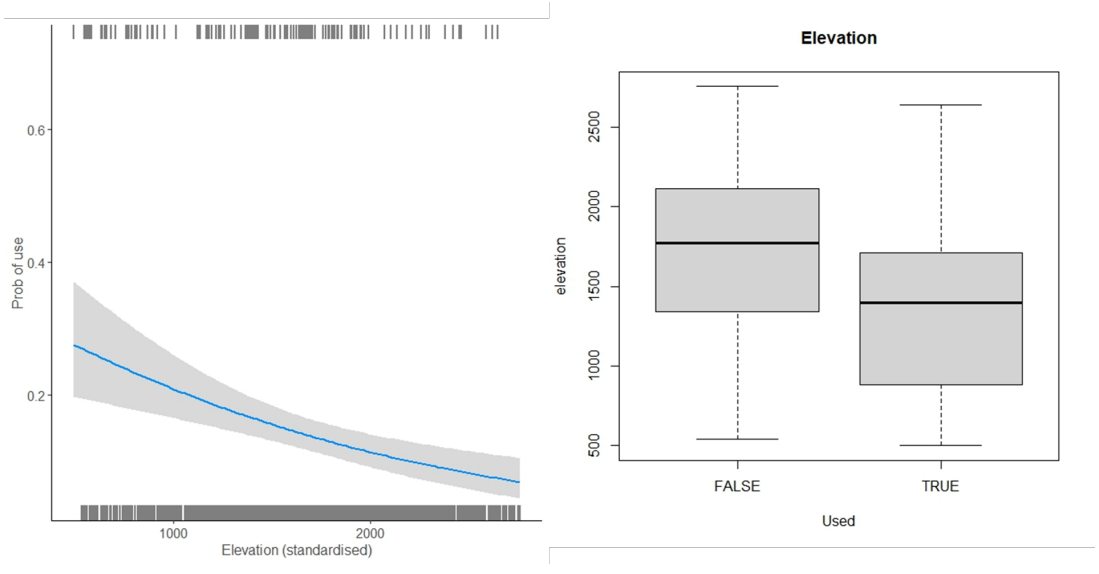


Figure S66. Probability of habitat use by dhole_1 in relation to tree cover. Figure legends area same as Figure S1.

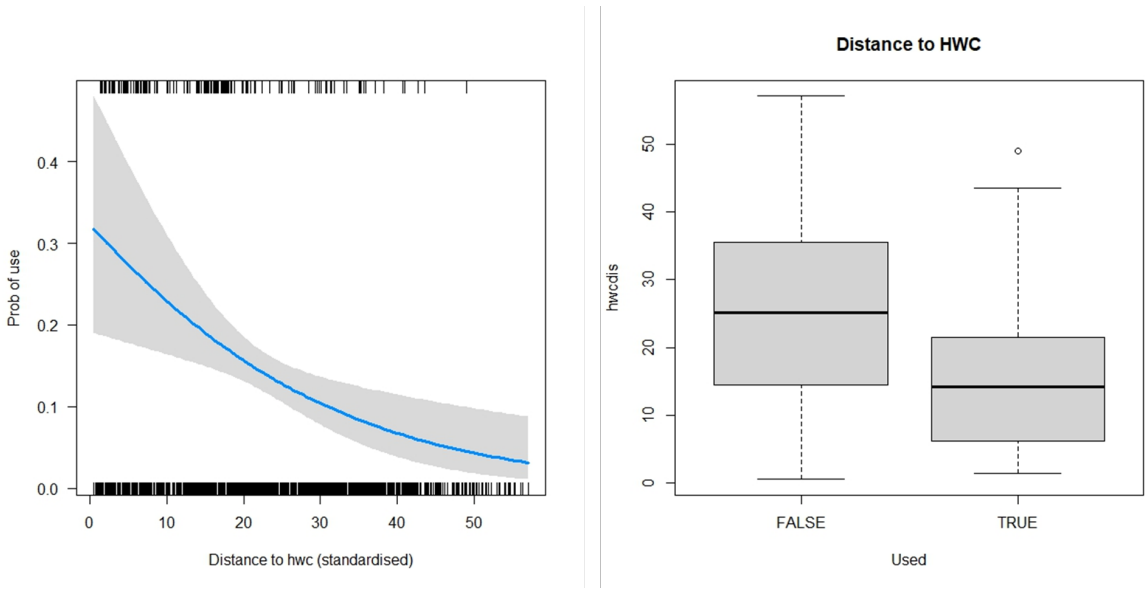


Figure S67. Probability of habitat use by dhole_2 in relation to the distance from human carnivore conflict sites. Figure legends area same as Figure S1.

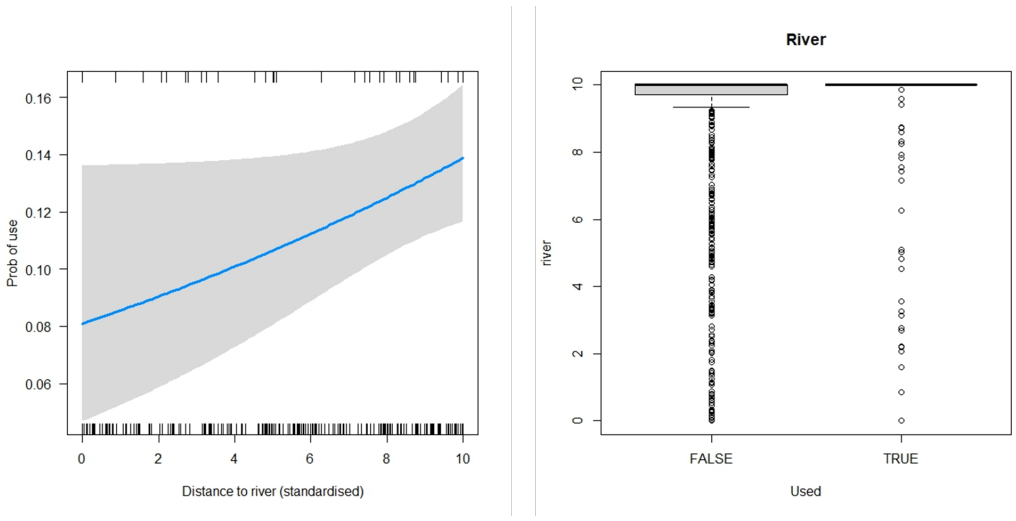


Figure S68. Probability of habitat use by dhole_2 in relation to the distance from rivers. Figure legends area same as Figure S1.

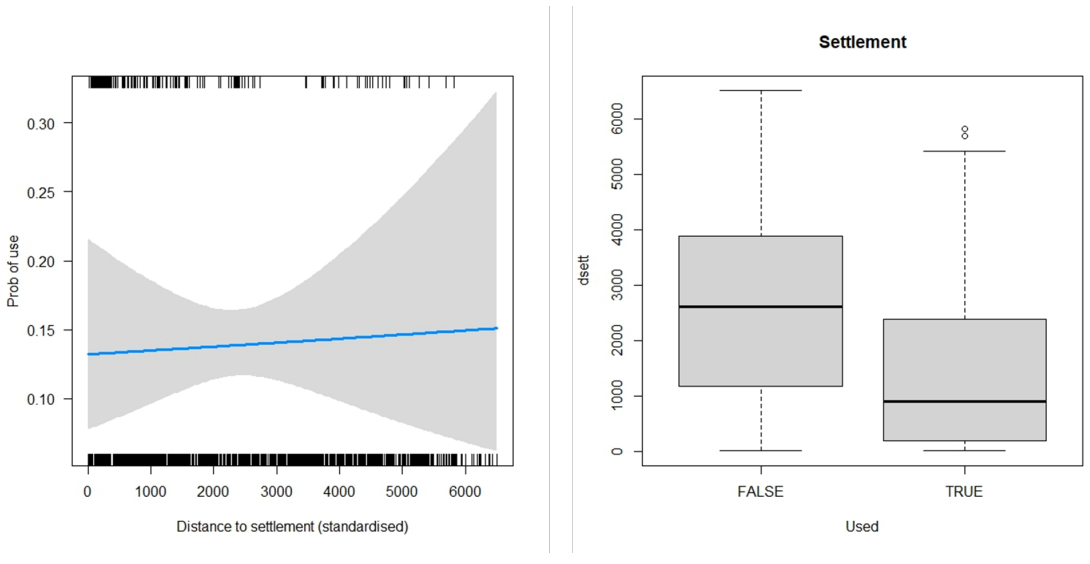


Figure S69. Probability of habitat use by dhole_2 in relation to the distance to settlement.

Figure legends area same as Figure S1.

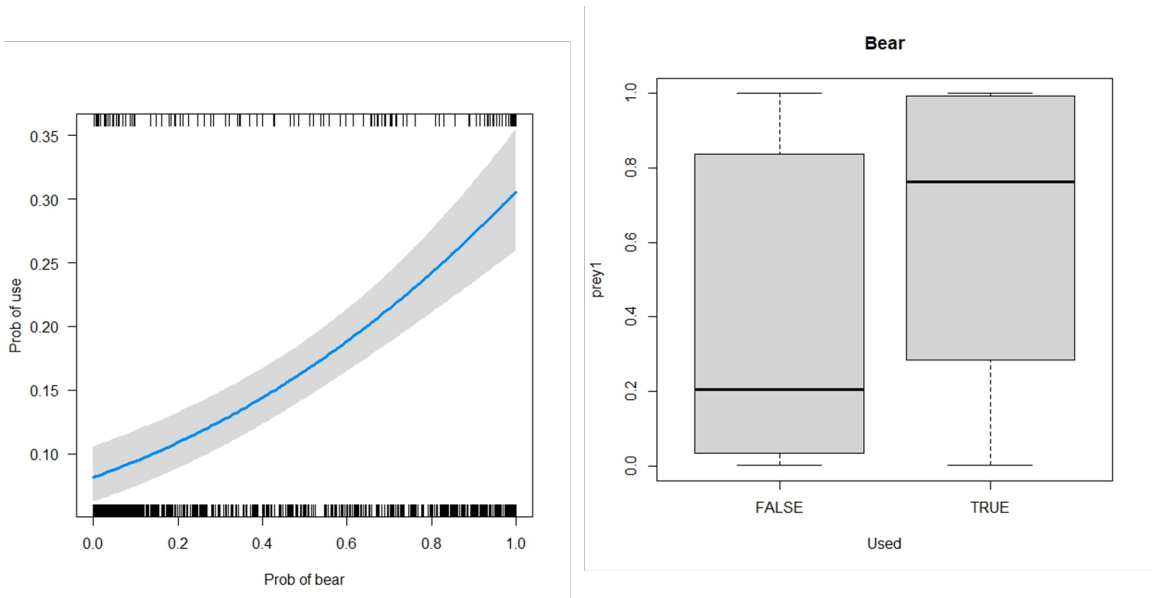


Figure S70. Probability of habitat use by leopard dhole_2 in relation to the site occupancy of bear. Figure legends area same as Figure S1.

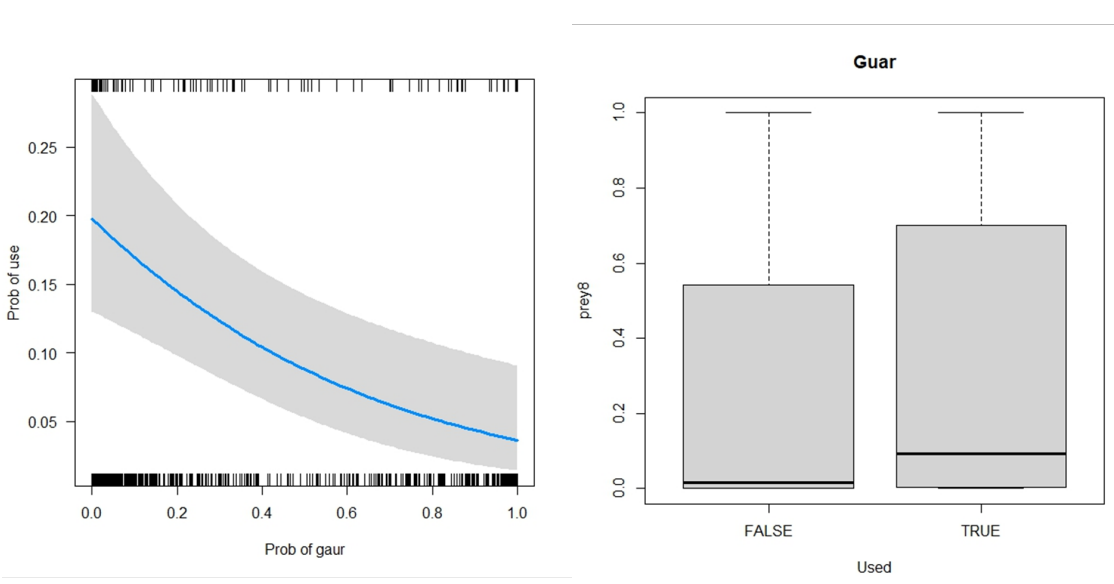


Figure S71. Probability of habitat use by leopard dhole_2 in relation to the site occupancy of gaur. Figure legends area same as Figure S1.

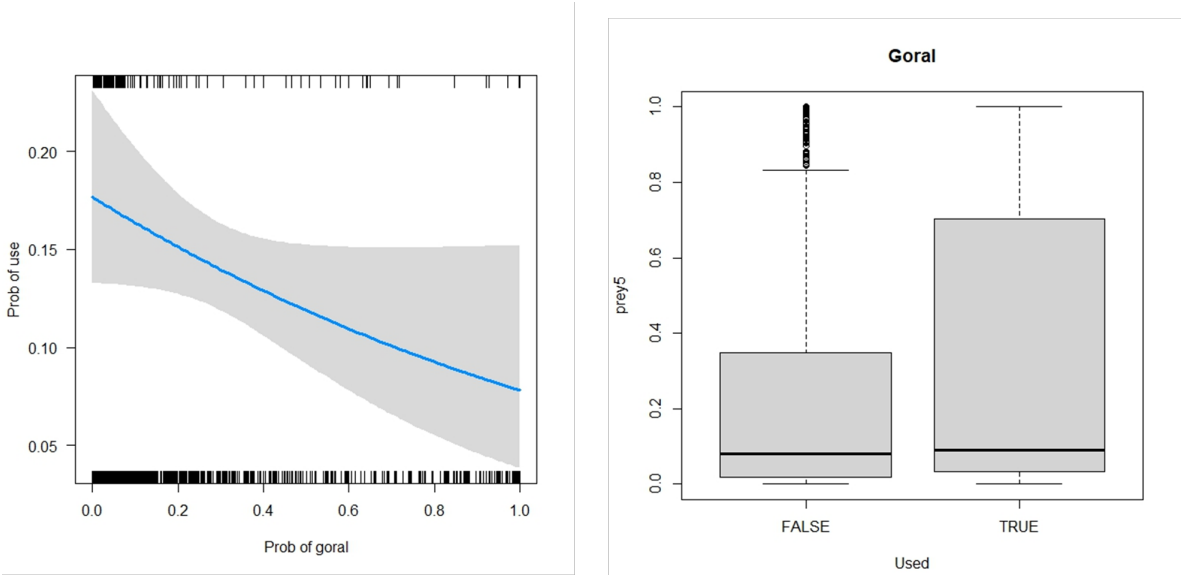


Figure S72. Probability of habitat use by dhole_2 in relation to the site occupancy of goral. Figure legends area same as Figure S1.

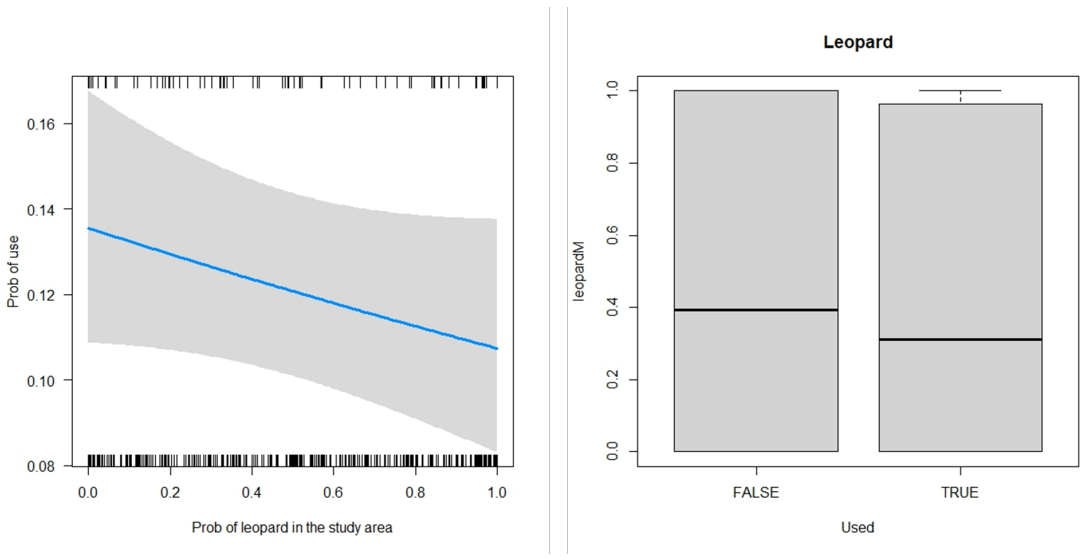


Figure S73. Probability of habitat use by dhole_2 in relation to the site occupancy of common leopard. Figure legends area same as Figure S1.

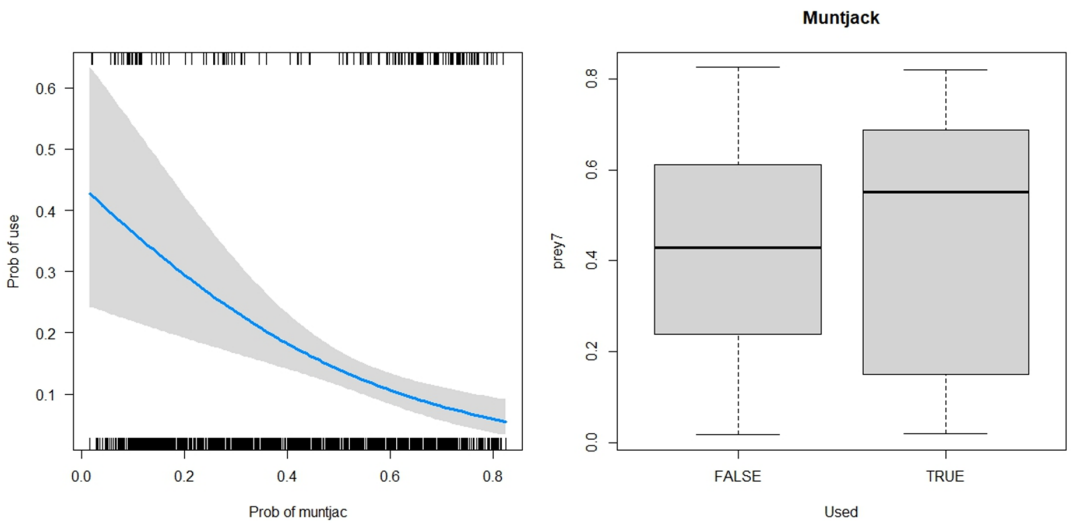


Figure S74. Probability of habitat use by dhole_2 in relation to the site occupancy of muntjac

Figure legends area same as Figure S1.

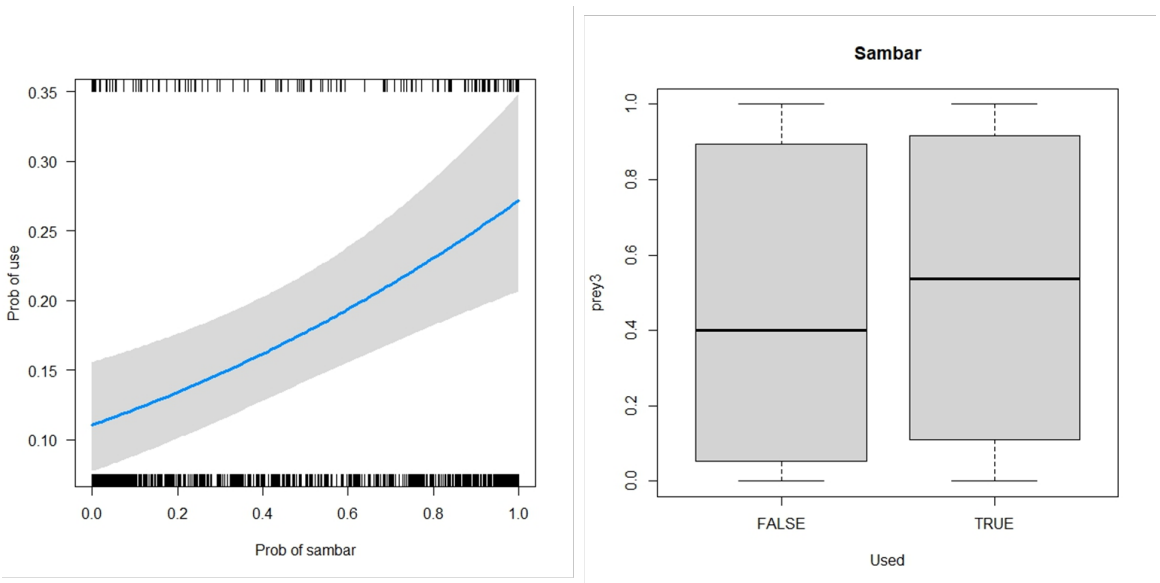


Figure S75. Probability of habitat use by dhole_2 in relation to the site occupancy of sambar.

Figure legends area same as Figure S1.

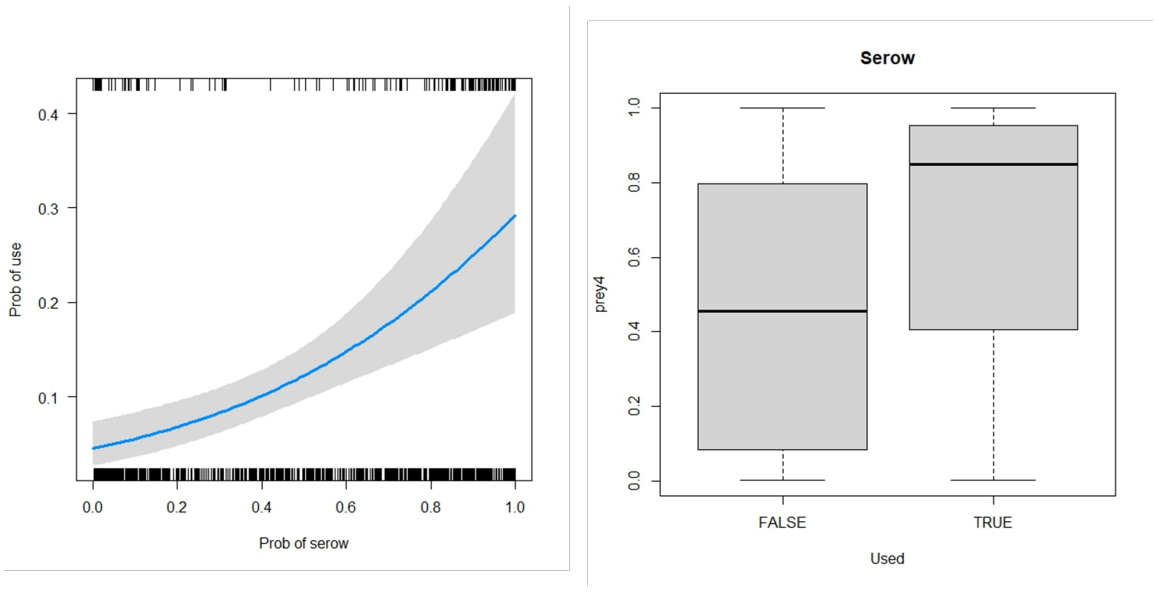
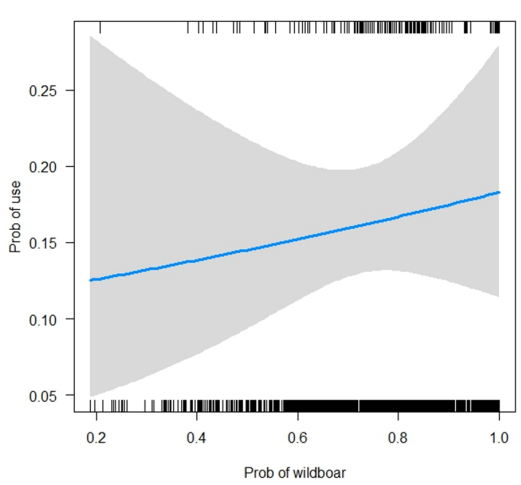


Figure S76. Probability of habitat use by dhole_2 in relation to the site occupancy of serow

Figure legends area same as Figure S1.



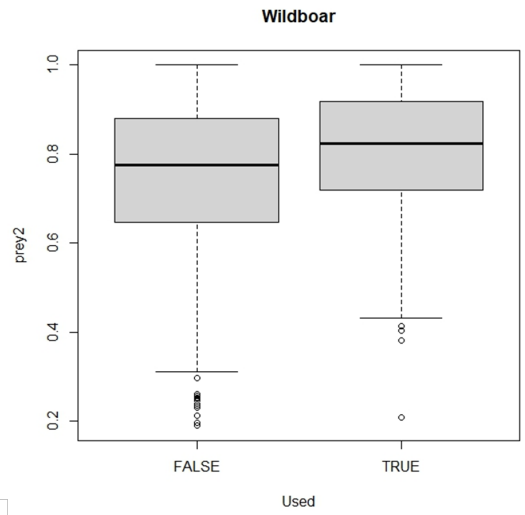


Figure S77. Probability of habitat use by dhole_2 in relation to the site occupancy of wild boar Figure legends area same as Figure S1.

Appendix 3l: Supplementary materials for occupancy model

We observed that the site occupancy is significantly high at trail stations for all the cat species except for clouded leopard compared to the random stations (Figure 3.4 and Table). There is similar site occupancy of clouded leopard at trail and random stations but higher when estimated from trail plus random stations (Figure 3.4). The site occupancy estimate was higher from the combination of trail plus random stations for all the cat species except for the common leopard (Figure 3.4). The lower site occupancy for common leopard from combined station is likely due to the influence of covariates as the naïve occupancy (number of camera station with the leopard capture divided by total camera stations without taking account of detection probability) was higher than the trail only station ($\Psi_{navie(100T+100R)} = 0.16$, $\Psi_{navie(100T+0R)} = 0.11$).

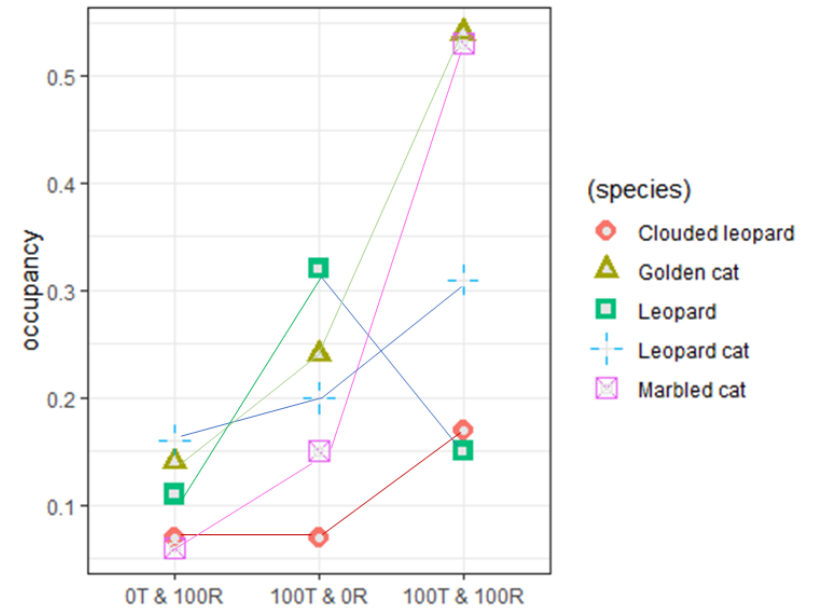


Figure 1. Site occupancy of wild cats at random and trail locations. X-axes represent the combination of trail (T) and random (R) stations.

The detection probability of common leopard and marbled cat was highest from random only stations (Table 3.5). Whereas the detection probability of Asiatic golden and leopard cat was highest from trail only stations. We observed equal probability of detection at random and trail stations for clouded leopard. The site occupancy derived from combination of trail plus random station is always lower than the trail stations for all the cat species (Table 3.5). We observed there are differences in site occupancy and detection probability from random and trail stations signifying presence of detection heterogeneity within the study area. The occupancy estimates only provides number of sites occupied by the animal giving less significance compared to that relative abundance and point density estimates.

We observed nuanced effect of covariates and choice of scale for different species and the station combinations (Table 3.5). Out of eight covariates applied for our study, closed forest, distance from settlement, distance from river, human density and elevation at different scale saw maximum influence on probability of occupancy (Table, detail of the effect on site occupancy form covariates are provided in Appendix VI).

Table 3.5. Occupancy of clouded leopard from different combinations of the trail (T) and random cameras (R). Paired cameras at trail and a single camera at random.

Species	Station combination	Model	Estimate	LCI	UCI
Clouded leopard	100T & 100R	Ψ *(human density4km + Elevation500m)*	0.17	0.07	0.32
		$p_{(.)}$	0.05	0.03	0.11
	0T & 100R	Ψ *(closed forest 4km) + settlement distance 500m +human density 4km)*	0.07	0.03	0.17
		$p_{(.)}$	0.06	0.03	0.17
	100T & 0 R	Ψ *(Elevation 500m +human density 4km)*	0.07	0.04	0.12
		$p_{(.)}$	0.06	0.02	0.15
Common leopard	100T & 100R	Ψ *(human density4km + Elevationc500m)*	0.15	0.03	0.50
		$p_{(.)}$	0.03	0.01	0.11
	100T & 0R	Ψ *(Closed Forest 1km + River distance 1km + settlement distance 500m)*	0.32	0.03	0.86
		$p_{(.)}$	0.01	0.01	0.07
	0R + 100R	Ψ *(Elevation 500m +human density 4km)*	0.11	0.02	0.40
		$p_{(.)}$	0.05	0.01	0.21
Asiatic golden cat	100T & 100R	Ψ *(NULL)*	0.54	0.15	0.90
		$p_{(.)}$	0.04	0.02	0.11
	100T & 0R	Ψ *(Elevation 2km + Open Forest 4km)*	0.24	0.14	0.36

		$p_{(.)}$	0.07	0.05	0.12
	0R +100T	Ψ *(Closed Forest 2km + River distance 500m + settlement distance 2km)*	0.14	0.04	0.37
		$p_{(.)}$	0.03	0.01	0.08
Marbled cat	100T & 100R	Ψ *(Closed Forest 2km + River distance 500m + settlement distance 2km)*	0.53	0.19	0.84
		$p_{(.)}$	0.05	0.02	0.09
	100T & 0R	Ψ *(Closed Forest 4km + Settlement distance 500m)*	0.15	0.03	0.50
		$p_{(.)}$	0.03	0.01	0.10
	0T & 100R	Ψ *(NULL)*	0.06	0.03	0.10
		$p_{(.)}$	0.11	0.06	0.17
Leopard cat	100T & 100R	Ψ *(Closed Forest 1km + River distance 4km + human density 4km)*	0.31	0.23	0.39
		$p_{(.)}$	0.13	0.10	0.16
	100T & 0R	Ψ *(NULL)*	0.20	0.14	0.25
		$p_{(.)}$	0.16	0.13	0.21
	100T & 100R	Ψ *(Closed Forest 1km + settlement distance 4km)*	0.16	0.07	0.32
		$p_{(.)}$	0.05	0.03	0.11

Table 1. MacKenzie-Bailey goodness of fit test. Chi-square probability ($\chi^2 p$) and over dispersion statistic ($\hat{c}$) site covariates tested were elevation, percentage of forest coverage (closed forest, open forest, and non-forest). Of the 120 days sampling period, 90 days subset was used for analysis. Data was collapsed to 7, 10, 12, and 15 days and collapse rate with dispersion statistic >7 and <1 was used for further occupancy analysis.

- **Species**	- **Station combination**	- **Collapsing period**	- $\chi^2 p$	- $\hat{c}$
- Common leopard	- 100T & 100R	- 7-days sampling occasions	- 0.22	- 1.21
-	-	- 10-days sampling occasions	- 0.20	- 0.72
-	-	- 15-days sampling occasions	- 0.08	- 2.72
-	- 100T & 0R	- 7-days sampling occasions	- 0.26	- 1.36
-	-	- 10-days sampling occasions	- 0.22	- 0.74
-	-	- 15-days sampling occasions	- 0.1	- 1.06

-	-	0T & 100R	- 7-days sampling occasions	-	0.14	-	1.41
-	-		- 10-days sampling occasions	-	0.40	-	1.26
-	-		- 15-days sampling occasions	-	0.32	-	0.72
- Clouded leopard	- 100R	100T &	- 7-days sampling occasions	-	0.22	-	0.72
-	-		- 10-days sampling occasions	-	0.025	-	3.94
-	-		- 15-days sampling occasions	-	0.013	-	5.77
-	-	100T & 0R	- 7-days sampling occasions	-	0.28	-	0.84
-	-		- 10-days sampling occasions	-	0.68	-	0.23
-	-		- 15-days sampling occasions	-	0.12	-	0.71
-	-	0T & 100R	- 7-days sampling occasions	-	0.80	-	0.73
-	-		- 10-days sampling occasions	-	0.48	-	0.75
-	-		- 15-days sampling occasions	-	0.44	-	0.63
- Asiatic golden cat	- 100R	100T &	- 7-days sampling occasions	-	0.28	-	0.85
-	-		- 10-days sampling occasions	-	0.42	-	0.21
-	-		- 15-days sampling occasions	-	0.02	-	1.76
-	-	100T & 0R	- 7-days sampling occasions	-	0.16	-	1.19
-	-		- 8-days sampling occasions	-	0.3	-	0.73
-	-		- 10-days sampling occasions	-	0.44	-	0.54
-	-	0T & 100R	- 7-days sampling occasions	-	0.52	-	1.2
-	-		- 10-days sampling occasions	-	0.35	-	0.8
-	-		- 15-days sampling occasions	-	1.14	-	0.16
- Marbled cat	- 100R	100T &	- 7-days sampling occasions	-	0.22	-	0.85
-	-		- 10-days sampling occasions	-	0.12	-	2.17
-	-		- 15-days sampling occasions	-	0.04	-	2.85
-	-	100T & 0R	- 7-days sampling occasions	-	0.24	-	0.85
-	-		- 10-days sampling occasions	-	0.22	-	1.17

-		-		- 15-days sampling occasions	-	0.02	-	3.82
-		-	0T & 100R	- 7-days sampling occasions	-	0.50	-	1.0
-		-		- 10-days sampling occasions	-	0.04	-	3.17
-		-		- 15-days sampling occasions	-	0.02	-	4.82
-	Leopard cat	-	100T & 100R	- 7-days sampling occasions	-	0.22	-	0.85
-		-		- 10-days sampling occasions	-	0.12	-	2.17
-		-		- 15-days sampling occasions	-	0.04	-	2.85
-		-	100T & 0R	- 7-days sampling occasions	-	0.22	-	0.85
-		-		- 10-days sampling occasions	-	0.32	-	1.22
-		-		- 15-days sampling occasions	-	0.04	-	2.85
-		-	0T & 100R	- 7-days sampling occasions	-	0.74	-	0.66
-		-		- 10-days sampling occasions	-	0.16	-	0.78
-		-		- 15-days sampling occasions	-	0.02	-	7.76

Table 2: Site occupancy model with site covariates optimised at a scale of 500m, 1km, 2km and 4km.

Species	**Station combination**	**Model**	**AIC**	**AIC$_{wt}$**	**K**
Clouded leopard	100T & 100R	Ψ *(human density4km + Elevationc500m)*	215.07	0.37	4
		Ψ *(settlement 500m + settlement500m + humandesnity4km)*	216.62	0.17	5
		Ψ *(closedfores4km + Elevation 500m + human dnsity4km)*	216.75	0.16	5
		Ψ *(humandensity4km + Elevationc500m + river distance 500m)*	216.85	0.15	5
		Ψ_{NULL}	218.65	0.06	2
	0T & 100R	Ψ *(closed forest 4km) + settlement distance 500m +human density 4km)*	77.05	0.28	5
		$\Psi_{(NULL)}$	77.15	0.26	2
		Ψ *(closed forest 4km + settlement distance 500m + human density 4km + river distance 500m)*	77.62	0.21	6
		Ψ *(closed forest 4km + Elevation 500m + river distance 500m + human density 4km)*	78.43	0.14	6

	100T & 0 R	Ψ *(Elevation 500m +human density 4km)*	182.58	0.25	4
		Ψ *(Settlement 500m + human density 4km + Elevation 500m)*	182.83	0.22	5
		Ψ *(Elevation 500m + river distance 500m + human density 4km)*	182.92	0.21	4
		Ψ *(Elevation 500m + closed forest 4km + human density 4km)*	183.23	0.18	5
Common leopard	100T & 100R	Ψ *(Closed Forest 1km +settlement distance 500m)*	126.47	0.41	4
		Ψ *(NULL)*	127.3	0.27	2
		Ψ *(Closed Forest 1km + elevation 500m + human density 4km)*	128.24	0.17	5
		Ψ *(River distance 1km + settlement distance 500m + human density 500m)*	129.85	0.08	5
	100T & 0R	Ψ *(Closed Forest 1km + River distance 1km + settlement distance 500m)*	157.48	0.28	5
		Ψ *(Closed Forest 1km + River distance 1km + Elevation 500m)*	157.69	0.26	5
		Ψ *(Closed Forest 1km + Settlement distance 500m + Elevation 500m + River distance 1km)*	157.82	0.24	6
		Ψ *(NULL)*	158.25	0.19	2
	0R + 100R	Ψ *(NULL)*	63.28	0.55	2
		Ψ *(Closed Forest 1km + River distance 1km)*	64.87	0.25	4
		Ψ *(Closed Forest 1km + Human density 500m + Elevation 500m)*	66.57	0.11	5
		Ψ *(Closed Forest 1km + Human density 500m)*	68.08	0.05	5
Asiatic golden cat	100T & 100R	Ψ *(NULL)*	304.01	0.68	2
		Ψ *(Closed Forest 2km + Settlement distance 2km)*	307.09	0.14	4
		Ψ *(Closed Forest 2km + River distance 500m + settlement distance 2km)*	308.12	0.09	4
		Ψ *(Closed Forest 2km + Human density 4km)*	309.09	0.05	5
	100T & 0R	Ψ *(Elevation 2km + Open Forest 4km)*	358.3	0.236	3
		Ψ *(NULL)*	358.4	0.229	2
		Ψ *(River distance 500m + settlement distance 2km)*	358.7	0.197	4
		Ψ *(Open Forest 2km + Human density 4km)*	358.9	0.179	4
	0T & 100R	Ψ *(Closed Forest 2km + River distance 500m + settlement distance 2km)*	151.6	0.31	5
		Ψ *(Closed Forest 2km + River distance 500m)*	151.82	0.28	4
		Ψ *(Closed Forest 2km + settlement distance 2km))*	152.57	0.19	4
		Ψ *(Open Forest 2km + River distance 500m+ Elevation 2km)*	152.71	0.18	5
Marbled cat	100T & 100R	Ψ *(Closed Forest 4km + Elevation 500m)*	295.19	0.53	4
		Ψ *(Settlement distance 500m + River distance 4km + Human density 4km)*	296.5	0.28	5

		Ψ *(Closed Forest 4km + settlement distance 500m)*	297.3	0.18	5
		Ψ *(NULL)*	304.01	0.01	2
100T & 100R		Ψ *(Closed Forest 4km + Settlement distance 500m)*	126.47	0.41	4
		Ψ *(NULL)*	127.3	0.27	2
		Ψ *(Closed Forest 4km + Human density 4km + Elevation 500m)*	128.24	0.17	5
		Ψ *(River distance 4km + Human density 4km)*	129.85	0.08	5
0T & 100R		Ψ *(NULL)*	179.72	0.61	2
		Ψ *(Closed Forest 4km + settlement distance 500m)*	182.16	0.18	4
		Ψ *(River distance 4km + settlement distance 500m +Human density 4km)*	183.49	0.09	5
		Ψ *(River distance 4km + Settlement distance 4km)*	183.49	0.09	5
Leopard cat	100T & 100R	Ψ *(Closed Forest 1km + River distance 4km + human density 4km)*	607.28	0.35	5
		Ψ *(NULL)*	607.72	0.28	2
		Ψ *(River distance 4km + human density 4km)*	607.98	0.25	4
		Ψ *(Closed Forest 1km + Settlement distance 4km)*	610.3	0.08	4
	100T & 0R	Ψ *(NULL)*	458.19	0.51	2
		Ψ *(River distance 4km+ human density 4km)*	459.59	0.25	4
		Ψ *(River distance 4km + settlement distance 4km + human density 4km)*	460.9	0.13	5
		Ψ *(Closed Forest 1km + River distance 4km)*	462.04	0.07	4
	0T & 100R	Ψ *(Closed Forest 1km + settlement distance 4km)*	207.42	0.69	4
		Ψ *(Closed Forest 1km+settlement distance 4km+ elevation1km)*	209.52	0.24	5
		Ψ *(Elevation 1km + Settlement distance 4km+ human density 4km)*	213.26	0.04	5
		Ψ *(NULL)*	213.76	0.03	5

Table 3. Mean parameter estimates of habitat use probability and 95 % confidence intervals for Common leopard, clouded leopard, Asiatic golden cat, marbled cat, leopard cat.

- **Clouded leopard**

Station combination		**Parameters ($\widehat{\beta}$)**	**Mean**	**LCI**	**UCI**
100T & 100R	Ψ	Intercept	-1.66	-2.59	-0.74
		Open forest 4km	-0.13	-0.77	0.51
		Closed forest 4km	0.29	-0.36	0.93
		River distance 500m	-0.37	-1.33	0.58
		Settlement distance 500m	-0.32	-1.02	0.38
		Human density 4km	0.68	-0.01	1.37
		Elevation 500m	-0.34	-1.07	0.40
	p	Intercept	-2.86	-3.62	-2.10

	Ψ	Intercept	-2.56	-3.52	-1.60
		Open forest 4km	-0.31	-1.05	0.44
		Closed forest 4km	0.44	-0.27	1.16
0T & 100R		River distance 500m	-0.10	-0.84	0.65
		Settlement distance 500m	-0.33	-1.12	0.47
		Human density 4km	0.23	-0.44	0.90
		Elevation 500m	0.02	-0.79	0.84
	p	Intercept	-2.66	-3.61	-1.72
100T & 0R	Ψ	Intercept	-2.37	-3.33	-1.41
		Open forest 4km	-0.47	-1.21	0.26
		Closed forest 4km	0.04	-0.62	0.70
		River distance 500m	-1.00	-2.23	0.24
		Settlement distance 500m	-0.16	-0.93	0.62
		Human density 4km	0.63	-0.06	1.31
		Elevation 500m	-0.28	-1.08	0.52
	p	Intercept	-2.66	-3.42	-1.90

- **Common leopard**

Station combination		**Parameters ($\widehat{\beta}$)**	**Mean**	**LCI**	**UCI**
	Ψ	Intercept	-1.76	-3.71	0.19
		Open forest 4km	-0.62	-1.66	0.42
100T & 100R		Closed forest 4km	0.70	-0.40	1.79
		River distance 500m	-0.45	-1.66	0.77
		Settlement distance 500m	0.22	-0.71	1.14
		Human density 4km	-0.55	-1.67	0.57
		Elevation 500m	-0.51	-1.70	0.68
	p	Intercept	-3.63	-5.17	-2.10
100T & 0R	Ψ	Intercept	-1.89	-2.38	-1.39
		Open forest 4km	-0.46	-0.98	0.06
		Closed forest 4km	0.07	-0.36	0.50
		River distance 500m	0.33	-0.01	0.67
		Settlement distance 500m	0.26	-0.29	0.82
		Human density 4km	0.33	-0.10	0.76
		Elevation 500m	-0.72	-1.29	-0.15
	p	Intercept	-3.81	-4.16	-3.46
0T & 100R	Ψ	Intercept	-2.76	-4.45	-1.07
		Closed forest 4km	0.68	-0.28	1.64
		Settlement distance 500m	0.11	-0.92	1.14
		Human density 4km	-0.63	-2.29	1.03
		Elevation 500m	0.28	-0.93	1.51
	p	Intercept	-2.33	-3.76	-0.91

- **Asiatic golden cat**

Station combination		**Parameters ($\widehat{\beta}$)**	**Mean**	**LCI**	**UCI**
	Ψ	Intercept	0.25	-1.99	2.50

		Open forest 4km	-0.05	-0.80	0.71
100T & 100R		Closed forest 4km	-0.38	-1.31	0.55
		River distance 500m	0.27	-1.56	2.09
		Settlement distance 500m	-0.04	-1.39	1.32
		Human density 4km	0.19	-1.02	1.40
		Elevation 500m	0.04	-1.23	1.31
	p	Intercept	-3.10	-4.08	-2.11
	Ψ	Intercept	-1.12	-1.75	-0.50
		Open forest 4km	0.37	-0.14	0.88
		Closed forest 4km	-0.56	-1.11	0.00
100T & 0R		River distance 500m	0.10	-0.44	0.63
		Settlement distance 500m	0.16	-0.41	0.73
		Human density 4km	0.25	-0.27	0.77
		Elevation 500m	0.16	-0.40	0.72
	p	Intercept	-2.50	-3.02	-1.99
0T & 100R	Ψ	Intercept	-2.34	-3.62	-1.06
		Open forest 4km	-1.07	-2.02	-0.11
		Closed forest 4km	1.46	0.32	2.60
		River distance 500m	1.07	-0.22	2.37
		Settlement distance 500m	-0.69	-1.82	0.43
		Human density 4km	0.11	-0.74	0.97
		Elevation 500m	-0.32	-1.52	0.88
	p	Intercept	-3.18	-4.07	-2.29

- **Marbled cat**

Station combination		**Parameters ($\widehat{\beta}$)**	**Mean**	**LCI**	**UCI**
	Ψ	Intercept	-1.76	-3.71	0.19
		Open forest 4km	-0.62	-1.66	0.42
100T & 100R		Closed forest 4km	0.70	-0.40	1.79
		River distance 500m	-0.45	-1.66	0.77
		Settlement distance 500m	0.22	-0.71	1.14
		Human density 4km	-0.55	-1.67	0.57
		Elevation 500m	-0.51	-1.70	0.68
	p	Intercept	-3.63	-5.17	-2.10
	Ψ	Intercept	-3.00	-4.39	-1.60
		Open forest 4km	4.04	0.04	8.04
		Closed forest 4km	-0.64	-1.17	-0.11
100T & 0R		River distance 500m	0.41	-0.14	0.97
		Settlement distance 500m	0.03	-0.54	0.60
		Human density 4km	0.22	-0.45	0.89
		Elevation 500m	-0.11	-0.67	0.44
	p	Intercept	-2.22	-2.75	-1.70
0T & 100R	Ψ	Intercept	-2.98	-3.69	-2.26
		Open forest 4km	0.29	-1.00	1.59
		Closed forest 4km	0.01	-0.63	0.66
		River distance 500m	0.24	-0.38	0.86
		Settlement distance 500m	-0.54	-1.30	0.22
		Human density 4km	-0.06	-0.82	0.71
		Elevation 500m	0.20	-0.47	0.88
	p	Intercept	-2.09	-2.62	-1.56

- **Leopard cat**

Station combination		Parameters ($\widehat{\beta}$)	Mean	LCI	UCI
100T & 100R	Ψ	Intercept	-1.50	-1.88	-1.13
		Open forest 4km	-0.12	-0.48	0.24
		Closed forest 4km	0.10	-0.28	0.49
		River distance 500m	0.44	0.00	0.88
		Settlement distance 500m	0.20	-0.27	0.67
		Human density 4km	0.37	-0.08	0.83
		Elevation 500m	-0.09	-0.55	0.36
	p	Intercept	-1.63	-1.93	-1.33
100T & 0R	Ψ	Intercept	-1.50	-1.88	-1.13
		Open forest 4km	-0.12	-0.48	0.24
		Closed forest 4km	0.10	-0.28	0.49
		River distance 500m	0.44	0.00	0.88
		Settlement distance 500m	0.20	-0.27	0.67
		Human density 4km	0.37	-0.08	0.83
		Elevation 500m	-0.09	-0.55	0.36
	p	Intercept	-1.63	-1.93	-1.33
0T & 100R	Ψ	Intercept	-1.74	-2.63	-0.85
		Open forest 4km	-0.20	-0.87	0.47
		Closed forest 4km	0.76	0.16	1.36
		River distance 500m	0.30	-0.28	0.88
		Settlement distance 500m	-0.37	-1.12	0.38
		Human density 4km	0.33	-0.33	0.99
		Elevation 500m	-0.16	-0.88	0.57
	p	Intercept	-2.80	-3.57	-2.04

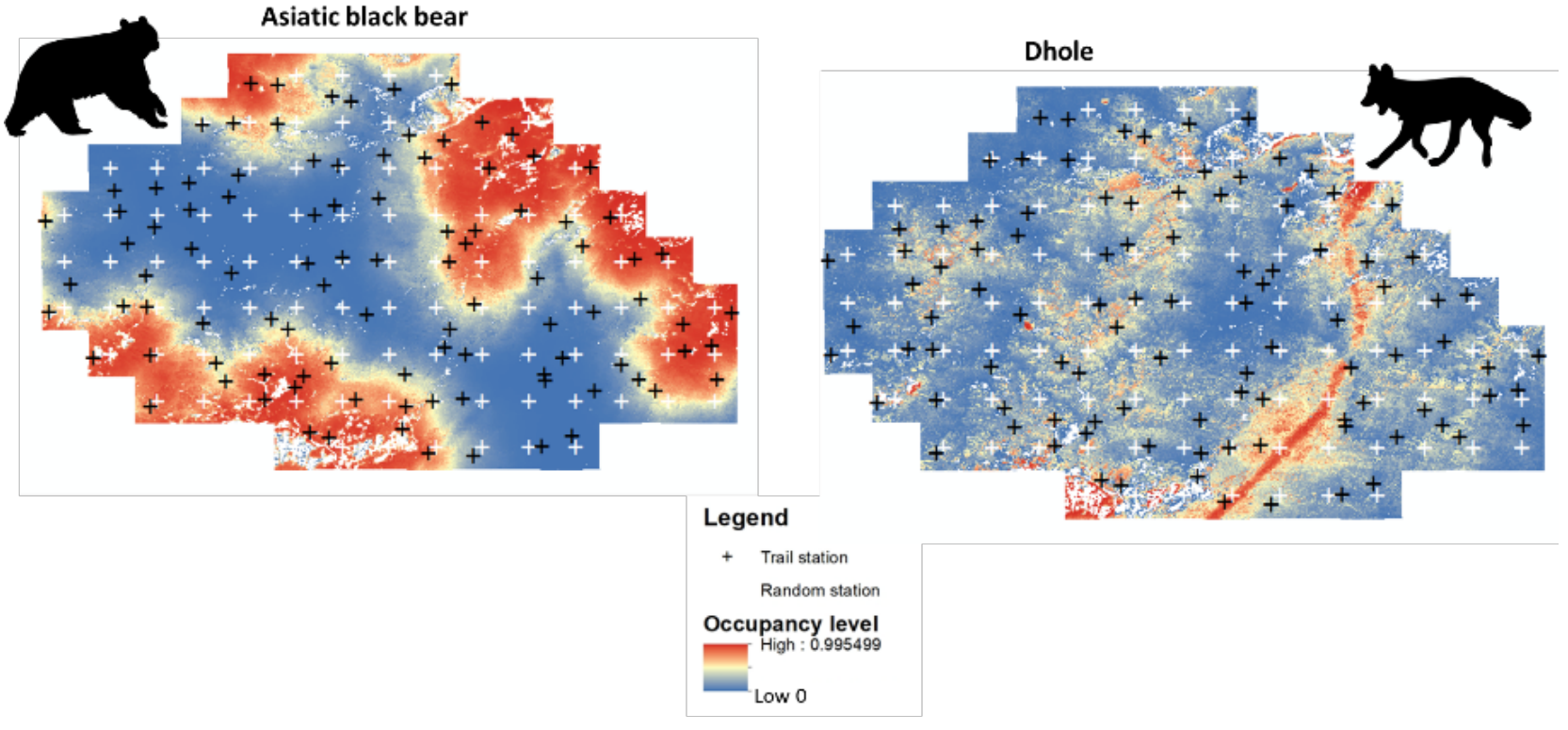


Figure 2. Predicted site occupancy of sympatric carnivores in the study area (left Asiatic black bear, right dhole). The occupancy probability is shown from 0 (blue) to 0.99 (red). The black plus sign represent the trail camera stations and white plus sign represents the random camera stations.

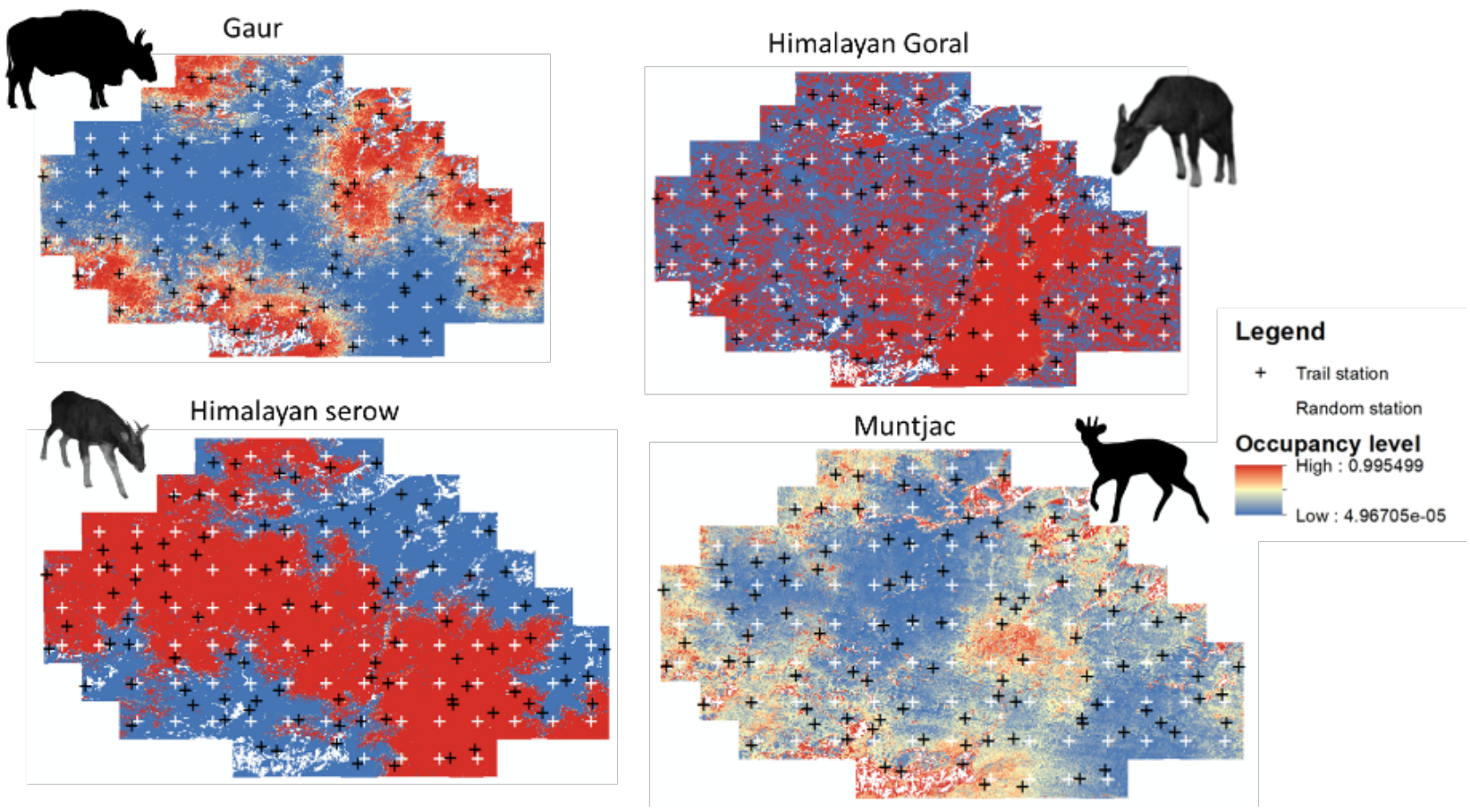


Figure 3. Predicted occupancy of prey species in the study area. Figure legend are same for Figure 2.

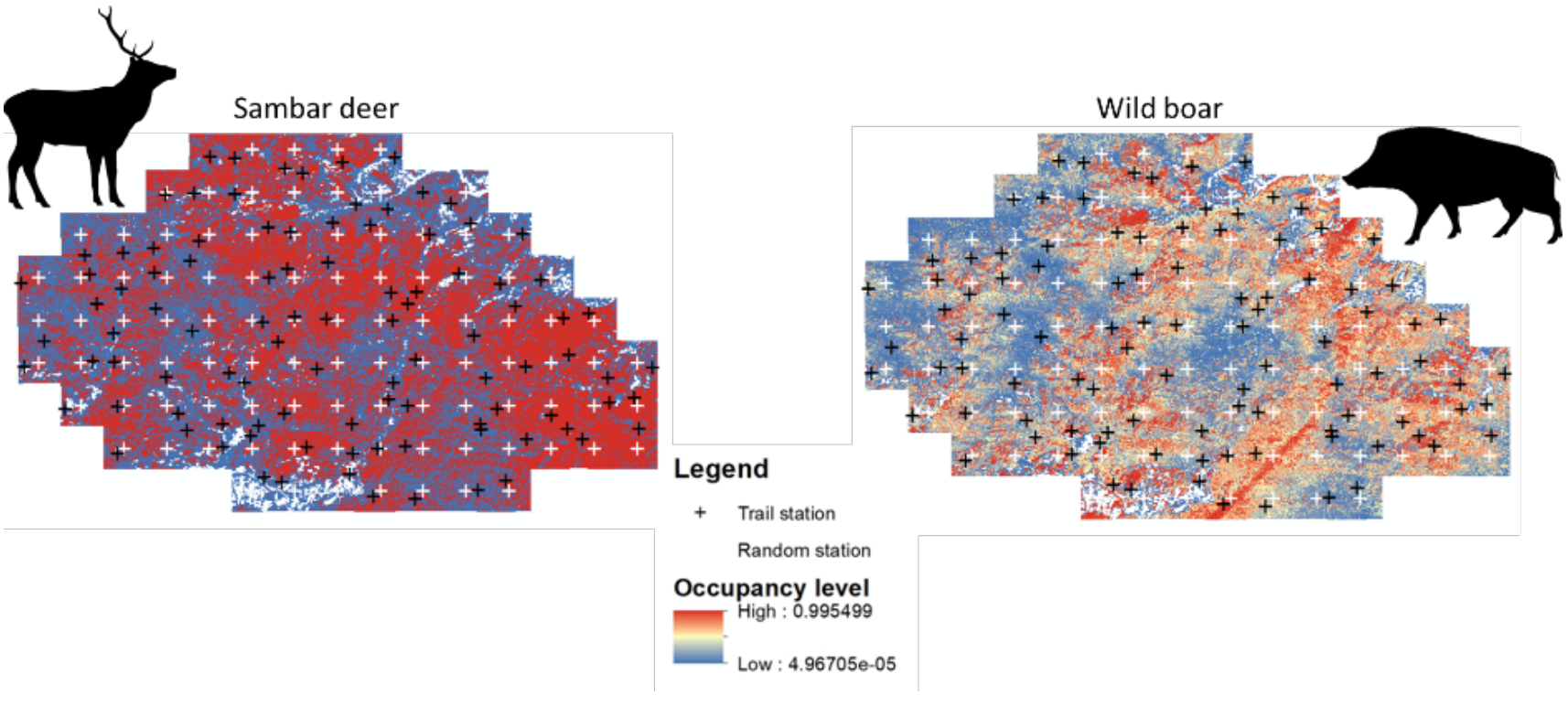


Figure 4. Predicted occupancy of prey species in the study area. Figure legend are same for the Figure 2.



Fig 5. Leopard_3 (female) recorded near live trap with a subadult cub 8 months after GPS collaring. The magnified image shows the subadult cub near live trap while mother inspects the live trap.

Appendix 4. Supplementary information for Chapter 5

Figure S1. Research permits for conducting camera trapping, live trapping and social survey in Jigme Singye Wangchuck National Park and Royal Manas National Park

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ཨོ་རྒྱན་དབང་ཕྱུག་མཐའ་འཁོར་དང་ཉམས་སྤྱད་ཞིབ་འཚོལ་སྡེ་ཚན།

Ugyen Wangchuck Institute for Conservation and Environmental Research
Department of Forests and Park Services
Ministry of Agriculture and Forests
ROYAL GOVERNMENT OF BHUTAN

RESEARCH PERMIT

Date: 2020-03-06

Applicant ID : **8423233545E33B9316C6F7**
Name of Researcher : **Lungten Dorji**
Address : **Wangchuck Centennial National Park, Department of Forest and Park Services, Ministry of Agriculture and Forests**

With reference to the approval of the Research Steering Committee and in accordance with Forest and Nature Conservation Rules and Regulations, 2017, this permit is issued to the above applicant to conduct research in State Reserved Forests/Community Forest/ Protected Areas/any other management regimes w.e.f. **2020-09-01** till **2023-01-31**

Research Site : **Jigme Singye Wangchuck National Park , Royal Manas National Park (Gomphu Range)**

Research Topic : **Resolving biases in big cat population density estimation for conservation**

Note : The researcher is instructed to meet the CFO of the above Park/Division office before the start of his/her research work in the field. The researcher is also instructed to submit a set of his/her research data and a copy of his/her research thesis to UWICER.

The research work shall adhere to the provisions of the Forest and Nature Conservation Rules and Regulations 2017.

OFFICIAL SEAL

Signature of Chairman
Research Steering Committee

Table S1: Input variables for ordinal logistic regression model where response variable was “negative attitude towards wild felids”. Q-represent the question number in survey questionnaire.

Predictor variable	Item in the questionnaire	Response Variable
Occupation	Q4. Occupation	Negative attitude towards wild felids (Q32. Carnivores in the forest are not important to everybody)
Education level	Q6. Education level	
Conservation group members	Q12. Are you member of the following group (coded to "Yes" if member of any conservation group and "No", if not a member)	
Rate of conflict, dhole	Q18a. As per your understanding, rank, which is the most conflicted animal in your locality (dhole)	
Rate of conflict, common leopard	Q18b. As per your understanding, rank, which is the most conflicted animal in your locality (common leopard)	
Rate of conflict, small felids	Q18c. As per your understanding, rank, which is the most conflicted animal in your locality (Small felids)	
Rate of conflict, tiger	Q18d. As per your understanding, rank, which is the most conflicted animal in your locality (tiger)	
Species importance, dhole	Q27a. Which carnivore do you think contributes most to ecosystem health (dhole)	
Species importance, clouded leopard	Q27b. Which carnivore do you think contributes most to ecosystem health (clouded leopard)	
Species importance, common leopard	Q27c. Which carnivore do you think contributes most to ecosystem health (common leopard)	
Species importance, small felids	Q27d. Which carnivore do you think contributes most to ecosystem health (small felids)	
Species importance, tiger	Q27e. Which carnivore do you think contributes most to ecosystem health (tiger)	
Missing household chores	Q49. We miss our daily chores guarding cattle against carnivores	
Lower compensation	Q51. The compensation we get from the government is very low	
Satisfaction with government	Q84.How satisfied are you with the grievance redressal mechanism developed by local government related to human-carnivore conflicts?	

Frequency of monitoring by authorities	Q85. How do the concerned organizations monitor human-carnivore conflict (1. Frequently, 2. Less frequently, 3. Never, 4. Don't know
Tolerance, not attending complains	Q76a. The following factors reduces the community's tolerance towards the conservation of the carnivores (Official not attending the complaints)
Tolerance, Productive breed lose	Q76b. The following factors reduces the community's tolerance towards the conservation of the carnivores (Losing productive breeds to carnivores)
Tolerance, Less compensation	Q76c. The following factors reduces the community's tolerance towards the conservation of the carnivores (Less compensation)
Tolerance, Late compensation	Q76d. The following factors reduces the community's tolerance towards the conservation of the carnivores (When compensation reaches late)

Table S2. Input variables for ordinal logistic regression model where response variable was "support towards wild felids". Q-represent the question number in survey questionnaire.

Variable name	**Item in questionnaire**	**Response Variable (item in questionnaire)**
Occupation	Q4. Occupation	Support towards wild felids (Q33. I can tolerate livestock depredation by carnivores)
Education level	Q6. Education level	
Rate of conflict, dhole	Q18a. As per your understanding, rank, which is the most conflicted animal in your locality (dhole)	
Rate of conflict, common leopard	Q18b. As per your understanding, rank, which is the most conflicted animal in your locality (common leopard)	
Rate of conflict, small felids	Q18c. As per your understanding, rank, which is the most conflicted animal in your locality (small felids)	

Rate of conflict, tiger	Q18d. As per your understanding, rank, which is the most conflicted animal in your locality (tiger)
Species importance, dhole	Q27a. Which carnivore do you think contributes most to ecosystem health (dhole)
Species importance, clouded leopard	Q27b. Which carnivore do you think contributes most to ecosystem health (clouded leopard)
Species importance, common leopard	Q27b. Which carnivore do you think contributes most to ecosystem health (common leopard)
Species importance, small felids	Q27b. Which carnivore do you think contributes most to ecosystem health (small felids)
Species importance, tiger	Q27b. Which carnivore do you think contributes most to ecosystem health (tiger)
Missing household chores	Q49. We miss our daily chores guarding cattle against carnivores
Lower compensation	Q51. The compensation we get from the government is very low
Satisfaction with government	Q84.How satisfied are you with the grievance redressal mechanism developed by local government related to human-carnivore conflicts?
Frequency of monitoring by authorities	Q85. How do the concerned organizations monitor human-carnivore conflict (1. frequently, 2. Less frequently, 3. Never, 4. Don't know)

Appendix 4

Table S3. Input variables for binomial logistic regression model where response variable was “risk of livestock depredation by wild felids”. Q-represent the question number in survey questionnaire.

Variable name	Item in questionnaire	Response Variable
Encroachment of habitat	Q19a. Rate the causes of human-carnivore conflicts as per your understanding (Habitat encroachment by humans)	Risk of livestock depredation by wild felids
Carnivore population expulsion	Q19b. Rate the causes of human-carnivore conflicts as per your understanding (Carnivore population expulsion)	(Q61. Have you ever faced incidences of livestock depredation from carnivores?)
Ecosystem imbalance	Q19c. Rate the causes of human-carnivore conflicts as per your understanding (Ecosystem imbalance)	
Rate of conflict, dhole	Q18a. As per your understanding, rank, which is the most conflicted animal in your locality (dhole)	
Rate of conflict, common leopard	Q18b. As per your understanding, rank, which is the most conflicted animal in your locality (common leopard)	
Rate of conflict, small felids	Q18c. As per your understanding, rank, which is the most conflicted animal in your locality (small felids)	
Rate of conflict, tiger	Q18d. As per your understanding, rank, which is the most conflicted animal in your locality (tiger)	
Risk of free raring of livestock	Q29. Domestic animals entering forests are at hight risk of depredation from carnivores	
Mode of livestock raring	Q56. What mode of cattle rearing do you practice (1. Stall feeding, 2. free roaming, 3. herding)	
Conflict habitat (near human settlement)	Q14a. Which is the location where most of the HWC occurs (Near human settlement)	

Conflict habitat (in the animal habitat)	Q14b. Which is the location where most of the HWC occurs (carnivore habitat)

Figure S2. Missing value in variable used for modelling local understanding of the factors influencing risk of livestock depredation from wild felids. The missing values are represented by white shading and blue shading indicates the observed data. Q are survey items in questionnaire (S4) and R represent the response variable.

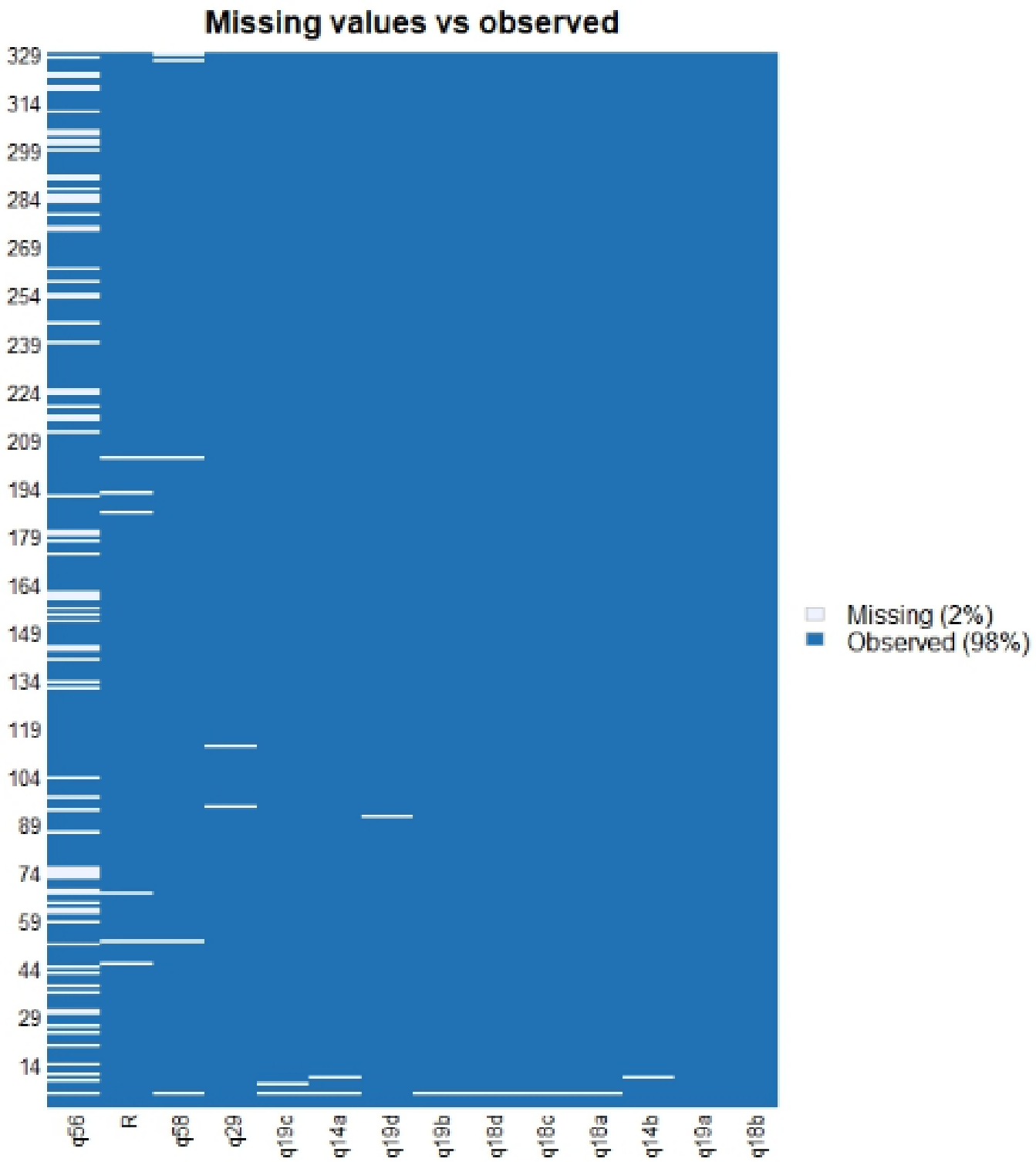
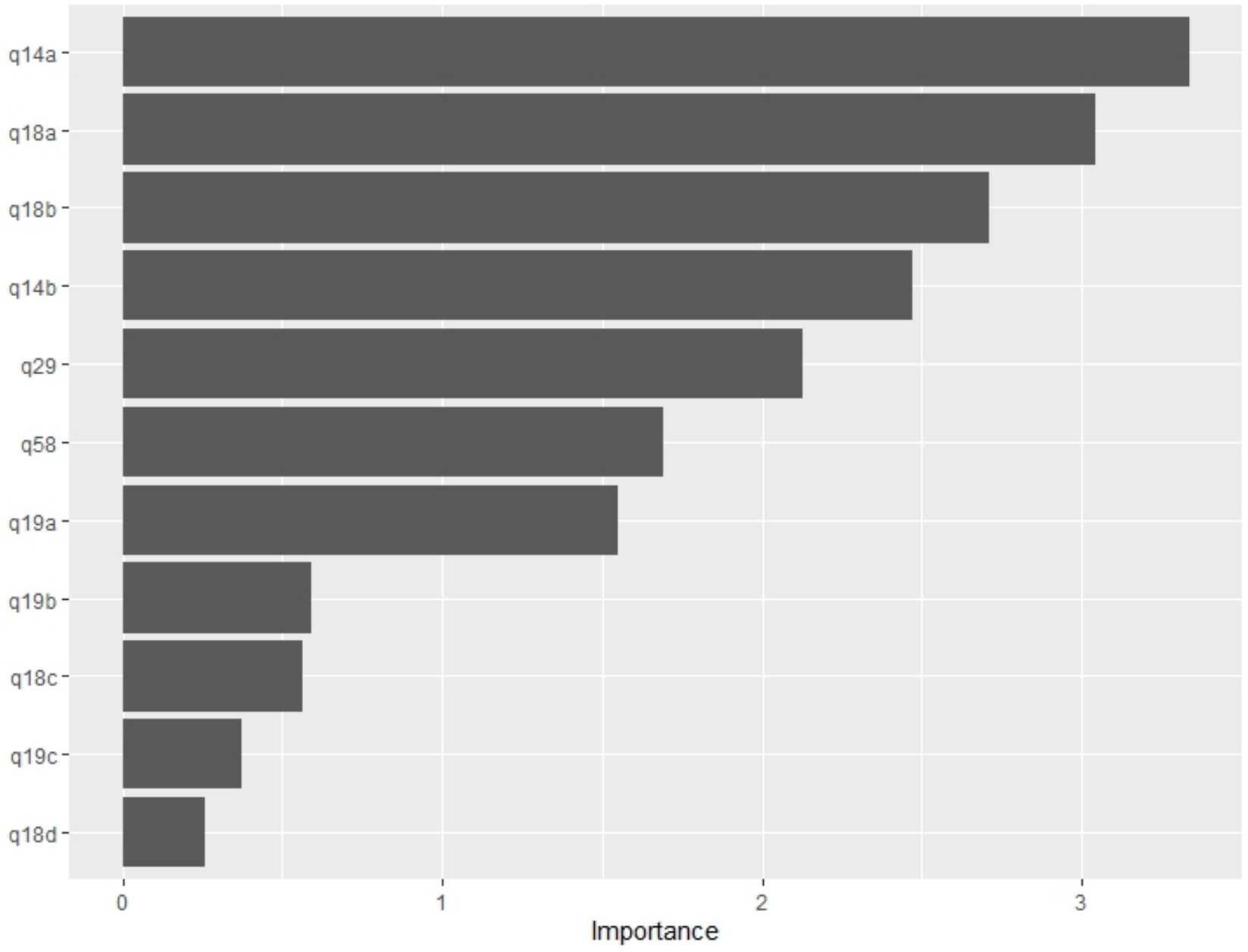


Figure S3. Variable importance against the response variable Q on y-axis are the survey items in questionnaire (S4) and the bar chart represents the importance on each variables.



Appendix 4

Table S4. Qualitative findings and content analysis of key informant survey. Tsogpa refers to elected head of village, gup refers to chairman of block administration under districts (Dzongkhags).

Occupation	Perceived causes of Human-carnivore conflict	Positive Impact of human-carnivore interaction	Negative impact of human carnivore interaction	Recommendation of reduction of HCC
Tsogpa	Because sometimes carnivores accidently attack livestock. Can be climate change or human population explosion and agriculture expansion.	Reduce herbivore near the human settlement as well as in the locality	Harming human and domestic animal	Help people to protect domestic animal and people will help to reduce retaliatory killing. To stay safe, people should keep surrounding safe. Guarding animal well.
Tsogpa	There is no adequate prey in the forest and development activities might be the cause.	Control herbivores	Depredation of cattle	No comments
Ranger	Settlement located near forests, Habitat disturbances, may be more number of carnivore	Control herbivores leading to less crop depredation. Good for ecotourism	Risk for human life, livestock depredation which reduces interest in raring livestock	Proper reporting system for compensation. Government and concerned authorities should focus on awareness. More number of households in the locality to reduce barren land which harbour wildlife.
Ranger	Encroachment of habitat by development activities, ecosystem imbalance, climate change, loss of ecosystem and encroachment	Gewog tiger conservation fund for Korphu area	No comments	More consultation with the people. including local people for consultation and planning at Dzongkhag level. Regularly providing education and awareness.

Gewog administrati on officer	Because human destroy their (carnivores) habitat, lack of food for survival in the wild. The human-carnivore conflict tends to increase over the past since human tend to destroy their habitat and hunt their prey, in order to survive carnivore attack cattle for food.	Balance ecosystem	Great loss for human	Preserve their habitat strictly and not letting human to destroy their habitat. Compensating farmers, the actual loss of their cattle due to carnivores. Overall, I find important to conserve the carnivores as they are endangered and may get extinct and future generations may not see them like dinosaurs. Creating awareness face to face rather than sending notifications. Creating awareness regarding the carnivores as they are endangered species. Strict monitoring of species, human behaviour and imposing strict fines as per the rules and regulations. Giving training or financial subsidies to improve livestock.
Teacher	It is because we are living in the area with heavy forest cover and the habitat shared by the wild animals and carnivores. Therefore, HWC is more likely to occur anytime. Moreover, I feel that conflict will accelerate when the competition for food and shelter increases. It is because human population is increasing and thereby increasing the demand for resources and space use simultaneously.	Presence of tiger will drive other carnivore to deeper forests. People fear will be reduced if the carnivores move deeper into the forests, herders will take extra care of cattle, People will learn for stall feeding instead of free raring	Loss of property livelihood and even life, threat to carnivores form human, HWC leads to decline and potential eradication of species	Communities and carnivores share the same landscape, therefore poor co-existence strategies lead to rise of human-carnivore conflicts over the years. Well planned and holistic and integrated management plan and strategies. Compensating the livestock kills. By maintaining good relationship with carnivores and maintaining healthy co-existence strategy. Making people aware about the direct and indirect benefits of having carnivores in the forest. People should be made more aware about the importance of carnivores in the ecosystem. A proper, integrated, and holistic plan is

				required to management human-carnivore conflicts.
Gewog Livestock extension officer	Mainly due to the geographic location of the place, the place is more remote with thick forests and there are many countless creatures including the carnivores. Due to habitat destruction, which includes shifting cultivation. The management and solution don't match with the scale of problem, and management are often implemented with just conservation focus. There are lack of support and coordination amongst the sectors despite issue being so important and global in nature	No comments	Loss of property livelihood and even life	In order to reduce human wildlife conflict, we need to assess the relationship between human and wildlife, especially the direct relationship between human and wildlife to improve the coexistence in the future. We need to identify the approaches that will address the deeper cause of the human-carnivore conflicts developing systematic and context-specific solution with affected communities as equal participant for solution and equal involvement of community in decision making. Habitat conservation.
Tsogpa	Because of the location of settlements. More number of protected areas around the human settlement	Controls herbivore population and even carnivore population by tiger.	Loss of property and impact on human life	Putting more effort on the preservation of habitat. There should be well planned management plan within the forestry sector and the local community. Making the local communities more about the rules and regulations. Strict monitoring and patrolling.

Gewog administrative officer	Achieving co-existence between human and carnivore is pressing challenge at global level. It manifests in many ways, to killing livestock and pets. Competition for food and resources. Many forms of interaction and climate change	Help to regulate ecosystem services, help to save endangered species, It can lower the herbivore population	Habitat destruction, decreasing livestock grazing site	Chain-link fencing, Education human to encounter wild animal. Avoid feeding wild animal. Creating more protected areas and buffer zone. Compensation to the kill will reduce retaliatory killings.
Tsogpa	Because of increasing population and increasing destruction of carnivore habitat leads to increasing human-carnivore conflicts. It can be also due to increase in the number of carnivores.	Controlling population of other species like sambar	Casualties and depredation of livestock	Awareness on importance of wildlife and rules. Using more technological advancement like use of chain-link fencing. More compensation. Imposing fines and penalties.
Agriculture extension officer	Rural places are mostly covered by rich forests. Clearing habitat for developmental activities and climate change. It can be also due to lack of food for carnivores.	No comments	Threat to human life and domestic animals	Maintain their habitat in the natural setting. With government and NGOs taking more conservation effort and to reduce human-carnivore conflicts, it can not only prevent human-carnivore conflict but also help in preserving endangered species. Ensure safe surroundings of village like lighting system, clearing bushes and use of technologies to chase away wild animals.
Tshogpa	May be due to shortage of food in the forests, could be because of settlement near the forests. Due to loss of habitat and climate change.	No comments	Threat to human life and domestic animals	Ensure safe surroundings around the village, providing electric fencing and proper lighting facilities. Awareness to public.

Facilitator, community information centre	Due to the disturbances to their habitat by various human activities by rising population. Habitat destruction. Climate change	Opportunities to receive funds for conservation of carnivores improves the livelihood of local people	With rising settlement and human interference to the forests increases the livestock depredation by carnivores causing great loss to the farmers	Advocacy to people on human-carnivore conflict and adaptation with the change in ecosystem. Make their farming easier and more eco-friendly by providing inputs in regard to electric fence, replacement of electric fence poles with HDPE pipes and farm mechanizations.
Tsogpa	No food for animals in the forests. Destruction of habitat by human being.	No comments	No comments	Awareness to public. Killing animals is not going to help reduce the conflicts, so, we must maintain safe village for ourselves. Compensation to farmers/people.
Gup (Head of local government)	Because of food chain. Removal of forests by human and no habitat for animals. Climate change	Loss of habitat	No comments	Plant more trees where tigers stay. Not killing animals like deer, boar, as they are main food for tigers. Let's plant more trees and keep a forest safe place to live for animals. Pay compensation for killing domestic animals.
Community information centre (facilitator)	Human-carnivore conflicts continue to rise over the year because of human character, as they kill all the animals and tigers are left without food, so they are attracted to the locality	No comments	Harmful to cattle and people	To plant more trees. Fine more if people kill tiger. To save other animals.

Gup	Because of insufficient food for them and human are unaware of wildlife. Increasing amount of wildlife. No proper care for domestic animals in the community.	No comments	No comments	To do awareness in the community. To take care of domestic animals with proper shelter. To compensate the public not through insurance scheme but directly to their account. Need to do shifting cultivation in order to clear trees, bushes, so that there won't be placed to hide wild animals around the village.
Ranger	Due to increasing human population and developmental activities in their habitat. lack of awareness	No comments	Killing and attacking of domestic cattle, Attack on human by common leopard in 2021	Need to give more awareness on the presence of wild animals especially carnivores and its advantages and disadvantages on their presence. My suggestion is to give more awareness and make people understand.
Ranger	Due to carnivores coming to human settlement for easy prey such as livestock and domestic animals. Due to increase in forest cover near the settlement and reduction of prey in the wild. People letting their livestock freely in the forests.	No comments	Chances of getting animals bullied by humans and reducing the population, and human getting injured by carnivores	The use of fences in communities help minimize contact between human and wildlife. Engage people though awareness, newsletters, television on human-carnivore conflicts. Compensate the owner by simplifying the process. Set nonlethal traps, tranquilize and relocate the problem animal.
Ranger	It is because their habitat is being disturbed, prey species is getting decreased with more poachers. It is because more developmental activities are coming to the locality or in nation whereby their home range are damaged.	They always maintain the balance in ecosystem	Sometimes high yielding domestic animals are being killed whereby public face great loss.	We should keep or maintain some place totally un-touched or disturbed for them to stay or feed on. We should increase the fine amount. We should give time to time awareness. Hotspot area should be monitored/ patrolled regularly. Management should encourage field staff by giving some extra incentives to take

				active role in conservation of those important carnivore species.
Ranger	Human settlement is near the forests. Encroachment of habitat by human. Carnivores' population increase in the community. Loss of habitat increases in population of wild animals in the community. Letting their livestock freely roam in the forest and due to climate change.	No comments	Carnivore killed their livestock as well as attract to the humans	Electric fence around the cultivation land. awareness to the communities. Compensation for their livestock killed. By giving awareness to the community time to time by forests department, parks on the importance of wildlife. Insurance scheme. Change the livestock raring practices in the community. Relocate the conflicted animals. Awareness to the communities and make people understand. Increase the penalties and fines.
Tsogpa	While the wild animal start to harm in human fields. Because of human population growth, agriculture expansion, infrastructure development, climate change, and other drivers of habitat loss.	No comments	The negative point is it is very risky for both human and domestic animal as they are being killed	The measure to reduce human-carnivore conflicts are by creating buffer zones between wild and urban areas. By giving awareness to the human by forest department. By preserving the endangered animal in zoos.
Tsogpa	Human settlement is near the forests, Encroachment of habitat by human. Loss of habitat and letting their livestock freely in the forest.	No comments	Carnivores kill their livestock as well attack to the people	Electric fence around the cultivation land. Awareness to the communities. Compensation for livestock killed. Increase the penalties. Insurance scheme.

Livestock extension officer	May be due to lack of food. Increase in the carnivore population.	No comments	No comments	Compensation for crop and livestock depredation/damage. Provide improve breed of cattle.
Gewog administrative officer	Due to rural urban migration the lands are uncultivated so that the wildlife habitat in and around the settlement causing increase of herbivore population in the locality.	Positive impacts are it control herbivore	It kills domestic animals	The agriculture lands to be chain-link fenced and concrete wall fencing. Compensation payment for loss of livestock.
Ranger	This is because it might be lack of food in the forest, it might be killing of wild animals by humans and disturbing the habitat. It might be due to the human have been doing illegal poaching for doing business and killing herbivore animal which disturbs food for carnivores.	No comments	The far-flung cattle herders have lost their cattle to tiger, leopard and wild dog. Infinite numbers of cattle have lost their life by these predators	The severe and hard laws, rules and regulation should be implemented. The regulatory body should do strict monitoring and patrolling. Impose high penalty to the kills and minimum sentence to them and everybody living in the village should be aware on conservation of carnivores.
Ranger		No comments	Loss of cattle is negative impact	Lack of awareness is main issue, cattle herding, strict rules, and law
Ranger	Since most of the settlement are surrounded by forests, constant interaction between wildlife and human and most of livestock keeping in herding. Hunting of herbivore species.	Positive impacts will control herbivore population when number of carnivores increase in locality.	Negative impact will be increased number of livestock depredation case	Improving pastureland near by settlement. Paying more compensation, supply breed cattle and introducing human-wildlife endowment fund. Improving pastureland near by settlement. Impose more fines. 1. Supplying of improve where there is high frequency of human-carnivore conflict. 1. Educating communities about carnivore behaviour and conservation importance

Ranger	1. Habitat loss and fragmentation, 2. Competition for resources, 3. Livestock predation, 4. Lack of awareness and understanding, 5. Illegal wildlife trade. Due to increase of carnivore population. Most people nowadays prefer free ranging methods for livestock rearing, unlike the past. Additionally, young people are more inclined to choose urban living over residing in rural communities. As a result, there is an increase in human-carnivore conflict due to the absence of younger individuals in the villages who would normally carry out necessary work. This leaves only the elderly parents behind to handle all responsibilities and tasks.	No comments	1. Livestock predation, 2. Human safety concerns	2. Educating communities about carnivore-behaviour and conservation importance. 2. Avoiding free-grazing practices. 3. Reducing the intrusion of human activities into natural habitats.

Ranger	Carnivores are often conflicted with human due to habitat overlapping, having surrounding forest being thickly populated, less pressures to carnivores from hunting and poaching and people let their domestic animal freely graze in nearby forest. 1. Overpopulations and habitat degradation by occupying their space, food, and shelter. 2.Strict conservations policies they stops poaching and hunting carnivores. 3. Due to Rural-urban migrations, leaving field with thick bushes allowing prey to live.	1. Ecological balance, Promotes Nature Tourism. 3. Helps in reducing animal disease breakouts in ungulates. 4. Provides Ecosystem services. 5. They are trophic cascades, controls other prey populations within ecosystem. 6. Gives cultural and spiritual significance. Act as indicator species	1. Livestock predations. 2. Human-wildlife conflicts, 3. Decline in prey populations. 4. Disease transmission. 5. Endangered species impact. And disruption of human activities	Provide conservation awareness, let people not to raise unproductive cattle more and let freely graze in forest, provide and encourage people with high-breed cattle. Encourage people in stall feeding of their cattle and provide other facilities at rural areas to stop rural-urban migration: Strict enforcement, and let people pay 100% fine and penalties, and imprisonment too if carnivores are killed. Introduce livestock insurance scheme. Identify highly conflicted carnivores and prepare conservation management plan based on species –location wise.

Ranger	The carnivores conflicted with humans due to proximity of the village and free cattle grazing in the jungle. ii. Inter-competition for survival. iii. Hunting/culling is prohibited by laws. iv. Settlement close to Forest. v. Dependency on Forest resources utilization. vi. Free grazing of cattle in the forest.	Positive-control population explosion of herbivores.	Negative-Risk to Human and Livestock	Provide Chain-link fencing and compensation scheme coverage for all carnivores. 1.Compensation scheme for livestock depredation of all cat species. The retaliatory killing/hunting may not stop unless the people are provided with adequate compensation for livestock depredation, crop damage and other property damage. 2.Institution of Gewog level committee for carnivores' conservation. 3.Importance of cat species for human survival.
Ranger	This is due to the increases of herbivore population in an around the human settlements, so the carnivore species come to depredation to domestic animals.	The carnivore controls the herbivore from crop damage	In negative impacts carnivore depredates the livestock in the locality	It is due to band of pastureland, so people use to graze the cattle only nearby and more. It is recommended to construct chaining fence to reduce herbivore to damage agriculture field crops, so that it reduces human- carnivore conflicts. Need time to time awareness to human-carnivore for most conflicted areas. Over the herbivore population increases.

jj

S1. ERGO II Ethics application form – FELS

1. Applicant Details

1.1 Applicant name	Lungten Dorji
1.2 Supervisor	Professor Charles Patrick Doncaster
1.3 Other researchers / collaborators (if applicable): *Name, address, email*	Nagdrel Lham World Wildlife Fund, Bhutan program nlhamo@wwfbhutan.org.bt Kuenley Tenzin World Wildlife Fund, Bhutan program ktenzin@wwfbhutan.org.bt

2. Study Details

2.1 Title of study	Assessing knowledge, attitude, and practices on the conservation of wild felids in two protected areas of Bhutan
2.2 Type of project (e.g. undergraduate, Masters, Doctorate, staff)	Doctorate

2.3 Briefly describe the rationale for carrying out this project and its specific aims and objectives.
This study is part of the overall Ph.D. project on "Enhancing Wild-felid Conservation by Resolving Biases in Population-density Estimation and Evaluating Human Perceptions of Felids". The entire Ph.D. project has three major study components: a comparison of alternative methods of estimating big-cat population densities, a study of big-cat movement ecology by GPS collaring, and a survey of social perceptions of big-cat conservation. The studies of big-cat population estimation and movement ecology have ERGO approval 53715. The present ERGO application relates to the social survey. This part of the project aims to study the social and ecological interaction between local communities and wild felids in two protected areas of Bhutan: Jigme Singye Wangchuck National Park and Royal Manas National Park. The information collected will help the government formulate policy and strategies to enhance the co-existence between the wild felids and the local communities. Wild felids number 37 species, of which 21 occur in Asia[1]. Wild felids influence the structure and function of diverse ecosystems worldwide [2]. Large felids, including tigers, lions, leopards, jaguars, and snow leopards, act as keystone species, essential for

maintaining biodiversity and ecosystem balance [3]. Bhutan supports 11 wild-felid species [4]. They form an integral part of Bhutan's rich biodiversity, and Bhutan is one of the biological hotspots in the world for rich biodiversity.[5].

Wild felids receive significantly more conservation priority worldwide than many other mammals due to the decline in their populations caused in large part by human-induced habitat degradation [2]. In Bhutan, they enjoy large tracts of undisturbed natural habitat and political and religious support [5]. Bhutan has committed to conserving wild felids, notably to doubling the current number of tigers (*Panthera tigris*) and snow leopards (*Panthera uncia*) by 2030 [6]. In 2019, two protected areas of Bhutan, Jigme Singye Wangchuck National Park and Royal Manas National Park, received accreditation from Conservation Assured Tiger Standards (CA|TS) for global Tiger Conservation standards [7].

Due to their requirement of extensive home range and dietary needs, wild felids are the most conflicted large wild carnivore with humans in Asia [8]. Tiger and common leopard alone account for eighty-two percent of livestock depredation in Bhutan's South-central region [4]. The snow leopard is a major conflicted felid in the country's Northern part [9], with a loss of more than ten percent of yak herder's earnings. In 2020 within seven months, Bhutan recorded more than 200 livestock depredation by tigers incurring massive loss to the livelihood of farmers [10, 11]. The negative interaction between felines and humans impacts the livelihood of forest-dependent communities and negatively impacts the wild animals in retaliatory killing [9, 12].

There are various mitigation measures to reduce incidences of human felid conflict worldwide, from financial compensations to modifying animal husbandry practices [2]. However, these management interventions have limited success. The interventions often fail to align with the conflict situations, due to a lack of in-depth study on the nature of conflicts [13]. The lack of fundamental understanding of the social and ecological factors influencing human-wildlife conflicts also hampers proper mitigation planning [14]. In Bhutan, the government formulated a strategy a decade ago to mitigate conflicts by providing compensation and alternative livelihood [15]. Nevertheless, human-felid conflicts have continued to rise over the years, posing concern to the government [16]. Therefore, there is a requirement to properly analyse human-felid interactions in Bhutan to revise the mitigation measures with evidence-based strategic actions.

We will study the relationship between the social, cultural, and ecological factors to characterize the causes of human-felid conflict for the first time in these two protected areas of Bhutan which will contribute to a better understanding of the nature of interactions between humans and felids. My overall PhD project will evaluate conflicts in the human dimension by studying the socio-cultural dependence on forest resources by communities, and in the animal dimension by studying movement ecology and habitat utilization by clouded leopard (*Neofelis nebulosa*) and common leopard (*Panthera pardus*) as model felid species. The social study will also quantify the trend of human-felid conflicts in Bhutan over the past decades and mitigation measures taken by conservation

authorities. The study will generate a comprehensive picture of the social and ecological components of human-felid conflicts in Bhutan, to develop an enhanced mitigation plan for peaceful co-existence.

1. Macdonald, D.W., A.J. Loveridge, and K. Nowell, *Dramatis personae: an introduction to the wild felids.* Biology and conservation of wild felids, 2010. 1: p. 3-58.
2. Krafte Holland, K., L.R. Larson, and R.B. Powell, *Characterizing conflict between humans and big cats Panthera spp: A systematic review of research trends and management opportunities.* PLOS ONE, 2018. 13(9): p. e0203877.
3. Newsome, T.M., et al., *Top predators constrain mesopredator distributions.* Nature Communications, 2017. 8(1): p. 15469.
4. Wang, S.W. and D.W. Macdonald, *Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan.* Biological Conservation, 2006. 129(4): p. 558-565.
5. Wang, S.W. and D.W. Macdonald, *The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan.* Biological Conservation, 2009. 142(3): p. 606-613.
6. NCD, *Snow Leopard Conservation Action Plan (2018-2023) & Tiger Action Plan of Bhutan 2018-2023*, DoFPS, Editor. 2018, Ministry of Agriculture and Forests: Thimphu, Bhutan.
7. WWF. *TWO PARKS IN BHUTAN RECEIVE INTERNATIONAL CA|TS ACCREDITION*. 2019; Available from: https://wwf.panda.org/wwf_news/?356671/TWO-PARKS-IN-BHUTAN-RECEIVE-INTERNATIONAL-CATS-ACCREDITION.
8. Inskip, C. and A. Zimmermann, *Human-felid conflict: a review of patterns and priorities worldwide.* Oryx, 2009. 43(01): p. 18.
9. Lham, D., et al., *Ecological determinants of livestock depredation by the snow leopard Panthera uncia in Bhutan.* Journal of Zoology, 2021. 314(4): p. 275-284.
10. Dorji, N., *Farmers receive semso for cattle lost to tiger* in *Kuensel*. 2020, Kuensel Corporation Bhutan Limited.
11. Jamtsho, Y. and O. Katel, *Livestock depredation by snow leopard and Tibetan wolf: Implications for herders' livelihoods in Wangchuck Centennial National Park, Bhutan.* Pastoralism, 2019. 9(1).
12. Sangay, T. and K. Vernes, *Human–wildlife conflict in the Kingdom of Bhutan: patterns of livestock predation by large mammalian carnivores.* Biological Conservation, 2008. 141(5): p. 1272-1282.
13. Baynham-Herd, Z., et al., *Conservation conflicts: Behavioural threats, frames, and intervention recommendations.* Biological Conservation, 2018. 222: p. 180-188.
14. Dickman, A.J., *Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict.* Animal Conservation, 2010. 13(5): p. 458-466.
15. NCD, *Bhutan National Human-Wildlife Conflicts Management Strategy*, DoFPS, Editor. 2008, Ministry of Agriculture and Forests: Thimphu, Bhutan.
16. Sharma, P., N. Chettri, and K. Wangchuk, *Human–wildlife conflict in the roof of the world: Understanding multidimensional perspectives through a systematic review.* Ecology and Evolution, 2021.
17. RMNP, *Conservation Management Plan of Royal Manas National Park 2015-2020*, D.o.F.a.P. Services, Editor. 2015, Department of Forests and Park Services, Royal Government of Bhutan: Gelephu, Bhutan.

18. JSWNP, *Conservation Management Plan of Jigme Singye Wangchuck National Park 2016-2021*, D.o.F.a.P. Services, Editor. 2016, Department of Forests and Park Services, Royal Government of Bhutan: Trongsa, Bhutan.
19. JSWNP, *Conservation Management Plan of Jigme Singye Wangchuck National Park 2016-2021*, D.o.F.a.P. Services, Editor. 2022, Department of Forests and Park Services, Royal Government of Bhutan: Trongsa, Bhutan.
20. Acharya, A.S., et al., *Sampling: Why and how of it.* Indian Journal of Medical Specialties, 2013. 4(2): p. 330-333.

2.4 Provide a brief outline of the basic study design. Outline what approach is being used and why.

We will assess the perception of park residents (people living in the protected areas) on wild felid conservation through a Knowledge, Attitude, and Practices (KAP) questionnaire and through a key informant survey (KIS). We will sample respondents from park communities, local leaders, and government officials working in the jurisdiction of the two protected areas. The KAP survey will cover the park communities and the local leaders. The KAP survey questionnaire contains 85 questions under three sections: knowledge on wild felid conservation, attitude on wild felid conservation and negative interaction of humans with wild felids, and the practices on wild felid conservation and negative interaction with wild felids. We kept the negative interaction of human and wild felid as human-carnivore conflict for better understanding of the term by local communities to whom the term “felid” seems more technical and difficult to understand. We will conduct a KIS for government officials and the local leaders.

The KAP survey will help us to understand social perspectives on wild felid conservation and the extent of negative interactions of human-felids from the people residing in these protected areas of Bhutan. The information on perception and experiences of conflicts will help conservation authorities to better balance negative with positive interactions. It will also help them to know the attitude of communities for conservation of wild felids, and the level of satisfaction with government interventions to mitigate negative human-felid interactions. The Ph.D. project along with this study will help us to know about interactions from both human and felid points of view, which is rarely encompassed by conservation authorities worldwide.

The study will conduct verbal interviews with those respondents who have no educational background, and paper-based interview with those respondents who can read and write. We have identified a representative sample of 389 individuals from the total of 2,271

households in these two protected areas (detailed in Sect. 3.2). It will take about 15 days including travel time for five enumerators plus the lead researcher to complete the survey. Of these 389 individuals, we will conduct the KAP questionnaire containing multiple choice questions with 329 individuals, and the KIS containing open questions with 60 individuals. The variables in both questionnaires are developed based on the known range of human-felid interactions in Bhutan recorded by previous studies on felid-human conflicts in the region. I consulted the experts from World Wildlife Fund Bhutan program to develop the questions.

2.5 What are the key research question(s)? Specify hypotheses if applicable.

This study aims to explore the social and ecological interactions between farmers in rural communities and wild felids in protected areas of Bhutan, which will help the government formulate policy and strategies to enhance co-existence between the wild felids and the local communities. This study will test the followings hypotheses:

- Increases in negative interactions between humans and wild felids are associated with the rise in the felid population towards the forest fringes.
- Negative attitudes of local communities towards felid conservation increase with negative interactions between human and wild felids.
- Changes in cultural practices of local communities increase with negative human-felid interactions.
- Socio-political changes in the local communities have negative impacts on people's perceptions towards wild felids.

3. Sample and setting

3.1 Who are the proposed participants and where are they from (e.g. fellow students, club members)? List inclusion / exclusion criteria if applicable.

We identified three target groups of adults (18 years old and above) for the interview with specific sets of questionnaires for each group. The first group of participants will be the park communities having direct dependence on natural resources of park for their livelihood. The Park communities in our study site comprises farmers, nomads, and religious organizations. They will receive the KAP questionnaire. The second group for interview will be the local leaders, who are the elected representatives of local communities residing in the protected areas. They will receive the KAP and KIS questionnaires. The third target group is government officials working as park rangers, agriculture and livestock officers, planning officer and education officers. They will receive the KIS. In this study we will not sample the respondents based on equal representation for gender and age in a group as it is logistically not feasible, and the different household have different representations of gender and the age. However, we will ensure that at least 30 percent of the respondents are from the gender that is less represented in this

study. For this the lead researcher will provide the minimum number of males and females to be interviewed from each community to the enumerators. The only inclusion/ exclusion criteria for this survey are the respondent should be above the age of 18 years.

3.2. How will the participants be identified and approached? Provide an indication of your sample size. If participants are under the responsibility of others (e.g., parents/carers, teachers) state if you have permission or how you will obtain permission from the third party).

For choosing an adequate sample size, the Royal Manas National Park and Jigme Singye Wangchuck National Park boundaries are selected as the sampling frame from which the household falling within the park boundary is chosen as sampling units. The total households in these two protected areas as per their conservation management plan is 2271 in 2018[17-19] which includes populations living within and in the periphery of the protected areas. We calculated the sample size using an open-access web program (https://www.surveysystem.com/sscalc.htm), which is based on the following formula:

$$n = \frac{\frac{Z^2.P(1-P)}{e^2}}{1+\left(\frac{Z^2.P(1-P)}{e^2 N}\right)}$$

Z is the standard error of 95% confidence interval, calculated from the proportion of population P and marginal error e. We assigned the general conservative social science values of 50% and 3% for *P* and *e*, respectively, to determine our sample size of 329 households of 2171 total households. We will sample following probability-based stratified random sampling, a straightforward sampling method for small population[20]. The village blocks (Gewogs) falling under each protected area are selected as the sub-strata, and the households falling within these sub-strata are sampled following Probability Proportional to Size (PPS) method as shown in Table 1.

Table.1: Sampling plan and determination of sampling weights

Sl.No	Protected area	Gewog	HHs	Sampled HHs	SF	W_b	Respondents for KIS	Total sampled respondents
1	JSWNP	Jigmechoeling	746	113	0.15	6.60	15	128
		Korphu	525	80	0.15	6.60	15	95
		Langthel	322	49	0.15	6.60	15	64
2	RMNP	Trong	578	88	0.15	6.60	15	103
Total			**2,171**	**329**	**0.15**	**6.60**	**60**	**389**

We have also determined the sampling weights for each stratum to represent its entire household population. The ratio of sampled household to the entire household population of each stratum represents the sampling fraction SF, and the inverse of the sampling fraction is base weight W_b (*see the details in Table 1).*

For the KIS we will select 15 respondents consisting of local government functionaries and the civil servants from each Gewogs as per the following lists in Table. 2:

Table.2: Respondents for KIS

Category of respondents	Designation	Number of individuals
Local government officials	Gup (village chairman)	1
	Magmi (village vice chairman)	1
	Tsogpa	4
Civil servants	Gewong administration officer	1
	Park Rangers	3
	Agriculture supervisor	1
	Livestock supervisor	1
	Community forests chairman	2
	Education officer	1
	Total	**15**

We will approach the potential participants in each local community by visiting their farm after informing them through their local leaders. We will communicate through official channels with the local leaders in the protected areas. We will approach the government officials in the protected areas by visiting their office with the official research permit and the request for interview letter from Department of Forests and Park Services of Bhutan.

This study will not involve any respondents below 18 years old and there are no participants under the responsibility of others. However, for conducting research in the protected areas of Bhutan, we already have the required research permit from the Department of Forests and Park Services of Bhutan (attached with the submission).

References:

17. RMNP, *Conservation Management Plan of Royal Manas National Park 2015-2020*, DoFPS, Editor. 2015, Department of Forests and Park Services, Royal Government of Bhutan: Gelephu, Bhutan.
18. JSWNP, *Conservation Management Plan of Jigme Singye Wangchuck National Park 2016-2021*, DoFPS, Editor. 2016, Department of Forests and Park Services, Royal Government of Bhutan: Trongsa, Bhutan.

19. JSWNP, *Conservation Management Plan of Jigme Singye Wangchuck National Park 2016-2021*, DoFPS, Editor. 2022, Department of Forests and Park Services, Royal Government of Bhutan: Trongsa, Bhutan.
20. Acharya, A.S., et al., *Sampling: Why and how of it.* Indian Journal of Medical Specialties, 2013. 4(2): p. 330-333.

3.3 Describe the relationship between researcher and sample. Describe any relationship e.g., teacher, friend, boss, clinician, etc.

The lead researcher has no relationship with the two groups of participants who are the communities and local leaders residing in these two protected areas. However, the lead researcher works in the same organization (Department of Forests and Park Services of Bhutan) as some of the participants from the group which will be the focus for the key informant interviews. The lead researcher has experience working in one of the largest protected areas in Bhutan, primarily dealing with the projects to help in uplifting the livelihood of rural communities and has previously conducted socio-economic surveys of rural communities for formulating conservation management plan of that protected area. The lead researcher also has experiences of communicating with rural communities through training and interviews. He has no previous contact with the communities of the two protected areas of this study. His previous experience will be useful in identification of potential participants and in the development of the interviews, and training the temporary enumerators. The temporary enumerators have experiences of interviewing rural communities and most of them are familiar with the local communities.

3.4 How will you obtain the consent of participants? (*please upload a copy of the consent form if obtaining written consent*) NB. Consent form is not needed for studies collecting data online.

The researcher will approach the local government authorities before proceeding with the questionnaire survey. The researcher will explain the rationale of the questionnaire survey to the local leaders and seek help to identify the potential participants. We have developed the uploaded participant information sheet, which is translated into local languages and dialects. The researcher will explain the information sheet to the community leaders, who will explain it to the participant in their local dialects. This is the normal procedure followed while conducting social research in Bhutan as most of the rural respondents are illiterate.

For interviews and the KIS with local leaders, who have all received higher levels of education, the researcher will provide them with the participant information sheet directly. The researcher will answer any questions they may have from the participants information sheet.

3.5 Is there any reason to believe participants may not be able to give full informed consent? If yes, what steps do you propose to take to safeguard their interests?
There are no reasons to believe participants may not give fully informed consent after being informed by the participants information sheet.

4. Research procedures, interventions and measurements

4.1 Give a brief account of the procedure as experienced by the participant. Make it clear who does what, how many times and in what order. Make clear the role of all assistants and collaborators. Make clear the total demands made on participants, including time and travel. *Upload copies of questionnaires and interview schedules to ERGO.*
We will adopt different interview schedule and strategies for the three groups of respondents (local communities, local leaders, and government officials). The first group will comprise of local communities residing within the protected areas. For them, we will employ 5 temporary enumerators for 15 days to conduct the KAP survey. The enumerators will be trained on the participant information sheet, the questionnaire, and data collection in android data forms. They will already be trained on basic ecological terminologies and interviewing techniques, having backgrounds on basics of ecology, anthropology, and rural studies. The lead researcher Lungten Dorji will arrange the interview schedule in consultation with the local leaders for different communities in the protected areas. The KAP questionnaire interview will not last more than 60 minutes for individual respondents, which then allows time for the 5 enumerators to conduct 4-5 interviews per day over the 15 days. To reduce interviewer bias, the enumerators will pre-test the questionnaire with at least 5 people before beginning of the real interview, and the lead researcher will assess their pre-testing outcome. The lead researcher will prepare a guide for enumerators, containing a description of terminologies, questioning techniques, and detailed descriptions of each question. Moreover, the enumerators will have access to the lead researcher throughout the survey over telephone or social media for clarifications. Lead researcher Lungten Dorji will conduct KAP and KIS interviews for the other two groups of respondents. The KIS with the government officials will take about 30 minutes per respondent, and the KAP + KIS with local leaders might last 1 hr 30 minutes. The field survey will be conducted entirely by the lead researcher Lungten Dorji and 5 temporary enumerators. Collaborators Kuenley Tenzin and Nagdrel Lham will be involved only during sharing of results. The course supervisor Professor Doncaster will guide lead researcher Lungten Dorji for the entire duration of this study.

4.2 Will the procedure involve deception of any sort? If yes, what is your justification?
The survey will not involve any kind of deception. It already has approval by the local survey approving authority of Bhutan: Ugyen Wangchuck Institute for Conservation and Environmental Research (UWICER), vide permit number 8423233545E33B9316C6F7 (http://www.uwice.gov.bt/rcs/track-application.php).

4.3. Detail any possible (psychological or physical) discomfort, inconvenience, or distress that participants may experience, including after the study, and what precautions will be taken to minimise these risks to ensure the well-being, health, and safety of the participants. **Health & Safety policies and resources are available here: https://sotonac.sharepoint.com/teams/HealthSafetyRisk?e=1%3Af902a94a6c14407fbe44e40e5066cb91** If the study involves lone working please state the risks and the procedures put in place to minimise these risks (please refer to the lone working policy). Please seek advice from your local Health and Safety contact if there are significant wellbeing or safety considerations.
The participant information sheet gives respondents the choice to not answer any question if it makes them uncomfortable. We will be recruiting temporary survey enumerators who are trained well on questionnaire for conducting interviews. The entire interview will be conducted upon approval from the local and the community leaders. The community leaders will prohibit researchers approaching respondents who are not fit physically and psychologically. These measures will minimise psychological discomfort for the respondents. For the KIS and local leaders' interviews, we will provide options to fill in the questionnaire by themselves on an online form suitable for a computer or mobile device, to remove potential discomfort in responding to an in-person interview. We will allow the respondents to take breaks if required in between the interview. The lead research has piloted the study with 5 individuals, and it takes less than 60 minutes of some respondents.

4.4 Detail any possible (psychological or physical) discomfort, inconvenience, or distress that YOU as a researcher may experience, including after the study, and what precautions will be taken to minimise these risks and ensure health and safety. **Health & Safety policies and resources are available here: https://sotonac.sharepoint.com/teams/HealthSafetyRisk?e=1%3Af902a94a6c14407fbe44e40e5066cb91**

If the study involves lone working please state the risks and the procedures put in place to minimise these risks (please refer to the lone working policy). Please seek advice from your local Health and Safety contact if there are significant wellbeing or safety considerations.
The potential for discomfort to the researcher and temporary enumerators is in their first approach to the respondents. To reduce this, the lead researcher Lungten Dorji will train the enumerators in interview techniques, questionnaire, and pre-testing of questionnaire before proceeding to the survey. The respondents will be pre-informed by their respective local leaders regarding the survey and the enumerators will asked to fix the interview schedule during the daytime. The enumerators will approach the respondents in early morning (7-9:00 Am Bhutanese time), when respondents are generally free from their daily chores. The lead researcher will ensure that no enumerator approaches the respondents before prior approval of local leaders.

4.5 Explain how you will care for any participants in 'special groups' e.g., those in a dependent relationship, are vulnerable or are lacking mental capacity), if applicable:
We will avoid children below 18 years old and differentially abled persons for this questionnaire survey. However, for the vulnerable groups such as old-aged persons, the surveyors will approach them at their homes only on recommendation by local leaders.

4.6 Please give details of any payments or incentives being used to recruit participants, if applicable:
The study will not provide any incentives or financial payments to recruit the participants.

5. Access and storage of data

5.1 How will participant confidentiality be maintained? Confidentiality is defined as non-disclosure of research information except to another authorised person. Confidential information can be shared with those already party to it and may also be disclosed where the person providing the information provides explicit consent. Consider whether it is truly possible to maintain a participant's involvement in the study confidential, e.g. can people observe the participant taking part in the study? How will data be anonymised to ensure participants' confidentiality?
The questionnaire will not record any personal information of the participants or respondents. This study will not report any names of individual, village, communities, and religious organization in the report. All the findings will only be reported at the aggregated level referring to the two protected areas in which we will conduct the interview. The enumerator will ensure that no local leaders and government officials will

be present during the interview. The local leaders will be used only for identification of the participants and reading out the participant information sheet if necessary.

5.2 How will personal data and study results be stored securely during and after the study. Who will have access to these data?
The questionnaire will be designed in the password protected google form or android phone-based application epicollect-5 (https://five.epicollect.net/) to avoid loss of questionnaires or data which are often in paper-based data enumeration. The enumerator will only have the option to fill in the survey forms. The data viewing option will be available only to the lead researcher Lungten Dorji and the course supervisor Professor Charles Patrick Doncaster. Collaborators Kuenley Tenzin and Nagdrel Lham will have access to the results of data analysis and the report.

5.3 How will it be made clear to participants that they may withdraw consent to participate? Please note that anonymous data (e.g. anonymous questionnaires) cannot be withdrawn after they have been submitted. If there is a point up to which data can be withdrawn/destroyed e.g., up to interview data being transcribed please state this here.
We will inform each participant that they can withdraw their consent to participate while reading out the participant Information sheet prior to the interview, and they can withdraw at any time during the interview, in which case we will destroy their record then and there. Because the data collected does not include personal identification, it will not be possible to withdraw consent after compiling the data.

6. Additional Ethical considerations

6.1 Are there any additional ethical considerations or other information you feel may be relevant to this study?
The above information covers all known ethical issues in this study.

S2. Participant Information Sheet for KIS

Study Title:Assessing Knowledge, Attitude, and Practices on the conservation of wild felids in two protected areas of Bhutan (Jigme Singye Wangchuck National Park and Royal Manas National Park).

Researcher: Lungten Dorji
ERGO number: 76113.A1
You are being invited to take part in the above research study. To help you decide whether you would like to take part or not, it is important that you understand why the research is being done and what it will involve. Please read the information below carefully and ask questions if anything is not clear or you would like more information before you decide to take part in this research. You may like to discuss it with others but it is up to you to decide whether or not to take part. If you are happy to participate you will be asked to express your verbal consent.

What is the research about?
This questionnaire survey is part of Mr. Lungten Dorji's Ph.D. project on "Enhancing Wild-felid Conservation by Resolving Biases in Population-Density Estimation and Evaluating Human Perceptions of Felids" in two protected areas of Bhutan (Jigme Singye Wangchuck National Park and Royal Manas National Park). He works as a Forestry Officer in the Department of Forests and Park Services of Bhutan, and is currently on study leave pursuing the Ph.D. at the University of Southampton in the UK, on resolving biases in density estimation of wild felids and studying the interaction of wild felids with humans in protected areas of Bhutan. This study is being done by evaluating movement ecology of wild felids and social perceptions on the wild felids.

This questionnaire survey aims to evaluate the knowledge, attitude, and practices of park residents of Jigme Singye Wangchuck National Park (JSWNP) and Royal Manas National Park (RMNP) on conservation and interaction with wild felids. On Mr. Lungten's behalf, I will be asking questions on your knowledge of the conservation of wild felids in Bhutan and in the protected area where you live in. You will be asked questions on your perceptions about the conservation status of wild felids and their interaction with the humans. The questionnaire also contains questions on your herding practices, and practices when you have negative interactions with the wild felids. The finding will be used for recommending park management. They will contribute to the development of management strategies by the Department of Forests and Park Services of Bhutan, aimed at achieving peaceful coexistence between humans and wild felids, and reducing the negative interaction which is often referred to as Human-Carnivore conflicts.

The project is funded by the World Wildlife Fund (WWF), which is one of the oldest conservation partners of the Royal Government of Bhutan for wildlife conservation and the sustainable livelihood program for communities living in the forests.

Why have I been asked to participate?
You have been asked to participate in this interview because you reside in one of the two focal protected areas (JSWNP/RMNP), which have high densities of wild felids and interactions between them and people. Your inputs in this study will be vital for framing strategies to better manage the wild felids and wild felid's interaction with the people. We will interview about 389 individuals residing in these two protected areas at end of this study.

What will happen to me if I take part?
If you take part in this survey, you will answer a questionnaire, which will take around 60 minutes to complete. I will ask questions about your personal knowledge, attitude and local practices about wild felids and their interactions with human. It is a onetime interview, and you will be visited only once, and we won't have any follow up interview or data collection after completing the questionnaire. I will transcribe your answers on my phone using an online application for data collection. No video or audio will be recorded in this process of interview. You will be able to view this transcription at any time during this process and change your views as an when you require.

Are there any benefits in my taking part?
There are no benefits in kind or cash for participating in this survey. However, the results from this study will benefit your community in the long term, with improved management strategies on human-felid interactions. Your responses will help park authorities to formulate mitigation plans for any negative human-felid interactions. For example, if community lacks knowledge on the compensation measures from the government, the concerned government offices should provide education and awareness program to the community.

Are there any risks involved?
This study will gather only your views on conservation of wild felids in protected areas of Bhutan, no questions are sensitive which might impact you. The questions regarding your attitude and practices are mostly aimed to enhance the current human-carnivore conflicts mitigation measures by the government and we won't trace any individuals or community for your response in the future.

What data will be collected?
This survey will mainly collect data on your knowledge, views, and practices in relation to human felid interaction in the protected areas where you live. We will also collect data on your yearly income, occupation, education level, gender, religion, and some information on your local community. The data will be collected by lead researcher Lungten Dorji and 5 enumerators who are well trained on the questionnaire.

Will my participation be confidential?
Your participation and the information we collect about you during the course of the research will be kept strictly confidential.

Only members of the research team and responsible members of the University of Southampton may be given access to data about you for monitoring purposes and/or to carry out an audit of the study to ensure that the research is complying with applicable regulations. Individuals from regulatory authorities (people who check that we are carrying out the study correctly) may require access to your data. All of these people have a duty to keep your information, as a research participant, strictly confidential.

Your entire response from this survey will be kept confidential and all the reporting will be at the aggregate level we will not report any individual views in our analysis and results. The individual response form will be accessible only to the lead researcher Mr. Lungten Dorji and we will not record any of your personal details such as name, phone number, house number or identity card.

Do I have to take part?

No, it is entirely up to you to decide whether or not to take part. If you decide you want to take part, you will need to sign a consent form to show you have agreed to take part.

If you want to take part in this survey, we will consider upon your verbal consent to any of our enumerators or the lead researcher. If you are not comfortable in answering any of the questions, you have full right to skip those questions and to opt-out the entire interview in between.

What happens if I change my mind?
You have the right to change your mind and withdraw at any time without giving a reason and without your participant rights being affected.

You may withdraw your responses in between the interview, or you may opt to not submit your response for the survey. However, after completing the interview, we will not be able to withdraw your responses as the questionnaire maintains anonymity and researcher won't be able to trace back to your responses or questionnaire.

If you withdraw from the study, we will keep the information about you that we have already obtained for the purposes of achieving the objectives of the study only.

What will happen to the results of the research?
Your personal details will remain strictly confidential. Research findings made available in any reports or publications will not include information that can directly identify you without your specific consent.

The results from this study will be published as a part Mr.Lungten's Ph.D. thesis and will be also published in scientific journals. He will also share the outcomes of this study with the park management of Jigme Singye Wangchuck National Park and Royal Manas National Park to incorporate in their conservation management plan. The results will be also made available to your local leaders and government officials. The results will be shared to you by local government and the park officials while formulating the park management plan.

Where can I get more information?*.*
For any clarification you can contact the lead researcher Mr. Lungten Dorji at L.Dorji@soton.ac.uk or phone +97517997062. You may also ask directly to our enumerators for any clarifications as they are well trained on the questionnaire and are provided with the enumerators guide.

What happens if there is a problem?
If you have a concern about any aspect of this study, you should speak to the researchers who will do their best to answer your questions.
If you remain unhappy or have a complaint about any aspect of this study, please contact the University of Southampton Research Integrity and Governance Manager (023 8059 5058, rgoinfo@soton.ac.uk).

Data Protection Privacy Notice
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agreed to take part in research. This means that when you agree to take part in a research study, we will use information about you in the ways needed, and for the purposes specified, to conduct and complete the research project. Under data protection law, 'Personal data' means any information that relates to and is capable of identifying a living individual. The University's data protection policy governing the use of personal data by the University can be found on its website (https://www.southampton.ac.uk/legalservices/what-we-do/data-protection-and-foi.page).

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http://www.southampton.ac.uk/assets/sharepoint/intranet/ls/Public/Research%20and%20Integrity%20Privacy%20Notice/Privacy%20Notice%20for%20Research%20Participants.pdf

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For the purposes of data protection law, the University of Southampton is the 'Data Controller' for this study, which means that we are responsible for looking after your information and using it properly. The University of Southampton will keep identifiable information for 10 years after the study has finished after which time any link between you and your information will be removed.

To safeguard your rights, we will use the minimum personal data necessary to achieve our research study objectives. Your data protection rights – such as to access, change, or transfer such information - may be limited, however, in order for the research output to be reliable and accurate. The University will not do anything with your personal data that you would not reasonably expect.

If you have any questions about how your personal data is used, or wish to exercise any of your rights, please consult the University's data protection webpage (https://www.southampton.ac.uk/legalservices/what-we-do/data-protection-and-foi.page) where you can make a request using our online form. If you need further assistance, please contact the University's Data Protection Officer (data.protection@soton.ac.uk).

The data will be retained at the University of Southampton data repository for 10 years as per the University data management policy. Mr. Lungten and his course supervisor will be fully responsible for controlling data. He is required to share only results and processed

data after completing his Ph.D. project to Department of Forests and Park Services of Bhutan.

There are no 3rd parties who can hold and process these data and except for the lead researcher and the course supervisor. He is only required to submit the findings from the study to the donor and the processed data to the Department of Forests and Park Services of Bhutan.

Thank you.
Thank you for taking the time to read the information sheet and considering taking part in the research.

S3. Participant Information Sheet for KAP survey

Study Title: Key Informant Survey (KIS) on wild felid conservation in Jigme Singye Wangchuck National Park and Royal Manas National Park.
Researcher: Lungten Dorji
ERGO number:

You are being invited to take part in the above research study. To help you decide whether you would like to take part or not, it is important that you understand why the research is being done and what it will involve. Please read the information below carefully and ask questions if anything is not clear or you would like more information before you decide to take part in this research. You may like to discuss it with others but it is up to you to decide whether or not to take part. If you are happy to participate you will be asked to express your verbal consent.

What is the research about?
This questionnaire survey is part of my Ph.D. project on "Enhancing Wild-felid Conservation by Resolving Biases in Population-Density Estimation and Evaluating Human Perceptions of Felids" in two protected areas of Bhutan (Jigme Singye Wangchuck National Park and Royal Manas National Park). I work as a Forestry Officer in the Department of Forests and Park Services of Bhutan and I am currently on study leave pursuing the Ph.D. at the University of Southampton in the UK, on resolving biases in density estimation of wild felids and studying the interaction of wild felids with humans in protected areas of Bhutan. This study is being done by evaluating movement ecology of wild felids and social perceptions on the wild felids.

This questionnaire survey aims to evaluate the social perceptions on wild felid conservation in Jigme Singye Wangchuck National Park (JSWNP) and Royal Manas National Park (RMNP). I will be asking questions on your knowledge of the conservation of wild felids in Bhutan and in the protected area where you live in. You will be asked questions on your knowledge and perceptions about the conservation status of wild felids and their interaction with the humans. The finding will be used for recommending park management. They will contribute to the development of management strategies by the Department of Forests and Park Services of Bhutan, aimed at achieving peaceful coexistence between humans and wild felids, and reducing the negative interaction which is often referred to as Human-Carnivore conflicts.

The project is funded by the World Wildlife Fund (WWF), which is one of the oldest conservation partners of the Royal Government of Bhutan for wildlife conservation and the sustainable livelihood program for communities living in the forests.

Why have I been asked to participate?
You have been asked to participate in this interview because you reside in one of the two focal protected areas (JSWNP/RMNP), which have high densities of wild felids and interactions between them and people. Your inputs in this study will be vital for framing strategies to better manage the wild felids and wild felid's interaction with the people. We will interview about 389 individuals residing in these two protected areas at end of this study.

What will happen to me if I take part?
If you take part in this survey, you will answer a questionnaire, which will take around 40 minutes to complete. I will ask key questions about wild felids and their interactions with

human. It is a onetime interview, and you will be visited only once, and we won't have any follow up interview or data collection after completing the questionnaire. I will transcribe your answers on my phone using an online application for data collection or you may fill in the paper version of this questionnaire based on your preference. No video or audio will be recorded in this process of interview. You will be able to view this transcription at any time during this process and change your views as an when you require.

Are there any benefits in my taking part?

There are no benefits in kind or cash for participating in this survey. However, the results from this study will benefit your community in the long term, with improved management strategies on human-felid interactions. Your responses will help park authorities to formulate mitigation plans for any negative human-felid interactions. For example, your recommendation on human-felid coexistence can be incorporated in park's conservation management plan.

Are there any risks involved?

This study will gather only your views on conservation of wild felids in protected areas of Bhutan, no questions are sensitive which might impact you. The questions regarding recommendations and views on human-wild felid interactions are mostly aimed to enhance the current human-carnivore conflicts mitigation measures by the government and we won't trace any respondents for your response in the future.

What data will be collected?

This survey will mainly collect data on your knowledge, views, and management recommendations in relation to human felid interaction in the protected areas where you live in.

Will my participation be confidential?

Your participation and the information we collect about you during the course of the research will be kept strictly confidential.

Only members of the research team and responsible members of the University of Southampton may be given access to data about you for monitoring purposes and/or to carry out an audit of the study to ensure that the research is complying with applicable regulations. Individuals from regulatory authorities (people who check that we are carrying out the study correctly) may require access to your data. All of these people have a duty to keep your information, as a research participant, strictly confidential.

Your entire response from this survey will be kept confidential and all the reporting will be at the aggregate level we will not report any individual views in our analysis and results. The individual response form will be accessible only to the lead researcher Mr. Lungten Dorji and we will not record any of your personal details such as name, phone number, house number or identity card.

Do I have to take part?

No, it is entirely up to you to decide whether or not to take part. If you decide you want to take part, you will need to sign a consent form to show you have agreed to take part.
If you want to take part in this survey, we will consider upon your verbal consent to any of our enumerators or the lead researcher. If you are not comfortable in answering any of the questions, you have full right to skip those questions and to opt-out the entire interview in between.

What happens if I change my mind?

You have the right to change your mind and withdraw at any time without giving a reason and without your participant rights being affected.
You may withdraw your responses in between the interview, or you may opt to not submit your response for the survey. However, after completing the interview, we will not be able to

withdraw your responses as the questionnaire maintains anonymity and researcher won't be able to trace back to your responses or questionnaire.
If you withdraw from the study, we will keep the information about you that we have already obtained for the purposes of achieving the objectives of the study only.

What will happen to the results of the research?
Your personal details will remain strictly confidential. Research findings made available in any reports or publications will not include information that can directly identify you without your specific consent.
The results from this study will be published as a part of my Ph.D. thesis and will be also published in scientific journals. I will share the outcomes of this study with the park management of Jigme Singye Wangchuck National Park and Royal Manas National Park to incorporate in their conservation management plan. The results will be also made available to your concerned offices upon completion of this study.

Where can I get more information?
For any clarification you can contact the lead researcher Mr. Lungten Dorji at L.Dorji@soton.ac.uk or phone +97517997062. You may also ask directly to our enumerators for any clarifications as they are well trained on the questionnaire and are provided with the enumerators guide.

What happens if there is a problem?
If you have a concern about any aspect of this study, you should speak to the researchers who will do their best to answer your questions.
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The data will be retained at the University of Southampton data repository for 10 years as per the University data management policy. My course supervisor Professor Patrick and I will be fully responsible for controlling data. I am required to share only results and processed data after completing of his Ph.D. project to Department of Forests and Park Services of Bhutan.
There are no 3rd parties who can hold and process these data and except for the lead researcher and the course supervisor. I am only required to submit the findings from the study to the donor and the processed data to the Department of Forests and Park Services of Bhutan.

Thank you.
Thank you for taking the time to read the information sheet and considering taking part in the research.

S4. KAP questionnaire

Assessing Knowledge, Attitude, and Practice on conservation of wild felids in Royal Manas National Park and Jigme Singye Wangchuck National Park

Dear Respondents,

The Department of Forests and Park Services would like to request your kind cooperation to smoothly execute this survey by Mr. Lungten Dorji, Forestry Officer (Ph.D. student, University of Southampton) of the department, to collect information from you to assess the level of knowledge, attitude, and practices related to wild felid conservation in your locality. Your identity will not be recorded throughout the analysis of data and reporting, and your personal views will be used to formulate these parks' management strategies.

Charles Patrick Doncaster
Professor of Ecology (Supervisor)
School of Biological Sciences
University of Southampton
SO17 1BJ, United Kingdom

Sonam Wangdi
Chief Forestry Officer
Nature Conservation Division
Department of Forests and Park Services

Chief Forestry Officer
Nature Conservation Division
DOFPS, Thimphu

Verbal consent of respondents

I got verbal consent from the respondent to carry out this questionnaire interview, and they are fully aware of the participant's information sheet

- Yes (continue the interview)

- No (discontinue the interview)

Name of the enumerator…… Signature…….Date……

Circle the responses or write the corresponding code

A: GEOGRAPHICAL IDENTIFICATION:
Q1. Dzongkhag:……
Q2. Name of the protected area…….....

B. SOCIO-DEMOGRAPHIC CHARACTERISTICS:
Q3. Age (in completed years):…….
Q4.Occupation:
1. Farmer
2. Civil servant
3. Armed forces
4. Herder
5. Student
7. Govt. employee
8. Private/corporate
9. Others (Specify)…….....

Q5. Mother Tongue:
1. Ngalop
2. Sharchop
3. Lotsam
4. Khengkha
5. Others (Specify)…….....

Q6. What is your Highest Educational level?
1. No education
2.Classes 1-12
3. Diploma
4. College & above
5.Monastic/shedra
6. NFE

Q7. The number of individuals in the household……..
Q8. What is your primary source of earning?
1. Agriculture
2. Sell of fruits/cardamon
3. Livestock
4.Others (Specify)…….....

Q9. Your yearly earning: ……..(Nu) (I don't know)
Q10. Yours yearly expenditure……..(Nu) (I don't know)
Q11. How many acres of land do you or your family own?.....(I don't know)

Q12. Are you a member of the following groups?
1. Community Forest Management Group

2. Human-Wildlife conflict response team
3. Community Fishing group
4. Eco-Camp Group
5. River Rafting Group
6. Others(Specify):……..

C.KNOWLEDGE

Q13. Human-carnivore conflicts are the negative interaction between humans and carnivores residing in the same location

1. Strongly agree
2. Agree
3. Neither agree nor disagree
4. Disagree
5. Strongly disagree

Q14. Which is the location where most of the Human-carnivore conflicts occur? [*5=Strongly agree; 4=Agree; 3= Don't know; 2=Disagree; 1= Strongly disagree*]

1. Near Human settlement
2. In the carnivore habitat
3. Both
4. Others (specify):……..

Q15. Did anyone tell you about human-carnivore conflicts?

1. Yes
2. No (>>**Q17**)

Q16. From whom did you get information regarding Human-carnivore?

1. Elders
2. Teachers
3. Friends
4. Television
5. social media
6. Forestry personnel
7. Personal observation

Q17. How is the carnivore conflicted with a human?

1. Livestock depredation
2. Direct conflict with humans
3. Don't know
4. Others (specify):……..

Q18. As per your understanding, rank, which is the most conflicted animal in your locality? *[5=Most conflicted; 4=Conflicted; 3: Neither conflicted nor not conflicted, 2: Not conflicted; 1= Never conflicted]*

1. Leopard
2. Tiger
3. Small felids
4. Dhole
5. Others (specify)…….

Q19. Rate the causes of Human-carnivore conflicts as per your understanding [*5=Strongly agree; 4=Agree; 3= Neither agree nor disagree; 2=Disagree; 1= Strongly disagree*]

1. Encroachment of habitat by human
2. carnivore population expulsion
3. Ecosystem imbalance
4. Curse of local deities
5. Don't know
6. Others (specify):…….

Q20. Do you know about Human-carnivore management?

1. Yes
2. No (>>**Q22**)

Q21. How do you rate the effectiveness of the following mitigation *measures [5=Very effective; 4=Effective; 3= Neither effective nor not effective; 2=Not effective;1=Not at all effective]*

1. Compensation for livestock lost
2. Relocation of conflicted animal
3. Changing livestock raring practices
4. Education and awareness
5. Insurance scheme

Q22. Do you think the conservation of carnivores is important to forest or ecosystems?

1. Yes
2. No

Q23. Are you aware of the cultural and ecological significance of carnivores?

1. Yes
2. No

Q24. Conservation of carnivores and interaction with humans have following positive impacts: *[5=Strongly agree; 4=Agree; 3= Neither agree nor disagree; 2=Disagree; 1= Strongly disagree]*

1. Good for ecosystem
2. Good for ecotourism
3. Controls herbivores
4. Cultural significance

Q25. Do you think Human-carnivore interactions have negative impacts on communities?

1. Yes
2. No (>>**Q27**)

Q26. Do you think the following will be negative or positive impacts from human-carnivore conflicts [*1=Positive, 2=Negative, 3=None]?*

1.Livelihood	
2. Mental wellbeing of human being	
3. Ecosystem	
4. Carnivores	
5. Conservation of iconic or umbrella species	
6. Rural-Urban migration	
7. Loss of social and community ties	
8. Retaliatory killing	

Q27. Which carnivore do you think contributes most to ecosystem health? Rate as per your understanding *[5=Very important; 4=Important; 3=Neither important nor not important; 2=Not important; 1=Not at all important]*

1. Tiger	
2. Leopard	
3. Clouded leopard	
4. Dhole	
5. Small felids	

D. ATTITUDE

Sl.No	Item	Strongly Agree (1)	Agree (2)	Neither Agree nor disagree (3)	Disagree (4)	Strongly disagree (5)
Q.28	Cattles/domestic animals should not be allowed to enter the core forests					
Q.29	Domestic animals entering forests are at high risk of depredation from carnivores					
Q.30	Farmers develop a negative attitude towards carnivores with livestock depredation					
Q.31	Wildlife should not be allowed to come toward the village periphery					
Q.32	Carnivores in the forests are not important to everybody					
Q.33	I can tolerate livestock depredation by carnivores					
Q.34	I am happy living in proximity to carnivores					
Q.35	I get mentally depressed with Human-carnivore conflicts					
Q.36	Blaming wildlife for Human-carnivore conflict is not good					
Q.37	Communities blaming low livestock productivity due to carnivores is an excuse					
Q.38	It is important to discuss and plan with communities for proper management of Human-carnivore conflicts					
Q.39	Communities should be responsible for reducing livestock depredation from carnivores					
Q.40	I will not retaliate against carnivores					
Q.41	Authorities and government are responsible for managing human-carnivore conflicts					
Q.42	The government is addressing human-carnivore conflicts effectively					
Q.43	Communities fail to report to the concerned authorities					
Q.44	There should be compensation from the government for the loss of livestock					
Q.45	Communities should also invest in Insurance schemes for livestock					
Q.46	Government authorities respond to our complaints and requests					
Q.47	There is no technological advancement from the government or from communities to reduce and mitigate Human-carnivore conflicts					

Q.48	People should be allowed to kill the conflicted animal					
Q.49	We miss our daily chores guarding cattle against carnivores					
Q.50	People should not be allowed to rare cattle in the forests or herding practices					
Q.51	The compensation we get from the government is very low					
Q.52	Tiger and other iconic species are our local deities					
Q.53	Conservation of carnivores is more important than losing livestock					
Q.54	Rural-urban migration might be the cause of Human-carnivore conflicts					
Q.55	Human-carnivore conflicts increased over the past years					

E. PRACTICES

Q56. What mode of cattle rearing do you practice?

1. Stall feeding
2. Free roaming in the forests and collecting in the evening
3. Herding
4. Others (specify):……..

Q57. Which one of the above do you prefer the most? *(Enter the corresponding serial number)*

Q58. How often do you see people following the free raring of cattle in the forests?

1. Once a week
2. Everyday
3. Once a month
4. Not at all

Q59. How often do you leave your cattle unattended in the forests?

1. Once a week
2. Everyday
3. Once a month
4. Not at all

Q60. How often do you take livestock to forests?

1. Once a week
2. Everyday
3. Once a month
4. Not at all

Q61. Have you ever faced incidences of livestock depredation from carnivores?

1. Yes
2. No (>>**Q64**)

Q62. If yes, how often?

1. Monthly
2. Weekly
3. Annually

Q63. What number of livestock over 5 years…….and wort of loss in Nu…….

Q64. Have you informed the concerned authorities?

1. Yes
2. No (>>**Q66**)

Q65. To which organization do you inform?

1. Forest Range Office
2. Local Government
3. RNR office
4. NGOs

Q66. Which of the following organization is effective in the mitigation of Human-carnivore conflicts? Rank based on your agreement *[5=Strongly agree; 4=Agree; 3= Neither agree nor disagree;2=Disagree; 1= Strongly disagree]*

1. Forest Range Office
2. Local Government
3. RNR office
4. NGOs
5. Others (Specify)…….

Q67. Does the organization respond to your request or grievances?

1. Yes
2. No **(>>Q69**)

Q68. How do you rate the effectiveness of the following mitigation measures based on your experience *[5=Highly effective; 4=Effective; 3=Neither effective nor not effective; 2=Not effective; 1=Not at all effective]*

1. Just inspects the damage
2. Compensation for the loss
3. Replacement of lost livestock
4. Provide improved breeds
5. Others (specify)…….

Q69. Do authorities such as the Department of Forests and Park Services, local government, and NGOs implement any projects to mitigate Human-carnivore conflicts?

1. Yes
2. No

Q70. Have you ever retaliated against the loss of livestock from the carnivores?

1. Yes
2. No (>>**Q72**)
3. Prefer not to say

Q71. If 'Yes,' how have you retaliated?

1. Put snares
2. Poison the carcasses
3. Put traps
4. Others (specify)…….

Q72. Have you ever heard of retaliation to livestock depredation from carnivores in your village?

1. Yes
2. No (>>**Q74**)
3. Prefer not to say

Q73. If 'Yes,' how have you retaliated?

1. Put snares
2. Poison the carcasses
3. Put traps
4. Others (specify)…….

Q74. How often do you hear about Human-carnivore conflicts in your village?

1. Once a week
2. Everyday
3. Once a month
4. Not at all

Q75. Rate followings based on your agreement: *[5=Strongly agree; 4=Agree; 3=Neither Agree nor disagree;2=Disagree; 1= Strongly disagree]*

1. Timely compensation will increase tolerance of the community
2. Projects on Human-carnivore conflicts will increase the community's interest in the conservation of carnivores
3. I am not at all interested in the conservation of carnivores

Q76. The following factors reduce the community's tolerance towards the conservation of the carnivores: *[5=Strongly agree; 4=Agree; 3= Neither agree or nor disagree;2=Disagree; 1= Strongly disagree]*

1. Officials not attending the complaints
2. Losing productive breeds to carnivores
3. Less compensation
4. When compensation reaches late
5. Others (Specify).....

Q77. Do you have insurance for your livestock?

1. Yes
2. No (>>**Q79**)

Q78. If 'Yes,' where do you insure?

1. Government Insurance scheme
2. Public/private insurance company
3. Others (specify).....

Q79. Do you practice any traditional methods to mitigate Human-carnivore conflicts?

1. Yes
2. No

Q80. What kind of practice do you follow? *[Tick the possible answers]*

1. Make noise
2. Burn firewood and crackers
3. Burn herbs
4. Please local deities
5. Others (specify).....

Q81. What kind of conservation-related activities do you participate in?

1. Rapid response to Human-wildlife conflicts
2. Porter to local foresters
3. Others (Specify).....

Q82. Do you take preventative measures to avoid the negative interaction between humans and carnivores?

1. Yes
2. No (>>**Q84**)

Q83. What are those prevention measures?

1. Avoid free roaming of cattle
2. Spend all time guarding the livestock in the forests
3. Rare improve the breed and avoid open grazing in forests
4. More stall feeding of livestock
5. Pray and seek guidance from local deities
6. Others (Specify)…….

Q84. How satisfied are you with the grievance redressal mechanism developed by local government relating to Human-carnivore conflicts?

1. Very satisfied
2. Satisfied
3. I Don't know
4. Not satisfied
5. Not at all satisfied

Q85. How do the concerned organizations monitor human-carnivore conflict?

1. Frequently
2. Less frequently
3. Never
4. Don't know

Thank you for your time!

S5. Key Informant Survey on wild felid conservation in Royal Manas National Park and Jigme Singye Wangchuck National Park

Verbal consent of respondents

I got verbal consent from the respondent to carry out this questionnaire interview, and they are fully aware of the participant's information sheet

- Yes (continue the interview)
- No (discontinue the interview)

Name of the enumerator…… Signature……Date……

Name of Agency:…….

Designation:…….

Gender: 1. Female

2. Male

Age: …..

Questions

- To what extent do you think that you understand the term Human-carnivore conflict?
    - Fully understand
    - Understand
    - Neutral
    - Don’t understand
    - Don’t understand at all

- Why are carnivores often conflicted with humans in your area?

- Is there one carnivore that is most conflicted with humans in your area?

- Why is conservation of carnivores important? [Tick the answers based on your understanding]
    - Carnivores are keystone species

- Controls herbivore population
- People like carnivores
- They are endangered
- Carnivores are ecosystem engineers
- Others (specify)……

- Are you aware of any of the following responses to human-carnivore conflicts from the Department of Forests and Park Services, and NGOs such as WWF? If you can, please mention the year of publication in the …….. space below.

  [Scale: 5=Fully aware; 4=aware; 3=Neither aware nor not aware; 2= Not aware; 1=Not aware at all]

1. National Human-wildlife conflict management strategies …… ☐
2. Conservation management plan of protected areas (Conservation management plan of Jigme Singye Wangchuck National Park ……..& Conservation management plan of Royal Manas National Park……..) ☐
3. Gewog (village block) Human-wildlife conflict endowment fund……. ☐
4. Livestock insurance scheme against Tiger depredation……. ☐

- Can you identify some impacts (both positive and negative) of human-carnivore interaction in your locality?

- Do you have a view as to why human-carnivore conflicts continue to rise over the years, despite government efforts and mitigation measures?

- Do you have a view on what can be done to improve the current mitigation measures and new ideas to reduce human-carnivore conflicts?

- Can you suggest one or more ways to reduce the retaliatory killing of carnivores?

- Any other comments?

List of References

Acharya, A. S., Prakash, A., Saxena, P., & Nigam, A. (2013). Sampling: Why and how of it. *Indian Journal of Medical Specialties*, *4*(2), 330-333.

Acharya, B., Johnsingh, A., & Sankar, K. (2010). Dhole telemetry studies in Pench Tiger Reserve, central India. *Telem Wildl Sci*, *13*, 69-79.

Ahrestani, F. S., & Karanth, K. U. (2014). Gaur (Bos gaurus CH Smith, 1827). *Ecology, evolution and behaviour of wild cattle (M. Melletti and J. Burton, eds.). Cambridge University Press, Cambridge, United Kingdom*, 174-193.

Aipanjiguly, S., Jacobson, S. K., & Flamm, R. (2003). Conserving Manatees: Knowledge, Attitudes, and Intentions of Boaters in Tampa Bay, Florida. *Conservation Biology*, *17*(4), 1098-1105. https://doi.org/10.1046/j.1523-1739.2003.01452.x

Ajzen, I. (1991). The theory of planned behavior. *Organizational behavior and human decision processes*, *50*(2), 179-211.

Alibhai, S., Jewell, Z., & Evans, J. (2017). The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. *PLOS ONE*, *12*(3), e0172065. https://doi.org/10.1371/journal.pone.0172065

Aliperti, J. R., Davis, B. E., Fangue, N. A., Todgham, A. E., & Van Vuren, D. H. (2021). Bridging animal personality with space use and resource use in a free-ranging population of an asocial ground squirrel. *Animal Behaviour*, *180*, 291-306.

Amstrup, S. C., McDonald, T. L., & Manly, B. F. (2005). *Handbook of capture-recapture analysis*. Princeton University Press.

Anderson, D. R., Burnham, K. P., & Otis, D. L. (1982). Capture-recapture and removal methods for sampling closed populations. *Los Alamos National Laboratory*.

Anderson, J. C., & Gerbing, D. W. (1988). Structural equation modeling in practice: A review and recommended two-step approach. *Psychological bulletin*, *103*(3), 411.

Andreasen, J. K., O'Neill, R. V., Noss, R., & Slosser, N. C. (2001). Considerations for the development of a terrestrial index of ecological integrity. *Ecological indicators*, *1*(1), 21-35.

Anile, S., Devillard, S., Ragni, B., Rovero, F., Mattucci, F., & Valvo, M. L. (2019). Habitat fragmentation and anthropogenic factors affect wildcat Felis silvestris silvestris occupancy and detectability on Mt Etna. *Wildlife Biology*, *2019*(1). https://doi.org/10.2981/wlb.00561

Aryal, A., Panthi, S., Barraclough, R. K., Bencini, R., Adhikari, B., Ji, W., & Raubenheimer, D. (2015). Habitat selection and feeding ecology of dhole (Cuon alpinus) in the Himalayas. *Journal of Mammalogy*, *96*(1), 47-53.

Ashraf, N., Anwar, M., Hussain, I., & Mirza, S. (2015). Population parameters of Grey goral (Naemorhedus goral goral) at two different sites in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *JAPS: Journal of Animal & Plant Sciences*, *25*(1).

Augustine, B. C., Royle, J. A., Kelly, M. J., Satter, C. B., Alonso, R. S., Boydston, E. E., & Crooks, K. R. (2018). Spatial capture–recapture with partial identity: An application to camera traps. *The Annals of Applied Statistics*, *12*(1), 67-95.

Austin, S., & Tewes, M. E. (1999). Ecology of the clouded leopard in Khao Yai National Park, Thailand. *Cat News/IUCN SSC*, *31*, 17-18.

Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, *7*(5), 619-630. https://doi.org/10.1111/2041-210x.12528

Bagchi, S., & Mishra, C. (2006). Living with large carnivores: predation on livestock by the snow leopard (Uncia uncia). *Journal of Zoology*, *268*(3), 217-224.

Bai, W., Connor, T., Zhang, J., Yang, H., Dong, X., Gu, X., & Zhou, C. (2018). Long-term distribution and habitat changes of protected wildlife: giant pandas in Wolong Nature Reserve, China. *Environmental Science and Pollution Research*, *25*, 11400-11408.

Bailey, T. N. (1993). *The African leopard: ecology and behavior of a solitary felid*. Columbia University Press.

Balestrieri, A., Ruiz-González, A., Vergara, M., Capelli, E., Tirozzi, P., Alfino, S., Minuti, G., Prigioni, C., & Saino, N. (2016). Pine marten density in lowland riparian woods: a test of the Random Encounter Model based on genetic data. *Mammalian Biology*, *81*(5), 439-446.

Balme, G. A., Batchelor, A., de Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D. W., & Hunter, L. T. (2013). Reproductive success of female leopards P anthera pardus: the importance of top-down processes. *Mammal Review*, *43*(3), 221-237.

Balme, G. A., Hunter, L. T., & Slotow, R. (2009). Evaluating methods for counting cryptic carnivores. *The Journal of Wildlife Management*, *73*(3), 433-441.

Barmoen, M., Bærum, K. M., Johansson, M., & Mathiesen, K. E. (2021). Trust in large carnivore science in Norway. *European Journal of Wildlife Research*, *67*(6). https://doi.org/10.1007/s10344-021-01538-7

Barton, K., & Barton, M. K. (2015). Package 'mumin'. *Version*, *1*(18), 439.

Baruzzi, C., Snow, N. P., Vercauteren, K. C., Strickland, B. K., Arnoult, J. S., Fischer, J. W., Glow, M. P., Lavelle, M. J., Smith, B. A., Steakley, D., & Lashley, M. A. (2023). Estimating body mass of wild pigs (Sus scrofa) using body morphometrics. *Ecology and Evolution*, *13*(3). https://doi.org/10.1002/ece3.9853

Bashir, T., Bhattacharya, T., Poudyal, K., Roy, M., & Sathyakumar, S. (2014). Precarious status of the Endangered dhole Cuon alpinus in the high elevation Eastern Himalayan habitats of Khangchendzonga Biosphere Reserve, Sikkim, India. *Oryx*, *48*(1), 125-132. https://doi.org/10.1017/s003060531200049x

Bashir, T., Bhattacharya, T., Poudyal, K., Sathyakumar, S., & Qureshi, Q. (2014). Integrating aspects of ecology and predictive modelling: implications for the conservation of the

leopard cat (Prionailurus bengalensis) in the Eastern Himalaya. *Acta theriologica*, *59*(1), 35-47. https://doi.org/10.1007/s13364-013-0145-x

Baskarada, S. (2014). Qualitative case study guidelines. *Baškarada, S.(2014). Qualitative case studies guidelines. The Qualitative Report*, *19*(40), 1-25.

Batavia, C., & Nelson, M. P. (2017). For goodness sake! What is intrinsic value and why should we care? *Biological Conservation*, *209*, 366-376. https://doi.org/10.1016/j.biocon.2017.03.003

Baynham-Herd, Z., Redpath, S., Bunnefeld, N., Molony, T., & Keane, A. (2018). Conservation conflicts: Behavioural threats, frames, and intervention recommendations. *Biological Conservation*, *222*, 180-188. https://doi.org/10.1016/j.biocon.2018.04.012

Bhalla, P., Coghlan, A., & Bhattacharya, P. (2016). Homestays' contribution to community-based ecotourism in the Himalayan region of India. *Tourism Recreation Research*, *41*(2), 213-228. https://doi.org/10.1080/02508281.2016.1178474

Bhattacharya, A., Chatterjee, N., Angrish, K., Meena, D., Sinha, B. C., & Habib, B. (2022). Population estimation of Asiatic black bear in the Himalayan Region of India using camera traps. *Ursus*, *2022*(33e8), 1-10.

Bhattarai, B. R., & Fischer, K. (2014). Human–tiger Panthera tigris conflict and its perception in Bardia National Park, Nepal. *Oryx*, *48*(4), 522-528. https://doi.org/10.1017/s0030605313000483

Bischof, R., Brøseth, H., & Gimenez, O. (2016). Wildlife in a politically divided world: Insularism inflates estimates of brown bear abundance. *Conservation Letters*, *9*(2), 122-130.

Blanc, L., Marboutin, E., Gatti, S., & Gimenez, O. (2013). Abundance of rare and elusive species: empirical investigation of closed versus spatially explicit capture–recapture models with lynx as a case study. *The Journal of Wildlife Management*, *77*(2), 372-378.

Borchers, D. (2012). A non-technical overview of spatially explicit capture–recapture models. *Journal of Ornithology*, *152*(S2), 435-444. https://doi.org/10.1007/s10336-010-0583-z

Borchers, D. L., & Efford, M. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, *64*(2), 377-385.

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, *11*(6), 637-650. https://doi.org/10.1111/j.1461-0248.2008.01182.x

Boudreau, M. R., Seguin, J. L., Lavergne, S. G., Sonnega, S., Scholl, L., Kenney, A. J., & Krebs, C. J. (2020). Please come again: attractive bait augments recapture rates of capture-naive snowshoe hares. *Wildlife Research*, *47*(3), 244-248. https://doi.org/10.1071/wr18200

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity <html_ent glyph="@amp;" ascii="&"/> Distributions*, *12*(3), 269-276. https://doi.org/10.1111/j.1366-9516.2006.00243.x

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecological modelling*, *157*(2-3), 281-300.

Broekman, M. J. E., Hoeks, S., Freriks, R., Langendoen, M. M., Runge, K. M., Savenco, E., Ter Harmsel, R., Huijbregts, M. A. J., & Tucker, M. A. (2023). HomeRange: A global database of mammalian home ranges. *Global Ecology and Biogeography*, *32*(2), 198-205. https://doi.org/10.1111/geb.13625

Bruskotter, J. T., & Wilson, R. S. (2014). Determining Where the Wild Things will be: Using Psychological Theory to Find Tolerance for Large Carnivores. *Conservation Letters*, *7*(3), 158-165. https://doi.org/10.1111/conl.12072

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2004). *Advanced distance sampling: estimating abundance of biological populations*. OUP Oxford.

Bumham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. *Spnnger-Veflag, New York, New York*.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23-35. https://doi.org/10.1007/s00265-010-1029-6

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*(3), 346-352.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*(3), 675-685. https://doi.org/10.1111/1365-2664.12432

Butler, A. R., Bly, K. L., Harris, H., Inman, R. M., Moehrenschlager, A., Schwalm, D., & Jachowski, D. S. (2020). Home range size and resource use by swift foxes in northeastern Montana. *Journal of Mammalogy*, *101*(3), 684-696.

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). ctmm: an <scp>r</scp> package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*(9), 1124-1132. https://doi.org/10.1111/2041-210x.12559

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., Rowcliffe, M. J., & Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, *3*(3), 109-122. https://doi.org/10.1002/rse2.48

Carbone, C., & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science*, *295*(5563), 2273-2276.

Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J., & Purvis, A. (2008). The predictability of extinction: biological and external correlates of decline in mammals.

Proceedings of the Royal Society B: Biological Sciences, *275*(1641), 1441-1448. https://doi.org/10.1098/rspb.2008.0179

Carter, N. H., Riley, S. J., & Liu, J. (2012). Utility of a psychological framework for carnivore conservation. *Oryx*, *46*(4), 525-535. https://doi.org/10.1017/s0030605312000245

Cavalcanti, S. C., Marchini, S., Zimmermann, A., Gese, E. M., & Macdonald, D. W. (2010). Jaguars, livestock, and people in Brazil: realities and perceptions behind the conflict.

Chandler, R. B., & Royle, J. A. (2013). Spatially explicit models for inference about density in unmarked or partially marked populatioins. *The Annals of Applied Statistics*, 936-954.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, *9*(2), 129-136.

Chauvenet, A. L., Gill, R. M., Smith, G. C., Ward, A. I., & Massei, G. (2017). Quantifying the bias in density estimated from distance sampling and camera trapping of unmarked individuals. *Ecological modelling*, *350*, 79-86.

Choki, K., Dhendup, P., Tenzin, J., Dorji, D., Tenzin, K., Wangmo, T., & Penjor, U. (2023). Conservation potential of non-protected area for sympatric carnivores in Bhutan. *Global Ecology and Conservation*, *42*, e02392.

Christensen, R. H. B., & Christensen, M. R. H. B. (2015). Package 'ordinal'. *Stand*, *19*(2016).

Comrey, A. L., & Lee, H. B. (2013). *A first course in factor analysis*. Psychology press.

Cordier, C. P., Smith, D. A. E., Smith, Y. E., & Downs, C. T. (2022). Camera trap research in Africa: A systematic review to show trends in wildlife monitoring and its value as a research tool. *Global Ecology and Conservation*, *40*, Article e02326. https://doi.org/10.1016/j.gecco.2022.e02326

Cressie, N. (2015). *Statistics for spatial data*. John Wiley & Sons.

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, *16*(2), 488-502.

Cubaynes, S., Macnulty, D. R., Stahler, D. R., Quimby, K. A., Smith, D. W., & Coulson, T. (2014). Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). *Journal of Animal Ecology*, *83*(6), 1344-1356. https://doi.org/10.1111/1365-2656.12238

Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus Game Trail-Based Camera Trap Placement Strategy for Monitoring Terrestrial Mammal Communities. *PLOS ONE*, *10*(5), e0126373. https://doi.org/10.1371/journal.pone.0126373

Cusack, J. J., Swanson, A., Coulson, T., Packer, C., Carbone, C., Dickman, A. J., Kosmala, M., Lintott, C., & Rowcliffe, J. M. (2015). Applying a random encounter model to estimate lion density from camera traps in Serengeti National Park, Tanzania. *The Journal of Wildlife Management*, *79*(6), 1014-1021. https://doi.org/10.1002/jwmg.902

Dalerum, F., Somers, M. J., Kunkel, K. E., & Cameron, E. Z. (2008). The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation*, *17*(12), 2939-2949. https://doi.org/10.1007/s10531-008-9406-4

Danish, M., Mahmood, T., Akrim, F., Nadeem, M. S., Noreen, S., Munawar, N., Shakil, M., & Arshad, M. (2023). Spatio-temporal patterns of human-carnivore conflict and mitigation in Pakistan. *Journal for Nature Conservation*, *76*, 126479.

Darwin, C. (1860). *On the origin of species by means of natural selection: or, the preservation of favoured races in the struggle for life*. Murray.

Dash, G., & Paul, J. (2021). CB-SEM vs PLS-SEM methods for research in social sciences and technology forecasting. *Technological Forecasting and Social Change*, *173*, 121092.

Debata, S., & Swain, K. K. (2019). Group Size and Population Structure of Vulnerable Gaur in an Isolated Tropical Deciduous Forest of Eastern India. *Proceedings of the National*

Academy of Sciences, India Section B: Biological Sciences, *89*(1), 89-94. https://doi.org/10.1007/s40011-017-0926-0

Decker, D., Forstchen, A., LeClaire-Mitchell, A., & Jacobson, C. (2012). Seeking common ground for collaborative conservation: Overcoming barriers and building bridges to a wildlife conservation institution for "all wildlife for all people",". Transactions of the 76th North American Wildlife and Natural Resources Conference (Milwaukee, WI),

Decker, D. J., & Purdy, K. G. (1988). Toward A Concept of Wildlife Acceptance Capacity in Wildlife Management. *Wildlife Society Bulletin (1973-2006)*, *16*(1), 53-57. http://www.jstor.org/stable/3782353

Delisle, Z. J., Flaherty, E. A., Nobbe, M. R., Wzientek, C. M., & Swihart, R. K. (2021). Next-generation camera trapping: systematic review of historic trends suggests keys to expanded research applications in ecology and conservation. *Frontiers in Ecology and Evolution*, *9*, 617996.

Dendup, P., Lham, C., Wangchuk, W., & Jamtsho, Y. (2023). Tiger abundance and ecology in Jigme Dorji National Park, Bhutan. *Global Ecology and Conservation*, *42*, e02378.

Dheer, A., Samarasinghe, D., Dloniak, S. M., & Braczkowski, A. (2022). Using camera traps to study hyenas: challenges, opportunities, and outlook. *Mammalian Biology*, *102*(3), 847-854. https://doi.org/10.1007/s42991-021-00188-1

Di Bitetti, M. S., Paviolo, A., & De Angelo, C. (2006). Density, habitat use and activity patterns of ocelots (Leopardus pardalis) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology*, *270*(1), 153-163.

Dickie, M., Serrouya, R., Avgar, T., McLoughlin, P., McNay, R. S., DeMars, C., Boutin, S., & Ford, A. T. (2022). Resource exploitation efficiency collapses the home range of an apex predator. *Ecology*, *103*(5), e3642.

Dickman, A. J. (2009). *Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania* University College London (University of London)].

Dickman, A. J. (2010). Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. *Animal Conservation*, *13*(5), 458-466. https://doi.org/10.1111/j.1469-1795.2010.00368.x

Dickman, C. R., Glen, A. S., Jones, M. E., Soulé, M. E., Ritchie, E. G., & Wallach, A. D. (2014). Strongly interactive carnivore species: maintaining and restoring ecosystem function. Carnivores of Australia: past, present and future, 301.

Distefano, E. (2005). Human-Wildlife Conflict worldwide: collection of case studies, analysis of management strategies and good practices. *Food and Agricultural Organization of the United Nations (FAO), Sustainable Agriculture and Rural Development Initiative (SARDI), Rome, Italy. Available from: FAO Corporate Document repository http://www. fao. org/documents*.

Domencich, T. A., & McFadden, D. (1975). *Urban travel demand-a behavioral analysis*.

Donadio, E., & Buskirk, S. W. (2006). Diet, morphology, and interspecific killing in Carnivora. *The American Naturalist*, *167*(4), 524-536.

Dorji, N. (2020, 30/07/2020). Farmers receive semso for cattle lost to tiger *Kuensel*. https://kuenselonline.com/farmers-receive-semso-for-cattle-lost-to-tiger/

Dorresteijn, I., Schultner, J., Nimmo, D. G., Fischer, J., Hanspach, J., Kuemmerle, T., ... & Ritchie, E. G. (2015). Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. Proceedings of the Royal Society B: Biological Sciences, 282(1814), 20151602.

Driscoll, J. W. (1992). Attitudes toward animal use. *Anthrozoös*, *5*(1), 32-39.

Duľa, M., Bojda, M., Chabanne, D. B., Drengubiak, P., Hrdý, Ľ., Krojerová-Prokešová, J., Kubala, J., Labuda, J., Marčáková, L., & Oliveira, T. (2021). Multi-seasonal systematic camera-trapping reveals fluctuating densities and high turnover rates of Carpathian lynx on the western edge of its native range. *Scientific Reports*, *11*(1), 9236.

Dupont, P., Milleret, C., Gimenez, O., & Bischof, R. (2019). Population closure and the bias-precision trade-off in spatial capture–recapture. *Methods in Ecology and Evolution*, *10*(5), 661-672. https://doi.org/10.1111/2041-210x.13158

ECIU. (2019). *COUNTDOWN TO ZERO, Plotting progress towards delivering net zero emmission by 2050*. E. a. C. I. Unit. https://ca1-eci.edcdn.com/reports/ECIU_Countdown_to_Net_Zero.pdf

Edwards, S., Fischer, M., Wachter, B., & Melzheimer, J. (2018). Coping with intrasexual behavioral differences: Capture-recapture abundance estimation of male cheetah. *Ecology and Evolution*, *8*(18), 9171-9180. https://doi.org/10.1002/ece3.4410

Efford, M. (2019). Habitat masks in the package secr. *R Package version*, 1-18.

Efford, M., & Efford, M. M. (2022). Package 'secr'. https://cran.r-project.org/web/packages/secr/index.html. Assessed 10 September 2022.

Efford, M., & Efford, M. M. (2023). Package 'secr'. https://cran.r-project.org/web/packages/secr/index.html. Assessed 2 April 2023.

Efford, M. G. (2014a). Bias from heterogeneous usage of space in spatially explicit capture-recapture analyses. *Methods in Ecology and Evolution*, *5*(7), 599-602. https://doi.org/10.1111/2041-210x.12169

Efford, M. G. (2014b). Bias from heterogeneous usage of space in spatially explicit capture–recapture analyses. *Methods in Ecology and Evolution*, *5*(7), 599-602. https://doi.org/10.1111/2041-210x.12169

Efford, M. G., & Boulanger, J. (2019). Fast evaluation of study designs for spatially explicit capture–recapture. *Methods in Ecology and Evolution*, *10*(9), 1529-1535. https://doi.org/10.1111/2041-210x.13239

Efford, M. G., Dawson, D. K., & Borchers, D. L. (2009). Population density estimated from locations of individuals on a passive detector array. *Ecology*, *90*(10), 2676-2682. https://doi.org/10.1890/08-1735.1

Efford, M. G., Dawson, D. K., & Robbins, C. S. (2004). DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation*, *27*(1), 217-228.

Efford, M. G., & Fewster, R. M. (2013). Estimating population size by spatially explicit capture-recapture. *Oikos*, *122*(6), 918-928. https://doi.org/10.1111/j.1600-0706.2012.20440.x

Eizirik, E., Yuhki, N., Johnson, W. E., Menotti-Raymond, M., Hannah, S. S., & O'Brien, S. J. (2003). Molecular genetics and evolution of melanism in the cat family. *Current biology*, *13*(5), 448-453.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics*, *40*, 677-697.

ENETWILD-consortium, Vicente, J., Palencia, P., Plhal, R., Blanco-Aguiar, J. A., Laguna, E., Soriguer, R., López, J. F., Podgórski, T., & Petrović, K. (2019). Harmonization of the use of hunting statistics for wild boar density estimation in different study areas: Report based on comparison of case studies in different wild boar populations representative of the different management and habitat conditions across Europe. *EFSA Supporting Publications*, *16*(9), 1706E.

Epskamp, S. (2015). semPlot: Unified Visualizations of Structural Equation Models. *Structural Equation Modeling: A Multidisciplinary Journal*, *22*(3), 474-483. https://doi.org/10.1080/10705511.2014.937847

Esmaeili, S., Hemami, M.-R., & Goheen, J. R. (2019). Human dimensions of wildlife conservation in Iran: Assessment of human-wildlife conflict in restoring a wide-ranging endangered species. *PLOS ONE*, *14*(8), e0220702. https://doi.org/10.1371/journal.pone.0220702

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., & Jackson, J. B. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040), 301-306.

Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S. R., Park, H., & Shao, C. (2016). Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecological Processes*, *5*(1). https://doi.org/10.1186/s13717-016-0063-3

Farhadinia, M. S., Heit, D. R., Montgomery, R. A., Johnson, P. J., Hobeali, K., Hunter, L. T. B., & Macdonald, D. W. (2020). Vertical relief facilitates spatial segregation of a high density large carnivore population. *Oikos*, *129*(3), 346-355. https://doi.org/10.1111/oik.06724

Fieberg, J. (2007). Utilization Distribution Estimation Using Weighted Kernel Density Estimators. *Journal of Wildlife Management*, *71*(5), 1669-1675. https://doi.org/10.2193/2006-370

Fieberg, J., & Kochanny, C. O. (2005). QUANTIFYING HOME-RANGE OVERLAP: THE IMPORTANCE OF THE UTILIZATION DISTRIBUTION. *Journal of Wildlife Management*, *69*(4), 1346-1359. https://doi.org/10.2193/0022-541x(2005)69[1346:qhotio]2.0.co;2

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'How to'guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, *90*(5), 1027-1043.

Fisher, R. A. (1999). *The genetical theory of natural selection: a complete variorum edition*. Oxford University Press.

Fiske, I., & Chandler, R. (2011). Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of statistical software*, *43*, 1-23.

Fleming, C. H., & Calabrese, J. M. (2017). A new kernel density estimator for accurate home-range and species-range area estimation. *Methods in Ecology and Evolution*, *8*(5), 571-579. https://doi.org/10.1111/2041-210x.12673

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: a new autocorrelated

kernel density estimator. *Ecology*, *96*(5), 1182-1188. https://doi.org/10.1890/14-2010.1

Fleming, C. H., Noonan, M. J., Medici, E. P., & Calabrese, J. M. (2019). Overcoming the challenge of small effective sample sizes in home-range estimation. *Methods in Ecology and Evolution*, *10*(10), 1679-1689. https://doi.org/10.1111/2041-210x.13270

Fleming, C. H., Sheldon, D., Fagan, W. F., Leimgruber, P., Mueller, T., Nandintsetseg, D., Noonan, M. J., Olson, K. A., Setyawan, E., Sianipar, A., & Calabrese, J. M. (2018). Correcting for missing and irregular data in home-range estimation. *Ecological Applications*, *28*(4), 1003-1010. https://doi.org/10.1002/eap.1704

Fleming, C. H., Subaşı, Y., & Calabrese, J. M. (2015). Maximum-entropy description of animal movement. *Physical Review E*, *91*(3). https://doi.org/10.1103/physreve.91.032107

Foster, R. (2008). The ecology of jaguars (Panthera onca) in a human-influenced landscape (Doctoral dissertation, University of Southampton).

Foster, R. J., & Harmsen, B. J. (2012). A critique of density estimation from camera-trap data. *The Journal of Wildlife Management*, *76*(2), 224-236. https://doi.org/10.1002/jwmg.275

Fretwell, S. D., & Calver, J. S. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*(1), 37-44. https://doi.org/10.1007/bf01601954

Fulton, D. C., Manfredo, M. J., & Lipscomb, J. (1996). Wildlife value orientations: A conceptual and measurement approach. *Human Dimensions of Wildlife*, *1*(2), 24-47.

Gálvez, N., Guillera-Arroita, G., Morgan, B. J. T., & Davies, Z. G. (2016). Cost-efficient effort allocation for camera-trap occupancy surveys of mammals. *Biological Conservation*, *204*, 350-359. https://doi.org/10.1016/j.biocon.2016.10.019

Gandiwa, E., Zisadza-Gandiwa, P., Muboko, N., Libombo, E., Mashapa, C., & Gwazani, R. (2014). Local People's Knowledge and Perceptions of Wildlife Conservation in

Southeastern Zimbabwe. *Journal of Environmental Protection*, *05*(06), 475-481. https://doi.org/10.4236/jep.2014.56050

Gardner, B., Royle, J. A., Wegan, M. T., Rainbolt, R. E., & Curtis, P. D. (2010). Estimating Black Bear Density Using DNA Data From Hair Snares. *Journal of Wildlife Management*, *74*(2), 318-325. https://doi.org/10.2193/2009-101

Garrote, G., Pérez De Ayala, R., Álvarez, A., Martín, J. M., Ruiz, M., De Lillo, S., & Simón, M. A. (2021). Improving the random encounter model method to estimate carnivore densities using data generated by conventional camera-trap design. *Oryx*, *55*(1), 99-104. https://doi.org/10.1017/s0030605318001618

Gerber, B. D., Karpanty, S. M., & Kelly, M. J. (2012). Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology*, *54*(1), 43-54. https://doi.org/10.1007/s10144-011-0276-3

Ghasemi, B., & Kyle, G. T. (2021). Toward moral pathways to motivate wildlife conservation. *Biological Conservation*, *259*, 109170.

Gilbert, M., Dvornicky-Raymond, Z., & Bodgener, J. (2023). Disease threats to tigers and their prey. *Frontiers in Ecology and Evolution*, *11*, 1135935.

Gilbert, N. A., Clare, J. D. J., Stenglein, J. L., & Zuckerberg, B. (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology*, *35*(1), 88-100. https://doi.org/10.1111/cobi.13517

Gimenez, O., Rossi, V., Choquet, R., Dehais, C., Doris, B., Varella, H., Vila, J.-P., & Pradel, R. (2007). State-space modelling of data on marked individuals. *Ecological modelling*, *206*(3-4), 431-438.

Gizachew, G. (2022). Spatial-temporal and factors influencing the distribution of biodiversity: a review. ASEAN Journal of Science and Engineering, 2(3), 273-284.

Goldman, M. (2003). Partitioned Nature, Privileged Knowledge: Community-based Conservation in Tanzania. *Development and Change*, *34*(5), 833-862. https://doi.org/10.1111/j.1467-7660.2003.00331.x

Goodrich, J., Kerley, L., Smirnov, E., Miquelle, D., McDonald, L., Quigley, H., Hornocker, M., & McDonald, T. (2008). Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *Journal of Zoology*, *276*(4), 323-329.

Gopalaswamy, A., Royle, J., Meredith, M., Jathanna, D., Kumar, N., & Karanth, K. (2014). SPACECAP: An R package for estimating animal density using spatially explicit capture-recapture models. *Bangalore, India: Wildlife Conservation Society, India Program, Centre for Wildlife Studies. Version*, *1*(0).

Gopalaswamy, A. M., Karanth, K. U., Delampady, M., & Stenseth, N. C. (2019). How sampling-based overdispersion reveals India's tiger monitoring orthodoxy. *Conservation Science and Practice*, *1*(12). https://doi.org/10.1111/csp2.128

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program <scp>SPACECAP</scp> : software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067-1072. https://doi.org/10.1111/j.2041-210x.2012.00241.x

Gopalaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: software for estimating animal density using spatially explicit capture–recapture models. *Methods in Ecology and Evolution*, *3*(6), 1067-1072.

Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological bulletin*, *127*(1), 45.

Grassman Jr, L. I., Austin, S. C., Tewes, M. E., & Silvy, N. J. (2004). Comparative immobilization of wild felids in Thailand. *Journal of Wildlife Diseases*, *40*(3), 575-578.

Grassman, L. (2000). Movements and diet of the leopard cat Prionailurus bengalensis in a seasonal evergreen forest in south-central Thailand. *Acta theriologica*, *45*(3), 421-426.

Grassman, L. I., Tewes, M. E., Silvy, N. J., & Kreetiyutanont, K. (2005a). ECOLOGY OF THREE SYMPATRIC FELIDS IN A MIXED EVERGREEN FOREST IN NORTH-CENTRAL THAILAND. *Journal of Mammalogy*, *86*(1), 29-38. https://doi.org/10.1644/1545-1542(2005)086<0029:eotsfi>2.0.co;2

Grassman, L. I., Tewes, M. E., Silvy, N. J., & Kreetiyutanont, K. (2005). Spatial ecology and diet of the dhole Cuon alpinus (Canidae, Carnivora) in north central Thailand.

Grassman, L. I., Tewes, M. E., Silvy, N. J., & Kreetiyutanont, K. (2005b). Spatial organization and diet of the leopard cat (Prionailurus bengalensis) in north-central Thailand. *Journal of Zoology*, *266*(1), 45-54. https://doi.org/10.1017/s095283690500659x

Gray, T. N. E., & Prum, S. (2012). Leopard density in post-conflict landscape, Cambodia: Evidence from spatially explicit capture-recapture. *The Journal of Wildlife Management*, *76*(1), 163-169. https://doi.org/10.1002/jwmg.230

Green, A. M., Chynoweth, M. W., & Şekercioğlu, Ç. H. (2020). Spatially explicit capture-recapture through camera trapping: a review of benchmark analyses for wildlife density estimation. *Frontiers in Ecology and Evolution*, *8*, 563477.

Greenwell, B. M., Boehmke, B. C., & Gray, B. (2020). Variable Importance Plots-An Introduction to the vip Package. *R J.*, *12*(1), 343.

Gregory, T., Carrasco Rueda, F., Deichmann, J., Kolowski, J., & Alonso, A. (2014). Arboreal camera trapping: taking a proven method to new heights. *Methods in Ecology and Evolution*, *5*(5), 443-451. https://doi.org/10.1111/2041-210x.12177

Haidt, J. (2003). The moral emotions. *Handbook of affective sciences*, *11*(2003), 852-870.

Haines, A. M., Grassman Jr, L. I., & Tewes, M. E. (2022). Ecological Separation and Coexistence in a Carnivore Community in North-Central Thailand. *Small Carnivores: Evolution, Ecology, Behaviour, and Conservation*, 309-322.

Hair, J. F., Black, W. C., Babin, B. J., Anderson, R. E., & Tatham, R. L. (2014). Pearson new international edition. *Multivariate data analysis, Seventh Edition. Pearson Education Limited Harlow, Essex*.

Hair, J. F., Hult, G. T. M., Ringle, C. M., Sarstedt, M., Danks, N. P., & Ray, S. (2021). An Introduction to Structural Equation Modeling. In (pp. 1-29). Springer International Publishing. https://doi.org/10.1007/978-3-030-80519-7_1

Hamilton, W. (1967). A sex-ratio theory for sex linkage and inbreeding. *Science*, *156*, 47.

Han, F., Yang, Z., Shi, H., Liu, Q., & Wall, G. (2016). How to Promote Sustainable Relationships between Heritage Conservation and Community, Based on a Survey. *Sustainability*, *8*(9), 886. https://doi.org/10.3390/su8090886

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., & Loveland, T. R. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*(6160), 850-853.

Happold, M., & Happold, D. (2013). *Mammals of Africa* (Vol. 3). Bloomsbury London.

Harestad, A. S., & Bunnel, F. (1979). Home range and body weight--A reevaluation. *Ecology*, *60*(2), 389-402.

Harestad, A. S., & Bunnel, F. L. (1979). Home Range and Body Weight--A Reevaluation. *Ecology*, *60*(2), 389-402. https://doi.org/10.2307/1937667

Harman, H. H. (1976). *Modern factor analysis*. University of Chicago press.

Harmsen, B. J., Foster, R. J., & Doncaster, C. P. (2011). Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. *Population ecology*, *53*(1), 253-259.

Harmsen, B. J., Foster, R. J., & Quigley, H. (2020). Spatially explicit capture recapture density estimates: Robustness, accuracy and precision in a long-term study of jaguars (Panthera onca). *PLOS ONE*, *15*(6), e0227468.

Harmsen, B. J., Foster, R. J., Sanchez, E., Gutierrez-González, C. E., Silver, S. C., Ostro, L. E., Kelly, M. J., Kay, E., & Quigley, H. (2017). Long term monitoring of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize; Implications for camera trap studies of carnivores. *PloS one*, *12*(6), e0179505.

Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2010). Differential Use of Trails by Forest Mammals and the Implications for Camera-Trap Studies: A Case Study from Belize. *Biotropica*, *42*(1), 126-133. https://doi.org/10.1111/j.1744-7429.2009.00544.x

Harrell, F. E. (2001). *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis* (Vol. 608). Springer.

Harrell, J., Frank E, & Harrell, F. E. (2015). Ordinal logistic regression. *Regression modeling strategies: with applications to linear models, logistic and ordinal regression, and survival analysis*, 311-325.

Hauser, C. E., Pople, A. R., & Possingham, H. P. (2006). Should managed populations be monitored every year? *Ecological Applications*, *16*(2), 807-819.

Hayward, M. W., Lyngdoh, S., & Habib, B. (2014). Diet and prey preferences of dholes (<scp>C</scp>uon alpinus): dietary competition within<scp>A</scp>sia's apex predator guild. *Journal of Zoology*, *294*(4), 255-266. https://doi.org/10.1111/jzo.12171

Hearn, A. J., Ross, J., Bernard, H., Bakar, S. A., Goossens, B., Hunter, L. T., & Macdonald, D. W. (2017). Responses of Sunda clouded leopard population density to anthropogenic disturbance and refining estimates of their conservation status in Sabah. *Oryx*.

Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2303-2312. https://doi.org/10.1098/rstb.2010.0087

Hendry, A., Amir, Z., Decoeur, H., Mendes, C. P., Moore, J. H., Sovie, A., & Luskin, M. S. (2023). Marbled cats in Southeast Asia: Are diurnal and semi-arboreal felids at greater risk from human disturbances? *Ecosphere*, *14*(1). https://doi.org/10.1002/ecs2.4338

Herfindal, I., Linnell, J. D. C., Odden, J., Nilsen, E. B., & Andersen, R. (2005). Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). *Journal of Zoology*, *265*(1), 63-71. https://doi.org/10.1017/s0952836904006053

Hernandez-Blanco, J. A., Naidenko, S. V., Chistopolova, M. D., Lukarevskiy, V. S., Kostyrya, A., Rybin, A., Sorokin, P. A., Litvinov, M. N., Kotlyar, A. K., Miquelle, D. G., & Rozhnov, V. V. (2015). Social structure and space use of Amur tigers (Panthera tigris altaica) in Southern Russian Far East based on GPS telemetry data. *Integrative Zoology*, *10*(4), 365-375. https://doi.org/10.1111/1749-4877.12140

Hijmans, R. J., Van Etten, J., Mattiuzzi, M., Sumner, M., Greenberg, J., Lamigueiro, O., Bevan, A., Racine, E., & Shortridge, A. (2013). Raster package in R. *Version. https://mirro rs. sjtug. sjtu. edu. cn/cran/web/packa ges/rast e r/raster. pdf*.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism1. *The canadian entomologist*, *91*(7), 385-398.

Honaker, J., King, G., Blackwell, M., & Blackwell, M. M. (2010). Package 'Amelia'. *Version. View Article*.

Horwich, R. H., & Lyon, J. (2007). Community conservation: practitioners' answer to critics. *Oryx*, *41*(3), 376-385. https://doi.org/10.1017/s0030605307001010

Hothorn, T., Hornik, K., Strobl, C., Zeileis, A., & Hothorn, M. T. (2015). Package 'party'. *Package Reference Manual for Party Version 0.9-998*, *16*, 37.

Hothorn, T., Hornik, K., & Zeileis, A. (2015). ctree: Conditional inference trees. *The comprehensive R archive network*, *8*.

Howe, E. J., Buckland, S. T., Després-Einspenner, M. L., & Kühl, H. S. (2017). Distance sampling with camera traps. *Methods in Ecology and Evolution*, *8*(11), 1558-1565. https://doi.org/10.1111/2041-210x.12790

Hsieh, H.-F., & Shannon, S. E. (2005). Three approaches to qualitative content analysis. *Qualitative health research*, *15*(9), 1277-1288.

Hunter, L. (2015). *Wild cats of the world*. Bloomsbury Publishing.

Iijima, H. (2020). A Review of Wildlife Abundance Estimation Models: Comparison of Models for Correct Application. *Mammal Study*, *45*(3), 177. https://doi.org/10.3106/ms2019-0082

Inskip, C., & Zimmermann, A. (2009). Human-felid conflict: a review of patterns and priorities worldwide. *Oryx*, *43*(01), 18. https://doi.org/10.1017/s003060530899030x

IUCN. (2023). *Family Felidae* https://www.iucnredlist.org/search?taxonomies=101738&searchType=species

Jackman, S., Tahk, A., Zeileis, A., Maimone, C., Fearon, J., Meers, Z., Jackman, M. S., & Imports, M. (2015). Package 'pscl'. *Political Science Computational Laboratory*, *18*(04.2017).

Jackson, R. M., Mishra, C., McCarthy, T. M., & Ale, S. B. (2010). Snow leopards: conflict and conservation. *The biology and conservation of wild felids*, *2*, 417-430.

Jamtsho, Y., & Katel, O. (2019). Livestock depredation by snow leopard and Tibetan wolf: Implications for herders' livelihoods in Wangchuck Centennial National Park, Bhutan. *Pastoralism*, *9*(1). https://doi.org/10.1186/s13570-018-0136-2

Johnson, A. R., Wiens, J. A., Milne, B. T., & Crist, T. O. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology*, *7*(1), 63-75. https://doi.org/10.1007/bf02573958

Johnson, C. J., Nielsen, S. E., Merrill, E. H., McDonald, T. L., & Boyce, M. S. (2006). Resource Selection Functions Based on Use–Availability Data: Theoretical

Motivation and Evaluation Methods. *Journal of Wildlife Management*, *70*(2), 347-357. https://doi.org/10.2193/0022-541x(2006)70[347:rsfbou]2.0.co;2

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65-71. https://doi.org/10.2307/1937156

Johnston, A., Hochachka, W., Strimas-Mackey, M., Gutierrez, V. R., Robinson, O., Miller, E., Auer, T., Kelling, S., & Fink, D. (2019). Best practices for making reliable inferences from citizen science data: case study using eBird to estimate species distributions. *BioRxiv*, *574392*.

Jones, B. T. (1999). Policy lessons from the evolution of a community-based approach to wildlife management, Kunene Region, Namibia. *Journal of International Development: The Journal of the Development Studies Association*, *11*(2), 295-304.

Jöreskog, K. G., Olsson, U. H., & Wallentin, F. Y. (2016). *Multivariate analysis with LISREL*. Springer.

Jorgensen, T. D., Pornprasertmanit, S., Schoemann, A. M., Rosseel, Y., Miller, P., Quick, C., Garnier-Villarreal, M., Selig, J., Boulton, A., & Preacher, K. (2016). Package 'semtools'. *Website: https://cran. r-project. org/web/packages/semTools/semTools. pdf*.

JSWNP. (2016). *Conservation Management Plan of Jigme Singye Wangchuck National Park 2016-2021*. Trongsa, Bhutan: Department of Forests and Park Services, Royal Government of Bhutan

JSWNP. (2022). *Conservation Management Plan of Jigme Singye Wangchuck National Park 2016-2021*. Trongsa, Bhutan: Department of Forests and Park Services, Royal Government of Bhutan

Kamath, A., & Wesner, A. B. (2020). Animal territoriality, property and access: a collaborative exchange between animal behaviour and the social sciences. *Animal Behaviour*, *164*, 233-239.

Kamler, J. F., Inthapanya, X., Rasphone, A., Bousa, A., Vongkhamheng, C., Johnson, A., & Macdonald, D. W. (2020). Diet, prey selection, and activity of Asian golden cats and leopard cats in northern Laos. *Journal of Mammalogy*, *101*(5), 1267-1278. https://doi.org/10.1093/jmammal/gyaa113

Karanth, K. (1993). Predator-prey relationships among large mammals of Nagarahole National Park, India. *PhD Dissertation, Mangalore University*.

Karanth K.U., N. J. D., Harihar A., Miquelle D.G., Kumar N.S., Dorazio R.M. (2017). Field Practices: Assessing Tiger Population Dynamics Using Photographic Captures. *Springers, Singapore*. https://doi.org/https://doi.org/10.1007/978-981-10-5436-5_10

Karanth, K. U., Nichols, J. D., Kumar, N. S., Link, W. A., & Hines, J. E. (2004). Tigers and their prey: predicting carnivore densities from prey abundance. Proceedings of the National Academy of Sciences, 101(14), 4854-4858.)

Karanth, K. K., Nichols, J. D., Karanth, K. U., Hines, J. E., & Christensen Jr, N. L. (2010). The shrinking ark: patterns of large mammal extinctions in India. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1690), 1971-1979.

Karanth, K. U. (1995). Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. *Biological Conservation*, *71*(3), 333-338.

Karanth, K. U., Miquelle, D. G., Goodrich, J., & Gopalaswamy, A. (2017). Statement of Concern by Tiger Biologists on the WWF-GTF Report.

Karanth, K. U., & Nichols, J. D. (1998). Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*, *79*(8), 2852-2862.

Karanth, K. U., Nichols, J. D., Goodrich, J. M., Reddy, G. V., Mathur, V. B., Wibisono, H. T., Sunarto, S., Pattanavibool, A., & Gumal, M. T. (2017). Role of monitoring in global tiger conservation. *Methods for monitoring tiger and prey populations*, 1-13.

Karanth, K. U., Nichols, J. D., Kumar, N. S., & Hines, J. E. (2006). Assessing tiger population dynamics using photographic capture–recapture sampling. *Ecology*, *87*(11), 2925-2937.

Karanth, K. U., & Sunquist, M. E. (1992). Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. *Journal of Tropical Ecology*, *8*(01), 21-35. https://doi.org/10.1017/s0266467400006040

Karanth, K. U., & Sunquist, M. E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*, 439-450.

Karanth, K. U., & Sunquist, M. E. (2000). Behavioural correlates of predation by tiger (Panthera tigris), leopard (Panthera pardus) and dhole (Cuon alpinus) in Nagarahole, India. *Journal of Zoology*, *250*(2), 255-265. https://doi.org/10.1111/j.1469-7998.2000.tb01076.x

Kawanishi, K., & E. Sunquist, M. (2008). Food habits and activity patterns of the Asiatic golden cat (Catopuma temminckii) and dhole (Cuon alpinus) in a primary rainforest of Peninsular Malaysia. *Mammal Study*, *33*(4), 173-177. https://doi.org/10.3106/1348-6160-33.4.173

Kavčić, K., Palencia, P., Apollonio, M., Vicente, J., & Šprem, N. (2021). Random encounter model to estimate density of mountain-dwelling ungulate. European Journal of Wildlife Research, 67(5), 87. (Kavčić et al., 2021)

Kays, R., Arbogast, B. S., Baker-Whatton, M., Beirne, C., Boone, H. M., Bowler, M., Burneo, S. F., Cove, M. V., Ding, P., Espinosa, S., Gonçalves, A. L. S., Hansen, C. P., Jansen, P. A., Kolowski, J. M., Knowles, T. W., Lima, M. G. M., Millspaugh, J., McShea, W. J., Pacifici, K., . . . Spironello, W. R. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution*, *11*(6), 700-713. https://doi.org/10.1111/2041-210x.13370

KE, K. (2003). Ecology, conservation, and restoration of large carnivores in western North America. *Mammal community dynamics: management and conservation in the coniferous forests of Western North America*, 250-295.

Kelly, M. J. (2008). Design, evaluate, refine: camera trap studies for elusive species. *Animal Conservation*, *11*(3), 182-184.

Kelt, D. A., & Van Vuren, D. H. (2001). The ecology and macroecology of mammalian home range area. *The American Naturalist*, *157*(6), 637-645.

Keneisenuo, K., Choudhary, O. P., Kalita, P. C., Duro, S., Kalita, A., Doley, P. J., Arya, R. S., Debroy, S., & Priyanka, P. (2022). A comparative study on the morphology, radiography and computed tomography of the skull bones of barking deer (Muntiacus muntjak) and sambar deer (Rusa unicolor). *Folia Morphologica*, *81*(1), 164-174. https://doi.org/10.5603/fm.a2021.0015

Khosravi, R., Hemami, M. R., Malakoutikhah, S., Ashrafzadeh, M. R., & Cushman, S. A. (2021). Prey availability modulates predicted range contraction of two large felids in response to changing climate. Biological Conservation, 255, 109018.

Klaassen, B., & Broekhuis, F. (2018). Living on the edge: Multiscale habitat selection by cheetahs in a human-wildlife landscape. *Ecology and Evolution*, *8*(15), 7611-7623. https://doi.org/10.1002/ece3.4269

Kline, R. B. (2023). *Principles and practice of structural equation modeling*. Guilford publications.

Kohlberg, L. (1969). The cognitive-developmental approach to socialization. *Handbook of socialization theory and research. Chicago: Rand McNally*, 347-480.

Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLOS ONE*, *12*(10), e0186679. https://doi.org/10.1371/journal.pone.0186679

Kolowski, J. M., Oley, J., & McShea, W. J. (2021). High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. *Ecosphere*, *12*(2). https://doi.org/10.1002/ecs2.3350

Koolhaas, J., Korte, S., De Boer, S., Van Der Vegt, B., Van Reenen, C., Hopster, H., De Jong, I., Ruis, M., & Blokhuis, H. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, *23*(7), 925-935.

Kozakai, C., Seryodkin, I., Pigeon, K. E., Yamazaki, K., Wangchuk, S., Koike, S., Tsubota, T., & Jamtsho, Y. (2021). Asiatic black bear (Ursus thibetanus). In *Bears of the world: Ecology, conservation and management* (pp. 110-121). Cambridge University Press.

Krafte Holland, K., Larson, L. R., & Powell, R. B. (2018). Characterizing conflict between humans and big cats Panthera spp: A systematic review of research trends and management opportunities. *PLOS ONE*, *13*(9), e0203877. https://doi.org/10.1371/journal.pone.0203877

Kristensen, T. V., & Kovach, A. I. (2018). Spatially explicit abundance estimation of a rare habitat specialist: implications for <scp>SECR</scp> study design. *Ecosphere*, *9*(5), e02217. https://doi.org/10.1002/ecs2.2217

Lancia, R. A., Kendall, W. L., Pollock, K. H., & Nichols, J. (2005). Estimating the number of animals in wildlife populations.

Lande, R., Engen, S., & Saether, B.-E. (2003). *Stochastic population dynamics in ecology and conservation*. Oxford University Press, USA.

Laver, P. N., & Kelly, M. J. (2008). A Critical Review of Home Range Studies. *Journal of Wildlife Management*, *72*(1), 290-298. https://doi.org/10.2193/2005-589

Law, G., & Tatner, P. (1998). Behaviour of a captive pair of clouded leopards (Neofelis nebulosa): introduction without injury. *Animal Welfare*, *7*(1), 57-76.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008). Home Range Utilisation and Territorial Behaviour of Lions (Panthera leo) on Karongwe Game Reserve, South Africa. *PLOS ONE*, *3*(12), e3998. https://doi.org/10.1371/journal.pone.0003998

Lester, P. A., Moore, R. M., Shuster, K. A., & Myers, D. D. (2012). Anesthesia and analgesia. In *The laboratory rabbit, guinea pig, hamster, and other rodents* (pp. 33-56). Elsevier.

Levshina, N. (2020). Conditional Inference Trees and Random Forests. In (pp. 611-643). Springer International Publishing. https://doi.org/10.1007/978-3-030-46216-1_25

Lewis, P.-M., Burns, G. L., & Jones, D. (2017). Response and responsibility: humans as apex predators and ethical actors in a changing societal environment. *Food Webs*, *12*, 49-55.

Lham, D., Cozzi, G., Sommer, S., Wangchuk, S., Lham, K., & Ozgul, A. (2021). Ecological determinants of livestock depredation by the snow leopard Panthera uncia in Bhutan. *Journal of Zoology*, *314*(4), 275-284. https://doi.org/10.1111/jzo.12883

Linnell, J. D., Swenson, J. E., & Andersen, R. (2000). Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiversity & Conservation*, *9*, 857-868.

Lischka, S. A., Teel, T. L., Johnson, H. E., Reed, S. E., Breck, S., Carlos, A. D., & Crooks, K. R. (2018). A conceptual model for the integration of social and ecological information to understand human-wildlife interactions. *Biological Conservation*, *225*, 80-87.

Lo, A. Y., Chow, A. T., & Cheung, S. M. (2012). Significance of Perceived Social Expectation and Implications to Conservation Education: Turtle Conservation as a Case Study. *Environmental Management*, *50*(5), 900-913. https://doi.org/10.1007/s00267-012-9926-2

Loonam, K. E., Ausband, D. E., Lukacs, P. M., Mitchell, M. S., & Robinson, H. S. (2021). Estimating abundance of an unmarked, low-density species using cameras. The Journal of Wildlife Management, 85(1), 87-96.

Lovari, S., Pokheral, C. P., Jnawali, S. R., Fusani, L., & Ferretti, F. (2015). Coexistence of the tiger and the common leopard in a prey-rich area: the role of prey partitioning. *Journal of Zoology*, *295*(2), 122-131. https://doi.org/10.1111/jzo.12192

Loveridge, A., Wang, S. W., Frank, L., & Seidensticker, J. (2010). People and wild felids: conservation of cats and management of conflicts. *Biology and conservation of wild felids*.

Lozano, J., Olszańska, A., Morales-Reyes, Z., Castro, A. A., Malo, A. F., Moleón, M., Sánchez-Zapata, J. A., Cortés-Avizanda, A., von Wehrden, H., & Dorresteijn, I.

(2019). Human-carnivore relations: a systematic review. *Biological Conservation*, *237*, 480-492.

Lute, M. L., & Attari, S. Z. (2017). Public preferences for species conservation: choosing between lethal control, habitat protection and no action. *Environmental Conservation*, *44*(2), 139-147. https://doi.org/10.1017/s037689291600045x

Lyet, A., Waller, S., Chambert, T., Acevedo, P., Howe, E., Kühl, H. S., Naidoo, R., O'Brien, T., Palencia, P., Soutyrina, S. V., Vicente, J., Wearn, O. R., & Gray, T. N. E. (2023). Estimating animal density using the <scp>Space-to-Event</scp> model and bootstrap resampling with motion-triggered camera-trap data. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/rse2.361

Macdonald, D., & Loveridge, A. (2010). *The biology and conservation of wild felids* (Vol. 2). Oxford University Press.

Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature*, *301*(5899), 379-384. https://doi.org/10.1038/301379a0

Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild felids. *Biology and conservation of wild felids*, *1*, 3-58.

Macdonald, D. W., Mosser, A., & Gittleman, J. L. (2010). Felid society. Biology and conservation of wild felids, 125-160.

Mackenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, *9*(3), 300-318. https://doi.org/10.1198/108571104x3361

Mackenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). ESTIMATING SITE OCCUPANCY RATES WHEN DETECTION PROBABILITIES ARE LESS THAN ONE. *Ecology*, *83*(8), 2248-2255. https://doi.org/10.1890/0012-9658(2002)083[2248:esorwd]2.0.co;2

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2017). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.

Mackenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, *42*(6), 1105-1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

Majumder, A., Qureshi, Q., Sankar, K., & Kumar, A. (2017). Long-term monitoring of a Bengal tiger (Panthera tigris tigris) population in a human-dominated landscape of Central India. *European Journal of Wildlife Research*, *63*(1). https://doi.org/10.1007/s10344-016-1070-5

Mangiafico, S., & Mangiafico, M. S. (2017). Package 'rcompanion'. *Cran Repos*, *20*, 1-71.

Manly, B., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.

Manly, B. F., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). Introduction to resource selection studies. *Resource selection by animals: statistical design and analysis for field studies*, 1-15.

Manstead, A. S. R., & Parker, D. (1995). Evaluating and Extending the Theory of Planned Behaviour. *European Review of Social Psychology*, *6*(1), 69-95. https://doi.org/10.1080/14792779443000012

Marcus Rowcliffe, J., Carbone, C., Jansen, P. A., Kays, R., & Kranstauber, B. (2011). Quantifying the sensitivity of camera traps: an adapted distance sampling approach. *Methods in Ecology and Evolution*, *2*(5), 464-476. https://doi.org/10.1111/j.2041-210x.2011.00094.x

Marcus Rowcliffe, J., Carbone, C., Kays, R., Kranstauber, B., & Jansen, P. A. (2012). Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in*

Ecology and Evolution, *3*(4), 653-662. https://doi.org/10.1111/j.2041-210x.2012.00197.x

Maronde, L., McClintock, B. T., Breitenmoser, U., & Zimmermann, F. (2020). Spatial capture–recapture with multiple noninvasive marks: An application to camera-trapping data of the European wildcat (Felis silvestris) using R package multimark. *Ecology and Evolution*, *10*(24), 13968-13979. https://doi.org/10.1002/ece3.6990

Martins, Q., & Harris, S. (2013). Movement, activity and hunting behaviour of leopards in the Cederberg mountains, South Africa. *African Journal of Ecology*, *51*(4), 571-579. https://doi.org/10.1111/aje.12068

Mary, P., Debbarma, J., & Kumar Awadhesh, G. A. (2015). Population Density and Conservation Status of Indian Gaur (Bos gaurus gaurus) in Trishna Wildlife Sanctuary, Tripura, Northeast India. *Biodiversity Conservation-Challenges for the Future*, 97.

Mazerolle, M. J., & Mazerolle, M. M. J. (2017). Package 'AICcmodavg'. *R package*, *281*.

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E., & Contasti, A. L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, *79*(1), 4-12. https://doi.org/10.1111/j.1365-2656.2009.01613.x

McNab, B. K. (1963). Bioenergetics and the determination of home range size. *The American Naturalist*, *97*(894), 133-140.

McWherter, B., Bauchet, J., Ma, Z., Grillos, T., Asquith, N., Rathjen, M., & Markos, A. (2022). Compliance under control: Insights from an incentive-based conservation program in rural Bolivia. *Ecological Economics*, *194*, 107317.

Meeyai, S. (2016). Logistic regression with missing data: a comparisson of handling methods, and effects of percent missing values. *Journal of Traffic and Logistics Engineering*, *4*(2).

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, 1561-1571.

Messinger, L. N., Stuber, E. F., Chizinski, C. J., & Fontaine, J. J. (2019). Mortality, perception, and scale: Understanding how predation shapes space use in a wild prey population. *PLOS ONE*, *14*(9), e0222272.

Michalski, F., Boulhosa, R., Faria, A., & Peres, C. (2006). Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Animal Conservation*, *9*(2), 179-188.

Miller, J. R., Ament, J. M., & Schmitz, O. J. (2014). Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *Journal of Animal Ecology*, *83*(1), 214-222.

Miller, J. R. B., Jhala, Y. V., & Schmitz, O. J. (2016). Human Perceptions Mirror Realities of Carnivore Attack Risk for Livestock: Implications for Mitigating Human-Carnivore Conflict. *PLOS ONE*, *11*(9), e0162685. https://doi.org/10.1371/journal.pone.0162685

Miquelle, D. G., Smirnov, E. N., Quigley, H. G., Hornocker, M. G., Nikolaev, I. G., & Matyushkin, E. N. (1996). Food habits of Amur tigers in Sikhote-Alin Zapovednik and the Russian Far East, and implications for conservation. *Journal of Wildlife Research*, *1*(2), 138-147.

Moeller, A. K., & Lukacs, P. M. (2021). spaceNtime: an R package for estimating abundance of unmarked animals using camera-trap photographs. *Mammalian Biology*. https://doi.org/10.1007/s42991-021-00181-8

Moeller, A. K., Lukacs, P. M., & Horne, J. S. (2018). Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere*, *9*(8), e02331. https://doi.org/10.1002/ecs2.2331

Mohamed, A., Sollmann, R., Wong, S. T., Niedballa, J., Abrams, J. F., Kissing, J., & Wilting, A. (2021). Counting Sunda clouded leopards with confidence: incorporating

individual heterogeneity in density estimates. *Oryx*, *55*(1), 56-65. https://doi.org/10.1017/s0030605318001503

Mondal, K., Bhattacharjee, S., Gupta, S., Sankar, K., & Qureshi, Q. (2013). Home range and resource selection of'problem'leopards trans-located to forested habitat. *Current Science*, 338-345.

Mondal, K., Chourasia, P., Gupta, S., Sankar, K., & Qureshi, Q. (2022). Investigating resource selection of the Indian leopard Panthera.

Mondol, S., Karanth, K. U., & Ramakrishnan, U. (2009). Why the Indian Subcontinent Holds the Key to Global Tiger Recovery. *PLoS Genetics*, *5*(8), e1000585. https://doi.org/10.1371/journal.pgen.1000585

Montalvo, V. H., Sáenz-Bolaños, C., Cruz-Díaz, J. C., Kamilar, J. M., Carrillo, E., & Fuller, T. K. (2023a). Effects of camera trap placement on photo rates of jaguars, their prey, and competitors in northwestern Costa Rica. *Wildlife Society Bulletin*, *47*(2). https://doi.org/10.1002/wsb.1428

Morris, L. R., Proffitt, K. M., & Blackburn, J. K. (2016). Mapping resource selection functions in wildlife studies: Concerns and recommendations. *Applied Geography*, *76*, 173-183. https://doi.org/10.1016/j.apgeog.2016.09.025

Mugerwa, B., Niedballa, J., Planillo, A., Sheil, D., Kramer-Schadt, S., & Wilting, A. (2023). Global disparity of camera trap research allocation and defaunation risk of terrestrial mammals. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/rse2.360

Forests and Nature Conservation Act of Bhutan, 2023, (2023). https://www.nab.gov.bt/en/business/acts/

Nagy-Reis, M. B., Nichols, J. D., Chiarello, A. G., Ribeiro, M. C., & Setz, E. Z. (2017). Landscape use and co-occurrence patterns of Neotropical spotted cats. *PLOS ONE*, *12*(1), e0168441.

Nagy-Reis, M. B., Nichols, J. D., Chiarello, A. G., Ribeiro, M. C., & Setz, E. Z. F. (2017). Landscape Use and Co-Occurrence Patterns of Neotropical Spotted Cats. *PLOS ONE*, *12*(1), e0168441. https://doi.org/10.1371/journal.pone.0168441

Nakashima, Y., Fukasawa, K., & Samejima, H. (2018). Estimating animal density without individual recognition using information derivable exclusively from camera traps. Journal of Applied Ecology, 55(2), 735-744.

Naing, H., Ross, J., Burnham, D., Htun, S., & Macdonald, D. W. (2019). Population density estimates and conservation concern for clouded leopards Neofelis nebulosa, marbled cats Pardofelis marmorata and tigers Panthera tigris in Htamanthi Wildlife Sanctuary, Sagaing, Myanmar. *Oryx*, *53*(4), 654-662. https://doi.org/10.1017/s0030605317001260

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059.

NCD. (2008). *Bhutan National Human-Wildlife Conflicts Management Strategy*. Thimphu, Bhutan: Ministry of Agriculture and Forests

NCD. (2018). *Snow Leopard Conservation Action Plan (2018-2023) & Tiger Action Plan of Bhutan 2018-2023*. Thimphu, Bhutan: Ministry of Agriculture and Forests

Negi, C. S. (2005). Religion and biodiversity conservation: not a mere analogy. *The International Journal of Biodiversity Science and Management*, *1*(2), 85-96.

Newsome, T. M., Greenville, A. C., Ćirović, D., Dickman, C. R., Johnson, C. N., Krofel, M., Letnic, M., Ripple, W. J., Ritchie, E. G., Stoyanov, S., & Wirsing, A. J. (2017). Top predators constrain mesopredator distributions. *Nature Communications*, *8*(1), 15469. https://doi.org/10.1038/ncomms15469

Ngoprasert, D., Reed, D. H., Steinmetz, R., & Gale, G. A. (2012). Density estimation of Asian bears using photographic capture–recapture sampling based on chest marks. *Ursus*, *23*(2), 117-133.

Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in ecology & evolution*, *21*(12), 668-673.

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, *7*(12), 1457-1462. https://doi.org/10.1111/2041-210x.12600

Nielsen, S. E., Boyce, M. S., Stenhouse, G. B., & Munro, R. H. (2002). Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus*, 45-56.

Nijhawan, S., Mitapo, I., Pulu, J., Carbone, C., & Rowcliffe, J. M. (2019). Does polymorphism make the Asiatic golden cat the most adaptable predator in the Eastern Himalayas? *Ecology*, *100*(10), 1-4.

Nilsen, E. B., Herfindal, I., & Linnell, J. D. C. (2005). Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience*, *12*(1), 68-75. https://doi.org/10.2980/i1195-6860-12-1-68.1

NLCS. (2010). *Digital Elevation Model of Bhutan* Bhutan Geospatial Portal. https://www.nlcs.gov.bt/?page_id=38

Noonan, M. J., Tucker, M. A., Fleming, C. H., Akre, T. S., Alberts, S. C., Ali, A. H., Altmann, J., Antunes, P. C., Belant, J. L., Beyer, D., Blaum, N., Böhning-Gaese, K., Cullen, L., De Paula, R. C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., . . . Calabrese, J. M. (2019). A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*, *89*(2), e01344. https://doi.org/10.1002/ecm.1344

Norbu, L., Koirala, B. K., Dechen, U., Dorji, T., Tshering, D., Dorji, P., Dorji, L., Phuntsho, U., Lhendup, U., & Tobgay, S. (2022). Camera Trap Evidence of Polymorphic Golden Asiatic Cat (Catopuma temminckii) in Trashigang Forest Division, Eastern Bhutan. *Bhutan Journal of Natural Resources and Development*, *9*(1), 54-61.

Northrup, J. M., Hooten, M. B., Anderson, C. R., & Wittemyer, G. (2013). Practical guidance on characterizing availability in resource selection functions under a use–availability design. *Ecology*, *94*(7), 1456-1463. https://doi.org/10.1890/12-1688.1

Noss, A. J., Gardner, B., Maffei, L., Cuéllar, E., Montaño, R., Romero-Muñoz, A., Sollman, R., & O'Connell, A. F. (2012). Comparison of density estimation methods for mammal populations with camera traps in the Kaa-Iya del Gran Chaco landscape. *Animal Conservation*, *15*(5), 527-535. https://doi.org/10.1111/j.1469-1795.2012.00545.x

Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T., & Paquet, P. C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology*, *10*(4), 949-963.

NSB. (2017). *Population and Housing Census of Bhutan*. Thimphu Bhutan: National Statistic Bureau, Royal Government of Bhutan Retrieved from https://www.nsb.gov.bt/

O'Brien, S. J., & Johnson, W. E. (2005). BIG CAT GENOMICS. *Annual Review of Genomics and Human Genetics*, *6*(1), 407-429. https://doi.org/10.1146/annurev.genom.6.080604.162151

O'Connell, A. F., & Bailey, L. L. (2011). Inference for occupancy and occupancy dynamics. *Camera traps in animal ecology: methods and analyses*, 191-204.

Obbard, M. E., Howe, E. J., & Kyle, C. J. (2010). Empirical comparison of density estimators for large carnivores. *Journal of Applied Ecology*, *47*(1), 76-84. https://doi.org/10.1111/j.1365-2664.2009.01758.x

Oberosler, V., Tenan, S., Groff, C., Krofel, M., Augugliaro, C., Munkhtsog, B., & Rovero, F. (2022). First spatially-explicit density estimate for a snow leopard population in the Altai Mountains. *Biodiversity and Conservation*, *31*(1), 261-275. https://doi.org/10.1007/s10531-021-02333-1

Odden, M., Wegge, P., & Fredriksen, T. (2010). Do tigers displace leopards? If so, why? *Ecological research*, *25*, 875-881.

Ofstad, E. G., Herfindal, I., Solberg, E. J., Heim, M., Rolandsen, C. M., & Sæther, B. E. (2019). Use, selection, and home range properties: complex patterns of individual habitat utilization. *Ecosphere*, *10*(4), e02695.

Oliveira, T., Urra, F., López-Martín, J. M., Ballesteros-Duperón, E., Barea-Azcón, J. M., Moléon, M., Gil-Sánchez, J. M., Alves, P. C., Díaz-Ruíz, F., Ferreras, P., & Monterroso, P. (2018). Females know better: Sex-biased habitat selection by the European wildcat. *Ecology and Evolution*, *8*(18), 9464-9477. https://doi.org/10.1002/ece3.4442

Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife monographs*(62), 3-135.

Owen-Smith, N., & Mills, M. G. L. (2008). Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, *77*(1), 173-183. https://doi.org/10.1111/j.1365-2656.2007.01314.x

Palencia, P., Barroso, P., Vicente, J., Hofmeester, T. R., Ferreres, J., & Acevedo, P. (2022). Random encounter model is a reliable method for estimating population density of multiple species using camera traps. *Remote Sensing in Ecology and Conservation*. https://doi.org/10.1002/rse2.269

Palencia, P., Fernández-López, J., Vicente, J., & Acevedo, P. (2021). Innovations in movement and behavioural ecology from camera traps: day range as model parameter. *Methods in Ecology and Evolution*, *12*(7), 1201-1212. https://doi.org/10.1111/2041-210x.13609

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, *153*(5), 492-508.

Penjor, U., Macdonald, D. W., Wangchuk, S., Tandin, T., & Tan, C. K. W. (2018). Identifying important conservation areas for the clouded leopard Neofelis nebulosa in a mountainous landscape: Inference from spatial modeling techniques. *Ecology and Evolution*, *8*(8), 4278-4291. https://doi.org/10.1002/ece3.3970

Penjor, U., Tan, C. K. W., Wangdi, S., & Macdonald, D. W. (2019). Understanding the environmental and anthropogenic correlates of tiger presence in a montane conservation landscape. *Biological Conservation*, *238*, 108196.

Péron, G. (2019). Modified home range kernel density estimators that take environmental interactions into account. *Movement Ecology*, *7*(1). https://doi.org/10.1186/s40462-019-0161-9

Petersen, W. J., Steinmetz, R., Sribuarod, K., & Ngoprasert, D. (2020). Density and movements of mainland clouded leopards (Neofelis nebulosa) under conditions of high and low poaching pressure. *Global Ecology and Conservation*, *23*, e01117. https://doi.org/10.1016/j.gecco.2020.e01117

Piña-Covarrubias, E., Chávez, C., Chapman, M. A., Morales, M., Elizalde-Arellano, C., & Doncaster, C. P. (2022). Ecology of large felids and their prey in small reserves of the Yucatán Peninsula of Mexico. *Journal of Mammalogy*.

Pina Covarrubias, E. (2019). *Interactions of large felids with their prey and humans in the Yucatán Peninsula of Mexico and Belize* University of Southampton].

Pitimol, N., & Srikosamatara, S. (2023). Population ecology and genetic study of gaur (Bos gaurus) in a small protected area in Thailand. *Biodiversitas Journal of Biological Diversity*, *24*(6). https://doi.org/10.13057/biodiv/d240631

Pledger, S., & Efford, M. (1998). Correction of bias due to heterogeneous capture probability in capture-recapture studies of open populations. *Biometrics*, 888-898.

Pollock, K. H. (1982). A Capture-Recapture Design Robust to Unequal Probability of Capture. *The Journal of Wildlife Management*, *46*(3), 752. https://doi.org/10.2307/3808568

Pollock, K. H., Nichols, J. D., Brownie, C., & Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife monographs*, 3-97.

Pomeranz, E. F., Hare, D., Decker, D. J., Forstchen, A. B., Jacobson, C. A., Smith, C. A., & Schiavone, M. V. (2021). Successful wildlife conservation requires good governance. *Frontiers in Conservation Science*, *2*, 753289.

Pomeranz, E. F., & Stedman, R. C. (2020). Measuring good governance: piloting an instrument for evaluating good governance principles. *Journal of Environmental Policy & Planning*, *22*(3), 428-440. https://doi.org/10.1080/1523908x.2020.1753181

Pooley, S. P., Mendelsohn, J. A., & Milner-Gulland, E. J. (2014). Hunting Down the Chimera of Multiple Disciplinarity in Conservation Science. *Conservation Biology*, *28*(1), 22-32. https://doi.org/10.1111/cobi.12183

Preisser, E. L., & Bolnick, D. I. (2008). The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLOS ONE*, *3*(6), e2465.

Pugesek, B. H., Tomer, A., & Von Eye, A. (2003). *Structural equation modeling: applications in ecological and evolutionary biology*. Cambridge University Press.

Punjabi, G. A., Havmøller, L. W., Havmøller, R. W., Ngoprasert, D., & Srivathsa, A. (2022). Methodological approaches for estimating populations of the endangered dhole Cuon alpinus. *PeerJ*, *10*, e12905. https://doi.org/10.7717/peerj.12905

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology*, *52*(2), 137-154. https://doi.org/10.1086/409852

QGIS.org. (2023). *QGIS Geographic Information System*. In Open Source Geospatial Foundation Project. http://qgis.org

Qi, J., Holyoak, M., Ning, Y., & Jiang, G. (2020). Ecological thresholds and large carnivores conservation: Implications for the Amur tiger and leopard in China. Global Ecology and Conservation, 21, e00837.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge university press.

Rahman, D. A., Gonzalez, G., & Aulagnier, S. (2017). Population size, distribution and status of the remote and Critically Endangered Bawean deer Axis kuhlii. *Oryx*, *51*(4), 665-672. https://doi.org/10.1017/s0030605316000429

Ramirez-Reyes, C., Sims, K. R. E., Potapov, P., & Radeloff, V. C. (2018). Payments for ecosystem services in Mexico reduce forest fragmentation. *Ecological Applications*, *28*(8), 1982-1997. https://doi.org/10.1002/eap.1753

Rasphone, A., Kamler, J. F., & Macdonald, D. W. (2020). Temporal partitioning by felids, dholes and their potential prey in northern Laos. *Mammal Research*, *65*(4), 679-689. https://doi.org/10.1007/s13364-020-00524-9

Ray, J., Redford, K. H., Steneck, R., & Berger, J. (Eds.). (2013). Large carnivores and the conservation of biodiversity. Island Press.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051-4063.

Riley, S. J., Ford, J. K., Triezenberg, H. A., & Lederle, P. E. (2018). Stakeholder trust in a state wildlife agency. *The Journal of Wildlife Management*, *82*(7), 1528-1535. https://doi.org/10.1002/jwmg.21501

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass'. *Cran r*, *538*, 113-120.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. Science, 343(6167), 1241484.

RMNP. (2015). *Conservation Management Plan of Royal Manas National Park 2015-2020*. Gelephu, Bhutan: Department of Forests and Park Services, Royal Government of Bhutan

Rode, J., Gómez-Baggethun, E., & Krause, T. (2015). Motivation crowding by economic incentives in conservation policy: A review of the empirical evidence. *Ecological Economics*, *117*, 270-282.

Rodríguez-Recio, M., Burgos, T., Krofel, M., Lozano, J., Moleón, M., & Virgós, E. (2022). Estimating global determinants of leopard home range size in a changing world. *Animal Conservation*, *25*(6), 748-758. https://doi.org/10.1111/acv.12777

Rodríguez, M., Montiel, S., Cervera, M. D., Castillo, M. T., & Naranjo, E. J. (2012). The practice and perception of batida (group hunting) in a Maya community of Yucatan, Mexico. *Journal of Ethnobiology*, *32*(2), 212-227.

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology*, *62*(2), 327-335.

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of statistical software*, *48*, 1-36.

Rota, C. T., Fletcher Jr, R. J., Dorazio, R. M., & Betts, M. G. (2009). Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, *46*(6), 1173-1181. https://doi.org/10.1111/j.1365-2664.2009.01734.x

Rovero, F., & Marshall, A. R. (2009). Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology*, *46*(5), 1011-1017. https://doi.org/10.1111/j.1365-2664.2009.01705.x

Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). " Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, *24*(2).

Rowcliffe, J. M. (2021). Protocol for generating distance data from camera trap images using a simple computer vision approach, CTtracking V0.3.2. https://github.com/MarcusRowcliffe/CTtracking

Rowcliffe, J. M., & Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation*, *11*(3), 185-186.

Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, *45*(4), 1228-1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x

Rowcliffe, J. M., Jansen, P. A., Kays, R., Kranstauber, B., & Carbone, C. (2016). Wildlife speed cameras: measuring animal travel speed and day range using camera traps. *Remote Sensing in Ecology and Conservation*, *2*(2), 84-94. https://doi.org/10.1002/rse2.17

Rowcliffe, J. M., Kays, R., Carbone, C., & Jansen, P. A. (2013). Clarifying assumptions behind the estimation of animal density from camera trap rates. *The Journal of Wildlife Management*, *77*(5), 876-876. https://doi.org/10.1002/jwmg.533

Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, *5*(11), 1170-1179. https://doi.org/10.1111/2041-210x.12278

Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, *60*(1), 108-115.

Royle, J. A. (2011). Hierarchical spatial capture–recapture models for estimating density from trapping arrays. *Camera traps in animal ecology: methods and analyses*, 163-190.

Royle, J. A., Chandler, R. B., Sollmann, R., & Gardner, B. (2013). *Spatial capture-recapture*. Academic Press.

Royle, J. A., & Converse, S. J. (2014). Hierarchical spatial capture-recapture models: modelling population density in stratified populations. *Methods in Ecology and Evolution*, *5*(1), 37-43. https://doi.org/10.1111/2041-210x.12135

Royle, J. A., & Dorazio, R. M. (2006). Hierarchical models of animal abundance and occurrence. *Journal of Agricultural, Biological, and Environmental Statistics*, *11*, 249-263.

Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Elsevier.

Royle, J. A., Karanth, K. U., Gopalaswamy, A. M., & Kumar, N. S. (2009). Bayesian inference in camera trapping studies for a class of spatial capture–recapture models. *Ecology*, *90*(11), 3233-3244.

Royle, J. A., Nichols, J. D., Karanth, K. U., & Gopalaswamy, A. M. (2009). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, *46*(1), 118-127. https://doi.org/10.1111/j.1365-2664.2008.01578.x

Russo, G., Milks, A., Leder, D., Koddenberg, T., Starkovich, B. M., Duval, M., Zhao, J. X., Darga, R., Rosendahl, W., & Terberger, T. (2023). First direct evidence of lion hunting and the early use of a lion pelt by Neanderthals. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-42764-0

Sagoe, A. A., Aheto, D. W., Okyere, I., Adade, R., & Odoi, J. (2021). Community participation in assessment of fisheries related ecosystem services towards the establishment of marine protected area in the Greater Cape Three Points area in Ghana. *Marine Policy*, *124*, 104336.

Sandell, M., & Gittleman, J. (1989). Carnivore behavior, ecology, and evolution. *The mating tactics and spacing patterns of solitary carnivores*, 164-182.

Sanderson, E. W., Forrest, J., Loucks, C., Ginsberg, J., Dinerstein, E., Seidensticker, J., Leimgruber, P., Songer, M., Heydlauff, A., & O'Brien, T. (2010). Setting priorities for tiger conservation: 2005–2015. In *Tigers of the World* (pp. 143-161). Elsevier.

Sangay, T., Rajaratnam, R., & Vernes, K. (2014). Wildlife camera trapping in the Himalayan kingdom of Bhutan with recommendations for the future. *Camera Trapping for Animal Monitoring. CSIRO Publishing, Collingwood*, 87-98.

Sangay, T., & Vernes, K. (2008). Human–wildlife conflict in the Kingdom of Bhutan: patterns of livestock predation by large mammalian carnivores. *Biological Conservation*, *141*(5), 1272-1282.

Santini, G., Abolaffio, M., Ossi, F., Franzetti, B., Cagnacci, F., & Focardi, S. (2022). Population assessment without individual identification using camera-traps: A comparison of four methods. *Basic and Applied Ecology*, *61*, 68-81.

Schaub, M., & Abadi, F. (2011). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, *152*, 227-237.

Schaub, M., Ullrich, B., Knötzsch, G., Albrecht, P., & Meisser, C. (2006). Local population dynamics and the impact of scale and isolation: a study on different little owl populations. *Oikos*, *115*(3), 389-400. https://doi.org/10.1111/j.2006.0030-1299.15374.x

Schaus, J., Uzal, A., Gentle, L. K., Baker, P. J., Bearman-Brown, L., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D. M., Sutherland, C. S., & Yarnell, R. W. (2020). Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation*, *6*(4), 514-528. https://doi.org/10.1002/rse2.153

Schelling, T. C. (1984). Incentives for environmental protection.

Schermelleh-Engel, K., Moosbrugger, H., & Müller, H. (2003). Evaluating the fit of structural equation models: Tests of significance and descriptive goodness-of-fit measures. *Methods of psychological research online*, *8*(2), 23-74.

Schreiber, J. B., Nora, A., Stage, F. K., Barlow, E. A., & King, J. (2006). Reporting Structural Equation Modeling and Confirmatory Factor Analysis Results: A Review. *The Journal of Educational Research*, *99*(6), 323-338. https://doi.org/10.3200/joer.99.6.323-338

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters* (Vol. 8). Blackburn press Caldwell, New Jersey.

Segerson, K. (2022). Group Incentives for Environmental Protection and Natural Resource Management. *Annual Review of Resource Economics*, *14*(1), 597-619. https://doi.org/10.1146/annurev-resource-111920-020235

Seidensticker, J., Jackson, P., & Christie, S. (1999). *Riding the tiger: tiger conservation in human-dominated landscapes*. Cambridge University Press.

Selvan, K., Lyngdoh, S., Habib, B., & Gopi, G. (2014). Population density and abundance of sympatric large carnivores in the lowland tropical evergreen forest of Indian Eastern Himalayas. *Mammalian Biology*, *79*(4), 254-258.

Shakeel, U., Minhas, R. A., Awan, M. S., Bibi, S. S., & Iftikhar, N. (2015). Conservation Status of Himalayan Grey Goral (Naemorhedus goral bedfordi Hardwicke, 1825) in Machiara National Park, Azad Jammu and Kashmir, Pakistan. *Pakistan Journal of Zoology*, *47*(5).

Sharma, P., Chettri, N., & Wangchuk, K. (2021). Human–wildlife conflict in the roof of the world: Understanding multidimensional perspectives through a systematic review. *Ecology and Evolution*.

Shi, C., Xu, J., Roberts, N. J., Liu, D., & Jiang, G. (2023). Individual automatic detection and identification of big cats with the combination of different body parts. *Integrative Zoology*, *18*(1), 157-168. https://doi.org/10.1111/1749-4877.12641

Sillero-Zubiri, C. (2001). (13 Interactions between carnivores and local communities: conflict or co-existence? CLAUDIO SILLERO-ZUBIRI AND M. KAREN LAURENSON. *Carnivore conservation*, *5*, 282.

Silmi, M., Putra, K., Amran, A., Huda, M., Fanani, A. F., Galdikas, B. M., Anggara S, P., & Traeholt, C. (2021). Activity and ranging behavior of leopard cats (Prionailurus bengalensis) in an oil palm landscape. *Frontiers in Environmental Science*, *9*, 651939.

Silverman, B. W. (2018). Density Estimation for Statistics and Data Analysis. https://doi.org/10.1201/9781315140919

Silverman, K., Jarvis, B. P., Jessel, J., & Lopez, A. A. (2016). Incentives and motivation. *Translational Issues in Psychological Science*, *2*(2), 97-100. https://doi.org/10.1037/tps0000073

Simcharoen, A., Savini, T., Gale, G. A., Simcharoen, S., Duangchantrasiri, S., Pakpien, S., & Smith, J. L. D. (2014). Female tiger Panthera tigris home range size and prey abundance: important metrics for management. *Oryx*, *48*(3), 370-377. https://doi.org/10.1017/s0030605312001408

Sinclair, A., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature*, *425*(6955), 288-290.

Sing, T., Sander, O., Beerenwinkel, N., & Lengauer, T. (2015). Package 'ROCR'. *Visualizing the performance of scoring classifiers*, 1-14.

Singh, P., & Macdonald, D. W. (2017). Populations and activity patterns of clouded leopards and marbled cats in Dampa Tiger Reserve, India. *Journal of Mammalogy*, *98*(5), 1453-1462. https://doi.org/10.1093/jmammal/gyx104

Singh, R., Qureshi, Q., Sankar, K., Krausman, P. R., & Goyal, S. P. (2014). Evaluating heterogeneity of sex-specific capture probability and precision in camera-trap population estimates of tigers. *Wildlife Society Bulletin*, *38*(4), 791-796. https://doi.org/10.1002/wsb.471

Skinner, C. J. (2014). Probability proportional to size (PPS) sampling. *Wiley StatsRef: Statistics Reference Online*, 1-5.

Skov, M. W., Hawkins, S. J., Volkelt-Igoe, M., Pike, J., Thompson, R. C., & Doncaster, C. P. (2011). Patchiness in resource distribution mitigates habitat loss: insights from high-shore grazers. *Ecosphere*, *2*(5), 1-17.

Smith, J. A., Suraci, J. P., Hunter, J. S., Gaynor, K. M., Keller, C. B., Palmer, M. S., Atkins, J. L., Castañeda, I., Cherry, M. J., Garvey, P. M., Huebner, S. E., Morin, D. J., Teckentrup, L., Weterings, M. J. A., & Beaudrot, L. (2020). Zooming in on mechanistic predator–prey ecology: Integrating camera traps with experimental methods to reveal the drivers of ecological interactions. *Journal of Animal Ecology*, *89*(9), 1997-2012. https://doi.org/10.1111/1365-2656.13264

Smith, K. D., Snider, R. J., Dembiec, D. P., Siegford, J. M., & Ali, A. B. (2023). Effects of a modern exhibit design on captive tiger welfare. *Zoo Biology*, *42*(3), 371-382.

Snider, M. H., Athreya, V. R., Balme, G. A., Bidner, L. R., Farhadinia, M. S., Fattebert, J., Gompper, M. E., Gubbi, S., Hunter, L. T. B., Isbell, L. A., Macdonald, D. W., Odden, M., Owen, C. R., Slotow, R., Spalton, J. A., Stein, A. B., Steyn, V., Vanak, A. T., Weise, F. J., . . . Kays, R. (2021). Home range variation in leopards living across the human density gradient. *Journal of Mammalogy*, *102*(4), 1138-1148. https://doi.org/10.1093/jmammal/gyab068

Sollmann, R., Furtado, M. M., Gardner, B., Hofer, H., Jácomo, A. T., Tôrres, N. M., & Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation*, *144*(3), 1017-1024.

Songorwa, A. N. (1999). Community-based wildlife management (CWM) in Tanzania: are the communities interested? *World development*, *27*(12), 2061-2079.

Srbek-Araujo, A. C. (2018). Do female jaguars (Panthera onca Linnaeus, 1758) deliberately avoid camera traps? *Mammalian Biology*, *88*, 26-30. https://doi.org/10.1016/j.mambio.2017.11.001

Srivathsa, A., Karanth, K. K., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2014). On a Dhole Trail: Examining Ecological and Anthropogenic Correlates of Dhole Habitat Occupancy in the Western Ghats of India. *PLOS ONE*, *9*(6), e98803. https://doi.org/10.1371/journal.pone.0098803

Srivathsa, A., Sharma, S., & Oli, M. K. (2020). Every dog has its prey: Range-wide assessment of links between diet patterns, livestock depredation and human interactions for an endangered carnivore. *Science of the Total Environment*, *714*, 136798.

Stabach, J. A., Wittemyer, G., Boone, R. B., Reid, R. S., & Worden, J. S. (2016). Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. *Ecosphere*, *7*(8), e01428. https://doi.org/10.1002/ecs2.1428

Stanton, R. A., Thompson, F. R., & Kesler, D. C. (2015). Site occupancy of brown-headed nuthatches varies with habitat restoration and range-limit context. *The Journal of Wildlife Management*, *79*(6), 917-926. https://doi.org/10.1002/jwmg.903

Stevenson, B. C., Fewster, R. M., & Sharma, K. (2022). Spatial correlation structures for detections of individuals in spatial capture–recapture models. *Biometrics*, *78*(3), 963-973. https://doi.org/10.1111/biom.13502

Street, G. M., Potts, J. R., Börger, L., Beasley, J. C., Demarais, S., Fryxell, J. M., McLoughlin, P. D., Monteith, K. L., Prokopenko, C. M., Ribeiro, M. C., Rodgers, A. R., Strickland, B. K., Van Beest, F. M., Bernasconi, D. A., Beumer, L. T., Dharmarajan, G., Dwinnell, S. P., Keiter, D. A., Keuroghlian, A., . . . Vander Wal, E. (2021). Solving the sample size problem for resource selection functions. *Methods in Ecology and Evolution*, *12*(12), 2421-2431. https://doi.org/10.1111/2041-210x.13701

Su, B., & Martens, P. (2017). Public attitudes toward animals and the influential factors in contemporary China. *Animal Welfare*, *26*(2), 239-247. https://doi.org/10.7120/09627286.26.2.239

Suksavate, W., Songsasen, N., Khiowsree, N., Charaspet, K., Pla-Ard, M., Chanachai, Y., Thomas, W., & Srinopawan, K. (2020). Home range, movement and habitat selection of dholes (Cuon alpinus) in Khao Yai National Park, Thailand. *Biodiversitas Journal of Biological Diversity*, *21*(12).

Sunarto, Sollmann, R., Mohamed, A., & Kelly, M. J. (2013). CAMERA TRAPPING FOR THE STUDY AND CONSERVATION OF TROPICAL CARNIVORES. *Raffles Bulletin of Zoology*, 21-42. <Go to ISI>://WOS:000327498800004

Sunquist, M., & Sunquist, F. (2002). Wild Cats of the World University of Chicago Press. *Chicago, USA*.

Sunquist, M., & Sunquist, F. (2017). *Wild cats of the world*. University of chicago press.

Suryawanshi, K. R., Khanyari, M., Sharma, K., Lkhagvajav, P., & Mishra, C. (2019). Sampling bias in snow leopard population estimation studies. *Population Ecology*, *61*(3), 268-276.

Sutherland, C., Royle, J. A., & Linden, D. W. (2019). oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. *Ecography*, *42*(9), 1459-1469. https://doi.org/10.1111/ecog.04551

Tallis, H., & Lubchenco, J. (2014). Working together: A call for inclusive conservation. *Nature*, *515*(7525), 27-28.

Tan, C. K. W., Rocha, D. G., Clements, G. R., Brenes-Mora, E., Hedges, L., Kawanishi, K., Mohamad, S. W., Rayan, D. M., Bolongon, G., & Moore, J. (2017). Habitat use and predicted range for the mainland clouded leopard Neofelis nebulosa in Peninsular Malaysia. *Biological Conservation*, *206*, 65-74.

Tarugara, A., Clegg, B. W., Gandiwa, E., & Muposhi, V. K. (2019). Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (Panthera pardus) population. *Global Ecology and Conservation*, *18*, e00627.

R Core Team. (2023). *R: A Language and Environment for Statistical Computing*. In R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Tempa, T., Hebblewhite, M., Goldberg, J. F., Norbu, N., Wangchuk, T. R., Xiao, W., & Mills, L. S. (2019). The spatial distribution and population density of tigers in mountainous terrain of Bhutan. *Biological Conservation*, *238*, 108192.

Tempa, T., Hebblewhite, M., Mills, L. S., Wangchuk, T. R., Norbu, N., Wangchuk, T., Nidup, T., Dendup, P., Wangchuk, D., & Wangdi, Y. (2013). Royal Manas National Park, Bhutan: a hot spot for wild felids. *Oryx*, *47*(2), 207-210.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., & Lambert, T. D. (2001). Ecological meltdown in predator-free forest fragments. *Science*, *294*(5548), 1923-1926.

Thinley, P., Rajaratnam, R., Lassoie, J. P., Morreale, S. J., Curtis, P. D., Vernes, K., ... & Dorji, P. (2018). The ecological benefit of tigers (Panthera tigris) to farmers in reducing crop and livestock losses in the eastern Himalayas: implications for conservation of large apex predators. Biological Conservation, 219, 119-125.

Thinley, P., Rajaratnam, R., Norbu, L., Dorji, L., Tenzin, J., Namgyal, C., Yangzom, C., Wangchuk, T., Wangdi, S., & Dendup, T. (2021). Understanding human–canid conflict and coexistence: socioeconomic correlates underlying local attitude and support toward the endangered dhole (Cuon alpinus) in Bhutan. *Frontiers in Conservation Science*, *2*, 691507.

Tighe, M., Muñoz-Robles, C., Reid, N., Wilson, B., & Briggs, S. V. (2012). Hydrological thresholds of soil surface properties identified using conditional inference tree analysis. *Earth Surface Processes and Landforms*, *37*(6), 620-632. https://doi.org/10.1002/esp.3191

Tobler, M. W., & Powell, G. V. N. (2013). Estimating jaguar densities with camera traps: Problems with current designs and recommendations for future studies. *Biological Conservation*, *159*, 109-118. https://doi.org/10.1016/j.biocon.2012.12.009

Treves, A., & Karanth, K. U. (2003). Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, *17*(6), 1491-1499. https://doi.org/10.1111/j.1523-1739.2003.00059.x

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., & Avgar, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466-469.

Turner, R. A., Fitzsimmons, C., Forster, J., Mahon, R., Peterson, A., & Stead, S. M. (2014). Measuring good governance for complex ecosystems: perceptions of coral reef-dependent communities in the Caribbean. *Global Environmental Change*, *29*, 105-117.

Turpie, J. K. (2003). The existence value of biodiversity in South Africa: how interest, experience, knowledge, income and perceived level of threat influence local willingness to pay. *Ecological Economics*, *46*(2), 199-216.

Twining, J. P., McFarlane, C., O'Meara, D., O'Reilly, C., Reyne, M., Montgomery, W. I., Helyar, S., Tosh, D. G., & Augustine, B. C. (2022). A comparison of density estimation methods for monitoring marked and unmarked animal populations. *Ecosphere*, *13*(10). https://doi.org/10.1002/ecs2.4165

Viollaz, J., Rizzolo, J. B., Long, B., Trung, C. T., Kempinski, J., Rawson, B. M., Reynald, D., Quang, H. X., Hien, N. N., Dung, C. T., Huyen, H. T., Thuy Dung, N. T., & Gore, M. L. (2022). Potential for informal guardianship in community-based wildlife crime prevention: Insights from Vietnam. *Nature Conservation*, *48*, 123-147. https://doi.org/10.3897/natureconservation.48.81635

Wang, M., & Grimm, V. (2007). Home range dynamics and population regulation: an individual-based model of the common shrew Sorex araneus. *Ecological modelling*, *205*(3-4), 397-409.

Wang, S. W. (2010). Estimating population densities and biomass of ungulates in the temperate ecosystem of Bhutan. *Oryx*, *44*(3), 376-382. https://doi.org/10.1017/s0030605310000487

Wang, S. W., & Macdonald, D. (2006). Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological conservation*, *129*(4), 558-565.

Wang, S. W., & Macdonald, D. W. (2006). Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biological Conservation*, *129*(4), 558-565. https://doi.org/10.1016/j.biocon.2005.11.024

Wang, S. W., & Macdonald, D. W. (2009). The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. *Biological Conservation*, *142*(3), 606-613. https://doi.org/10.1016/j.biocon.2008.11.023

Wang, Y., Nickel, B., Rutishauser, M., Bryce, C. M., Williams, T. M., Elkaim, G., & Wilmers, C. C. (2015). Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. *Movement Ecology*, *3*(1), 2. https://doi.org/10.1186/s40462-015-0030-0

Warton, D. I., Stoklosa, J., Guillera-Arroita, G., Mackenzie, D. I., & Welsh, A. H. (2017). Graphical diagnostics for occupancy models with imperfect detection. *Methods in Ecology and Evolution*, *8*(4), 408-419. https://doi.org/10.1111/2041-210x.12761

WBCSD. (2011). Guide to Corporate Ecosystem Valuation: A framework for improving corporate decision-making. *World Business Council on Sustainable Development*.

Wearn, O., & Glover-Kapfer, P. (2017). Camera-trapping for conservation: a guide to best-practices. *WWF conservation technology series*, *1*(1), 2019-2004.

Wearn, O. R., Bell, T. E. M., Bolitho, A., Durrant, J., Jessica, Nijhawan, S., Thorley, J., & Rowcliffe, J. M. (2022). Estimating animal density for a community of species using information obtained only from camera-traps. *Methods in Ecology and Evolution*(10), 2248-2261. https://doi.org/10.1111/2041-210x.13930

Wearn, O. R., & Glover-Kapfer, P. (2019). Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science*, *6*(3), 181748. https://doi.org/10.1098/rsos.181748

Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H., & Ewers, R. M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PloS one*, *8*(11), e77598.

Wegge, P., & Mosand, H. M. (2015). Can the mating system of the size-monomorphic Indian muntjac (Muntiacus muntjak) be inferred from its social structure, spacing behaviour and habitat? A case study from lowland Nepal. *Ethology Ecology & Evolution*, *27*(2), 220-232. https://doi.org/10.1080/03949370.2014.921794

West, S. G., Taylor, A. B., & Wu, W. (2012). Model fit and model selection in structural equation modeling. *Handbook of structural equation modeling*, *1*, 209-231.

Westley, P. A., Berdahl, A. M., Torney, C. J., & Biro, D. (2018). Collective movement in ecology: from emerging technologies to conservation and management. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1746), 20170004.

White, G. C., & Garrott, R. A. (2012). *Analysis of wildlife radio-tracking data*. Elsevier.

Wiik, E., Jones, J. P., Pynegar, E., Bottazzi, P., Asquith, N., Gibbons, J., & Kontoleon, A. (2020). Mechanisms and impacts of an incentive-based conservation program with evidence from a randomized control trial. *Conservation Biology*, *34*(5), 1076-1088.

Witmer, G. W. (2005). Wildlife population monitoring: some practical considerations. *Wildlife Research*, *32*(3), 259. https://doi.org/10.1071/wr04003

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. Royal Society open science, 4(7), 170052.

Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, *70*(1), 164-168. https://doi.org/10.2307/1938423

Worton, B. J. (1995). Using Monte Carlo simulation to evaluate kernel-based home range estimators. *The Journal of Wildlife Management*, 794-800.

Wright, W. J., Irvine, K. M., & Rodhouse, T. J. (2016). A goodness-of-fit test for occupancy models with correlated within-season revisits. *Ecology and Evolution*, *6*(15), 5404-5415. https://doi.org/10.1002/ece3.2292

Wu, J., Wang, J., Zhu, Y., Bu, X., Xiang, R., Lu, Q., Cui, S., Hao, Y., Sheng, Y., & Meng, X. (2020). Summer habitat selection and impacts of human disturbance on leopard cats (Prionailurus bengalensis). *Ecosystem Health and Sustainability*, *6*(1), 1856630.

WWF. (2016). https://wwf.panda.org/wwf_news/?265197/Global-wild-tiger-population-increases-but-still-a-long-way-to-go

WWF. (2019a). Two Parks In Bhutan Receive International CA|TS Accreditation. http://www.wwfbhutan.org.bt/?uNewsID=356671

WWF. (2019b). *TWO PARKS IN BHUTAN RECEIVE INTERNATIONAL CA|TS ACCREDITION*. https://wwf.panda.org/wwf_news/?356671/TWO-PARKS-IN-BHUTAN-RECEIVE-INTERNATIONAL-CATS-ACCREDITION

WWF. (2023). WWF congratulates Bhutan for increase in wild tiger population. https://wwf.panda.org/wwf_news/?9396441/WWF-congratulates-Bhutan-for-increase-in-wild-tiger-population

Wysong, M. L., Hradsky, B. A., Iacona, G. D., Valentine, L. E., Morris, K., & Ritchie, E. G. (2020). Space use and habitat selection of an invasive mesopredator and sympatric, native apex predator. *Movement Ecology*, *8*(1). https://doi.org/10.1186/s40462-020-00203-z

Xu, L., Xu, W., Jiang, C., Dai, H., Sun, Q., Cheng, K., Lee, C.-H., Zong, C., & Ma, J. (2022). Evaluating Communities' Willingness to Participate in Ecosystem Conservation in Southeast Tibetan Nature Reserves, China. *Land*, *11*(2), 207. https://doi.org/10.3390/land11020207

Yang, T., Druică, E., Zhang, Z., Hu, Y., Cirella, G. T., & Xie, Y. (2022). Predictors of the Behavioral Intention to Participate in Saiga Antelope Conservation among Chinese Young Residents. *Diversity*, *14*(5), 411. https://doi.org/10.3390/d14050411

Young, S., Rode-Margono, J., & Amin, R. (2018). Software to facilitate and streamline camera trap data management: A review. *Ecology and evolution*, *8*(19), 9947-9957. https://doi.org/10.1002/ece3.4464

Zero, V. H., Sundaresan, S. R., O'Brien, T. G., & Kinnaird, M. F. (2013). Monitoring an endangered savannah ungulate, Grevy's zebra Equus grevyi: choosing a method for estimating population densities. *Oryx*, *47*(3), 410-419.

Zhang, W. (2016). *Analysis of the Supply and Perception of the Recreation Service from Urban Forests in Beijing* Beijing Forestry University Beijing, China].

Zimmermann, F., & Foresti, D. (2016). Capture-recapture methods for density estimation In Rovero F. & Zimmermann F.(Eds.), Camera trapping for wildlife research (pp. 95–141). In: Exeter, UK: Pelagic Publishing.[Google Scholar].