UNIVERSITY OF SOUTHAMPTON

FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES

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The ecology of jaguars (*Panthera onca*) in a human-influenced landscape

by

Rebecca Foster

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Correction Sheet

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ABSTRACT

FACULTY OF MEDICINE, HEALTH AND LIFE SCIENCES, SCHOOL OF BIOLOGICAL SCIENCES

Doctor of Philosophy

THE ECOLOGY OF JAGUARS IN A HUMAN-INFLUENCED LANDSCAPE

by Rebecca Jacqueline Foster

Despite intense persecution over the last century, the jaguar (*Panthera onca*) has sustained a wide geographic distribution, perhaps due to its elusive nature and rather flexible ecology. This study investigated jaguar ecology under anthropogenic pressures in Belize, Central America. A suite of methods including camera-trap surveys, diet analysis, discussions with local stakeholders, and population simulations were used to study a population of jaguars spanning the boundary of a protected forest.

Camera-trap data combined with capture-recapture population models are increasingly used to estimate the density of mammals such as jaguars with individually identifiable coat patterns. A review of current methods highlighted problems associated with estimating the sizes of low-density populations. Simulations to assess the robustness of the method found that camera failure can negatively or positively bias the abundance estimate, depending on the particular nature of capture histories. The most commonly used model estimator in the literature was nevertheless robust to failures of up to 10% of trap-occasions. Pooling trap-occasions reduced the effect of camera failure. Sub-sampling data from large-scale surveys indicated a threshold survey area of ~170 km^2, below which estimates of density were inflated and unreliable. For surveys exceeding this threshold size, jaguar density varied across the landscape from the protected forest to the human-influenced lands such that <30% contiguous forest precipitated reduction. Reduced densities with distance from contiguous forest and proximity to human habitation may result principally from direct conflicts with people.

The influence of anthropogenic factors on the coexistence of jaguars and pumas (*Puma concolor*) was investigated by comparing their habitat use and feeding ecology. Diet was analysed from the largest sample to date of scats from one area identified to species. Jaguars and pumas made similar use of the secondary rainforest, despite differences in diet. Although both cats relied heavily on one species of small prey (5-10 kg), for jaguars this was the nine-banded armadillo (*Dasypus novemcinctus*) while for pumas it was the paca (*Agouti paca*). Both cats took some larger prey, mainly white-lipped peccaries (*Dictolyes pecari*) by jaguars and red brocket deer (*Mazama americana*) by pumas. Energetics models indicated that reproduction may be limited for either species if large prey are unavailable for females with dependents. Outside the forest block, jaguars rarely ate large wild prey species; instead, a diet of smaller wild prey was supplemented with large domestic stock. Pumas were scarce outside the protected forest, possibly reflecting a reluctance to utilise domestic species near human developments and competition with humans for their preferred prey of paca and deer, which are also prized regionally as game species.

Human-induced mortality of jaguars outside the protected forest was mainly associated with livestock predation. Both sexes were equally active on pastures and were persecuted at a similar rate. Many of those killed were young individuals in good body condition, suggesting high turnover rates augmented by immigration. Population simulations indicated that the observed levels of human-induced mortality could be maintained only with immigration from the protected forest. Without natal dispersers (2-4 year olds) immigrating in, the hunted population had zero probability of persisting beyond 20 years. Simulations indicated that the jaguar populations inhabiting the two main protected forest blocks in Belize could persist in isolation and maintain low levels of emigration to the unprotected population. However the probability of all three populations persisting for 100 years fell to ~50% if the migration of natal dispersers from the protected to unprotected population exceeded ~12% per year.

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Declaration of authorship

I, Rebecca Foster, declare that the thesis entitled ‘The ecology of jaguars (*Panthera onca*) in a human-influenced landscape’ and the work presented in the thesis are both my own, and have been generated by me as the result of my own original research.

I confirm that:

- this work was done wholly or mainly while in the candidature for a research degree at this University;
- where any part of this thesis has been previously submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
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I have acknowledged all main sources of help;

- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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Definitions and abbreviations

BAS	Belize Audubon Society: co-manage CBWS for the Belize Government
BFD	Belize Forestry Department
BLPA	Belize Livestock Producers Association
CBWS	Cockscomb Basin Wildlife Sanctuary
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
ETA	Effective trapping area: *the area utilised by the study animals, may extend beyond the trapping grid*
GLM	General Linear Model
GIS	Geographic Information System
GPS	Global Positioning System
IUCN	International Union for the Conservation of Nature
λ	Finite rate of population growth (annual multiplicative growth rate)
MDM	Maximum distance moved: *maximum distance moved by an individual between captures in a trapping grid*
MMDM	Mean maximum distance moved: *maximum distance moved between captures in a trapping grid, averaged over all individuals*
MWVP	Mean weight of vertebrate prey: *a method for comparing diet between carnivores calculated as the geometric mean body mass of prey items taken*
OS	Ordnance Survey (maps)
p-hat	Estimate of capture (detection) probability modelled from the patterns of encounters with individuals
r	Exponential growth rate (net rate of population increase per capita)
Trap-night	Discrete trapping occasion at a given trap site, *e.g. 20 traps set every night for 7 days = 20 × 7 = 140 trap-nights*. (Also called trap-occasion).
UTM	Universal Transverse Mercator (coordinate system)
WCS	Wildlife Conservation Society
WRI	World Resources Institute

‘Rare, elusive, dangerous – carnivores are difficult to study’

Gittleman *et al.* (2001)

Chapter 1

Carnivores in human-influenced landscapes

Introduction

Twenty-three percent of terrestrial mammalian species are threatened with extinction, averaging approximately one third of the species in each order (mean ± SD = 0.35 ± 0.29, IUCN 2007). Contemporary declines in terrestrial mammal populations are associated with regions of high human density or their resultant impacts such as intensive agriculture, urbanisation and hunting (Ceballos and Ehrlich 2002, Cardillo *et al.* 2004). An estimated 83% of the land on Earth is influenced by human activity (Sanderson *et al.* 2002a). The current human population is predicted to increase from 6.6 billion to 9 billion by 2042 (US Census Bureau 2007). The survival of terrestrial mammal species will increasingly depend on their ability to co-exist with people in human-influenced landscapes.

Carnivores have a worldwide distribution. Many have suffered population declines and range contractions over the past 200 years; for example the range of tigers (*Panthera tigris*) has decreased by 93% (Dinnerstein *et al.* 2007), grizzly bears (*Ursus arctos horribilis*) by 95-98% (Pyare *et al.* 2004), and the range of grey wolves (*Canis lupus*), originally the widest of all mammals, has reduced by one-third (Mech and Boitani 2004). Twenty-eight percent of terrestrial carnivore species are now threatened (IUCN 2007). The population status of only 108 of 245 terrestrial carnivores is known, but of these 82% are in decline (IUCN 2007). It is not surprising then that biological characteristics associated with extinction vulnerability are frequently found in carnivore species (Gittleman *et al.* 2001): low genetic variability; small geographical range; few, small or declining populations; low population densities; large home ranges; large body size; and specialized niche requirements. The effect of these biological traits may be exacerbated by human activity and modification of the landscape. For example, Cardillo *et al.* (2004) showed that carnivore biology interacts with human population density to determine extinction risk: 38% of the variation in extinction risk of carnivore species with low exposure to humans was explained by biology, specifically density and geographic range; whilst in those with high exposure to humans, biology (geographic range, density and gestation length) explained 80% of the variation.

Carnivore declines may be expected where there is human population growth (Woodroffe 2000) because human activity, whether intentional or accidental, is major cause of carnivore mortality (Woodroffe and Ginsberg 1998, Woodroffe 2001, Riley *et al.* 2003) and this has been correlated with local human density (in Africa) (Harcourt *et* *al*. 2001). Despite this, human density alone is a weak indicator of carnivore extinction (Woodroffe 2000, Linnell *et al*. 2001) because there is variation in the ability of different carnivore species to adapt to human-modified habitats, and temporal and spatial variation in people's activities and attitudes towards carnivores (Woodroffe 2000); for example Linnell *et al*. (2001) showed that certain large carnivores are able to persist today in North America and Europe, even though human density is high and the landscape is heavily modified, because human behaviour is now controlled (reserves are protected effectively and hunting regulations are enforced). As such, social, cultural and economic factors, as well as carnivore biology, will influence the ability of carnivores to survive the threats arising from a growing human population in a landscape increasingly dominated by people.

This doctoral study was conceived with the aim of improving understanding of the ecology of jaguars (*Panthera onca*) in a human-influenced landscape. The jaguar has persisted despite intense persecution over the last century, perhaps due to its elusive nature and rather flexible ecology. However the limits of its adaptability to anthropogenic pressures are still unknown and in need of further research, the premise for this thesis. This study was designed to investigate the ecology of jaguars utilising a human-influenced landscape in Belize, Central America. The jaguar population in this region is considered to have a high probability of survival (Sanderson *et al*. 2002b) and provides an important link in the corridor through Central to South America. This study explores density, demographics, habitat use and diet in a jaguar population spanning the boundary of a protected forest; and assesses the sustainability of lethal control in response to livestock predation.

The aim of this chapter is to review contemporary anthropogenic threats faced by terrestrial carnivores and discuss factors which may influence their resilience in an increasingly human-dominated world. Cats are highlighted as a carnivore family at particular threat from human activities, and the jaguar as one which is relatively poorly known. The ecology and conservation of jaguars are then discussed, identifying gaps in our current knowledge and explaining how this thesis attempts to fill them. The specific thesis objectives and study area are described at the end of this chapter.

Threats facing carnivores

The over-riding human threat facing all terrestrial mammals is habitat transformation, which impacts ~86% of all threatened mammal species (Baillie *et al.* 2004). Habitat transformation degrades or destroys the habitat required for forage, prey or refugia; and, through fragmentation of the landscape, intensifies all other anthropogenic threats by bringing species into closer contact with humans and their activities.

Habitat fragmentation

Habitat fragmentation is of particular concern for large carnivores because they often have large home ranges and so are forced to move through, or utilise, human-influenced landscapes; for example in a retrospective study of 12 large carnivore species (> 11 kg), Woodroffe (2001) found that relative extinction ‘proneness’ increased with female home range size, regardless of body size or density. Indeed female home range size has been shown to determine the critical reserve size (size at which probability of survival is 50%) in large carnivores (Woodroffe and Ginsberg 1998). Ultimately the effectiveness of any reserve will depend not only on the ranging behaviour of the target species, but also the size and physiognomy of the reserve and the spatial needs of humans occupying the same landscape (Revilla *et al.* 2001).

As the size of optimal habitat decreases, not only do the available resources within the fragment decrease, but the effect of a smaller core to edge ratio increases the impact of human activity from the surrounding matrix (‘edge-effects’). For carnivores these ‘edge-effects’ may include the impact of hunters removing prey from further inside the core habitat, and, for wide-ranging carnivores, the overlapping of their home ranges or dispersal movements with the human matrix and its associated threats. It has been suggested that for extremely wide-ranging carnivores such as African wild-dogs (*Lycaon pictus*) which suffer high rates of human-induced mortality outside reserves, protected areas < 10,000 km^2 will be insufficient to ensure their survival (Woodroffe and Ginsberg 1999, Woodroffe *et al.* 2007b). Even species with relatively small home ranges may endure edge-effects; for example Revilla *et al.* (2001) showed that survival probability of a medium-sized carnivore (6-7 kg), the Eurasian badger (*Meles meles*), in a protected area of 550 km^2 in Spain increased with distance into the reserve. They estimated that edge-effects (human-related mortality of badgers living close to the edge of the reserve) reduced the effectiveness of the protected area by 36%. A study of Iberian lynx (*Lynx pardina*) from the same region attributed the high annual mortality of male dispersers (86%) compared to male residents (12%) to movement across high risk areas within a fragmented habitat (Ferreras *et al*. 1992). Smaller fragments or reserves are often indicative of more intense human activity outside the fragment, which in turn exacerbates the edge-effects further; for example reserve size in Africa and the USA is negatively correlated with the surrounding human population density, thus smaller reserves are located in more adverse landscapes and may suffer more intense edge-effects than large reserves (Harcourt *et al*. 2001, Parks and Harcourt 2002).

A subtle effect of habitat fragmentation is that the vulnerability of competitively inferior species within carnivore guilds may increase in human-influenced landscapes: fragmentation may prevent subordinate species re-colonising isolated habitats following competitive exclusion by dominant species, and so alter local extinction rates (Creel 2001). Subordinate species may be displaced to marginal areas by dominant competitors, potentially increasing the risk of contact with humans (Woodroffe 2001).

Extreme fragmentation can isolate populations, for example the Asiatic lion (*Panthera leo persica*) is restricted to a single site, the Gir Forest in north western India which is surrounded by human development (Sunquist and Sunquist 2002). Small isolated populations may be subject to inbreeding depression, for example the Florida panther (*Puma concolor coryi*) (Hendrick 1995).

The subsequent threats discussed here may be the direct result of, or intensified by, habitat fragmentation.

Reduction of wild prey abundance

Prey density is a key factor determining carnivore density both within and between species: within carnivore species, population density is positively correlated with prey biomass density; and as carnivore size increases the number of carnivores supported by a given prey biomass decreases (10,000 kg of prey supports ~90 kg of carnivore) (Carbone and Gittleman 2002). Reductions in prey availability, either through direct competition with man or indirectly through habitat loss, may have repercussions for carnivore survival; for example Karanth *et al*. (2004) demonstrated a functional relationship between abundances of tiger and their prey and suggest that wild prey depletion may be a principal cause of tiger population decline.

The response of carnivores to lowered prey availability varies: it may reduce fecundity, reduce neonatal, juvenile and adult survival, increase home range and increase the number of transients and dispersers (for a review see Fuller and Sievert 2001). Thus, within a human-dominated landscape it is likely that depletion of wild prey will both lower the ability of populations to compensate for human-related mortality, and further increase risk of contact with humans through home range expansion and utilisation of domestic livestock as an alternative to wild prey.

In some situations management of game species may be detrimental to carnivores. In African National Parks, where hunting is prohibited, high densities of large ungulates support high densities of large carnivores, lions (*Panthera leo*) and hyaenas, which in turn competitively exclude smaller carnivores, cheetahs (*Acinonyx jubatus*) and African wild dogs; in contrast cheetahs and wild dogs can exist in Game Reserves because there hunting is allowed which depresses prey densities, thus lion and hyaena densities are lower (Creel *et al.* 2001). The decline of the Iberian lynx in Spain has been linked to the introduction of myxomatosis to control rabbits (*Oryctolagus cuniculus*) the main prey of lynx (Rodriguez and Delibes 2002). More recently in Spain, high densities of wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) promoted for sport hunting have also been found to reduce the availability of rabbit, the preferred prey of the threatened wildcat (*Felis silvestris*) (Lozano *et al*. 2007).

Direct persecution

Many carnivore species are targeted for the harvest and trade of body parts, recreational sport hunting, and in response to real or perceived threats to human life or livelihood. Some carnivore populations, in particular canids such as coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), may persist despite intensive persecution because reproduction compensates for harvest mortality (e.g. Knowlton 1972, Harris and Saunders 1993, Knowlton 1999). Often populations cannot compensate for sustained exploitation; for example Stoner *et al.* (2006) found that hunting intensity > 40% of adult pumas for ≥ 4 years reduced density and resulted in a population that was younger, less productive and socially unstable compared to an un-hunted population. Novaro *et al*. (2005) demonstrated that the hunting of culpeo foxes (*Pseudalopex culpaeus*) in Argentina is non-compensatory: human-induced mortality and natural mortality were additive so the persistence of local populations was dependent on emigration from protected areas.

Historically many terrestrial carnivore populations were heavily exploited for the fur trade; this has declined since the 1980s following the 1973 implementation of an international treaty (CITES) banning trade in wildlife products derived from endangered species (Johnson *et al*. 2001). Although large-scale commercial hunting for the wildlife trade has diminished, illegal hunting and sale of body parts continues on the black market; for example international trade in tiger parts for traditional Chinese medicine remains extensive and threatens the few remaining tiger populations (Dinerstein *et al*. 2007).

Pro-active or retaliatory lethal control to defend human life and livelihood from threats of carnivore attack is common throughout the world (Thirgood *et al*. 2005, Sillero-Zuibiri and Laurenson 2001). In particular, efforts to protect livestock or game species can impact heavily on carnivore populations, for example this has led to the extinction of Falkland Island wolf (*Dusicyon australis*), and dramatic range contractions of grey wolves and red wolves (*Canis rufus*) in the US and the African wild dog (Woodroffe *et al*. 2005). Indiscriminate pro-active lethal control to pre-empt livestock predation may exacerbate the problem through the injuring of individuals such that they can no longer hunt wild prey, or the removal and replacement of ‘well-behaved’ residents with naïve immigrants who predate livestock (Rabinowitz 1986a, Frank and Woodroffe 2001).

Trophy hunting of large charismatic carnivores is popular and lucrative (Frank and Woodroffe 2001). It is often regarded as a conservation tool because off-take rates are considered low and high prices may offer economic incentives in areas where eco-tourism may not be suitable (Lindsey *et al*. 2007). However the selective harvesting of specific age or sex classes can disrupt the social system and demography of the population; although the extent to which this may influence population growth is not well known (Milner *et al*. 2007). Large males are often targeted for trophy hunting; the removal of resident males from a population has been documented to increase rates of infanticide by new males which move into the area, for example in lions (Loveridge *et al*. 2007), leopards (*Panthera pardus*) (Balme *et al*. 2007), and brown bears (Swenson *et al*. 1997). More subtle effects have also been noted, for example it has been suggested that the reproductive rates in a hunted population of brown bears were lower (smaller litter sizes) than a non-hunted population because females utilised sub-optimal foraging grounds in order to avoid potentially infanticidal immigrant males (Wielgus and

Bunnell 2000); and lion prides may suffer cleptoparasitism of kills by hyaenas where adult males have been removed (Milner *et al*. 2007).

Incidental deaths and disturbance

Carnivores may be killed 'accidentally' by human activities, for example in road traffic accidents or through the poisoning or trapping of non-target species in vermin control (e.g. Ferreras *et al*. 1992, Nielsen and Woolf 2002, Seiler *et al*. 2004, Fournier-Chambrillon *et al*. 2004, Haines *et al*. 2005, Virgos and Travaini 2005, Orlowski and Nowak 2006, Gaydos *et al*. 2007, Riley *et al*. 2007). Non-natural incidental deaths may have a considerable impact on the survival of small, endangered populations, especially if mortality is non-compensatory. For example a seven-year study of the endangered Iberian lynx population in the Doñana area of south-western Spain revealed that 75% of mortality (18/24 deaths) was due to human activities: 37% of deaths were attributed to capture in traps and snares set for fox and rabbits or attack by poachers' dogs, a further 21% were killed in road traffic accidents and 17% drowned in wells (Ferreras *et al*. 1992). Such high rates of non-natural mortality raised concerns for the survival of the population, estimated to be only 40-50 individuals.

Various studies have shown temporal and/ or spatial avoidance by carnivores of areas with high human activity, such as settlements and roads, or otherwise pristine areas disturbed by hunters, ecotourism or field researchers; for example sun bears (*Helarctos malayanus*) and tigers (Griffiths and van Schaik 1993), pumas (Janis and Clark 2002), bobcats (*Lynx rufus*) (George and Crooks 2006, Riley *et al*. 2003, Riley 2006) and wolves (Theuerkauf *et al*. 2003). The relationships between such behaviour and survival are not always clear, although behavioural plasticity can often facilitate persistence in human-dominated landscapes (discussed later). In sensitive species however, disturbance from human activities may negatively impact on normal activity budgets and potentially lower survival, for example Kerley *et al*. (2002) suggested that reduced foraging efficiency of female tigers caused by human disturbance at kill sites in Russia may lower survival and reproduction.

Large carnivores are frequently reported to avoid paved or high-use roads, for example wolves (Theuerkauf *et al*. 2003, Whittington *et al*. 2004) and pumas (Dickson *et al*. 2005). Such behaviour, whilst reducing vehicle mortality, could facilitate population isolation in highly fragmented habitats, for example a genetic study of bobcat and coyote populations on either side of a busy highway near Los Angeles found that individuals used it as a home range boundary and it limited gene flow between populations on either side (Riley *et al*. 2006).

Disease transmission from domestic carnivores

Domestic carnivores can act as reservoirs of parasites and infectious pathogens which may 'spill over' into wild carnivore populations; for example domestic dogs have been linked to outbreaks of rabies in African wild dogs and Ethiopian wolves (*Canis simensis*) and canine distemper in lions (RoelkeParker *et al*. 1996, Woodroffe *et al*. 1997, Randall *et al*. 2006, Cleaveland *et al*. 2007). Such diseases may lower the resilience of wild populations or drive them to extinction if populations are small, for example the African wild dog population of the Serengeti was extirpated by rabies originating from local domestic dogs (Woodroffe *et al*. 1997). The risk may be greater where veterinary care is low, populations of domestic carnivores are high and there is close contact with wild species; for example during the 1990s the annual growth of the Zimbabwean domestic dog population on reserve boundaries was estimated to be ~ 6.5%, raising concerns about risks of disease transmission to wild carnivores which prey on diseased dogs (Butler *et al*. 2004). More recently several studies have highlighted the potential risk of disease transmission to wild carnivores from domestic dogs and cats living in villages neighbouring national parks in South America (Fiorello *et al*. 2004, Fiorello *et al*. 2006, Fiorello *et al*. 2007, Whiteman *et al*. 2007). Evidence of exposure to domestic carnivore parasites and pathogens has been detected in at least six species of wild neotropical felids and canids (Deem and Emmons 2005, Whiteman *et al*. 2007). Whiteman *et al*. (2007) suggest that the solitary behaviour of many neotropical carnivores, with the exception of coati (*Nasua nasua*), may prohibit outbreaks of canine distemper virus in rainforest environments such as the Amazon, although they caution that escalating habitat fragmentation may increasingly bring wild and domestic carnivores into contact and reverse this trend.

Introduced species

Introduced and domestic mammals can negatively impact on endemic carnivore species in other ways, not only as potential disease reservoirs. Hybridisation with domestic cats threatens the genetic integrity of European wildcats (Beaumont *et al*. 2001, Pierpaoli *et al*. 2003). Endangered European mink (*Mustela lutreola*) have declined across their range, partly due to competition with the introduced American mink (*Mustela vison*) (Mustelid Specialist Group 1986, Dunstone 1993). Domestic dogs in India may compete with endangered Indian wolves (formerly *Canis lupus pallipes*, now *C. indica*) for blackbuck (*Antelope cervicapra*) prey (Jhala 1993). Less commonly a non-carnivore species may impact negatively on a carnivore. The island fox (*Urocyon littoralis*) declined following the introduction of feral pigs in the Californian Channel Islands because the pigs provided additional prey for the natural predator of the fox, the golden eagle (*Aguila chrysaetos*). Eagle numbers increased as did predation on the fox (Roemer *et al*. 2001).

The resilience of carnivores and concerns for cats

The preceding introductory review demonstrates how carnivores face a range of anthropogenic threats. Habitat fragmentation and ranging behaviour both play an important role in the level of exposure to these threats. However some carnivore species are more resilient than others; some may even flourish in human-dominated landscapes. The resilience of carnivores to anthropogenic threats depends on the ability of individuals to adapt their behaviour to human-disturbed environments; demographic compensation to mitigate effects of human-induced mortality; and dispersal to connect fragmented populations (Weaver *et al*. 1996). For instance, in a simplified scenario Weaver *et al*. (1996) demonstrated how, within the same landscape, the relative resilience of three sympatric carnivores to disturbance, persecution and fragmentation, may differ based on their foraging behaviour, fecundity and dispersal ability (illustrated in Table 1.1).

Table 1.1 The resilience of three sympatric carnivores to disturbance, persecution and fragmentation at the individual, population and meta-population level. Based on Weaver *et al.* (1996)

Species	Diet	Reproduction	Dispersal	Resilience
Gray wolf	Generalist omnivore	High annual productivity	High dispersal ability	HIGH
Puma	Generalist carnivore; requires specific habitat for stalking prey	Biennial productivity	Intermediate dispersal	↕
Grizzly bear	Omnivore; requires high quality forage at certain times of year	Triennial productivity	Females philopatric to maternal home range	LOW
Level	*individual*	*population*	*meta-population*	
Threat	*disturbance*	*persecution*	*fragmentation*	

In reality, mechanisms of resilience are complex, as shown in Figure 1.1. Individual resilience (through behavioural flexibility) will influence both population and meta-population resilience: it will affect the probability that individuals will avoid human-induced mortality during their life-time, allowing successful dispersal and reproduction. Local population resilience (through demographic compensation) will depend on reproductive and social flexibility (Frank and Woodroffe 2001) in response to anthropogenic threats. In highly exploited populations immigration (dispersal ability) may also be important if reproduction does not compensate for mortality. Finally, meta-population resilience (through successful dispersal between populations) will depend on (and influence) population resilience, and depend on dispersal ability, which in turn depends on individual resilience.

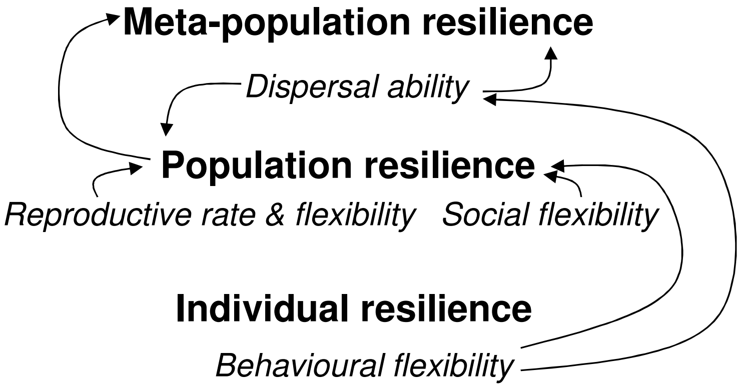


Figure 1.1 Levels and mechanisms of resilience to anthropogenic threat

Individual Resilience

Behavioural plasticity within a species allows individual adaptation to a changing environment, even in the face of rapid anthropogenic change (e.g. Beckmann and Berger 2003a). Frequently this involves shifts in activity to avoid contact with people or areas of high human activity; and/or changes in foraging behaviour related to the depletion of the preferred natural prey or the superabundance of anthropogenic sources of food such as garbage or livestock. Frank and Woodroffe (2001) suggest that selection for behavioural plasticity under conditions of competition from larger predators and a fluctuating prey base has pre-adapted certain species to survive in human-influenced landscapes. As such we may expect smaller, omnivorous carnivore species to be more resilient to many human threats than larger, strictly carnivorous species. It could also be argued that carnivores which hunt by stalking, such as many felids, have evolved cryptic behaviours with which to catch prey and that this elusive behaviour may pre-dispose them to successfully avoid humans.

Behavioural response to human activity

Behavioural adaptation to human disturbances which may pose a threat (e.g. hunters or traffic) usually involves spatial or temporal avoidance. For example, activity often becomes more nocturnal in highly exploited populations so as to avoid hunters (e.g. coyotes, Kitchen *et al*. 2000) and in or near urban areas, as documented in bobcats and coyotes (Riley *et al*. 2003, Riley 2006, George and Crooks 2006), black bears (*Ursus americanus*) (Beckmann and Berger 2003a) and grey wolves (Theuerkauf *et al*. 2003). Disturbance may range from hikers to hunters; and from relatively pristine habitat to more developed landscapes with agriculture, roads and urban settlements. Avoidance of ‘benign’ human activity may be disadvantageous if it disrupts foraging or other behaviours to such an extent that survival may be compromised (e.g. Kerley *et al*. 2002). In some cases, habituation to predictable human activities may be preferable to avoidance behaviour (George and Crooks 2006).

Different levels of ‘tolerance’ to urban areas are observed among carnivore species (e.g. Crooks 2002, Riley *et al*. 2003, Riley 2006). Urban tolerance is likely to be associated with the degree of diet flexibility and the availability of food resources within urban areas compared to rural or wild areas (next section), as well as species-specific responses to human activities, roads and the urban environment *per se*. Within developed areas some species are more sensitive to roads than others, for example Riley (2006) found that bobcats appeared to avoid crossing paved roads, whilst foxes crossed roads regularly. Intraspecific variation in use of urban areas has also been documented, for example, in southern and northern California male bobcats used areas near or in urban areas more than did female bobcats (Riley *et al*. 2003, Riley 2006). If female carnivores tend to be less tolerant of landscapes with high human activity this knowledge should be incorporated into management plans (Riley 2006). There is evidence to support the hypothesis that ‘street wise’ individuals which regularly use developed habitats may learn to utilise roads safely whilst naïve individuals who use urban areas less often are at greater risk of vehicle mortality; for example raccoons (*Procyon lotor*) in urban areas of north-eastern Illinois suffered less traffic mortalities than raccoons in suburban and rural areas (Prange *et al*. 2003).

Behavioural response to prey availability

Flexibility in foraging behaviour and diet will allow prey switching if the preferred prey become depleted; for example, African wild dogs are able to survive on small prey in areas where their preferred large ungulate prey is scarce (Woodroffe *et al.* 2007a). The narrower the diet, the less resilient the species will be to environmental changes, therefore omnivorous generalists will be more resilient than strictly carnivorous specialists. Many carnivore species utilise anthropogenic sources of food. Strictly carnivorous species such as large felids will predate on domestic livestock, bringing them into direct conflict with people, in the long run a negative adaptation; for example lions (Patterson *et al.* 2004), and pumas (Mazzolli *et al.* 2002). Omnivorous species however, such as canids, ursids, hyaenids and some mustelids, may greatly benefit from foraging on garbage, at relatively low risk. These species may thrive in urban habitats; for example urban densities exceeding rural densities have been recorded in many generalist carnivores including raccoons (Smith and Engeman 2002, Prange *et al.* 2003), grey foxes (*Urocyon cinereoargenteus*) (Riley 2006), black bears (Beckmann and Berger 2003b), coyotes (Fedriani *et al.* 2001) and San Joaquin kit foxes (*Vulpes macrotis mutica*) (Cypher and Frost 1999).

Population Resilience

High reproductive rates, reproductive and social flexibility (Frank and Woodroffe 2001) and dispersal ability between populations, will help a population compensate for human-induced mortality. There is high variability among carnivores and their resilience to human-induced mortality may be difficult to predict; for example mustelids and small felids are not resilient to non-selective methods of red fox control, yet the high reproductive rate, density dependent reproduction and broad diet of foxes allow them to persist under such conditions (Virgos and Travaini 2005).

Reproductive rate tends to scale with size: large species reproduce later and more slowly than small species, but, in the absence of human-induced mortality, also live longer. Under conditions of intense anthropogenic mortality it may be expected that smaller carnivores may be more resilient than larger carnivore species.

The energy requirements of a female increase when she is pregnant, lactating, or with dependents. In order to reproduce females must have access to abundant food. In fragmented and disturbed habitats generalist species will be more likely to secure sufficient food resources for reproduction than those with specialist diets, or those which compete with humans for wild prey; for example tigers (Sunsquist *et al.*1999). It is also likely that diet will influence the interval of dependency (period between birth and dispersal) and so influence reproductive rate. Species which must learn specialized hunting strategies from their mother will likely remain dependent longer than those with generalist diets.

Many mustelids are able to delay implantation of the embryo (Ferguson *et al.* 2006) so that females can select mates when they are available but delay development and birth until the environmental conditions are favourable. This flexible reproductive strategy may increase the resilience of the mother and her progeny to periods of resource scarcity. Spotted hyaenas (*Crocuta crocuta*) can alter the sex ratio of their off-spring in response to clan size (Holekemp and Smale 1995) this may also increase population resilience particularly against selective exploitation of a particular sex.

Coyotes have been show to increase their litter size in response to high levels of persecution (Knowlton 1972). Indeed the resilience of coyote populations to exploitation is formidable. Group-living in carnivores may facilitate larger litter sizes, or group-hunting; therefore species such as coyotes that are socially flexible (able to shift from solitary to pair or group-living) according to conditions will likely achieve higher reproductive rates. Social flexibility can also help secure mates, for example the formation of coalitions in male cheetahs (Sunquist and Sunquist 2002). In species which are not socially flexible the negative effects of increased mortality may be exacerbated by the disruption it causes to the social system, for example increased levels of infanticide.

Several studies of large carnivores suggest that reproduction does not increase in response to exploitation, for example pumas (Stoner *et al.* 2006); and the sustainability of heavily exploited carnivore populations may entirely depend on immigration from neighbouring unexploited populations, for example cuelpos (Novaro *et al.* 2005), wolverines (Krebs *et al.* 2004), wolves (Jedrzejewska *et al.* 1996), lynx (Slough and Mowat 1996) and pumas (Sweanor *et al.* 2000). This emphasises the importance of corridors of permeable habitat between exploited and un-exploited populations, as well as the need for flexible dispersal ability.

Usually in carnivores, as in other mammals, females tend to be philopatric, staying close to their natal range; their dispersal is generally governed by the availability of resources such as den and food. In contrast males disperse in search of a territory where they can secure females. Strong philopatry in females may be beneficial if conditions are favourable but detrimental if a population is suffering from intense human-induced mortality: the sex ratio may become male-biased and reproduction may decrease as new males are recruited into the area but resident females are killed (e.g. Robinson *et al*. 2008). Flexibility in male dispersal is also important in maintaining a balance between travelling far enough to promote genetic mixing but not so far that human-induced mortality during dispersal becomes a risk. For example, male red foxes and male badgers are more likely to disperse at low population densities (see Frank and Woodroffe 2001). This behaviour probably functions to increase the probability of finding a mate.

Concerns for cats

Understanding mechanisms of individual and population resilience can help to identify taxa which may be at particular risk from anthropogenic threats. As discussed, resource generalists with flexible reproduction, social systems and dispersal may be better adapted to a human-influenced landscape than more specialist species. In a study of habitat fragment use by carnivores in California, Crooks (2002) found that both body size and resource specialisation of carnivores were associated with patch occupancy. Small generalist carnivores such as raccoons, grey fox and domestic cats occupied most fragments; and within the larger carnivores, coyotes occurred in most patches whilst pumas were highly sensitive to fragmentation. A similar pattern was observed in a study of carnivores in the hyper-fragmented forest landscape of southern Brazil: all cat species, jaguar, puma, ocelot (*Leopardus pardalis*) and jaguarondi (*Herpailurus yaguarondi*), were only found in the larger fragments, whilst matrix-tolerant opportunistic omnivores, tayra (*Eira barbara*), crab-eating fox (*Cerdocyon thous*) and coati, occupied most forest fragments and were not sensitive to patch size (Michalski and Peres 2005).

Many extant carnivores are now adapted to omnivorous diets, an asset in human-influenced landscapes. Cats (family *Felidae*) are perhaps the most carnivorous of all the *Carnivora* families and therefore least adaptable to reductions in the availability of wild prey; whilst simultaneously posing the greatest perceived threat to humans and their livestock. Forty-seven percent of cat species are threatened and a further 22% are near threatened (IUCN 2007). All 36 cat species are facing population reduction, comprising 41% of all carnivore species known to be in decline (IUCN 2007). In comparison, only

23% (8/35) of dog species (family *Canidae*) are considered threatened (although six are data deficient); and of the 108 terrestrial carnivore species for which suitable data exist, stable or increasing populations are found only in canids (16 species) and mustelids (three species) (IUCN 2007). Prey depletion has been attributed to population decline in 92% (33/36) of cat species (IUCN 2007). In contrast only one canid is threatened due to prey depletion (the endangered dhole, *Cuon alpinus*) (IUCN 2007), presumably because of the more varied omnivorous diets of dog species.

Within the *Felidae* the larger species may be considered to be most at risk in human-influenced landscapes: in addition to reasons already discussed such as relatively large home ranges, low reproductive potential and decline in prey through habitat loss, they face direct competition with man for the same game species (e.g. Nuñez *et al.* 2000a, Leite *et al.* 2002) and the increased threat of direct persecution associated with both livestock predation and trophy-hunting of large charismatic carnivores. In particular, livestock loss is considered the greatest source of conflict between humans and large cats, and the major cause underlying their disappearance from considerable areas of their former range (Mazzolli *et al.* 2002). The current ranges of the two largest cats, the tiger and the lion, are 7% and 17% of their historic ranges respectively (Dinnerstein, 2007, Anon 2007). Both species are endangered; tigers are most at risk, with a total effective population size estimated at below 2,500 mature breeding individuals, and no subpopulation containing more than 250 (Cat Specialist Group 2002). In contrast, the range contraction of the third largest cat, the jaguar, has been less severe, despite intense exploitation for its skins throughout the 20th century (Smith 1976, McMahan 1982, Payán and Trujillo 2006) and on-going persecution to protect livestock (Rabinowitz 2005). Jaguars show wide variation in their diet, activity patterns and land tenure system (e.g. Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986) and their resilience thus far is undoubtedly linked to this behavioural and social flexibility. Unlike other widely distributed large carnivore species, the jaguar population has not yet been genetically isolated in any part of its range, suggesting that it is able to utilise human-dominated landscapes (Eizirik *et al.* 2001, Rabinowitz 2006). Maintaining population connectivity throughout the jaguar range will be essential for its long-term survival; however the limits of its adaptability to anthropogenic pressures are still unknown and in need of further research.

Jaguar ecology and conservation

Jaguars are the largest of the six felids which inhabit the neotropics (Table 1.2). They utilise a wide range of lowland habitats (up to about 2,000 m) including rainforest, wet grasslands, mangroves and even arid scrub, although they tend to be associated with water (Emmons and Feer 1990, Kitchener 1991, Nowell and Jackson 1996, Reid 1997). Historically (*circa* 1900) the jaguar ranged from the southern USA to southern Argentina, occupying ~19.1 million km^2. Over the past 100 years their range has contracted by at least 37%, mainly in northern Mexico, the southern US, northern Brazil and southern Argentina (Sanderson *et al*. 2002b). They have been completely extirpated from El Salvador, Uruguay, and the US, as well as from large areas of Argentina (the Argentine Monte and Pampas grasslands), Panama and Nicaragua (Emmons and Feer 1990, Sanderson *et al*. 2002b). Their status is currently unknown in 3.3 million km^2 of their historic range. Of the remaining 15.8 million km^2 where they once ranged, they now occupy just 8.75 million km^2 (Figure 1.2). This comprises 48 geographically distinct areas, varying from 114 km^2 to 7 million km^2. The largest is centred on the Amazon Basin in South America, and forms 88% of the known range of jaguars. In Central America the tropical moist lowland forest of the Selva Maya of Guatemala, Mexico and Belize forms another contiguous area and has been identified as one in which the probability of the long-term survival of the jaguar remains high (Sanderson *et al*. 2002b).

Jaguars are sympatric with another large cat, the puma, across their entire range. Together they are the top predators of the neotropics. Because the puma is a potential competitor of the jaguar, any discussion of jaguar ecology should consider the puma also. Pumas have the largest geographic range of any terrestrial mammal in the Western hemisphere, spanning Canada to southern Argentina and Chile; however, although widespread they are generally uncommon or rare (Emmons and Feer 1990, Sunquist and Sunquist 2002).

Table 1.2 Body size of the neotropical *Felidae* (from Emmons & Feer 1990 and Reid 1997)

		Head-Body (mm)	**Tail (mm)**	**Weight (kg)**
Jaguar	*Panthera onca*	1100 - 1850	440 - 560	30 - 158
Puma	*Puma concolor*	860 - 1540	610 - 960	24 – 120
Oceolot	*Leopardus pardalis*	640 - 875	260 - 419	7 – 14.5
Jaguarundi	*Herpailurus yaguarondi*	505 - 940	330 - 609	4 – 9
Margay	*Leopardus wiedii*	490 - 797	351 - 533	2.6 – 9
Oncilla	*Leopardus tigrinus*	426 - 648	245 - 340	1.4 – 3

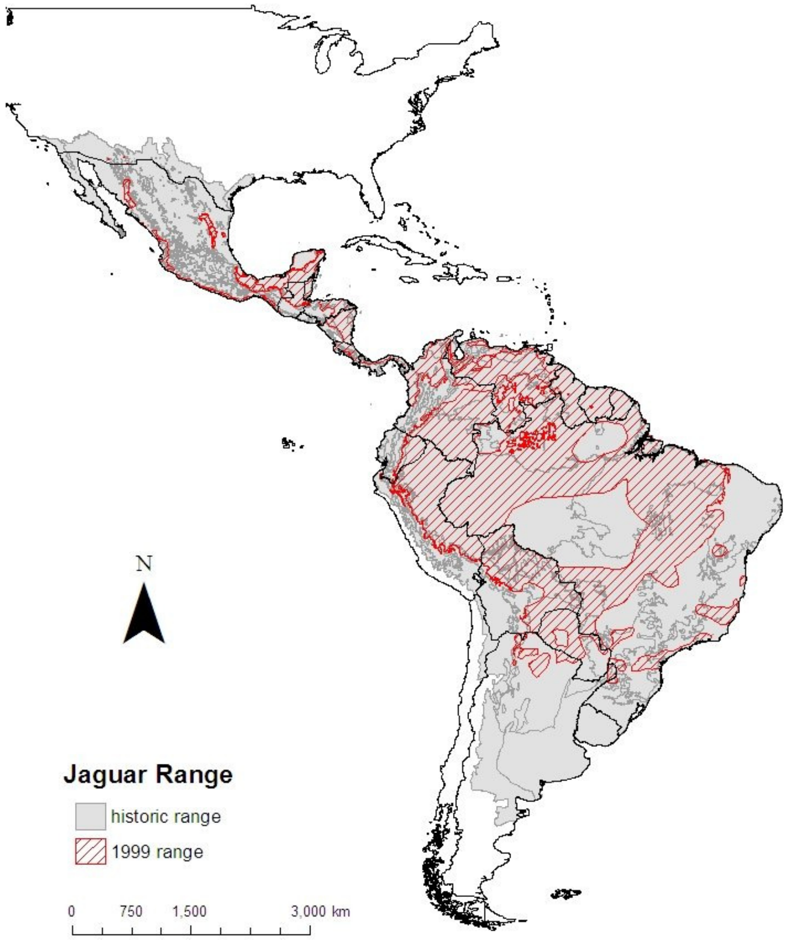


Figure 1.2 The historic and current (1999) known range of jaguars through Central and South America (from Sanderson *et al.* 2002b).

The conservation issue

Both jaguar and puma populations are in decline, with total effective populations estimated at less than 50,000 breeding individuals (Cat Specialist Group 2002). Compared to puma, the future of jaguar is more uncertain since their distribution is more restricted both in terms of geography and diversity of habitats utilized (Hoogesteijn 2000). The probability of the long-term survival of the jaguar is considered high in 70% of its known occupied range; however of those areas still considered to have a substantial jaguar population, adequate habitat and a stable and diverse prey base only 3% is effectively protected (Sanderson *et al*. 2002c). In order to survive, the species requires space, prey and connectivity between populations. Their need for huge interconnected areas makes informal protection of large areas between reserves, through participation of the land owners and users, critical for their conservation (Hoogesteijn 2000, Miller and Rabinowitz 2002).

The long-term survival of the jaguar through Mexico, Guatemala and Belize will require improved connectivity between reserves (Ceballos *et al*. 2002). However levels of ranching and arable agriculture are increasing, and suitable habitat is becoming surrounded by a contiguous matrix of human development. As their environment is fragmented by deforestation, and hunters remove available prey, the cats are forced into human habitation and face direct conflict with people. With an abundance of livestock as prey, farms and ranches that link forest fragments are potentially resource rich corridors for cats. However, predators are rarely tolerated, even in the absence of cases of livestock depredation in the area (Hoogesteijn 2000, Rabinowitz 1986a). Unless conflicts of interest between farmer and cats can be resolved, and lethal control is replaced with alternative methods of livestock protection, farms and villages may function as sinks for cats from surrounding areas.

Identifying solutions to conflicts between jaguars and people needs to become a research priority (Sunquist 2002), and first requires a sound understanding of the ecology of jaguars in these areas. The problem is being extensively investigated in South America, for example in Venezuela (Scognamillo *et al*. 2002, Polisar *et al*. 2003), Brazil (Crawshaw 2002, Crawshaw and Crigley 2002, Dalponte 2002, Conforti and Azevedo 2003, Zimmermann *et al*. 2005) and Argentina (Schiaffino *et al*. 2002). However livestock depredation and solutions to the illegal hunting of jaguars and their wild prey has not yet been sufficiently addressed in Central America (Vaughan and Temple 2002). Given the variation in jaguar ecology, habitat and prey availability across its range (next section), and the variation in culture and socio-economic development between range countries, site-specific research is required to understand the ecological processes and develop conservation strategies appropriate to each society.

Jaguar ecology

The jaguar has a stocky, heavy body with short massive limbs associated with reduced cursorial behaviour and dense forest habitat, and robust canines and large head allowing a more powerful bite than other large cats (Seymour 1989, Sunquist and Sunquist 2002). As in other cat species males are larger than females. Mean body weight varies by up to 100% across their range; those living further from the equator tend to be larger (Iriarte *et al.* 1990). This extreme variation in size is believed to reflect variation in the availability of large prey in different habitats: the largest jaguars occur in open flood plains areas, the Llanos in Venezuela and the Pantanal in Brazil, and take the largest prey, whilst the smallest jaguars inhabit the dense forest areas of Central America and Amazonia and take smaller prey (Hoogesteijn and Mondolfi 1996, de Oliveira 2002). Compared to jaguars, pumas are longer-limbed and more slender (Sunquist and Sunquist 2002). They are generally smaller than jaguars in areas where they co-exist (see Table 1.4) but increase in size outside the jaguar range (Iriarte *et al.* 1990). As with jaguars their body size increases with distance from the equator, again thought to be associated with prey availability and habitat characteristics (Iriarte *et al.* 1990).

Density

Estimating and monitoring population density is essential for ecological studies and wildlife conservation. Formerly, density estimates of elusive, wide-ranging species such as jaguars have been derived from long-term telemetry studies, using estimates of home range size based on relatively small sample sizes (n = 2 to 8, e.g. Schaller and Crawshaw 1980, Quigley and Crawshaw 1992, Ceballos *et al.* 2002, Núñez *et al.* 2002, Azevedo and Murray 2007). However the small sample sizes and presence of unknown individuals within the study area limits this technique. The recent development of camera-trap technology utilised in combination with standard capture-recapture population models has allowed non-invasive monitoring of large numbers of individuals and statistically rigorous density estimates (Karanth 1995, Karanth and Nichols 1998). The use of camera-trap capture-recapture methods to estimate density is becoming more popular; however it is not without problems (e.g. Harmsen 2006, Soisalo and Cavalcanti 2006, Dillon and Kelly 2007). Chapter 2 reviews methods of density estimation using camera-trap methodology with closed population capture-recapture population models, and the problems associated with contemporary estimates of abundance and density of low density, wide-ranging, large species such as jaguars. Chapter 3 manipulates empirical data to assess the influence of trap effort on abundance estimates.

Contemporary estimates of jaguar density in different areas of their range vary by an order of magnitude from ~1 to ~12 per 100 km^2 with no obvious relationship with broad habitat type (Table 1.3). This to be expected since site-specific factors such as levels of prey availability and direct persecution from humans, and fine-scale habitat variables, such as seasonal flooding or the availability of permanent water sources, will influence population size in an area. Density estimates from sites where there has been long-term protection with no human persecution may give good estimates of the local carrying capacity, for example those from Gallon Jug Private Estate and Cockscomb Basin Wildlife Sanctuary both located within the Belizean rainforest (Table 1.3).

Estimates of jaguar density are lacking outside of the borders of reserves or private lands such as the large ranches of Brazil and Venezuela, (Table 1.3). Although it is important to monitor jaguars in these potential source populations it is also necessary to assess their density in the human matrix outside of these lands; this will help to reveal whether stable resident populations of jaguars can co-exist with people or whether jaguars utilising these disturbed areas are mainly transients in search of suitable habitat to establish a home range. Chapter 4 uses large-scale camera-trap surveys to estimate and compare the density of jaguars inhabiting a protected rainforest with those utilising the neighbouring landscape, a matrix of agriculture, communities and unprotected forest and savannahs.

Table 1.3 Jaguar density at different sites in the neotropics based on telemetry and/ or camera-trap data. Repeated surveys at the same site are shown as separate estimates; alternate methods of estimation using the same data are shown as ranges.

Country	Habitat	Density /100 km^2 (SE)	Method	Study
Mexico	Dry tropical deciduous forest	1.7	telemetry	1
	Semi-deciduous & seasonally flooded forest	4.5-6.7	telemetry	2
Guatemala	Subtropical moist forest with seasonally inundated bajo forest	~ 0.7-1.7	camera	3
Belize	Subtropical moist forest with seasonally inundated bajo forest	8.8 (2.3), 11.3 (2.7)	camera	4a
	Tropical evergreen seasonal broadleaf secondary forest	5.3 (1.8)	camera	4b
	Tropical evergreen & semi-evergreen broadleaf lowland secondary forest	8.8 (3.7), 18.3 (5.2), 4.8 (1.0), 11.5 (5.5)	camera	5
	Deciduous semi-evergreen seasonal forest with pine	7.5 (2.7)	camera	6a
Costa Rica	Tropical lowland primary rainforest	7.0 (2.4)†	camera & telemetry	7
Brazil	**Atlantic forest** - Semi-deciduous rainforest	2.2 (1.3)	camera, telemetry	8
		3.7	telemetry	9
	Pantanal - Seasonally inundated alluvial plains: pasture, grassland, cerrado, gallery forest, deciduous & semi-deciduous forest	4.0	telemetry	10
		7	telemetry	11
		1.6	telemetry	12
		5.7 (0.8)-10.3 (1.5) 5.8 (1.0)-11.7 (1.9)	camera & telemetry	13
Bolivia	Open canopy forest with palms	1.7 (0.8), 2.8 (1.8)	camera	14, 6b
	Chaco alluvial plain forest	5.1 (2.1), 5.4 (1.8)	camera	15a, 6c
		2.1	camera	16a
	Chaco-chiquitano transitional dry forest	11.1	camera	16b
	…with scrub	4.0 (1.3)	camera	6d
		2.3 (0.9), 2.6 (0.8), 3.1 (1.0)	camera	15b

†effective sample area < 100 km^2 (86 km^2)

1 - Chamela-Cuixmala Biosphere Reserve, Jalisco, Núñez *et al.* (2002); **2** - Calakmul Biosphere Reserve, Campeche, Ceballos *et al.* (2002); **3** - Mirador-Rio Azul National Park, Novack (2003); **4** – a) Gallon Jug Private Estate b) Fireburn Private Reserve, Miller (2006); **5** - Cockscomb Basin Wildlife Sanctuary, Harmsen (2006); **6 a)** Chiquibul Forest Reserve, **b)** Madidi National Park, Tuichi Valley **c)** & **d)** Kaa-Iya National Park, Gran Chaco, Silver *et al.* (2004); **7**- Cocovado National Park, Salom-Pérez *et al.* (2006); **8** - Morro do Diabo State Park, Cullen *et al.* (2005); **9** - Iguaçu National Park, Crawshaw *et al.* (2004); **10** - Acurizal & Bela Vista Ranches, Pantanal, Schaller & Crawshaw (1980); **11** - San Francisco Ranch, Pantanal, Azevedo & Murray (2007); **12** – Pantanal, Quigley & Crawshaw (1992); **13** - Fazenda Sete Ranch, Pantanal, Soisalo & Cavalcanti (2006); **14** - Madidi National Park, Tuichi Valley, Wallace *et al.* (2003); **15 – a)** & **b)** Kaa-Iya National Park, Gran Chaco, Maffei *et al.* (2004); 16 – **a)** Kaa-Iya National Park, Gran Chaco, **b)** Kaa-Iya National Park, Gran Chaco Maffei *et al.* (2005).

Spacing and habitat utilisation

Assuming that there is no selection pressure for cooperation, female solitary carnivores may be expected to space themselves according to prey abundance and availability. As such exclusive female ranges are expected if resources are stable and even, shifting to larger overlapping ranges under conditions of temporally or spatially variable resources (Sandell 1989). Male solitary carnivores are expected to space themselves according to both the distribution of receptive females and the food resources. As such male home ranges should be larger than predicted from energy requirements alone; exclusive male home ranges are expected when females are abundant and evenly distributed, whilst overlapping ranges and ‘free-roaming’ males are expected if receptive females are scarce or unevenly distributed (Sandell 1989).

Jaguar home ranges, which tend to be larger for males, vary in size considerably throughout their geographic range (Table 1.4), are positively correlated to body size (Scognamillo *et al*. 2002), and are presumably associated with availability and distribution of prey in different habitats. Indeed variation in home range size with seasonal changes in resources has been documented at several sites (e.g. Crawshaw and Quigley 1991, Núñez *et al*. 2002, Scognamillo *et al*. 2003, Table 1.4). Jaguars, like most large cats, are generally considered solitary. As with other aspects of their ecology, their land tenure system appears to be flexible. In accordance with theory about the spacing of solitary carnivores (Sandell 1989), the male range often overlaps with several females (e.g. Schaller and Crawshaw 1980, Scognamillo *et al*. 2002). Overlap between the home ranges of individuals of the same sex (male-male and female-female) has been frequently documented, however in such situations temporal avoidance appears to be common (Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991, Núñez *et al*. 2002). Azevedo and Murray (2007) found that although the ranges of same sex jaguars in the Pantanal overlapped by up to 50% they still maintained exclusive core areas; in contrast the core areas of different sex individuals showed high levels of overlap. Female-female overlap appears to be greater for related individuals than non-kin, for example range sharing between mother and daughter (e.g. Crawshaw and Quigley 1991). Extensive male-male overlap with no stability in occupancy observed in the Belizean rainforest has been attributed to the limited availability of travel routes through the dense forest and the local super-abundance of small prey (Rabinowitz and Nottingham 1986, Harmsen 2006). Here males utilised small transient feeding areas (~2.5 km^2) for up to two weeks before shifting to another part of their range; similar behaviour has also been documented in the Peruvian Amazon (Rabinowitz and Nottingham 1986, Emmons 1987).

Activity patterns of jaguars are highly variable within and between study sites; primarily nocturnal activity was documented in the Venezuelan llanos (Scognamillo *et al*. 2003), the dry forests of Mexico (Núñez *et al*. 2002), and the Belizean rainforest (Rabinowitz and Nottingham 1986, Weckel *et al*. 2006a, Harmsen 2006); and crepuscular activity peaks were reported in the Bolivian Chaco (Maffei *et al*. 2004). Crawshaw and Quigley (1991) reported that jaguars were more active during the day in Brazilian Pantanal, whilst in the Peruvian Amazon jaguars were active equally day and night (Emmons 1987). Activity is probably influenced by a number of factors such as the ambient temperature (Crawshaw and Quigley 1991), the activity of prey species, the intensity of human disturbance and periods when females are in oestrus. Studies which collected data on both jaguars and pumas, found similar activity patterns in both species (Núñez *et al*. 2002, Scognamillo *et al*. 2003, Harmsen 2006).

Three telemetry studies have monitored jaguars and pumas simultaneously (see Table 1.4): in the Pantanal, Brazil, Schaller and Crawshaw (1980) found spatial separation between jaguars and a single puma; in contrast Núñez *et al*. (2002) found extensive overlap both within and between the pumas and jaguars inhabiting the dry forest of Jalisco, Mexico; in the llanos of Venezuela, Scognamillo *et al*. (2003) found up to 60% home range overlap between jaguars and pumas, however they noted that at a fine scale only 15% of puma locations were within 200 m of jaguar locations. Indeed broad assessments of home range overlap may fail to detect subtle differences in the temporal and spatial distribution of jaguars and puma. A recent camera-trap study in the Belizean rainforest revealed that jaguars and pumas avoid one another more than they avoid con-specifics: although jaguars and puma utilised all the same locations they did not do so at the same time; in contrast, no temporal avoidance was detected between jaguars (Harmsen *et al*. in press).

Studies of broad habitat preferences of jaguars and pumas based on telemetry are not unanimous but do show a tendency for jaguars to utilise forested areas and avoid more exposed areas such as open pasture (Schaller and Crawshaw 1980, Crawshaw and Quigley 1991, Silveira 2004, Cullen *et al*. 2005). In contrast pumas will utilise more open habitats, including disturbed areas such as croplands and pasture (Scognamillo *et al*. 2003, Silveira 2004). Little information is available regarding the extent to which jaguars and pumas utilize human-influenced landscapes, the impact of human activity, or how these factors may influence the spatio-temporal distribution of these species. Chapter 5 uses long-term camera-trap data to compare habitat use and activity within and between jaguars and pumas in an undisturbed protected forest with those of a neighbouring human-influenced landscape.

Diet

Jaguar diet is highly variable, with more than 85 prey species taken across their geographic range, and between eight and 24 prey species documented in the diet at any one site (Rabinowitz and Nottingham 1986, Emmons 1987, Seymour 1989, Aranda and Sánchez-Cordero 1996, Taber *et al.* 1997, Garla *et al.* 2001, Crawshaw and Quigley 2002, Dalponte 2002, Leite *et al.* 2002, Nuñez *et al.* 2000a, Polisar *et al.* 2003, Crawshaw *et al.* 2004, Novack *et al.* 2005, Azevedo 2008). Peccaries, deer, large cavimorph rodents, armadillos and coatis are the main prey taken (de Oliveira 2002). In an analysis of diet studies from 10 different geographic locations, González and Miller (2002) found that jaguars utilise medium (1-10 kg) and large prey (> 10 kg) equally however the use of medium prey may be a consequence of the removal of larger prey by humans hunting game. For example, the high proportion of small prey in the diet of jaguars in the Paraguayan Chaco has been attributed to a reduction in the peccary population caused by intensive commercial hunting of peccaries by people (Taber *et al.* 1997).

Optimal foraging theories predict that when prey are scarce they should be taken opportunistically according to their availability, but when prey are abundant predators should select large prey in order to maximize energy intake (Griffiths 1975). Emmons (1987) suggested that in rainforest environments solitary hunters such as jaguars have to be opportunistic because encounters with prey are unpredictable and vision is limited by dense vegetation; in an open environment, assuming that prey are abundant, predators can be more selective. Indeed a review of 16 jaguar diet studies confirmed that mean weight of vertebrate prey differed with habitat type, with larger prey taken in open floodplain areas (de Oliveira 2002).

It has been suggested that where jaguars and pumas co-exist, pumas take smaller prey species; particularly in closed environments such as dense forest where jaguars may be more efficient at hunting (Iriate *et al.* 1990, Taber *et al.* 1997). Harmsen (2006) reviewed seven diet studies of sympatric jaguars and pumas. Diet overlapped by ~80% in open habitats; however in closed rainforest environments the similarity between jaguar and puma diets was much lower (~20%) with pumas taking smaller prey species than did jaguars. The ability for pumas to exploit smaller prey such as cotton rats (100 g) may give them an advantage in disturbed habitats (Núñez *et al*. 2000a).

To date most studies of jaguar and puma diets have utilized scat diameter, footprints and other sign to identify scats to species level (for example Rabinowitz and Nottingham 1986, Emmons 1987, Aranda and Sánchez-Cordero 1996, Garla *et al*. 2001, Dalponte 2002, Leite *et al*. 2002, Nuñez *et al*. 2000a, Azevedo 2008). However, diameter width has been demonstrated to be < 40% accurate (Taber *et al*. 1997, Farrell *et al*. 2000), and the use of tracks to identify scats requires a suitable undisturbed substrate: footprints are rarely found in dense secondary rainforest where leaf litter may cover the ground, or in areas of human development where high levels of human traffic may obscure tracks or cats utilise man-made paved or rock roads (R. Foster pers. obs.). Farrell *et al*. (2000) developed a molecular assay to correctly distinguish jaguar and puma genetic sequences from mitochondrial DNA derived from scats, and the method has been used in more recent diet studies (Polisar *et al*. 2003, Novack *et al*. 2005, Weckel *et al*. 2006b). Chapter 6 compares the breadth and overlap of diets of jaguars and pumas utilizing a protected forest with those utilizing the neighbouring human-influenced landscape. Scats are identified to species level using genetic analysis allowing interspecific diet comparisons.

Reproduction

Jaguars may come together at any time of the year to breed during the 6-17 day period when the female is in oestrus. Gestation lasts 91-101 days (in captivity), after which the female gives birth to up to four cubs, usually two, which will stay with her for up to 24 months (Kitchener 1991, Sunquist and Sunquist 2002). Cubs are fully dependent on their mother's milk for the first 10-11 weeks, and will continue to suckle until 5-6 months old (Sunquist and Sunquist 2002). Cycling could resume 2-3 weeks following lactational anestrus (Soares *et al*. 2006). By the age of 15-18 months young jaguars travel and hunt independently within their mother's range, although they may still come together at kill sites (Quigley and Crawshaw 2002, Sunquist and Sunquist 2002). Pregnancy and the long period of association during which the mother is lactating and/or hunting to feed both herself and her off-spring, is energetically demanding for the female. In areas where humans have reduced the abundance of wild prey species, females may not be able to find sufficient prey in order to reproduce, or may begin hunting domestic animals in order to support herself and her off-spring.

Chapter 6 uses simple harvest models to determine the minimum sizes of wild prey populations necessary to sustain off-take by a breeding female, and indentifies the conditions under which livestock predation may become necessary for reproduction.

Jaguars are usually independent by the age of 24 months, however the age of dispersal or the social circumstances associated with it are poorly known (Sunquist and Sunquist 2002). Dispersal does not appear to be linked with the onset of sexual maturity, estimated at 24-30 months for females and 36-48 months for males (Sunquist and Sunquist 2002). Few data are available on dispersal distances however telemetry studies in the Brazilian Pantanal suggest that males disperse further than females (Quigley and Crawshaw 1992, Quigley and Crawshaw 2002). Dispersal through the human matrix may increase the likelihood of conflict with humans, particularly in areas where the habitat is highly fragmented (e.g. Sáenz and Carrillo 2002). Understanding such movement patterns is necessary in order to predict the risk of conflict with people and human-induced mortality in different sex and age classes.

Table 1.4 Adult jaguar mass and home range from telemetry studies. Data on sympatric pumas are included where available.

Country	**Habitat**	**Study**	**Jaguar**				**Puma**			
			Home range (km^2)		**Mass (kg)**		**Home range (km^2)**		**Mass (kg)**	
			male	**female**	**male**	**female**	**male**	**female**	**male**	**female**
Mexico	Dry tropical deciduous forest	1	-	25^{d}–60^{w}	$35^{\ddagger}$-$55^{\ddagger}$	$35^{\ddagger}$-$55^{\ddagger}$	60^{d}–90^{w}	25^{d}–60^{w}	$25^{\ddagger}$-$50^{\ddagger}$	$25^{\ddagger}$-$50^{\ddagger}$
	Semi-deciduous & seasonally flooded forest	2	33-41	32-59	-	-	-	-	-	-
Belize	Tropical evergreen & semi-evergreen broadleaf moist lowland secondary forest	$3^{?}$	28-40	$(10)^{t}$	57	-	-	-	-	-
Venezuela	**Llanos** – seasonally inundated: open pasture, grassland & savannah woodland; non-flooded evergreen forest & dry forest	4	93^{d}-100^{d}	51^{w} -80^{d}	82-93	46-58	17^{d}-104^{d}	23^{dw}-47^{d}	50-52	24-28
Brazil	**Pantanal** - Seasonally inundated: pasture, grassland, cerrado, gallery forest, deciduous & semi deciduous forest	$5^{?}$	$(90)^{t}$	25-38	-	61-75	≥32	-	55	-
		6	20^{w} -79^{d} $152^{\dagger}$	5^{w} -70^{d} $97^{\dagger}$-$168^{\dagger}$	-	75-85	-	-	-	-
		7^{fk}	67	38	100	62	-	-	-	-
		8	$57^{d\ddagger}$-$176^{d\ddagger}$	$57^{d\ddagger}$-$176^{d\ddagger}$	-	-	-	-	-	-
Brazil	**Atlantic forest** - Semi-deciduous rainforest	9	88-177	44-133	90-98	55-86	-	-	-	-
		10	87-139	70	-	-	-	-	-	-

1 - Chamela-Cuixmala Biophere Reserve, Jalisco, Núñez *et al.* (2002); **2** - Calakmul Biosphere Reserve, Campeche, Ceballos *et al.* (2002); **3** - Cockscomb Basin, Rabinowitz & Nottingham (1986); **4** - Hato Piñero Ranch, Scognamillo *et al.* (2003), **5** - Acurizal & Bela Vista Ranches, Pantanal, Schaller & Crawshaw (1980); **6** - Miranda Ranch, Pantanal, Crawshaw & Quigley (1991); **7** - San Francisco Ranch, Pantanal, Azevedo & Murray (2007); **8** - Fazenda Sete Ranch, Pantanal, Soisalo & Cavalcanti (2006); **9** - Morro do Diabo State Park, Cullen *et al.* (2005); **10** - Iguaçu National Park*,* Crawshaw *et al.* (2004).

Home ranges are 95% MCP unless indicated: **fk** 95% fixed kernel; **?** method not given; **t** minimum estimates based on track data
w wet season home range; **d** dry season home range; **†** dry & wet season home ranges combined
‡ Authors do not distinguish between sexes

Jaguars, people and livestock

Jaguar populations suffered intense persecution for the commercial skin trade throughout the 20th century; during 1969 alone ~10,000 jaguar skins were imported into the US (Smith 1976, McMahan 1982, Rabinowitz 2006). In 1973 the jaguar was included in an international treaty (CITES) to ban trade in wildlife products derived from endangered species. All countries within the jaguar range are now members of CITES and commercial jaguar hunting has declined (Sunquist and Sunquist 2002). Today direct persecution from livestock owners, combined with reductions in habitat and wild prey, pose the main threat to jaguars.

Cattle were introduced to South America during the 16th century by European colonisers (Jarrige and Auriol 1992), prior to this *Bovidae* never occurred on the continent (Polisar *et al*. 2003). Over the past 40 years the cattle population of Central and South America has doubled to ~380 million, concurrent with human population growth and deforestation (World Resources Institute, WRI, 2007). Because the extent and intensity of pastoral ventures differ across the continent, so too do people-jaguar-livestock interactions, and the ecological, economical and social factors which drive them. In particular it is important to distinguish between the extensive ranches of Brazilian Pantanal or Venezuelan llanos where essentially feral cattle roam freely with wild prey species through the natural mosaic of grasslands and forests, compared to regions where forested areas are cleared specifically for small intensive pastures such as the Atlantic forests of Brazil or the lowland rainforests of Belize (Crawshaw and Quigley 1992, Hoogesteijn 2000, Conforti and Azevedo 2003, R. Foster pers. obs.).

In some areas of Venezuela and Brazil the only jaguar habitat outside of protected areas exists within large expanses of ranch land. Here cattle ranches of 100 km^2 to 800 km^2 with tens of thousands of cattle are common (e.g. Polisar *et al*. 2003). Management is limited such that the cattle have become part of the natural ecosystem. The home ranges of several jaguars and pumas may fall easily within the ranch boundaries and they may come to rely heavily on the cattle as a prey source. Extensive on-going research is being conducted on the jaguars inhabiting such areas (e.g. Crawshaw 2002, Quigley and Crawshaw 2002, Polisar *et al*. 2003, Soisalo and Cavalcanti 2006, Azevedo and Murray 2007).

The situation in Belize is rather different. The cattle population of Belize has doubled since 1979, and is currently ~75,000 head, yet 72% of the land is still forested

(Belize Government 2006, WRI 2007) and, although livestock production is common and increasing, it is characterised by many small holdings and few large holdings. Of the 1600(+) registered livestock farmers, 11% own 71% of the cattle (Brechin and Buff 2005), and the larger established cattle ranches rarely exceed 10 km^2 (R. Foster pers. obs.). As a consequence, many farms and villages lie in close proximity to the forest and almost every livestock holding is at risk of predation. This can be particularly damaging to the small-scale farmer unless preventative action is taken when depredation begins (R. Foster pers. obs.). In areas with a high proportion of forest cover, such as Belize, research has not yet addressed how jaguars living near the forest edge utilise the boundary between forest and human habitation. The aim of this thesis, to understand the ecological processes occurring 'at the edge', will be instrumental in predicting the likely impact on the jaguar population of continued lethal control and the inevitable agricultural expansion and intensification that faces Belize (Chapter 7).

Factors influencing livestock predation

Both jaguars and pumas prey on livestock. Studies from different locations cite different levels of predation by either species. For example jaguars were reported to prey more heavily on livestock than did pumas in fragmented forest habitats of the Brazilian Amazon, southern Brazil and Belize (Michalski *et al.* 2006, Conforti and Azevedo 2003, Azevdeo 2008, Brechin and Buff 2005) and in the Brazilian Pantanal (Azevedo and Murray 2007). The reverse was reported in the Venezuela llanos (Polisar *et al.* 2003) and the cerrado/forest transition zone of central-western Brazil (Palmeira *et al* 2008). As such a suite of interacting factors may influence depredation. These include innate and learned behaviour; the health, status and sex of individual cats; habitat and the division of space and resources between jaguar and puma; the abundance and distribution of natural prey; and livestock husbandry practices (Linnell *et al.* 1999, Polisar *et al.* 2003).

Adult male carnivores are usually responsible for more depredation events than any other age or gender class and this appears to hold true for jaguars (Linnell *et al.* 1999, Rabinowitz 1986a, Sáenz and Carrillo 2002). The sex bias is not fully understood but may be due to greater risk taking in males and/or greater encounter rates with livestock due to their larger home range (Linnell *et al.* 1999). It has been proposed that the injuring of healthy jaguars through indiscriminate shooting may further exacerbate the problem. Evidence suggests that injured or infirm jaguars unable to hunt wild prey are forced to take easier domestic animals (Rabinowitz 1986a, Hoogsteijn 2000). Chapter 7 identifies specific characteristics of jaguars that are associated with livestock predation and are thus at risk of lethal control. Understanding which individuals within a population are most at risk is necessary in order to predict the effect of lethal control on population dynamics, for example the removal of females will directly lower the reproductive potential of the population whilst the removal of males may have more subtle effects through the disruption of social dynamics.

It has been argued that most large cats will occasionally kill accessible livestock that they encounter, even if the biomass of natural prey is adequate; however, work in Venezuela has shown that the highest depredation rates occur in areas where abundance of wild prey is relatively low (Linnell *et al*. 1999, Polisar *et al*. 2003). Indeed in Brazil the decline of white-lipped peccary has coincided with an increase of predation on domestic prey (Conforti and Azevedo 2003, Crawshaw *et al*. 2004); similarly the overexploitation of caiman in the Pantanal resulted in increased cattle predation (Hoogesteijn 2000). In contrast, ranches rich in wild prey may suffer little or no depredation, suggesting a preference for wild prey when it is available (e.g. Miller 2002). It is likely that there is an interaction between the availability of wild versus domestic prey. In Venezuela the frequency of cattle depredation was inversely related to availability and vulnerability of natural prey and directly related to availability and vulnerability of livestock (Polisar *et al*. 2003). Chapter 6 estimates the abundance of wild prey required to sustain off-take by the observed jaguar density, discussing competition with man for game species and the extent to which wild prey depletion may intensify livestock predation.

Livestock management plays a pivotal role in determining the level of depredation. If livestock are kept in open pastures or constantly herded or confined at night within a fence, depredation requires the development of specialised behaviour in the predator. In contrast, if the livestock are free-ranging and unattended there is unlikely to be any perceptual difference between the livestock and natural prey except that the domestic animal is easier to kill (Linnell *et al*. 1999). Under these circumstances depredation may be more common. However, it can also be argued that a fenced pasture enclosing a high density of livestock is equivalent to a patch whose value never becomes marginal (Polisar *et al*. 2003). If the fence keeps the livestock in, but fails to keep predators out, repeated predation events can be expected. Numerous authors suggest that improvements to livestock management are fundamental to lowering rates of depredation (e.g. Linnell *et al.* 1999, Hoogesteijn 2000, Miller 2002, Mazzolli *et al.* 2002). Habitat factors are equally important, indeed several studies indicate that higher predation rates are associated with proximity to forest cover (e.g. Polisar *et al.* 2003, Michalski *et al.* 2006, Azevedo and Murray 2007). Chapters 5 and 7 examine how habitat factors and livestock husbandry influence jaguar encounter rates with human habitation and livestock predation and thus the risk of lethal control.

The consequences of livestock predation

As discussed, the magnitude of cattle predation varies with many factors. Reports of annual stock loss to predation, on farms suffering from jaguar and puma attacks, range from 0.2% to 2% (Dalponte 2002, Mazzolli *et al.* 2002, Conforti and Azvedo 2003, Zimmerman *et al.* 2005, Michalski *et al.* 2006, Azevedo and Murray 2007). On extensive ranches where cattle roam freely, otherwise ‘unexplained’ losses (disease, accidents and theft) cause more deaths annually than depredation events but are often blamed on cats (Hoogesteijn 2000). Jaguars may range close without ever taking livestock however preconceptions about their behaviour mean that they are rarely tolerated, even in the absence of depredation in the area (Hoogesteijn 2000, Rabinowitz 1986a); for example, in the Pantanal 64% of ranchers interviewed said that they could not tolerate jaguars on their land (Zimmermann *et al.* 2005). Despite this, few studies of jaguar ecology have attempted to quantify levels of human-induced mortality, and those that do make no assessment of the likely impact on the local jaguar population (e.g. Crawshaw 2002, Conforti and Azvedo 2003, Brechin and Buff 2005, Michalski *et al.* 2006). Chapter 7 presents data on levels of lethal control of jaguars in southern Belize, and combined with estimates of jaguar density (Chapter 4) uses individual-based population simulations to investigate the impact of current levels of human-induced mortality on the population dynamics and long-term persistence of the Belizean jaguar population.

Thesis objectives

The goal of this thesis is to improve our understanding of the ecology of jaguars in a human-influenced landscape, and in doing so provide reliable data which can be used by policy makers and contribute to the long-term conservation of jaguars in Central America. Camera traps provided a non-invasive method of studying high numbers of these elusive cats for which large-scale live-trapping would not have been appropriate. However the method still needs to be refined so the research simultaneously addresses various methodological issues associated with studying jaguars effectively in this environment.

Camera-trap methodology is described in Chapter 2. The objective of Chapter 2 is to review methods of density estimation from camera-trap data using closed population capture-recapture population models and to identify the pitfalls of contemporary population estimates of low density, wide-ranging species. Because the humid tropics are a harsh environment for camera traps there is no guarantee of functional consistency throughout a survey, therefore the objective of Chapter 3 is to evaluate the robustness of the most commonly used closed population estimator to variable and reduced trap effort resulting from camera failure.

The main objective of Chapter 4 is to compare the demographics, ranging behaviour and density of jaguars inhabiting a protected lowland rainforest with those utilising the neighbouring human-influenced landscape in Belize, using camera-trap data. As density estimation from camera-trap data has not yet been perfected, Chapter 4 also has three methodological objectives which are a prerequisite to the main objective. The first is to assess the suitability of the ‘mean maximum distance moved’ (MMDM) as a proxy for home range diameter. MMDM is commonly derived from trapping data when home range is unknown to estimate the effective sampling area and so estimate density. The second auxiliary objective is to assess the influence of sexual variation in MMDM on density estimates. The third is to identify the minimum survey area required for reliable density estimates.

In Chapter 5 the habitat use of jaguars and pumas is explored using camera-trap data. The main objective is to compare habitat use of the two species between the protected lowland rainforest and the fragmented landscape. The second objective is to assess the relative tolerance of jaguars and pumas to human activity. The final objective is to investigate the habitat factors influencing jaguar and puma activity and livestock predation around cattle farms and evaluate potential options for managing habitats to reduce attacks on livestock.

Chapter 6 investigates the diet of jaguars and pumas. The main objective is to compare food habits between the protected lowland rainforest and the fragmented landscape, and to evaluate the level of dietary overlap between the two species, using scats genetically identified to species level. Because diet studies may underestimate diet richness if sample sizes are too small, the influence of sample size on number of prey taxa identified is investigated. The final objective is to assess how prey preferences and energy requirements may influence habitat use and livestock predation.

Chapter 7 quantifies human-induced mortality of jaguars in the study area and evaluates whether the current level is likely to be sustainable in the long-term. The first objective is to report and discuss causes and rates of human-induced mortality and the characteristics of jaguars killed for attacking livestock; and to assess the effectiveness of lethal control at reducing livestock losses. The second objective explore the probability of long-term persistence of the Belizean jaguar population under alternative scenarios of population isolation/ connectivity and human-induced mortality, using population simulations and field data collected during this study.

Chapter 8 reviews the main findings of this thesis and discusses the future of jaguar conservation in Belize. The first objective is to discuss methods of studying jaguars within a human-influenced landscape. The second objective is to discuss the adaptability of jaguars to anthropogenic pressures; and the third objective is to discuss ways in which humans and jaguars can coexist in the future.

Study area

Belize lies below Mexico and to the east of Guatemala (Figure 1.3). It is approximately 280 × 120 km, with a total land area of 22,970 km^2. With a population of just 292,000, Belize has the lowest human density in Latin America: 12 people/ km^2; however the population is growing at ~2% per year (WRI 2007, Belize Government 2006). Belize currently protects and manages 6280 km^2 of tropical forest in a network of wildlife sanctuaries, national parks and forest reserves across the country (Figure 1.4).

Figure 1.3 Location of Belize (green) in Central America. Inset shows Central America (shaded grey) within the Americas.

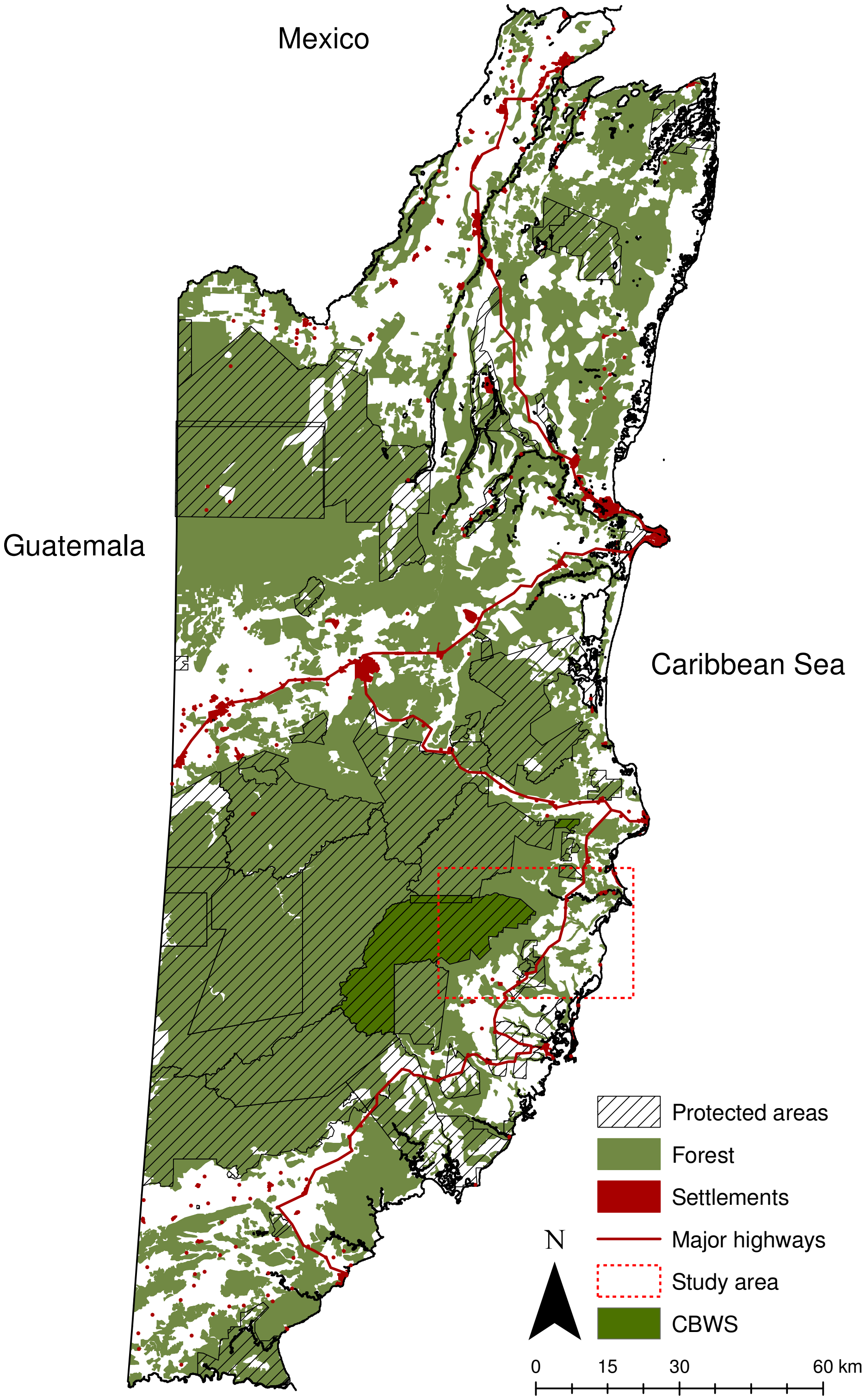


Figure 1.4 The protected areas of Belize and approximate forest cover (from Meerman and Sabido 2001). The Cockscomb Basin Wildlife Sanctuary (CBWS) and the study area are shown.

The study site lies in the Stann Creek district, southeast Belize, a region expected to become a major growth zone for the cattle industry in Belize (O. Salas, Belize Forestry Officer, pers. comm.). The research focuses on the lowland subtropical broadleaf forest of the Cockscomb Basin and the neighbouring farms and villages (Figure 1.5). The basin is bordered by the Cockscomb Mountains to the north and Maya Mountains to the west; and divided into an east and west basin by a series of small hills which delineate the watersheds of two major rivers. The forest was heavily logged from 1888 until a hurricane hit in 1961, after which selective logging continued until 1986, creating dense secondary forest in the basin. The basin received protected status in 1986 following the telemetry studies of jaguars by Rabinowitz and Nottingham (1986) which revealed a high density of jaguars in the area. Logging operations were ended, hunting was banned and the small community of milpa farmers which had settled at the logging camp were relocated to the established village of Maya Centre, 10 km outside the reserve boundary. Today the Cockscomb Basin Wildlife Sanctuary (CBWS) encloses 425 km^2 of forest and supports prospering populations of both jaguar and puma (Harmsen 2006). Maya Centre has a thriving economy based on ecotourism in the eastern part the sanctuary.

Nine villages and at least 11 cattle farms fringe the CBWS eastern border and/or the intermediate unprotected forest. Illegal subsistence hunting and fishing occurs at the edges of the sanctuary from the peripheral communities, and both villages and the farms suffer intermittent livestock predation. The area towards the sea forms a mosaic of community and private lands including unprotected broadleaf forest, shrublands, pine savannah, small-scale tourist resorts, shrimp farms, and citrus and banana plantations. The region has a distinct wet season (June to December) and receives ~270 cm rain/ year.

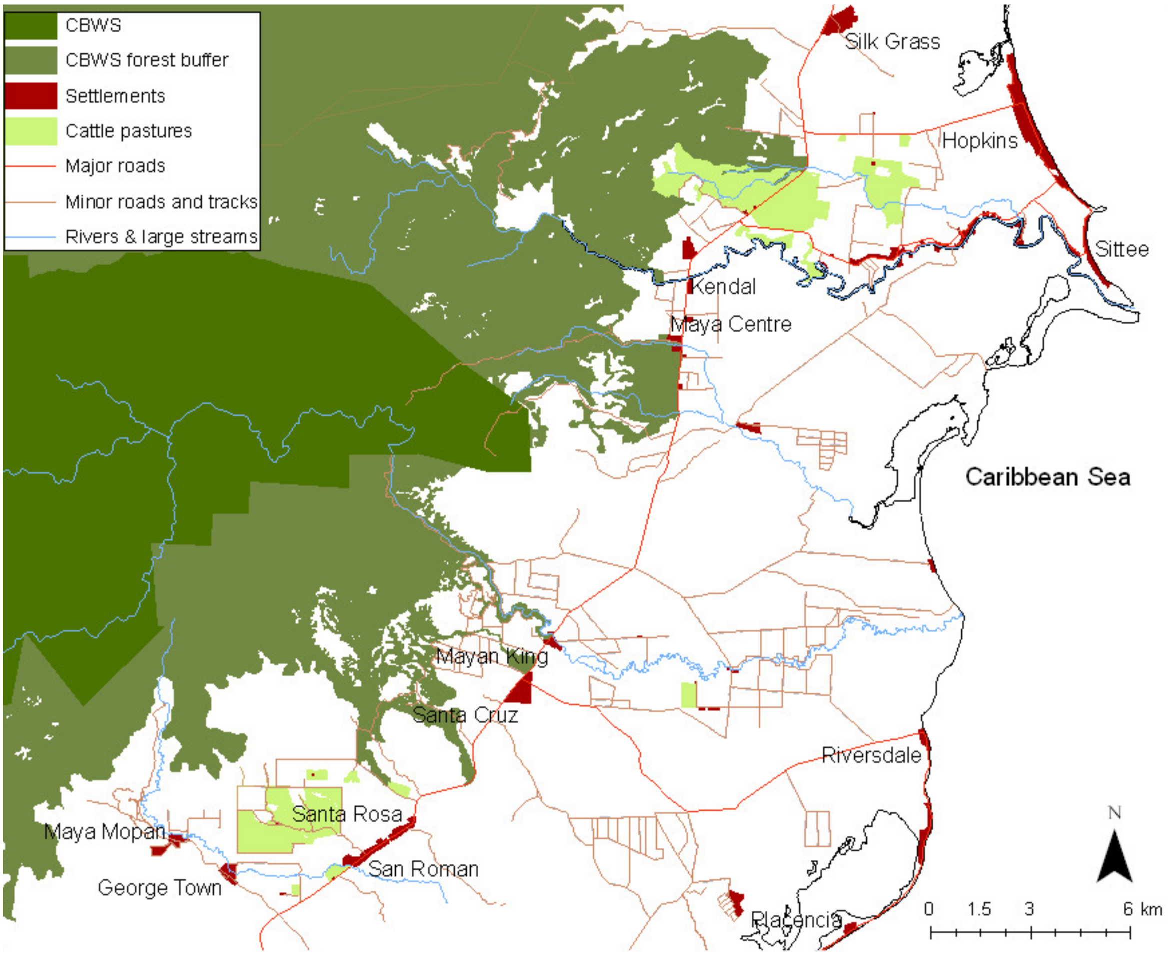


Figure 1.5 Detail of the study area showing the settlements and cattle farms neighbouring the eastern part of the Cockscomb Basin Wildlife Sanctuary and its forest buffer, Belize. Location of eastern tip of CBWS = UTM 0348113, 1854515 (WGS 84).

Chapter 2

Review of abundance and density estimation from camera-trap data

Abstract

Estimating and monitoring population density is essential for ecological studies and wildlife conservation. The recent development of camera-trap technology utilised in combination with standard capture-recapture population models has allowed non-invasive monitoring of large numbers of individuals and statistically rigorous density estimates of otherwise elusive species. Because camera-trapping is increasingly providing data for conservationists and policy makers, the methodology needs to be accurate, robust, reliable and comparable. This chapter reviews methods of density estimation using camera-trap methodology with closed population capture-recapture population models, and the problems associated with contemporary population estimates of low density, wide-ranging species.

Introduction

Populations of large wide-ranging carnivores are threatened due to anthropogenic factors (Chapter 1), yet basic ecological data are lacking for elusive species which occur at low densities such as forest felids. Formerly, density estimates of elusive, wide-ranging species were derived from home ranges and level of range of overlap estimated from long-term telemetry studies; for example tigers (*Panthera tigris*), leopards (*Panthera pardus*) (Rabinowitz 1989a) and jaguars (*Panthera onca*) (Schaller and Crawshaw 1980). This method of density estimation is labour intensive, expensive and invasive, requiring live-trapping and anaesthesia of the target species. Because of the cost and time constraints imposed by the method, sample sizes are generally small (e.g. for jaguars n = 2 to 8, Chapter 1) and the presence of unknown individuals within the study area limit the technique as a robust method of density estimation.

Over the past 30 years methods of population estimation from capture-recapture data have improved (e.g. Amstrup *et al*. 2005), however these methods have been restricted to species which can be live-trapped easily (e.g. small mammals) or observed in the field. The recent development of camera-trap technology has provided a non-invasive method of monitoring elusive, large mammals for which large-scale live-trapping would not be appropriate. Karanth (1995) made the first attempt to combine the two, estimating tiger density from camera-trap data using capture-recapture population models. Since then the use of camera-trap capture-recapture methods to estimate density has become popular. Unlike telemetry, the method is non-invasive and sampling periods are short (~ 3 months); however it is not without problems (e.g. Harmsen 2006, Soisalo and Cavalcanti 2006, Dillon and Kelly 2007).

Camera traps can be used to answer ecological questions other than estimating density. Rapid assessments can be conducted to determine presence/absence and describe diversity in little known regions (e.g. Azlan and Engkamat 2006, Azlan and Sharma 2006). In addition surveys of specific species can be in used to investigate habitat preferences (e.g. Maffei *et al*. 2005, di Bitetti *et al*. 2006, Harmsen 2006), activity patterns (Maffei *et al*. 2005, Harmsen 2006), spatial and temporal distribution (Harmsen 2006, Weckel *et al*. 2006a) and demographics (Harmsen 2006). However care must be taken when interpreting the data and making conclusions about species natural history, for example di Bitetti *et al*. (2006) suggested that the difference in ocelot (*Leopardus pardalis*) sex ratio between their study and that of Maffei *et al*. (2005) could reflect different social systems in the two populations; in fact skewed sex ratios may be an artefact of the sampling design arising from a difference between male and female movement patterns (e.g. Harmsen 2006) thus comparison between studies could be confounded by of choice of trap location.

Given the utility of camera-trapping, it is likely to be used increasingly to provide data for conservation policy (Trolle and Kéry 2005) therefore the methodology needs to be accurate, robust, reliable and comparable. The aim of this chapter is to review methods of population estimation of low density, wide-ranging, large species using camera-trap methodology with closed population capture-recapture population models. The first objective is to describe camera-trap methodology, capture-recapture closed population models and methods of density estimation from abundance estimates. The second objective is to discuss contemporary population estimates of low density wide-ranging large species, in particular highlighting the potential pitfalls associated with inadequate sample size and capture probability, and choice of method to estimate density, and to examine factors that may influence the reliability of the density estimate.

Camera-trap methodology

The utility of camera traps to study animals which cannot easily be live-trapped and marked relies on individual recognition of members of the study population. For large felids such as tigers or jaguars the pelt pattern is unique between individuals and is used to identify each member of the sample (Figure 2.1).

a) Right flank, female F05-06 **b)** Right flank, female F05-06 **c)** Right flank, female F05-13

Figure 2.1 Three jaguar flanks, the pattern of spots and rosettes is unique to each individual: **a)** and **b)** are separate photos of the same individual; **c)** is a different individual.

Camera traps can be ‘active’ or ‘passive’. Active camera traps are triggered when an animal passes between paired sensors, actively breaking an infrared beam. Passive camera traps are triggered when a warm-blooded animal passes a heat and motion sensor; simpler than active traps, they comprise a single unit containing the camera with a sensor below. For a comparison of the advantages and disadvantages of passive and active camera traps see Harmsen (2006). This study used passive cameras, primarily ‘CamTrak’ units (Cam Trak Inc.) which could be set to operate continuously or only at night, with an enforced delay of 3-45 minutes between each photograph. The delay prevents film being wasted by herding non-target species such as white-lipped peccary (*Dicotyles pecari*) or cattle; however it limits the detection of cubs or juveniles who may often be following behind their mother. The night setting is useful in areas where there is human activity during the day and the target species is primarily nocturnal. This study used a 3 minute delay, combined with continuous or night-only settings depending on the level of human disturbance at the camera location.

The choice of camera location on the large-scale depends on the statistical objectives of the study, and on maximising capture rate at the local-scale (Carbone *et al.* 2001). Given the large survey areas often required, camera location may be constrained by the logistics of accessing cameras to change film and batteries. Furthermore camera locations based in areas with human activity will be further limited by cooperation of local people and the risk of vandalism and theft of the cameras (Chapter 3). As such it is rare for trap configuration to form neat grids or webs which are preferable for accurate density estimates. However, wherever possible researchers should strive to maximise the core to edge ratio of the survey area.

Two cameras are positioned at each site roughly opposite each other, but slightly offset such that the flash of one camera will not over expose the photograph from the opposite camera. Two cameras are favoured over one at each site. This ensures that both flanks (left and right) of the target species are photographed for identification. In addition a double station reduces the risk of lost trap-nights through camera failure.

Capture-recapture closed-population models

Abundance can be estimated from the number of individuals detected and the probability of detection which is estimated from the encounter histories of each individual during a sampling period (Eqn. 2.1).

$$\hat{N} = \frac{C}{\hat{p}} \qquad \text{(Eqn 2.1)}$$

$\hat{N}$ = abundance estimate, C = number of individuals detected and $\hat{p}$ = estimate of detection probability modelled from the patterns of encounters with individuals. Individuals may be detected 'actively' (e.g. by an observer making instantaneous observations) or 'passively' via a detector at a fixed point (e.g. live traps, mist nets, camera traps) (Efford *et al*. 2004). Typically, active detection involves continuous data collection whilst passive detection involves trapping on a series of distinct occasions. 'Discrete-time' closed-population methods have received extensive attention in the literature and will be considered here. A camera trap is essentially a continuous passive detector, but the data can be divided into discrete trap occasions, usually 24h periods, and analysed with discrete time models. Multiple captures of the same individual during a single occasion are considered a single observation. Each encounter is a 'capture' and each occasion in an individual's history is coded either as 1 (captured) or 0 (not captured) (Otis *et al*. 1978).

Population estimation using capture-recapture methods dates back to the 17th century and was first applied to wildlife in the 1930s (Manly *et al*. 2005). Different capture-recapture methods are based on different assumptions about the population. Early models assumed that capture probabilities of all individuals in the sampled population are equal. This assumption is convenient mathematically but has no empirical justification and is often violated (Burnham and Overton 1978). A unifying assumption is that every individual in the population has a capture probability (p)

greater than zero; if this assumption is violated then the population estimate refers only to the ‘catchable’ population (Krebs 1999). Individuals must be identifiable throughout the entire sampling period, either through an artificial marker applied on their first capture (e.g. tags, fur clips, tattoos) or from unique natural identifiers such as pelt patterns, for example ocelots (Maffei *et al*. 2005), jaguars (Silver *et al*. 2004), tigers (Karanth 1995); or genotype, for example using hair traps e.g. martens (*Martes americana*) (Mowat and Paetkau 2002) or faecal samples e.g. otters (Arrendal *et al*. 2007), so that their capture histories can be recorded. Closed-population models assume that the total number of individuals in the population does not alter during the sampling period, i.e. demographic closure (no births, deaths, immigration or emigration) and geographic closure (home ranges of all individuals in the population are bounded by the study area).

The models

Closed-population capture-recapture models utilise the basic concept of the ratio of ‘marked’ (previously caught) to ‘unmarked’ (not previously caught) individuals within the population sample to estimate capture probability over repeated trapping occasions. The simplest closed-population models are based on two trapping occasions within the sampling period: the Peterson-Lincoln estimator and the Chapman estimator (see Krebs 1999). However, models based on multiple occasions give more reliable estimates.

Multi-occasion models can be classified according to the assumptions they make about capture probability which may vary with time (between trapping occasions) and/or behavioural response to capture and/or between individuals (Otis *et al*. 1978). These three sources of variation can be combined into eight models. The simplest, referred to as the ‘null model’ (M_0), assumes that capture probability does not vary between trapping occasions within the sampling period, or within or between individuals. The model M_t extends M_0 allowing variation in capture probability between trapping occasions but capture probability must remain equal between individuals. In natural populations this is rarely valid and models which assume equal capture probability within and between individuals may be biased despite having good precision (Chao and Huggins 2005a).

The model M_b allows capture probability to vary within individuals i.e. the probability of 1st capture (p) $\neq$ probability of recapture (c). This may occur if individuals show a behavioural response to capture: they become either 'trap-happy' ($c > p$) for example if traps are baited with food or a lure; or 'trap-shy' ($c < p$) for example if the trapping experience was stressful. Models which do not include the behavioural response may overestimate abundance if individuals are trap-shy or underestimate abundance if individuals are trap-happy (Chao and Huggins 2005a).

The model M_h allows capture probability to vary between individuals. Individual heterogeneity in capture probability can be expected in most wild animal populations because individual behaviour (thus the probability of capture) may vary with factors such as age, sex and social status; for example males may be more active, less risk-averse and have larger home ranges than females and so have greater a probability of being detected (e.g. encountering and entering a live trap or passing a camera trap). Models which assume equal capture probability in the presence of individual heterogeneity will underestimate abundance (Burnham and Overton 1978, Chao and Huggins 2005b). The four remaining closed-population models described by Otis *et al.* (1978) and White *et al.* (1982) correspond to each possible combination of the three types of variation in capture probability: M_{tb}, M_{bh}, M_{th} and M_{tbh}.

Model estimators

Approaches to formulating estimators (functions of the data that are used to estimate unknown parameters, e.g. p, c and N) for the eight model classes have developed rapidly since the 1970s, particularly as computer processing power has improved. Estimators have been described for all classes (M_0 to M_{tbh}) using a number of different approaches; for a summary review see Chao and Huggins (2005b).

Maximum likelihood estimators (MLE) were initially described for M_0, M_t, M_b, M_{bh} and M_{tb} (Otis *et al*, 1978, White *et al.* 1982, Pollock and Otto 1983, Rexstad and Burnham 1991). Maximum likelihood estimation involves the construction of a likelihood function which states the probability of observing the data (capture histories) as a function of the unknown target parameters. The unknown parameters are then estimated as those which maximise the likelihood function. One advantage of using likelihood estimation for a number of different models is that Akaike's Information Criterion (AIC) can be used for model selection (AIC is a measure of goodness of fit of a statistical model based on its complexity and precision).

MLEs could not be derived for M_h because it can have up to $N + 1$ parameters (where N = number of individuals observed and $p_1, p_2, p_3 \ldots p_N$ are the capture probabilities of *N* individuals). Burnham and Overton (1978) took a non-parametric approach and used a jack-knife technique for M_h. Jack-knife systematically re-computes the statistic omitting one observation at a time from the sample; in this case repeatedly computing the number of individuals, each time deleting successive trap occasions. The result is that the estimator is a linear function of the capture frequencies (Otis *et al.* 1978).

MLEs for M_h have now been developed under a unified framework for all eight models using finite mixture models (Pledger 2000). Individual heterogeneity is simplified down to a few (usually two) groups of individuals, such that all individuals within the same group have the same capture probability. This type of model is considered appropriate if there is a dichotomy in capture rates due to different age classes or sexes that cannot be observed and modelled as covariates. Finite mixture models are less appropriate for populations in which there is potentially infinite variation in capture rate, for example due to individual variation in activity, habitat and foraging preferences or differences in exposure of individuals to sampling relative to their home ranges (Pledger 2005). Conn (2006) used field data from a population of known abundance to demonstrate that models that included individual covariates performed better than mixture models alone.

Closed-population models (M_0 through to M_{tbh}) have also been developed which allow the incorporation of individual covariates (Huggins 1989, 1991). This is not possible for the original ML models because they include a term for the probability of capture of unknown animals (those never captured) and as these animals are unknown they do not have observable covariates. The inclusion of covariates was achieved by removing this term such that the likelihood is conditional on only the captured animals, thus covariates are only required for the captured individuals. Any covariates can be included, for example age or weight. If heterogeneity effects are fully explained by the covariates then the models can perform well, however they may perform less well than models with no covariates if heterogeneity effects are not fully determined by the covariates (Chao and Huggins 2005b).

Estimates from general models (e.g. M_{tbh} +/- covariates) are less biased than those from simple models (e.g. M_0) but they are also less precise (larger variances) because they have more parameters. It may not always be possible to fit general models to sparse data sets, for example those from populations with low capture and recapture rates. The models are complex (beyond the scope of this thesis) and often iterative such that estimation requires specially developed computer programs such as CAPTURE (White *et al*. 1982) and MARK (White and Burnham 1999).

Analysis of capture-recapture data

The program MARK supports the full range of models (M_0 through to M_{tbh}) for the full likelihood models of Otis *et al*. (1978), the finite mixture models of Pledger (2000) and the conditional likelihood models of Huggins (1989, 1991); and can also call up the program CAPTURE for the jack-knife and alternate M_h models, for example Chao's M_h estimator. Temporal and group covariates can be included in any of the likelihood models, and, as discussed, individual covariates can be included in the Huggins models (White 2005).

Objective model selection procedures such as AIC for likelihood estimators are available in closed-population computer programs such as MARK, but cannot be used to select between all the available models; for example AIC values of the full likelihood models cannot be compared with the AIC values of the conditional likelihood models. The model-averaging feature in MARK can be used when model selection is uncertain. Only models of the same data type (e.g. either full or conditional likelihood models) can be averaged. The output is an estimate and SE which takes into account the model selection uncertainty (White 2005, Lukacs 2007).

Heterogeneity models which do not use likelihood estimators, for example the jack-knife estimator for M_h, have no suitable model selection procedure (Chao and Huggins 2005b). The program CAPTURE does provide an automated model selection procedure based on goodness-of-fit tests of models M_h, M_b and M_t and between-model tests of M_0 and M_h, M_0 and $M_{b;}$ and M_0 and M_t (White *et al*. 1982); but the procedure does not perform well in simulations (Chao and Huggins 2005b).

Confidence intervals of the population estimate

Population size (*N*) does not have a normal distribution therefore the classical method of calculating confidence intervals from +/-1.96 SE(*N*) is not appropriate and results in poor coverage of the true population size; furthermore the lower bound may fall below the number of individuals captured during the survey (Rexstad and Burnham 1991). This problem is solved by constructing the confidence intervals under the assumption that the number of un-marked individuals in the population is log-normally distributed. The lower bound cannot fall below the number captured and the upper bound tends to be higher than N +1.96SE which gives better coverage (Rexstad and Burnham 1991).

Testing the closure assumption

Closed-population capture-recapture models assume that the population is both demographically and geographically closed during the sampling period. A valid test of demographic closure cannot be devised because behavioural responses in capture probabilities cannot be distinguished from failure of closure. For example an individual whose capture rate becomes very low during the study may not be differentiated from one who emigrates or dies (Otis *et al.* 1978, White *et al.* 1982). Closure tests have been developed which assume that M_0 or M_h or M_t is the underlying closed-population model (null hypothesis) and test it against the alternative hypothesis of an open-population model (Otis *et al.* 1978, White *et al.* 1982, Stanley and Burnham 1999). These tests are not valid if closure is true but a different model holds (e.g. M_b). For example, the program CAPTURE computes the closure test assuming that the underlying model is M_h however it often rejects the null hypothesis of closure even when it is true (Type I error) if capture probabilities vary with behaviour (Otis *et al.* 1978, White *et al.* 1982). The test has low power if sample size is small and it may fail to reject closure even when the population is open (Type II error) (e.g. Kawanishi and Sunquist 2004). Furthermore the test is only suitable to detect closure violation at the start or end of the study period, it is insensitive to individuals which emigrate during the middle of the study but return later (Otis *et al.* 1978).

In the absence of a suitable test, the assumption of demographic closure is generally reasonable as long as the length of the sampling period is appropriate for the target species. A period of 2 to 3 months is currently considered appropriate for big cats such as jaguars and tigers (Silver *et al.* 2004, Karanth and Nichols 1998). Such species are associated with low capture probability therefore some studies increase the sampling period in order to achieve sufficient captures for abundance estimation, for example 10 to 13 months of capture-recapture data were used to estimate tiger abundance in Malaysia (Kawanishi and Sunquist 2004). The authors condensed the data by pooling consecutive trapping occasions (~ 12 days per occasion) before analysis; closure was not rejected, but this is not unexpected given the small sample sizes (five to six individuals and 14 to 25 captures). Even if care is taken to optimise the sampling period for demographic closure, unexpected events may occur, such the death of a study animal in a live trap. It is possible to incorporate these anomalies into the final estimate; indeed Lukacs' (2007) definition of closed populations as those 'free of unknown changes in abundance' is fair since it is usually possible to account for known changes, for example White *et al*. (1982) recommend that if trap deaths are < 5% of total captures, the dead-animal data should be removed before analysis, and then the number of dead individuals added to the final population estimate.

The assumption of geographic closure is rarely attained in the field unless the study area encompasses an isolated habitat, for example a lake, an island or a habitat fragment. Most study areas do not bound the home ranges of every individual captured; consequently individuals living primarily outside the study area may be captured within the study area. This 'edge effect' is reflected in individual variation in capture rate, and regarding abundance estimation is partially resolved by population estimators robust to heterogeneity (e.g. M_h). Density estimation, however, requires knowledge of the area to which the abundance estimate is applicable and so must incorporate the edge effect if the population is not geographically closed.

Density estimation

Density, rather than abundance, is of ecological relevance in population biology, particularly for wildlife management. The conventional parameterization of density is in terms of the abundance estimate and the effective area sampled. The effective sampling (or trapping) area (often called ETA) refers to the area utilised by the study animals. Unless the sampled population is truly geographically closed, individuals at the edge of the trapping grid (study area) will live partially outside the study area. If the study area is large compared to average home range then the ETA approximates to the study area; density can be calculated from the area bounded by the outer most traps. If the study area is small compared to the average home range then the ETA exceeds the study area; density calculated from the area bounded by the outer most traps will overestimate the true density.

Density estimation and the ETA

The ETA is calculated by adding a boundary strip (width *W*) to the study area. *W* is some statistic based on movement data of the study animals, for example Dice (1938) proposed using half the diameter of the animal's home range. If telemetry data are available *W* may be based on the known average home range of the species. In the absence of telemetry data various *ad hoc* approaches are used based on the distances between captures from the trapping data; for example, half of the maximum distance moved between captures averaged over all individuals (½ mean maximum distance moved from here on referred to as ½ MMDM) (Wilson and Anderson 1985) or half of the asymptotic trap-revealed range length (½ARL) (Jett and Nichols 1987). Wilson and Anderson (1985) showed that using ½MMDM to estimate the effective sampling area produced density estimates that were less positively biased than those based on the study area alone.

Karanth and Nichols (1998) used ½MMDM to estimate tiger density using camera-trap data and following their recommendations the method has been used in many camera-trap studies of large cats, for example Silver *et al.* (2004). Nichols and Karanth (2002) summarise the method:

The mean maximum distance moved, $\hat{d}$, and its variance are estimated as:

(Eqns 2.2, 2.3)

$$\hat{d} = \frac{\sum_{i=1}^{m} d_i}{m} \qquad \hat{\text{var}}(\hat{d}) = \frac{\sum_{i=1}^{m} (d_i - \hat{d})^2}{m(m-1)}$$

where $\hat{d}$ is the mean maximum distance moved; d_i is the maximum distance moved between recaptures for individual i; and m is the number of individuals captured more than once.

The boundary strip width, W, and its variance are estimated as:

(Eqns 2.4, 2.5)

$$\hat{W} = \frac{\hat{d}}{2} \qquad \hat{\text{var}}(\hat{W}) = \frac{\hat{\text{var}}(\hat{d})}{4}$$

The effective sample area ($A(W)$) is obtained using a GIS program. Conventionally a strip of width W is added to the convex hull (minimum convex polygon) of the trap sites (i.e. the polygon which bounds the outer traps); however it is preferable to add a circle of radius W around each camera trap and then calculate the area bounded by the merged perimeter. This ‘concave’ approach will reveal whether there are any ‘holes’ (‘un-sampled’ areas between cameras) where individuals could have zero probability of capture (Maffei *et al.* 2005).

Density is then calculated as:

(Eqns 2.6, 2.7)

$$\hat{D} = \frac{\hat{N}}{\hat{A}(W)} \qquad \widehat{\mathrm{var}}(\hat{D}) = \hat{D}^2 \left[\frac{\widehat{\mathrm{var}}(\hat{A}(W))}{\left[\hat{A}(W)\right]^2} + \frac{\widehat{\mathrm{var}}(\hat{N})}{\hat{N}^2} \right]$$

where *N* is the abundance estimate, var(*N*) is the variance of the abundance estimate (obtained with *N* from the population analysis), var(*A*(*W*)) is the variance of the effective sampling area. Var(*A*(*W*)) can be calculated by approximating the shape of the sampled area to that of a circle of radius *c* + *W*, where *c* is a constant:

(Eqns 2.8, 2.9, 2.10)

$$\hat{A}(W) = \pi(c + \hat{W})^2 \qquad \widehat{\mathrm{var}}(\hat{A}(W)) = 4\pi^2 (c + \hat{W})^2 \, \widehat{\mathrm{var}}(\hat{W})$$

$$c = \sqrt{\frac{\hat{A}}{\pi}} - \hat{W}$$

Density estimation and the spatial detection model

The calculation of the ETA through the addition of a boundary strip (*W*) derived from trapping data is widely applied to density estimates but it is not optimal. *W* is a function of the specific trap spacing and is truncated at the edge of the study area (Wilson and Anderson 1985, Efford 2004) thus the ETA is underestimated and the density overestimated (Efford *et al.* 2005). An alternative method based on a spatial model of the detection (capture) process does not require the intermediate step of estimating the ETA and has performed well in field and simulation studies (Efford 2004, Efford *et al.* 2004, Efford *et al.* 2005). The method, described in detail elsewhere (Efford 2004, Efford *et al.* 2004), is summarised here.

Animals are assumed to occupy similar-sized, circular stationary home ranges whose centres have a Poisson distribution of density (*D*). A Poisson distribution assumes that home range centres occur independently with respect to each other. It is assumed that capture does not influence subsequent movement patterns of the animals. The probability that an animal is captured at a trap at distance (*d*) from the centre of its home range is a function of: the probability of capture when trap location equals home range centre (*g*(0)); and the decline in capture probability with increasing distance between trap and home range centre (σ). The shape of this detection function is assumed to be half-normal such that σ is one standard deviation from g(0) and the probability of capture is considered insignificant at ~3 σ (the edge of the home range) . Together *D*, *g*(0), *σ* and the configuration of the traps define the detection process. The trapping process is simulated for a range of known values of *D*, *g*(0) and *σ* based on the trap configuration of the field study, giving a set of capture-recapture data for each simulation. For each simulation, capture probability (*p*) and abundance (*N*) are estimated using any appropriate closed-population estimator that is robust to heterogeneity (e.g. M_h). A statistic ('*HR*') proportional to home-range size is also calculated for each set of simulated data. Inverse prediction is then used to infer *D*, *g*(0) and *σ* from field estimates of *p*, *N* and *HR*. It is assumed that the field data come from a study area that spans several home ranges and has sufficient recaptures (at least 20) to provide information on the spatial scale of movements (Efford *et al*. 2004).

The program DENSITY (Efford *et al*. 2004) can be used to estimate density from capture-recapture data using either the spatial detection function or traditional 'ETA statistics' such as ½MMDM. DENSITY allows habitats within the study area to be masked in areas where it is known that home-ranges can not be centred (e.g. in a river). The method of inverse prediction does not permit covariates to be included in the abundance estimators; however a new approach using maximum likelihood based methods is currently being developed which does allow inclusion of covariates (M. Efford, creator of DENSITY, pers. comm.).

Density estimates of wide-ranging, low density species

Over the past decade the utility of camera traps to monitor otherwise elusive species, and the pioneering work of Karanth (1995), which demonstrated how to use camera-trap data within a capture-recapture framework, have sparked numerous attempts to estimate densities of cryptic mammals. Most studies have focused on felids, for example tigers (Karanth and Nichols 1998, O'Brien *et al*. 2003, Wegge *et al*. 2004, Kawanishi and Sunquist 2004), jaguars (Wallace *et al*. 2003, Maffei *et al*. 2004, Silver *et al*. 2004, Miller and Miller 2005, Cullen *et al*. 2005, Harmsen 2006, Miller 2006, Soisalo and Cavalcanti 2006, Salom-Pérez *et al*. 2007), pumas (*Puma concolor*) (Kelly *et al*. 2008), ocelots (Trolle and Kéry 2003, Dillon 2005, Maffei *et al*. 2005, Trolle and Kéry 2005, Di Bitetti *et al*. 2006, Haines *et al*. 2006, Maffei and Noss 2008), Geoffroy's cat (*Oncifelis geoffroyi*) (Cuellar *et al*. 2006), snow leopards (*Uncia uncia*) (Jackson *et al*. 2006), and bobcats (*Lynx rufus*) (Heilburn *et al*. 2006); although recently the method has been used to estimate tapir (*Tapirus terretris*) (Noss *et al*. 2003) and giant armadillo (*Priodontes maximus*) (Noss *et al*. 2004) densities also. Many of the species studied in this way are wide-ranging and occur at low densities. This is in contrast to the development of capture-recapture theory which was based largely on small mammals that occur at high densities with relatively small ranges. As such it is prudent to discuss some of the problems associated with the application of these methods to the study of low density wide-ranging species; not least because the results of published studies are often used to make management decisions and drive policy.

Sample size

Samples sizes of ~10-20 individuals may be too small for reasonable estimates using capture-recapture closed population models (Otis *et al*. 1978, White *et al*. 1982). Because many of the species of interest occur at low numbers, relatively small sample sizes are inevitable; however this is no justification for applying an otherwise inappropriate method of population estimation. In 64 published abundance estimates based on camera-trap data of felids the mean sample size was 13 (SD = 10) with a mode of 5. In particular, some studies have used capture-recapture models to estimate abundance from exceptionally small samples, for example jaguars $n = 4$ (Wallace *et al*. 2003) and ocelot $n = 3$ (Haines *et al*. 2006). In such circumstances it may be more appropriate simply to report the minimum number alive as a conservative best guess.

Capture probability

Models which include behavioural variation in capture probability (e.g. M_b) may be appropriate in live-trapping studies where individuals may become trap-shy (in response to being trapped) or trap-happy (in response to bait). There is little evidence to date of a behavioural response to camera traps; however during one study which used a high density of camera traps (1 per km^2) in conjunction with impression pads to obtain pug marks, it seems that the tigers used the impression pads as cues to avoid the cameras (Wegge *et al*. 2004).

Models which include temporal variation in capture probability (e.g. M_t) may be appropriate if trap effort varies through time. M_h assumes constant trap effort on each trapping occasion (Burnham and Overton 1978) however trap failure during the survey will break this assumption. Camera traps may fail for a number of reasons yet few studies report levels of camera trap failure. Chapter 3 assesses the effect of trap failure on abundance estimates using the M_h jack-knife estimator.

Most abundance estimates based on camera-trap data use the M_h jack-knife model, and for good reason. Low sample sizes, common in studies of large felids, will limit the ability to correctly identify sources of variation in capture probability and select the appropriate model, for example M_h versus M_t or M_b (Karanth and Nichols 1998). Heterogeneous capture rates of individuals are expected due to a combination of biological and sampling biases such as sex, social status, age and trap location. Models which assume equal capture probability in the presence of individual heterogeneity will underestimate abundance (Burnham and Overton 1978, Chao and Huggins 2005b). Therefore Nichols and Karanth (2002) recommend the use of the M_h jack-knife estimator given the *a priori* belief that capture probabilities are heterogeneous, and because it tends to be more robust than other model estimators to deviations from the underlying assumptions. Note however that if nearly all individuals are captured it may overestimate abundance (Chao and Huggins 2005b); given the low capture probability of many target species this situation is unlikely.

As with other estimators, the M_h jack-knife estimator will underestimate abundance at capture probabilities less than ~0.05 (White *et al.* 1982). Low capture probabilities are common in camera surveys of wide-ranging species such as large cats, and abundance estimates based on samples with average capture probabilities < 0.05 are published, for example tigers, $\hat{p} = 0.03$ (O'Brien *et al.* 2003), ocelots, $\hat{p} = 0.02$ to 0.05 (Maffei *et al.* 2005). Simulation studies by Harmsen (2006) suggest that such estimates are likely to be unreliable, but that pooling consecutive trapping occasions before analysis will increase the capture probability hence the precision of the M_h jack-knife estimate. Many studies now take this approach to increase capture probability by increasing the occasion length and simultaneously decreasing the number of occasions (e.g. Kawanishi and Sunquist 2004, Heilburn *et al.*2006, Dillon and Kelly 2007, Kelly *et al.* 2008). The M_h jack-knife estimator requires at least five trapping occasions (Otis *et al.* 1978). Published camera-trap studies fulfil this requirement, with seven to 70 occasions of length 1 to 44 days per occasion. Although capture probability can be increased by increasing the sampling period care must be taken not to violate the assumption of demographic closure. Several published studies sampled for 6 to 12 months (Karanth 1995, Kawanishi and Sunquist 2004, Haines *et al.* 2006), which exceeds the recommended sampling period of 2 to 3 months for large cats (Silver *et al.* 2004). Because the closure test is not powerful with low sample sizes, the capture histories from such studies should be subjectively assessed for evidence of closure before population estimation.

The M_h jack-knife estimator does not quantify the degree of heterogeneity within the population (Chao and Huggins 2005b). Simulations have shown that high levels of heterogeneity (extreme variation between individuals in capture probability) can reduce the reliability of the abundance estimate (Harmsen 2006). Pooling occasions can reduce the level of heterogeneity and so improve the estimates (Harmsen 2006). No published studies report levels of heterogeneity; although this could be simply assessed through a frequency of distribution of captures. For example, a bimodal distribution would suggest that the population consists of two groups, one with a high probability of capture and one with a low probability of capture perhaps arising from behavioural differences between the sexes (e.g. Harmsen 2006) or social status (e.g. residents versus transients).

Methods of density estimation

This chapter has described two different methods of density estimation: the ETA method in which a buffer based on the home range size of the target species is added to the survey area, and the spatial detection method which uses inverse prediction. Camera-trap studies commonly use the ETA method with a buffer width of ½MMDM derived from the trap data. This is usually justified on the grounds that Wilson and Anderson (1985) found that a buffer width of ½MMDM performed well in simulation studies. However the simulations by Wilson and Anderson (1985) are based on densities of 2,500 to 5,000 individuals /km^2 which far exceed the natural densities of any large carnivore.

The spatial detection method has not been used in any published camera-trap study, yet it could provide a sensible alternative to the ETA method in the absence of good home range data. Again, simulations and field tests perform well but are based on relatively high densities (50 to 5,000 individuals /km^2) (Efford 2004, Efford *et al* 2005).

The precision and accuracy of both the ETA method (with ½MMDM) and the spatial detection method need to be investigated at a scale appropriate for population densities associated with large, wide ranging carnivores.

Home range and density estimation using ETA

A few studies do not calculate an ETA for density estimation but simply use the area bounded by a minimum convex polygon of the outer traps of study area, or the boundary of a park or reserve (e.g. Carbone *et al.* 2001, Cullen *et al.* 2005, Heilburn *et al.* 2006). This is acceptable if it is known that the members of the population do not leave the park boundaries; but failure to account for ETA when individuals do move beyond the trapping grid will overestimate the true density.

Most published studies do calculate the ETA prior to density estimation, using a proxy for home range radius (usually ½MMDM) derived from the trap data. Some studies use few individuals for calculation of MMDM; for example Trolle and Kéry (2003) and Cuellar *et al.* (2006) used $n = 2$, because only 2 individuals were captured at >1 station. Not only does this indicate that the stations were spaced too far apart (see later), but such small samples will likely underestimate the mean home range diameter so it may be preferable to use absolute MDM instead (Kawanishi and Sunquist 2004). Wallace *et al.* (2003) chose to use the most conservative estimate of jaguar home range available in the literature (10 km^2) to estimate ETA for their jaguar survey; an approach which will most likely have overestimated the true density.

Maffei and Noss (2008) emphasize that the only means to confirm whether MMDM derived from trap data is a valid proxy for home range diameter is to conduct telemetry and camera trapping simultaneously. Four studies to date have done this, with differing results: home range diameter derived from camera traps and from telemetry agreed in a study of jaguars in Costa Rica (Salom-Pérez *et al.* 2007) and tapirs in Bolivia (Noss *et al.* 2003); however camera-trap data underestimated home range diameter in a study of jaguars in the Pantanal (Soisalo and Cavalcanti 2006), and of ocelots in Belize (Dillon 2005) and in Bolivia if sample areas were small (Maffei and Noss 2008). This variation should be of no surprise. The relationship between a proxy of home range derived from camera-trap data will be a function of the spatial configuration of the traps in the particular study and the ranging behaviour of the individuals sampled. As such the suggestion that estimates of MMDM can be calibrated using telemetry and extrapolated to other studies (Soisalo and Cavalcanti 2006) should be treated with caution.

Factors influencing reliability of ETA density estimate

The ranging behaviour of the target species and the spatial configuration of traps within a survey (survey area, trap spacing and location) will influence sample size, capture probability and estimates of MMDM, all of which will all influence the reliability of the abundance and density estimate.

Ranging behaviour

Although it is common to use an average estimate of home range radius to estimate the ETA, variation in ranging behaviour within the sampled population needs to be considered before estimating densities. For example, Cuellar *et al*. (2006) noted distinct seasonal changes in the ranging behaviour of Geoffroy's cats in Bolivia, in addition this species utilises relatively small areas for 2 to 3 months before moving large distances (25 km) a behaviour which could lead to highly variable density estimates both within and between sites.

Most large carnivores display sexual differences in their ranging behaviour. However differences in home range radius between the sexes, and the resultant effect on the ETA and density estimation has not yet been formerly addressed. Harmsen (2006) suggested that for species with distinct differences in ranging behaviour (and capture probability), such as jaguars, it may be appropriate to estimate density separately for males and females. Not only would this allow a more appropriate ETA to be applied to the abundance estimate of each sex, but it would also remove extreme heterogeneity in capture rate from the capture histories and so increase the precision of the abundance estimate. Sexual differences in MMDM and the resultant affect on density estimates are investigated in Chapter 4.

Survey area

The study of wide-ranging species requires camera traps spaced over a large area but this is often limited by the costs and logistics of camera trapping. Various studies have reported that small survey areas give inflated density estimates (e.g. Cuellar *et al*. 2006, Harmsen 2006, Jackson *et al*. 2006, Dillon and Kelly 2007, Maffei and Noss 2008). This positive bias may arise because:

1) Individuals move further than the maximum distance between traps. Consequently the proxy for home range diameter derived from the camera data underestimates the true

home range and the ETA. For example, Dillon and Kelly (2007) demonstrate an inverse relationship between trap spacing and density based on camera-trap data of ocelots.
2) Individual ranges can overlap in relatively small areas (despite maintaining exclusive ranges elsewhere) particularly if traps are located near a favoured resource; for example the high densities reported for jaguars in the Belizean forest (Silver *et al*. 2004, Harmsen 2006) maybe an artefact of preferentially locating traps along logging roads which are favoured by jaguars as easy travel routes through the dense forest. Extrapolating this density to areas without logging roads may be unreliable.
3) Small survey areas may fail to sample the all available habitat types, again extrapolation to larger areas may not be appropriate.

Some published studies fail to recognise the positive bias of small survey area on their density estimates. For example, in a study of jaguars in Corcovado National Park, Costa Rica, Salom-Pérez *et al*. (2007) surveyed just 29 km^2 (ETA of 88 km^2); this is likely to overestimate the true density yet the authors claim the opposite arguing that density is likely underestimated because they only surveyed 20% of the park. This is a rash claim to make given that their findings suggest that the jaguars of Corcovado are in a critical condition anyway. In a study of jaguars in Bolivia, Maffei *et al*. (2004) extrapolated densities based on three study sites (sample areas of 49 to 130 km^2, ETAs of 128 to 308 km^2) to the entire Bolivian Gran Chaco, an area of 34,400 km^2 and concluded that the Chaco supports a viable jaguar population. Such broad claims should be treated with caution, particularly if used to drive Government policy. Soisalo and Cavalcanti (2006) demonstrate the consequences of overestimation and extrapolation using the Pantanal as an example; here they show that underestimation of MMDM by camera-trap data (compared to telemetry) overestimated the jaguar population by 3.8 to 5 individuals per 100 km^2. Extrapolating this estimate across the entire Pantanal (140,000 km^2) would overestimate the population by 5,320 to 7,000 individuals.

Maffei and Noss (2008) discuss the appropriate minimum survey area relative to the home range of the target species, using empirical camera-trap and telemetry data of ocelots (their study, and Dillon 2005), tapirs (Noss *et al*. 2003), and jaguars (Soisalo and Cavalcanti 2006). They recommend that if home ranges are known for the site, the camera survey area should cover at least four times the average home range. Of course many studies do not have the funds to combine telemetry with camera trapping, and home range may not be known for the target species at the study site. In these situations they suggest that MMDM can be considered a valid proxy for home range diameter and

ETA estimation if a large enough area is surveyed. They recommend surveying the largest area possible and sub-sampling the data to evaluate the threshold area above which the density estimates stabilize. For jaguars in the Belizean rainforest this has been estimated at about 100-150 km^2 (Harmsen 2006) and is investigated further in Chapter 4.

If cameras are limited, survey areas can be maximized by moving cameras within the sampling period and combining data from the sub-areas sampled. Various studies have used this technique, (e.g. Karanth and Nichols 1998, O'Brien *et al*. 2003, Wegge *et al*. 2004, Trolle and Kéry 2005, De Bitetti *et al*. 2006, Soisalo and Cavalcanti 2006). Most of these studies sequentially sample adjacent trapping grids which are then combined ignoring temporal variation such that the first day of each sampling block forms the same trapping occasion (e.g. Soisalo and Cavalcanti 2006). De Bitetti *et al*. (2006) used an alternative approach in which the entire area was surveyed throughout the sampling period with traps at half density which were shifted to new locations within the same area half-way through the sampling period. This method may be considered superior since it reduces the confounding effect of space and time.

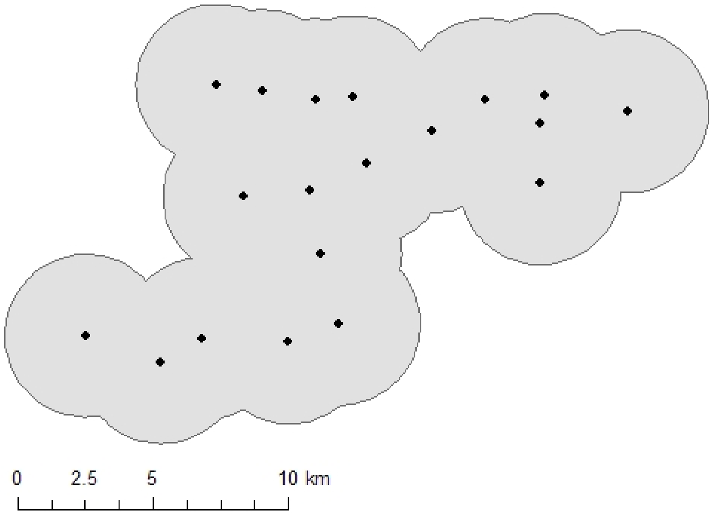
When resources are severely limited surveys can utilize single camera stations. This effectively doubles the area which can be surveyed but increases the risk of trap failure and variable trap effort. Because left and right flanks can not be identified as the same or different individuals the analysis must be limited to one side only. Although this lowers the capture probability it is still possible to use this method for estimation (Karanth 1995, O'Brien *et al*. 2003).

Trap spacing

Trap spacing, as well as overall survey area, is important. Dillon and Kelly (2007) suggest that camera spacing should seek to maximize capture probability by including at least two traps per average home range. Traps which are spaced too widely may fail to detect individuals if they occupy home ranges which fall between trap locations. Thus, a balance should be found between maximizing survey area (e.g. Maffei and Noss 2008) and optimizing trap spacing (e.g. Dillon and Kelly 2007).

'Gaps' within surveys, where individuals could theoretically maintain a home range and not be detected, can be identified when the buffer based on average home range radius (or a proxy thereof) is applied to each trap location (Figure 2.2). Essentially the presence of gaps within a survey breaks the assumption of capture-recapture models that the probability of capture of every individual is greater than zero. Noss *et al*. (2003) argue that whilst estimates based on such discontinuous surveys may be less precise because of the increased edge effect, but they are not invalid; and Maffei *et al*. (2005) demonstrated that at the same site density estimates of ocelots did not differ between continuous and discontinuous surveys. The extent to which ‘gaps’ influence the reliability of density estimates is likely to be dependent on the spatial aspects of the survey grid and the ranging behaviour of the target species and warrants further study.

a) Buffer width 3.0 km



b) Buffer width1.5 km

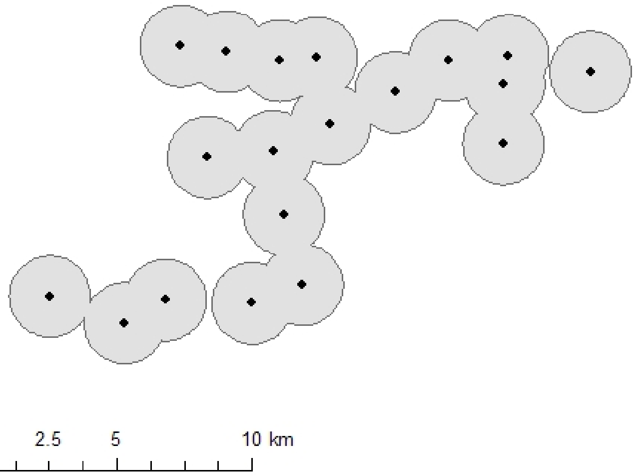


Figure 2.2 An example of continuous and discontinuous effective trapping areas (ETA). Cameras are spaced ~1-3 km apart. In **a)** the mean home range radius of the target species is 3 km therefore the ETA is continuous. In **b)** the mean home range radius of the target species is 1.5 km therefore the ETA is discontinuous.

Trap Location

Harmsen (2006) demonstrated that minor changes in trap location can influence abundance estimates if moved from a location of low capture probability to one of high capture probability. Several studies have detected subtle differences in capture rate associated with certain habitat features, in particular variation in capture rate with road and trail characteristics such as width, age and substrate (e.g. Maffei *et al*. 2004, Trolle and Kéry 2003, De Bitetti *et al*. 2006, Dillon and Kelly 2007). In order improve precision of abundance estimates researchers frequently select trap locations which will optimise capture probability. This is valid, but as discussed earlier, care should be taken when extrapolating the resultant density estimates to larger areas where habitat may be less optimal.

Multi-species surveys: pros and cons

Camera traps record any animal that passes, not just the target species, giving rise to huge datasets. Within the camera-trap literature there is a temptation to use the same survey to estimate the abundance of multiple species within the study area. For example, Noss *et al*. (2003, 2004) used surveys designed to study jaguars to estimate densities of tapir and giant armadillo. Certainly utilising the same database is cost efficient and can reveal interactions between sympatric species (e.g. Harmsen *et al*. in press); however using the same survey design for density estimations of multiple species should be treated with caution given that the optimal trap location, spacing and minimum survey area for one species may not be optimal for another species. Density estimates of similar species from the same survey may be valid if sufficient information is known about their ranging behaviour and preferably if the survey is designed *a priori* with this in mind; for example a survey originally designed to study jaguars (Maffei *et al*. 2004) has been used to estimate puma density (Kelly *et al*. 2008) and ocelot density (Maffei *et al*. 2005).

Recommendations

This chapter has reviewed the current method of density estimation of low-density, wide-ranging species using camera-trap technology and closed population capture-recapture models. This approach to density estimation has been instrumental in facilitating ecological research of elusive species. The technique has been used increasingly over the past decade with few attempts to refine the methodology since the original work of Karanth and Nichols (1998); although it is starting to receive attention now e.g. Harmsen (2006), Soisalo and Cavalcanti 2006, Dillon and Kelly (2007) and Maffei and Noss (2008). Researchers' should remember: '*garbage in, garbage out'* (Krebs 1999); for example the use of closed-population models for exceptionally low sample sizes is not appropriate; also consideration should be given to the potential biases which may arise from aspects of both the sampling design (survey area, trap spacing, trap location) and the ranging behaviour of the target species prior to commencing the study. The effects of all these factors on the reliability of density estimates require more research. Yet whilst the method itself needs to be refined it continues to be used to assess population of threatened species, and potentially drive conservation policy. As such researchers and policy makers alike must interpret findings with caution, taking into account the limitations of the method.

Chapter 3

Camera failure and closed population models

Abstract

Camera-trap data combined with capture-recapture closed population models are commonly used to estimate the abundance of elusive, low density mammals. Although camera-trap technology is improving there is no guarantee of functional consistency throughout a survey. This study assessed the robustness of the M_h jack-knife estimator to camera failure and night-only sampling in the estimation of jaguar (*Panthera onca*) abundance in Belize, Central America. The results suggest that the jack-knife estimator is robust to trap failure up to ~10% of trap-occasions based on manipulation of empirical data. Surveys with high capture and recapture rates were less affected by trap failure than those with low capture and recapture rates. Pooling trap-occasions reduced the effect of trap failure. Trap failure can negatively or positively bias the abundance estimate, dependent on the specific nature of the capture histories. Underestimation is likely if trap failure excludes individuals from the capture history, whilst the causes of overestimation are less clear; both warrant further investigation. These findings suggest that published abundance estimates based on camera-trap data should include information about the level of trap-failure within the survey. Jaguar activity is primarily nocturnal in the study area. Night-only sampling lowered the number of individuals detected and the overall capture probability; for surveys in which capture probability remained above the 0.03 threshold required for reliable estimates (Harmsen 2006) night-only sampling did not significantly affect the abundance estimate compared to continuous sampling.

Introduction

The recent development of passive camera traps has made possible the study of elusive species living at low densities (Karanth and Nichols 1998). Camera traps have the potential to provide data on large numbers of the population, more so than could be practically achieved by live-trapping. The use of camera-trap technology with capture-recapture closed population models is becoming a popular method to estimate the abundance of elusive, low density mammals (Chapter 2). Its utility means that it will be used increasingly to drive conservation policy (Trolle and Kéry 2005) therefore the methodology needs to be accurate, robust, reliable and comparable. The study of elusive species is, by its very nature, based on low sample sizes and low capture rates which will both reduce the reliability of population estimates (Chapter 2). This is further complicated by sampling biases arising from study design in relation to the ranging behviour of the target species (Chapter 2). Some of these issues are now beginning to be addressed (e.g. Harmsen 2006, Maffei *et al*. 2008). Variable trap effort, arising from camera failure during the survey period is not uncommon, particularly in sites where the terrain and logistics prevent daily visits to camera stations; or where human activity may interfere with cameras; and due to harsh environmental conditions. The extent to which moderate levels of trap failure bias abundance estimates based on small sample sizes associated with elusive mammals has not yet been addressed. This aim of this study is to assess the robustness of the M_h jack-knife estimator to variable and reduced trap effort resulting from camera failure when estimating the abundance of an elusive, low density mammal, the jaguar (*Panthera onca*) in Belize, Central America

By nature of their applicability to the detection of elusive mammals, camera traps are often employed in harsh environments such as humid rainforests, (e.g. Harmsen 2006) or exposed arid conditions (e.g. Jackson *et al*. 2006) so exposing them to conditions which may lower functionality. Even in favourable environmental conditions camera traps are not always reliable, due to design faults or field incompetence; furthermore when deployed in areas of human activity cameras are at additional risk of interference from people. Yet, human-influenced landscapes are exactly the areas requiring research into the population ecology of large elusive mammals (Chapter 4). In addition to heightened risks of camera failure through theft and vandalism, working in human-dominated areas may often necessitate limiting the trapping periods to night-only sampling. This prevents the wasting of film on high activity non-target species such as cattle or vehicles (e.g. Karanth and Nichols 1998, Heilbrun *et al*. 2006), and is also often preferred by local people going about their daily activities. Examples of the causes of camera failure experienced when conducting camera trap surveys for jaguars on unprotected lands in Belize, Central America are listed in Table 3.1.

Table 3.1 Examples of camera failure documented during camera-trap surveys of jaguars conducted in Belize, Central America

Failure	Examples
Technical	- Faulty circuitry e.g. ‘snapping’: the camera takes consecutive photos without the sensor being triggered such that the film is full within 24h - Field incompetence: staff may be well-trained but mistakes are inevitable e.g. exposing the film, forgetting to switch on the camera
Climate	- Heavy rains may flood cameras overnight - Heat blindness in exposed areas at high temperatures may prevent detection of body heat against the ambient temperature - Humidity can ruin film and drain batteries
People and animals	- Theft and vandalism can result in the loss of many weeks of data - Unexpectedly high levels of traffic of non-target species such as cows or vehicles may cause a film to run out sooner than anticipated, or necessitate night-only sampling - Invertebrates nest in camera lens or block sensors

Capture-recapture models are classified according to the assumptions they make about capture probability (Otis *et al.* 1978). The model M_h assumes capture probability varies between individuals. Heterogeneous capture rates of individuals within a population are expected due a combination of biological and sampling biases such as sex, social status, age and trap location. Models which assume equal capture probability in the presence of individual heterogeneity will underestimate abundance (Burnham and Overton 1978, Chao and Huggins 2005b). Published abundance estimates derived from camera-trap data commonly use the M_h jack-knife estimator (Burnham and Overton 1978), following the recommendations of Nichols and Karanth (2002) (see Chapter 2 for more detail).

Accurate capture-recapture abundance estimates require reliable methods of counting individuals during each occasion. Models of closed populations, such as M_h, assume constant trap effort among sampling occasions. If trap effort is variable through the survey period then the probability of capture of some individuals may fall to zero if the only station that they ever pass is a ‘failed’ camera. This will violate the assumption underlying capture-recapture models that all individuals have a probability of capture > 0. Few studies report levels of trap failure during surveys, yet given the range of factors which may result in camera failure (Table 3.1) it is unlikely that many camera-trap surveys maintain constant trap effort. It is therefore appropriate to investigate how robust are closed population models to variation in trap effort; and what level of trap failure, if any, is acceptable. In this study trap failure is simulated in three datasets for which camera failure was known to be minimal, to determine whether it is appropriate to apply standard methods of capture-recapture population estimation to poor datasets. The same datasets are also manipulated to determine the influence of night-only sampling on abundance estimates.

Methods

Camera-trap data collected during three surveys were manipulated in order to assess the effect of variable trap effort (camera failure) and reduced trap effort (continuous versus night-only sampling) on jaguar abundance estimates using the jack-knife estimator for model M_h. The surveys were conducted in a protected forest where human interference, thus camera failure, was minimal (B. Harmsen, Panthera Belize, pers. comm.). Estimates of camera failure during surveys conducted on neighbouring lands with human activity ranged from 1.9% to 17.6% of the trap-nights, spanning from 0% to 90% at any given camera station. Consecutive failures at the same station ranged from 0% to 45% of the trapping period. When stations with more than 10 failed nights were removed these failure rates fell, ranging from to 2.3% to 4.4% (0% to 20% at any given station), with consecutive failures at 0% to 20% (Chapter 4).

The effect of camera failure on abundance estimates

Data from three camera-trap surveys of jaguars conducted in a protected forest in 2004, 2005 and 2006 were manipulated in order to assess the effect of camera failure on abundance estimates using the jack-knife estimator for model M_h. A 62-day period was selected (22nd March to 22nd May) from each year. These datasets were complete (no camera failure) and identical in all 19 camera locations, giving 1178 trap-occasions per survey. The data for 2004 and 2005 came from Harmsen (2006).

Simulation of camera failure

Camera failure rate was set at 10% trap-night failure (118 failed trap-occasions during the entire survey period). The number of consecutive failures at the same station was set to a maximum of 30% of the survey period (19 consecutive occasions). Camera location (1-19), occasion (1-62) and number of consecutive failed occasions (1-19) were selected randomly, and repeated until the total number of failed trap-occasions was equal to 118. The final randomly selected value of consecutive failed occasions was constrained if it otherwise caused the total number of failed trap-occasions to exceed

118. Duplicate failures on the same trap-occasion were rejected. This process was repeated 20 times, giving 20 sets of failed trap-occasions. Each set of failed trap-occasions was applied to the trapping records of each survey such that captures were removed if they occurred on a simulated failed trap-occasion. Abundance was then estimated from the new trapping records, 20 for each survey plus the original estimate based on the complete trapping record. Abundance was estimated for every trapping record both as the number of individuals captured (minimum number alive), and using the jack-knife estimator for model M_h in the program CAPTURE (Rexstad and Burnham 1991). The full procedure was repeated with camera failure rate set at 5% and 20% (59 and 236 failed trap-occasions during the entire survey period, respectively). The number of consecutive failures at the same station was kept at a maximum of 30% of the survey period (19 consecutive nights).

Harmsen (2006) demonstrated that pooling data from consecutive trap occasions reduces the number of occasions with no captures and so increases the capture probability, which in turn can improve the precision of the estimate. It was hypothesised that pooling occasions would improve robustness to camera failure therefore the simulated capture histories were collapsed from 62 occasions (62 consecutive days) to nine occasions (nine consecutive weeks, note that the final week consisted of only six days) and the abundance estimates were repeated.

Robustness of the jack-knife M_h model to camera failure

The mean ($\hat{N}$), SE and 95% CI (+/-1.96SE) were calculated for each set of 20 abundance estimates. Three measures of performance of M_h were calculated in order to compare the actual estimate (*N*, no trap failure) with the simulated estimates under each level of trap failure for each survey:

1. *The coefficient of variation (CV) of the estimate* = $\dfrac{SE(\hat{N})}{N} \times 100$

2. *The relative bias* = $\dfrac{\left(\hat{N} - N\right)}{N} \times 100$

3. *Confidence interval coverage = % of nominal 95% CIs that contain the actual value*

The program CAPTURE calculates the average capture probability ($\hat{p}$, termed '*p-hat*') from the trapping record for each abundance estimate. Simulation studies by Harmsen (2006) showed that *p-hat* ≥ 0.03 is necessary for a reliable estimate using the jack-knife M_h estimator. Closed population models rely on recaptures, so high capture ratios are preferred. Trap failure may alter this ratio in either direction; with consequences for the abundance estimate. In order to quantify this, the capture frequency ratio was calculated as (Eqn 3.1):

$$\frac{\textit{Number of individuals with recaptures}}{\textit{Number of individuals with one capture}} \qquad \text{(Eqn 3.1)}$$

A capture frequency ratio >1 indicates that more than half of the individuals in the trapping record were recaptured. Together the *p-hat* and the capture frequency ratio reflect the nature of the capture history, thus will likely determine the effect of simulated trap failure on the abundance estimate. The mean *p-hat* and mean capture frequency ratio were calculated for each set of 20 simulations and compared at each level of trap failure and with the actual *p-hat* and capture frequency ratio of each survey.

Trap effort as a temporal covariate in MLE M_h mixture models

Trap effort was calculated for each occasion of every simulated dataset. Abundance was estimated for each simulated dataset using the maximum likelihood estimator (MLE) for the mixture model with two groups (M_{h2}) in the program MARK (White 2005). This was repeated with the addition of trap effort as a temporal covariate (model $M_{h2\text{-trap}}$) and the AIC values compared to determine whether inclusion of trap effort improved the model likelihood. The intention was to investigate whether the inclusion of trap effort as a temporal covariate in maximum likelihood models could improve the reliability estimate over the simple M_h model. This was attempted for several of the simulated datasets but had to be abandoned because the $M_{h2\text{-trap}}$ model generally failed to converge, probably because the data were too sparse (K. Burnham, creator of program MARK, pers. comm.).

The effect of continuous versus discrete trap effort on abundance estimates

Abundance was estimated as minimum number alive, and using the jack-knife estimator for model M_h, for the three surveys (2004, 2005 and 2006) including and excluding daytime captures to determine whether trapping only at night significantly affects the estimate. All photographs had a time and date stamp. Daytime captures were defined as those occurring between sunrise and sunset. Daily sunrise and sunset times (2004-2006) were acquired from the US Naval Observatory (2007).

Results

Jaguar abundance estimates based on the full trapping-records with continuous detection (day and night) for a 62-day period (March to May) in 2004, 2005 and 2006 are compared with abundance estimates based on variable and reduced trap effort to determine the robustness of the M_h jack-knife estimator. In 2004 20 individuals were captured a total of 74 times, giving an abundance estimate of 40 (95%CI 27-88). In 2005, 18 individuals were captured a total of 48 times, giving an abundance estimate of 20 (95%CI 19-37). In 2006, 17 individuals were captured a total of 103 times, giving an abundance estimate of 19 (95%CI 18-36).

The effect of camera failure on abundance estimates

The average number of individuals captured in each set of 20 trapping records was the same as for the original trapping records of each survey until trap failure reached 20%; at this level the average number of individuals captured reduced (Figure 3.1). This suggests that if the minimum number alive is considered a reasonable index of the actual population then trapping records which have suffered 5% or 10% trap failure may remain acceptable as conservative estimates of the actual population.

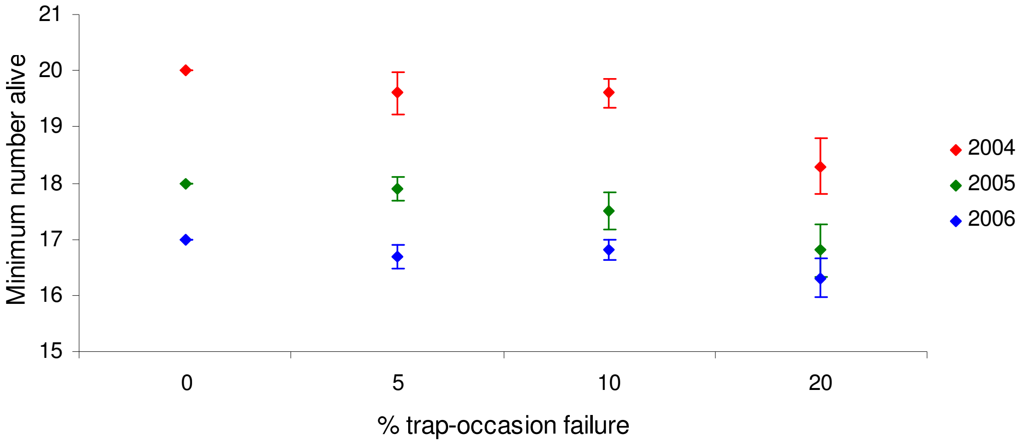


Figure 3.1 Effect of trap failure on number of individuals captured ('minimum number alive').Three levels of trap failure (5%, 10% and 20%) were applied 20 times to the trapping records of three surveys (2004, 2005 and 2006). The mean and 95% CI of the 20 counts for each level of simulated trap failure are shown for each of the three surveys. 0% trap-occasion failure is the count based on the original data.

Number of captures and number of individuals

The loss of captures from the trapping records tended to increase with increased trap failure, for both the un-pooled (62 occasions) and pooled (nine occasions) capture histories (Table 3.2). The proportional increase in loss of captures with increased randomly distributed trap failure indicates a random distribution of captures through time. The loss of individuals also increased with trap failure but varied less consistently (Table 3.3), presumably because the loss of an individual would depend on how many times it occurred in the trapping record. The variation between the three surveys in loss of captures and individuals probably reflects differences between the original trapping records of the three surveys; for example the ratio of captures to recaptures, and the number and distribution of captures throughout each survey period.

Table 3.2 Mean % loss of captures when three levels of trap failure (5%, 10% and 20%) were applied 20 times to the capture histories of three surveys (2004, 2005 and 2006). The % mean loss of captures are shown for the 62 one-day occasions; a similar pattern was observed for the same capture histories pooled into 9 one-week occasions.

% failure	**Mean % captures lost (SD)**		
	2004	**2005**	**2006**
5	4.9 (2.8)	4.5 (3.6)	4.3 (2.9)
10	7.8 (3.5)	7.2 (3.8)	7.8 (4.0)
20	18.0 (5.4)	17.2 (6.4)	18.2 (4.5)

Table 3.3 Mean % loss of individuals when three levels of trap failure (5%, 10% and 20%) were applied 20 times to the capture histories of three surveys (2004, 2005 and 2006).

% failure	**Mean % individuals lost (SD)**		
	2004	**2005**	**2006**
5	2.3 (4.1)	0.8 (2.7)	2.1 (2.9)
10	2.0 (3.0)	3.6 (4.1)	1.2 (2.4)
20	8.8 (5.6)	6.9 (5.9)	4.1 (4.7)

Capture probability ($\hat{p}$)

For the un-pooled capture histories, the average capture probability (*p-hat*) associated with each original trapping record was ≥ 0.03, the threshold required for a reliable estimate using the jack-knife estimator (Harmsen 2006). The average *p-hat* during the 2006 survey was more than twice that of the 2004 and 2005 surveys, > 0.05, the threshold required for a precise and reliable estimate (Harmsen 2006). *P-hat* tended to decline in 2005 and 2006, but increase in 2004, with increased trap failure (Figure

3.2a). When the capture histories were pooled from 62 one-day occasions to nine one-week occasions *p-hat* increased by an order of magnitude, and became more stable to increased trap failure (Figure 3.2b).

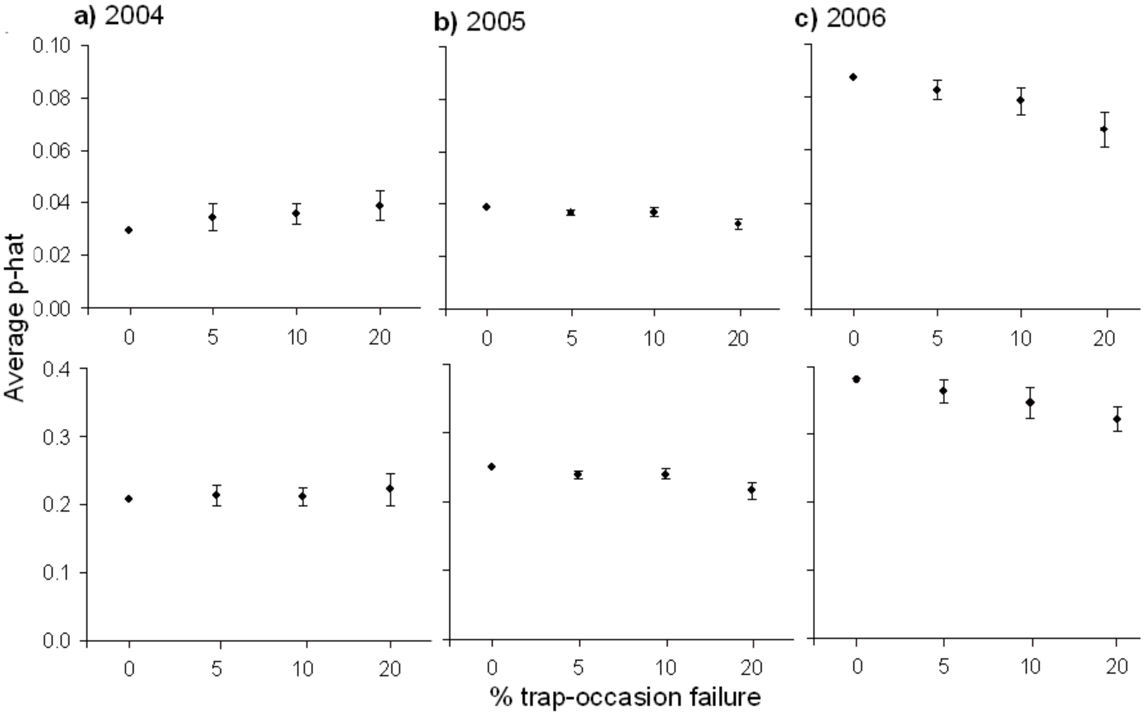


Figure 3.2 Effect of trap failure on average capture probability (*p-hat*) calculated using the jack-knife estimator for model M_h. Three levels of trap failure (5%, 10% and 20%) were applied 20 times to the capture histories of three 62-day surveys (2004, 2005 and 2006). Capture histories were pooled into nine one-week occasions. The mean and 95% CI of the 20 *p-hats* for each level of simulated trap failure are shown for each of the three surveys, for both the **un-pooled** (62 occasions, **upper panel**) and **pooled** (9 occasions, **lower panel**) capture histories. 0% trap-occasion failure is the *p-hat* based on the original data.

Capture frequency ratio

For all capture histories, the capture ratio was >1 indicating that more individuals were recaptured than not. For the un-pooled (62 occasion) capture histories, the capture frequency ratio was lowest in the original 2004 trapping record (Figure 3.3a upper); at 20% trap failure the average ratio increased, presumably because high levels of failure removed individuals with single captures from the trapping record. This increased proportion of individuals with multiple captures likely explains the increased average *p-hat* observed in 2004 with increased trap failure (Figure 3.2a upper). In contrast capture frequency ratio of the 2005 trapping record decreased at 20% trap failure (Figure 3.3b), presumably because high levels of failure increased the probability that individuals with recaptures were reduced to single capture individuals. The capture frequency ratio of the 2006 trapping record remained stable with increased trap failure (Figure 3.3c) The capture ratios were reduced when the capture histories were pooled in 2004 (Figure 3.3a lower). This is because multiple captures of the same individual within the same week were condensed into a single capture.

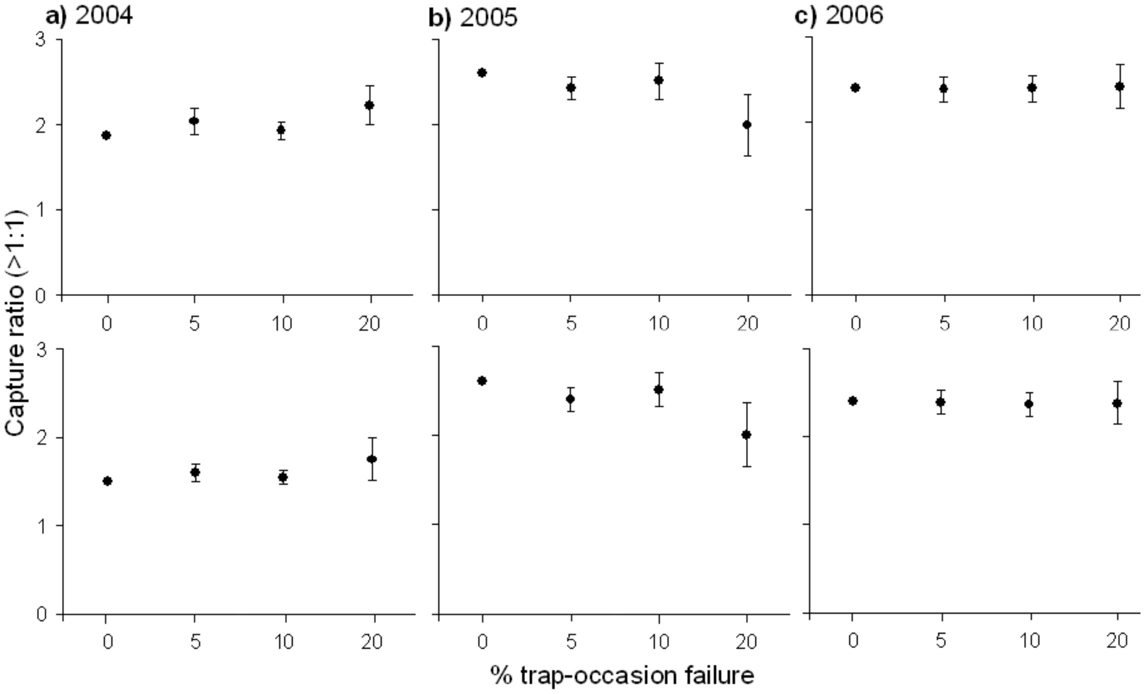


Figure 3.3 Effect of trap failure on capture frequency ratio (number of individuals captured more than once/ number of individuals captured once).Three levels of trap failure (5%, 10% and 20%) were applied 20 times to the trapping records of three 62-day surveys (2004, 2005 and 2006). Capture histories were pooled into nine one-week occasions. The mean and 95% CI of the 20 ratios for each level of simulated trap failure are shown for each of the three surveys, for both **un-pooled** (62 occasions, **upper panel**) and **pooled** (9 occasions, **lower panel**) capture histories. 0% trap-occasion failure is the ratio based on the original data.

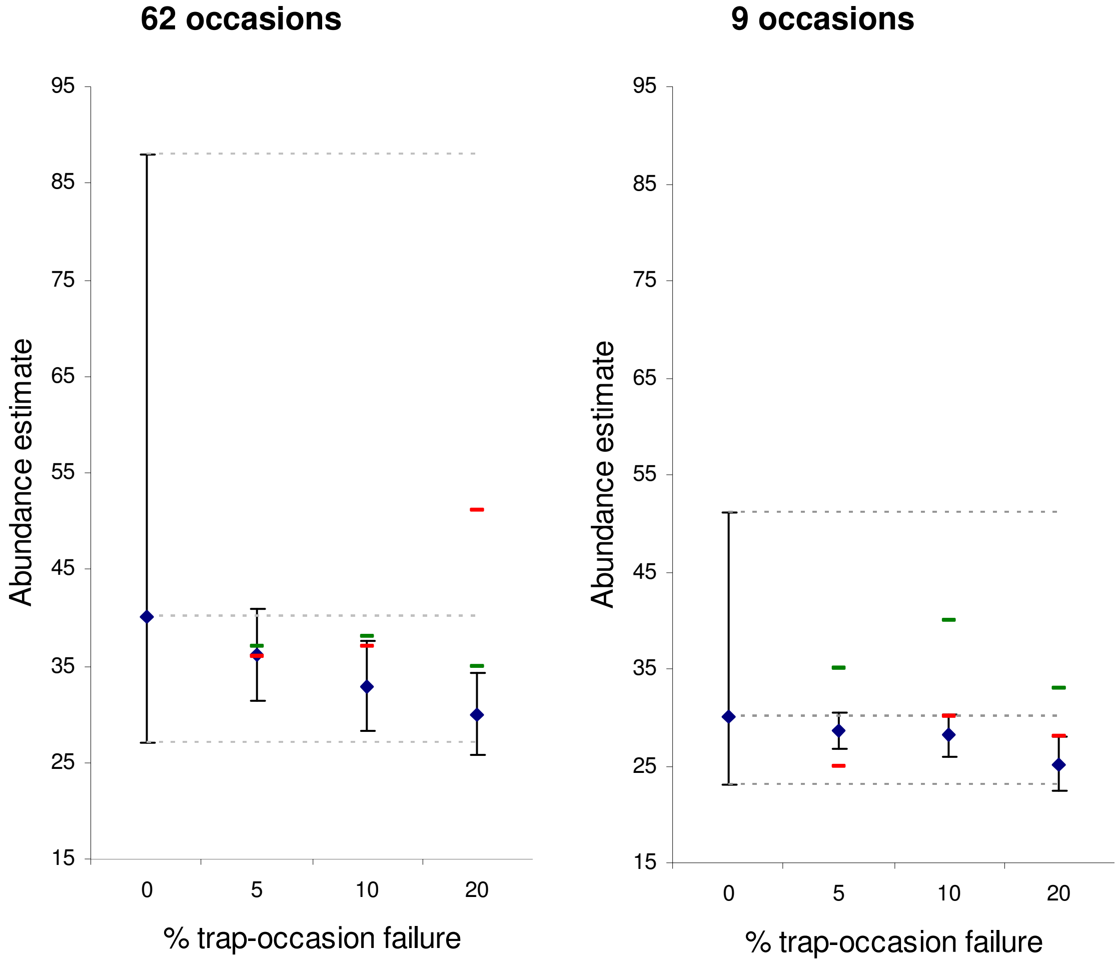
Abundance estimates

The mean of each set of 20 abundance estimates was within the 95% CI of the actual abundance estimate for each survey; and the 95% CI of every simulation estimate overlapped with the 95% CI of the actual abundance estimate for each survey (Figures 3.4a-c).

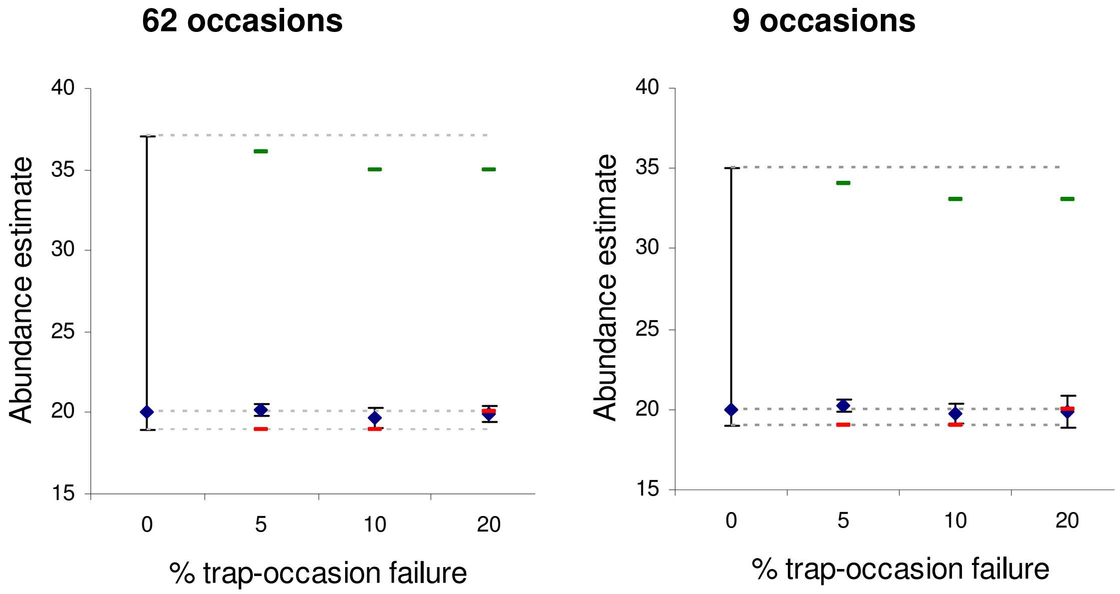
For the abundance estimates based on the un-pooled capture histories, the effect of trap failure varied between the three surveys. In 2004 simulated estimates tended to decrease with increased trap failure. In 2005 the simulated estimates were tight relative to the actual estimate at all levels of trap failure. The same is true for the 2006 survey at the 5% level of trap failure; however as trap failure increased to 10% and 20% the simulated estimates tended to increase.

The abundance estimates based on pooled capture histories responded to trap failure similarly as those based on un-pooled capture histories, with two exceptions: 1) the precision of the 2004 abundance estimate under conditions of zero trap failure increased when the capture histories were pooled; and 2) abundance estimates based on the 2006 pooled capture histories were more stable to increasing trap failure than were those based on the equivalent un-pooled capture histories.

a) 2004



b) 2005



c) 2006

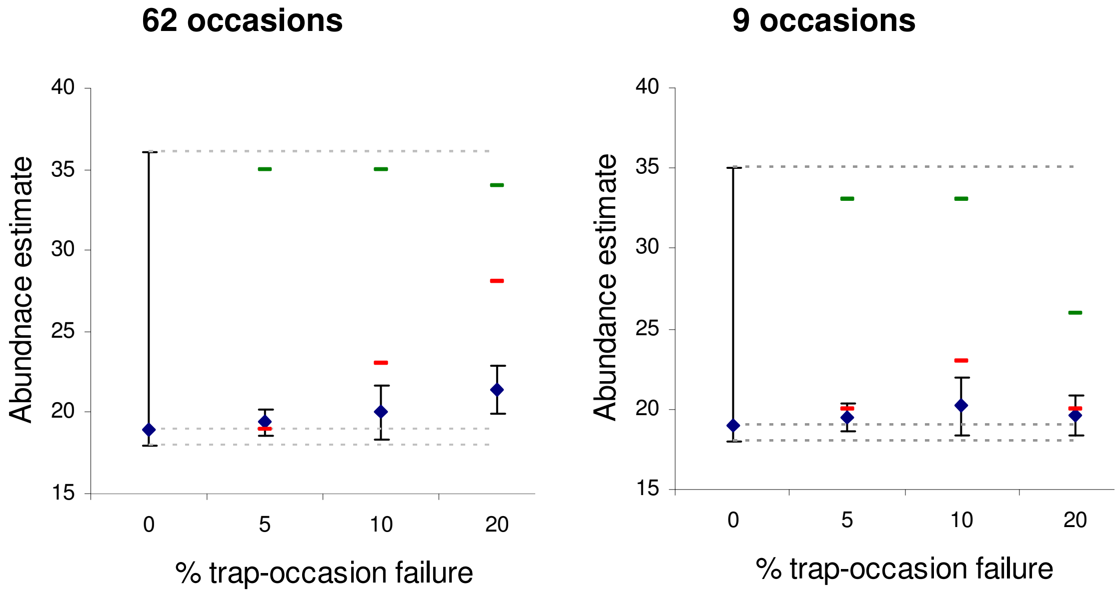


Figure 3.4 Abundance estimates based on manipulated trapping records of three 62-day surveys **a)** 2004, **b)** 2005 and **c)** 2006.Trap failure was simulated at 5%, 10% and 20% Capture histories were pooled into nine one-week occasions. The mean and 95% CI of the 20 abundance estimates for each level of simulated trap failure are shown for each of the three surveys, for both the un-pooled (62 occasions) and pooled (9 occasions) capture histories. The red markers show the highest lower 95% CI of the 20 estimates. The green markers show the lowest upper 95% CI of the 20 estimates. 0% trap-occasion failure is the abundance estimate and 95%CI based on the original data.

Performance of M_h jack-knife estimator

The coefficient of variation of the mean, the relative bias and the 95% CI coverage were compared between each set of 20 estimates relative to the estimate based on the original trapping record (un-pooled and pooled) for each survey. The M_h jack-knife estimator performed better at all levels of trap failure with estimates based on the pooled capture histories than with those based on the un-pooled capture histories (Table 3.4).

The coefficient of variation of the mean for each set of 20 simulations increased with increased trap failure indicating that, relative to the actual estimate, the simulated estimates became more variable as trap failure increased. The variation was lower for the estimates based on the pooled than the un-pooled capture histories.

Relative bias was negligible (<10%) for estimates simulated at 5% trap failure for the un-pooled capture histories and at 10% trap failure for the pooled capture history estimates; but both increased with trap failure. In 2004 the relative bias became increasingly negative (compared to the actual estimate) indicating a tendency to underestimate abundance with increased trap failure. In 2006 the relative bias became increasingly positive indicating a tendency to overestimate abundance as *p-hat* declined with increased trap failure.

The CI coverage of the estimates based on un-pooled capture histories was good (85%-100%) for all surveys under all levels of trap failure except for 20% trap failure in 2004, when only 13 (65%) of the 20 95% CIs included the actual abundance estimate. The CI coverage of the estimates based on pooled capture histories was consistently good (90%-100%).

Overall the 2004 dataset was least robust to trap failure. This is expected since the original 2004 capture history had a relatively low *p-hat* (Figure 3.2) and a low frequency of individuals with recaptures (Figure 3.3), resulting in an abundance estimate with wide confidence intervals (Figure 3.4). Because of the high number of individuals with single captures only, 20% trap failure resulted in a loss of up to 20% of the individuals from the 2004 trapping record, causing a negative bias in the abundance estimate with increased trap failure.

The 2005 dataset was most robust, even though individual loss and capture loss were almost as high as those in 2004 at 20% trap failure. This robustness is probably due to the high frequency of individuals with recaptures, and the relatively high *p-hat* in the original 2005 dataset (Figures 3.2 and 3.3).

The 2006 dataset was less robust to trap failure than was 2005 despite having fewer losses of individuals and captures from the simulated trapping records and a higher *p-hat* associated with the original trapping record. This indicates that the effect of trap failure is dependent on the specific nature of the capture histories as well as the magnitude of trap failure. Overall a high frequency of recaptures and a high capture probability in the original trapping record appear to reduce the variation in the abundance estimate under simulated trap failure.

Table 3.4 Performance of M_h jack-knife estimator at different levels of trap failure; based on 20 simulations at each level of trap failure. Abundance estimates based on manipulated trapping records of three 62-day surveys a) 2004, b) 2005 and c) 2006.Trap failure was simulated at 5%, 10% and 20% Capture histories were pooled into nine one-week occasions. The performance of the estimator at each level of trap failure is compared to the original estimate (0% trap-failure), for both the un-pooled (62 occasions) and pooled (9 occasions) capture histories.

Occasions:	**62 occasions**			**9 occasions**		
% trap failure:	**5**	**10**	**20**	**5**	**10**	**20**
2004						
CV of the estimate	6.2	5.9	10.4	3.0	3.7	4.8
Relative bias	-9.6	-17.8	-25.0	-4.8	-6.3	-16.2
CI coverage	85	95	65	100	100	100
2005						
CV of the estimate	1.0	1.6	2.5	1.0	1.6	2.5
Relative bias	1.0	-2.3	-0.5	0.8	-1.8	-0.5
CI coverage	100	100	100	100	100	100
2006						
CV of the estimate	2.1	4.7	8.1	2.5	4.7	3.4
Relative bias	2.1	5.3	12.4	2.6	6.3	3.2
CI coverage	100	95	90	90	95	90

The results suggest that, for surveys with similar trapping records as those investigated here, the M_h jack-knife estimator is robust to failure of 5% of the trap occasions. The accuracy of the abundance estimate decreases at higher levels of trap failure: under- or over-estimation of abundance is more likely to occur if ≥ 10% of the trap occasions fail. The estimator is sensitive to the specific trapping record: the effect of trap failure > 5% on the abundance estimate depends on whether *p-hat* increases or decreases with trap failure, which in turn depends on the ratio of individuals with recaptures to individuals captured only once. The effect of trap failure is least marked if the frequency of recaptures and the *p-hat* are both high in the original trapping record and so remain stable despite trap failure. Pooling capture histories increases *p-hat* and reduces the effect of trap failure.

The effect of continuous versus discrete trap effort on abundance estimates

The exclusion of daytime captures from the trapping records reduced the number of individuals captured by up to 17% (Table 3.5); as such the elimination of daytime captures reduced the capture probability of some individuals to zero. The exclusion of daytime captures from the trapping records had no significant effect on the abundance estimates of 2005 and 2006 surveys (Figure 3.5), even though in 2005 the capture frequency ratio was reduced by 42% (Table 3.6). The removal of the daytime captures from these two surveys did not lower the average *p-hat* below that of 0.03, the threshold considered necessary for a reliable estimate (Harmsen 2006), (Table 3.6). In contrast, removal of daytime captures from the 2004 data set decreased the average *p-hat* to 0.01 such that the resulting abundance estimate was inflated with wide confidence intervals (Figure 3.5).

Table 3.5 Effect of removal of daytime captures on the number of individuals present in the trapping record (minimum number alive) in three surveys (2004, 2005 and 2006). % underestimate is shown.

Trap Effort	**Minimum alive**					
	2004	**%**	**2005**	**%**	**2006**	**%**
Continuous	20		18		17	
Night only	19	5.0	15	16.7	16	5.9

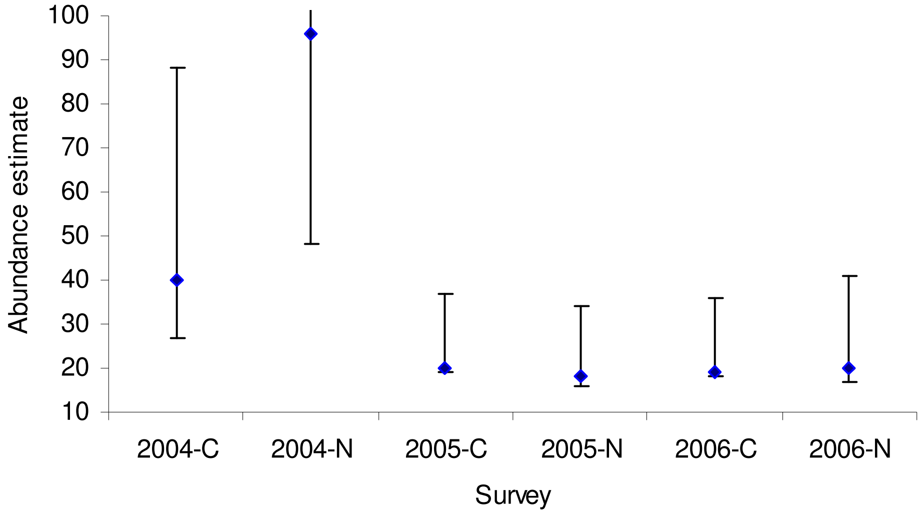


Figure 3.5 Effect of night only versus continuous trapping on abundance estimates based on three jaguar surveys in the CBWS (2004, 2005 and 2006). Each survey had 62 occasions and 19 stations in identical locations. Suffix '-C' indicates continuous trapping (day and night captures included). Suffix '-N' indicates night only trapping (daytime captures are excluded). 95%CI are shown. The upper 95%CI for 2004-N was 227, exceeding the y-axis shown here.

Table 3.6 Effect of removal of daytime captures on capture probability and capture frequency ratio in three surveys (2004, 2005 and 2006)

Trap Effort	Average *p-hat*			Capture frequency ratio		
	2004	2005	2006	2004	2005	2006
Continuous	0.03	0.04	0.09	1.9	2.6	2.4
Night only	0.01	0.03	0.06	1.7	1.5	2.2

Discussion

The use of camera-trap technology with capture-recapture closed population models is becoming a popular method to estimate the abundance of elusive, low density mammals (Chapter 2). Although camera-trap technology has greatly improved in recent years there is no guarantee that they will function consistently throughout a survey. This study assessed the robustness of the M_h jack-knife estimator to camera failure and night-only sampling in the estimation of jaguar abundance.

Camera failure

Continuous sampling over a period of 62 days detected 17-20 individuals in three separate surveys. Under these conditions the jack-knife estimator for the model M_h was fairly robust to camera failure up to ~10% of the trap-occasions. The effect was least marked in surveys with a high capture probability and a high recapture frequency;

pooling trap-occasions increased the capture probability and reduced the effect of trap failure.

When the number of individuals with single captures was relatively high (2004 survey), camera failure caused negatively biased population estimates. It appears that under conditions in which there are many individuals with single captures, trap failure is likely to exclude individuals from the trapping record, reducing the minimum number detected and under-estimating abundance. In contrast, when the recapture rate was high (2006 survey), increasing camera failure resulted in increasingly positively biased population estimates. The cause is less clear but maybe associated with a reduction in capture probability whilst the number of individuals remained relatively stable. Based on these observations it appears that the effect of trap failure on the reliability of an abundance estimate depends on specific properties of the trapping record associated with the distribution of captures and recaptures through the sampled population; which in turn can either positively or negatively bias the estimate. Further investigation using simulated capture histories with pre-defined capture probabilities and capture frequency ratios are warranted and will allow predictions of the likely influence of trap failure under different conditions. In particular the paradox that trap failure can result in an overestimate of abundance should be treated with concern. These findings indicate that published abundance estimates based on camera-trap data should include information about the level of trap-failure within the survey.

Predicting the likely influence of trap failure on the reliability of an abundance estimate will require some *a priori* knowledge of the expected capture histories of the sampled population under conditions of continuous trap effort. For example, in the human-influenced landscape studied in this thesis the habitat is heterogeneous, there are multiple alternative man-made travel routes and camera location may be sub-optimal in order to reduce risk of interference from people. This is expected to result in low capture probability and relatively high number of individuals with single captures. As such it can be expected that camera failure during surveys based in such an area will likely result in an underestimate rather than an overestimate of the population.

Continuous versus night-only sampling

The extent to which night-only sampling will affect the reliability of an abundance estimate will depend on the activity patterns of the target species. Jaguar activity in the area used for this simulation study is primarily nocturnal (Harmsen

2006); despite this, the exclusion of day-time sampling from the capture histories lowered the minimum number of individuals detected by up to 17% (from 18 to 15). When dealing with relatively small populations these differences should not be ignored.

Activity patterns of jaguars are highly variable within and between study sites; ranging from primarily nocturnal to equally active day and night to primarily diurnal (Rabinowitz and Nottingham 1986, Emmons 1987, Crawshaw and Quigley 1991, Núñez *et al*. 2002, Scognamillo *et al*. 2003, Maffei *et al*. 2004, Harmsen 2006, Weckel *et al*. 2006a). Many studies of carnivores report shifts to nocturnal activity areas with human disturbance (e.g. Kitchen *et al*. 2000, Beckmann and Berger 2003a, Riley *et al*. 2003, Theuerkauf *et al*. 2003, Riley 2006, George and Crooks 2006). It is expected that jaguars inhabiting areas with human activity will be more nocturnal than those utilising the protected area where disturbance from humans is minimal. Indeed reports of daytime sightings in the lands neighbouring the protected area were rare, as were daytime photographic captures on cameras which were operating both day and night (R. Foster pers. obs.). Therefore conducting night-only surveys in this area is unlikely to significantly reduce the detection of individuals. However it will reduce the utility of camera-trapping as a method of simultaneously monitoring multiple species, for example sympatric prey species which may have diurnal or crepuscular activity patterns.

Chapter 4

Jaguar densities inside and outside a protected area

Abstract

Central America is facing rapid human population growth and associated forest fragmentation; the long-term persistence of jaguars (*Panthera onca*) will increasingly depend on their ability to utilise the human-modified matrix between protected forests. Little is known of jaguar densities outside expansive forest blocks in this region. This chapter uses camera-trap data to investigate variation in jaguar density across the landscape from protected forest to the human-influenced fragmented lands in Belize. As density estimation from camera-trap data is not yet perfected, this chapter simultaneously addresses methodological issues involving 1) the estimation of sex-specific home range diameters from camera data and their inclusion in density estimates and 2) the minimum survey area required for reliable estimates.

During the 3-year study, six large-scale camera surveys detected 64-74 jaguar individuals over a total survey area of ~ 850 km^2. Males ranged further than females. Therefore, for a given camera array, the effective trapping area (ETA) was greater for males than for females. Single-sex density estimates based on single-sex ETAs were compared to total population density estimates based on average ETAs, and indicated that male density estimates were equivalent to more than half of the total population density estimates. This suggested that either the population was truly male-biased, or that the sampling method was biased. Closer inspection of the data suggested that the female component of the population could have been underestimated because 1) some cameras within the survey arrays were spaced further apart than the average female range and/or 2) females may avoid cameras locations placed on forest trails which are dominated by males.

Sub-sampling data from large-scale surveys indicated a threshold survey area of ~170 km^2 below which jaguar density estimates were inflated and unreliable. For surveys exceeding this threshold, jaguar density varied across the landscape from the protected forest to the human-influenced lands such that less than one-third contiguous forest cover precipitated a reduction in density. In the fragmented landscape, below ~ 20% contiguous forest cover, the average jaguar did not utilise the available land. Density was lower but larger ranges were not detected. This suggested that the declining density with distance from contiguous forest and proximity to human habitation may result principally from direct conflicts with people.

Introduction

The tropical moist lowland forests of the Selva Maya, Central America, have been identified as a region where the long-term persistence of the jaguar (*Panthera onca*) is considered high (Sanderson *et al*. 2002b); yet there are few detailed data on jaguar density outside of protected areas in this region. The aim of this Chapter is to compare the demographics, ranging behaviour and density of jaguars inhabiting a protected lowland rainforest with those utilising the neighbouring human-influenced landscape, in Belize, Central America. The study uses large-scale camera-trap surveys combined with capture-recapture closed population models. This method is becoming increasingly popular as a technique to estimate abundance of elusive, wide-ranging, low density species; however density estimation from camera-trap data is controversial, particularly due to difficulties associated with quantifying the effective trapping area of the sampling grid (Chapter 2). Thus an additional aim of this Chapter is to assess the influence of variation in ranging behaviour on jaguar density estimates.

The jaguar population ranges from southern Mexico to northern Argentina (Sanderson *et al*. 2002b); unlike populations of its larger African and Asian congeners, the tiger and lion (*Panthera tigris* and *P. leo*), it does not appear to be genetically isolated in any part of its current range (Eizirik *et al*. 2001, Cat Specialist Group 2002, Rabinowitz 2006). This is encouraging for the long-term survival of the jaguar; however the risk of population fragmentation and isolation due to continuous human development is of concern. The human population density in Latin America has tripled over the past 50 years (World Resources Institute, WRI, 2007). Currently estimated at 72 people /km^2 in Central America and 22 people /km^2 in South America, it is projected to reach 97 people /km^2 in Central America by 2050, when it will be second only to Asia as the region with the highest population density (WRI 2007). The growing human population is associated with an estimated loss of ~ 4,000 km^2 of forest per year in Central America (World Bank 2007). The limits of jaguars' adaptability to anthropogenic pressures are unknown, however it is clear that their ability to utilise human-dominated landscapes will become increasingly important for their long-term survival. The informal protection of large areas between reserves will be critical (Hoogesteijn 2000, Miller and Rabinowitz 2002), requiring conservation initiatives which transcend political boundaries. This is an ambitious goal, but the will is present:

the Mesoamerican Biological Corridor (MBC) program was created in 1998 to support a system of 600 protected areas and connecting corridors spanning Mexico and Central America. In 2006 the MBC consignees, all seven nations of Central America and Mexico, agreed to establish a network of protected areas and wildlife corridors, within the MBC, specifically to conserve jaguars.

Within Central America, regions of lowland tropical rainforest have the highest probability of jaguar survival; in particular the Selva Maya of Belize, Guatemala and Mexico (Sanderson *et al*. 2002b). Belize still retains 72% forest cover and ~ 28% of the land is protected (WRI 2007). Two principal forest blocks have been identified in Belize as important jaguar strongholds: the Maya Mountain block to the south (~5,200 km^2), and the Rio Bravo block to the north (~1,900 km^2) (Meerman 2004, see Figure 1.4 Chapter 1). It has been suggested that these two populations cannot persist in isolation and that long-term survival of jaguars in this region will require continued connection between these two blocks, and with populations in the Guatemalan Petén and southern Mexico (Meerman 2004). Despite the recognition that long-term jaguar survival will increasingly depend on their ability to utilise the human matrix between protected areas, few studies in the region have addressed aspects of jaguar ecology beyond the Maya Mountain and Rio Bravo forest blocks.

Density, sex ratio & ranging behaviour outside a protected area

Density estimates of jaguars in Belize have mainly been confined to protected areas: long-term monitoring studies have been running in Gallon Jug Private Reserve within the Rio Bravo forest block (Miller and Miller 2005) and in the Chiquibul Forest Reserve/ National Park and the Cockscomb Basin Wildlife Sanctuary, both in Maya Mountain forest block (Silver *et al*. 2004, Harmsen 2006). Although it is important to monitor jaguars in these potential source populations it is also necessary to assess jaguar density in the human matrix beyond the protected areas. Surveys of jaguar in marginal habitat will allow better predictions of the jaguar population at the national level. They will also help to reveal the extent to which these areas may function as sinks, and whether they can support stable populations of jaguars in co-existence with people or whether jaguars utilising these disturbed areas are mainly transients in search of better habitat. To date only two studies of jaguar density have been made outside the Rio Bravo and Maya Mountain forests blocks, and both in areas of limited or negligible human development (Miller 2006, M. Kelly unpubl. data).

The main objective of this chapter is to estimate and compare the density of jaguars inhabiting the protected tropical lowland rainforest of the Cockscomb Basin Wildlife Sanctuary (CBWS) with those utilising the neighbouring human-influenced landscape, a matrix of agriculture, communities and unprotected forest and savannahs where hunting of wild prey species, rearing of livestock and the lethal control of jaguars occur. Density is estimated using camera-trap data collected between 2004 and 2006.

Home ranges of solitary carnivores are expected to increase and overlap if resources are scarce (Sandell 1989); for example Chundawat *et al*. (2007) found that female tiger home range was larger in areas of poor quality habitat. However, predictions of ranging behaviour in a human-influenced landscape may be complicated by the interaction between the low availability of wild prey and clustered patches containing a high availability of domestic prey. We may expect a situation in which some individuals range widely, predominantly utilising wild prey; whilst others maintain smaller home ranges around communities and livestock holdings, preying on domestic animals. For example, telemetry of pumas (*Puma concolor*) on a Venezuelan ranch found that some pumas focused their activity around fenced maternity pastures, utilising patches which never became marginal (Polisar *et al*. 2003).

Camera-trap studies of jaguars in the CBWS previously revealed a male-biased sex ratio (Harmsen 2006). It is not clear whether this represents the true situation or is an artefact of the sampling regime and sexual differences in ranging behaviour, but similar male-skewed ratios have been reported from jaguar camera-trap studies from elsewhere in Belize and in Bolivia (Silver *et al*. 2004). The second objective of this chapter is to compare the jaguar sex ratio and range sizes derived from camera-trap data between the protected and unprotected area and discuss potential reasons for any disparity. Implications for population dynamics will be discussed in light of differences in sex ratio, ranging behviour and density inside and outside the protected area.

Methodological issues

Studies aiming to estimate the density of elusive wide-ranging species from abundance estimates based on camera-trap data usually follow the method of Karanth (1995). A proxy for the average home range diameter of the sampled population is derived from the trap data as the mean of the maximum distance moved by each individual captured at more than one location (MMDM). A buffer of width ½MMDM is then added to the sampling grid to calculate the effective trapping area (ETA), and density is calculated from the abundance and ETA. The extent to which MMDM is an appropriate proxy for home range diameter will depend on the survey area (Maffei and Noss 2008) and the spatial configuration of the trap locations (see Chapter 2 for details). Comparison with telemetry data can help to verify whether MMDM is an appropriate proxy at a given site. The third objective of this chapter is to assess the suitability of MMDM as a proxy for home range within this study by comparing estimates of MMDM derived from multiple surveys with each other and with estimates of home range based on previous telemetry data from the area (Rabinowitz and Nottingham 1986).

An average estimate of home range size may not be appropriate to estimate the ETA if variation in ranging behaviour exists between sub-groups of the sampled population. For example, differences between the ranges of male and female solitary carnivores are common, with males occupying larger areas than females; for example tigers (Sunquist 1981) and leopards (*Panthera pardus*) (Mizutani and Jewell 1998). Because of their smaller home range, female jaguars may not be captured at more than one location (B. Harmsen pers. comm., R. Foster pers. obs.) and so fewer females than males will contribute to the estimate of MMDM. As such, male-biased surveys combined with larger male home ranges will inflate the estimate of MMDM and potentially underestimate the female component of density. The effect of sexual differences in home range size on density estimation from camera-trap data has not yet been addressed in the literature. However it has been suggested that for species with distinct sexual differences in ranging behaviour, it may be appropriate to estimate density separately for males and females (Harmsen 2006). Thus the fourth objective of this chapter is compare density estimates based on single-sex abundances and home ranges with those based on the standard method of averaging over both sexes.

Methods

Camera-trap data were collected over three years (2004-2006) from a range of habitats and land-use systems: the protected secondary rainforest of the CBWS, forest buffer (unprotected forest contiguous with CBWS), unprotected fragmented forest, shrubland, pine savannah, cattle pastures, citrus and banana plantations, shrimp farms, and villages. In 2005 and 2006, three independent large-scale surveys were conducted with station locations extending out from the protected forest into the neighbouring lands towards the coast (Sit05, Zab05 and Arn06, Figure 4.1). In 2004, 2005 and 2006, a large-scale survey was repeated (Mar-May) in the protected forest. Data from the 2004 and 2005 protected forest surveys (CBWS04 and CBWS05) are from Harmsen (2006). The 2006 protected forest survey (CBWS06) was run concurrent with camera stations outside the reserve, using some locations from the both the Sit05 and Zab05 surveys, which were contiguous with the reserve stations but not with each other (Ext06). Survey information is shown in Table 4.1. Most survey cameras were also functional for variable periods outside of the survey dates between 2004 and 2006; as were additional camera stations throughout the study area (both inside and outside the protected forest). Camera station locations are shown in Figures 4.1a-f.

The spacing of survey stations followed the methodology of Silver *et al*. (2004) and Harmsen (2006) which was previously used to monitor jaguars in the reserve. Based on telemetry of jaguars in the Cockscomb Basin (Rabinowitz and Nottingham 1986), the conservative assumption was made that a jaguar would not have a home range less than 10 km^2. Cameras were located close enough to each other such that, theoretically, a 10 km^2 circle centred on the camera would overlap with the 10 km^2 circles of its nearest neighbours. This equates to a maximum average distance between neighbouring core stations of ~ 2746 m. A circular home range of 10 km^2 will fit between any pair of stations > 3568 m apart. Within this survey design, a jaguar with a home range $\geq$ 10 km^2 could not occupy an area that does not encompass at least one camera. As such the capture probability of every jaguar within the survey area is more than zero. This assumption must be upheld in order to accurately estimate the abundance using closed population capture-recapture data (Chapter 2).

For camera stations outside the reserve the approximate location for a camera was identified on OS maps using the above criteria, then permission was sought from the property owners to work on their land and, if granted, the area was surveyed for signs of cats and prey species. This information was combined with any available local knowledge on wildlife in the area as well as likelihood of theft, and used to choose a suitable camera site. At sites outside the reserve where high levels of non-target traffic were unavoidable (e.g. vehicles or cows) the cameras were set to operate only at night. All cameras were set with an enforced delay of three minutes between consecutive exposures.

Table 4.1 Survey information

Survey	**Date**	**Length (days)**	**Stations**	**Functional trap nights**	**Survey area (km^2)***
CBWS04	01Mar'04 to 01May'04	62	19	1,178	141
CBWS05	22Mar'05 to 22May'05	62	19	1,178	141
CBWS06	22Mar'06 to 22May'06	62	19	1,178	141
Ext06‡	22Mar'06 to 22May'06	62	46	2,749	297
Sit05	31Aug'05 to 31Oct'05	62	27	1,320	165
Zab05	13Dec'05 to 12Feb'06	62	22	958	130
Arn06	18Aug'06 to 26Sep'06	40	22	810	158
All 04-06	01Jan'04 to 31Dec'06	1096	180†	22,100	524

* Survey area calculated as a merged 10 km^2 circular buffer around each station
‡The Ext06 survey combines the CBWS06 data with additional station locations outside the reserve (Sit06 and Zab06)
† Stations < 100 m apart are combined as single locations; four stations from inside CBWS are excluded because GPS information was not available

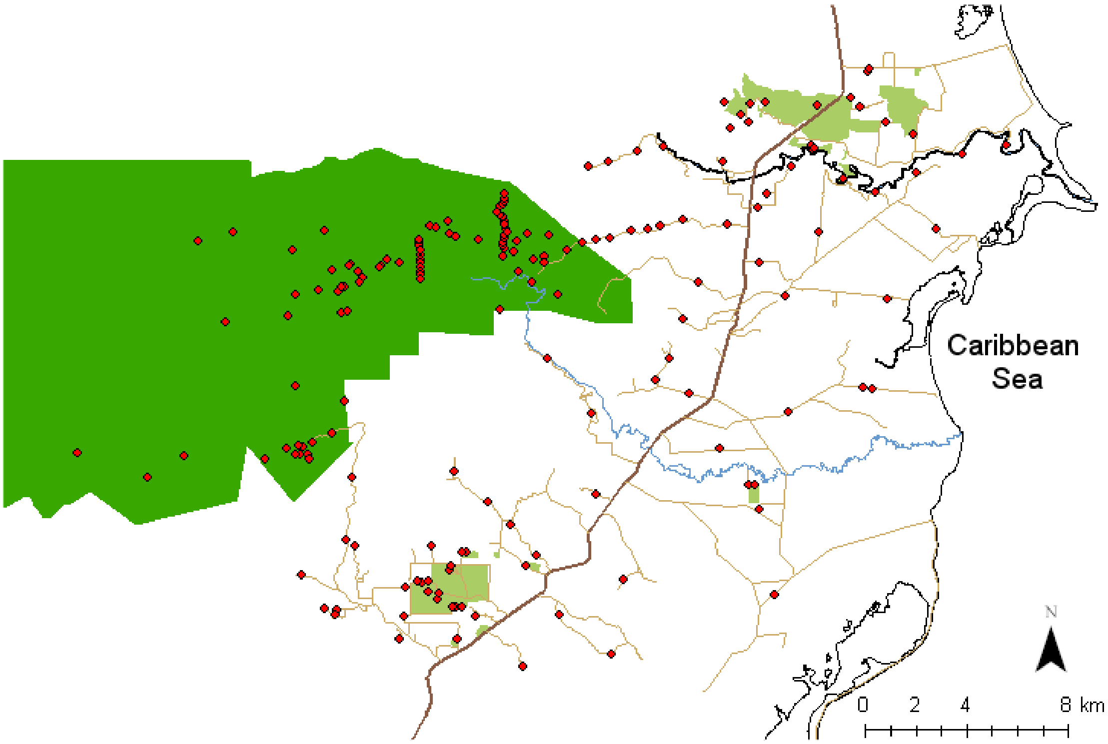


Figure 4.1a All camera locations 2004 to 2006 (All04-06)

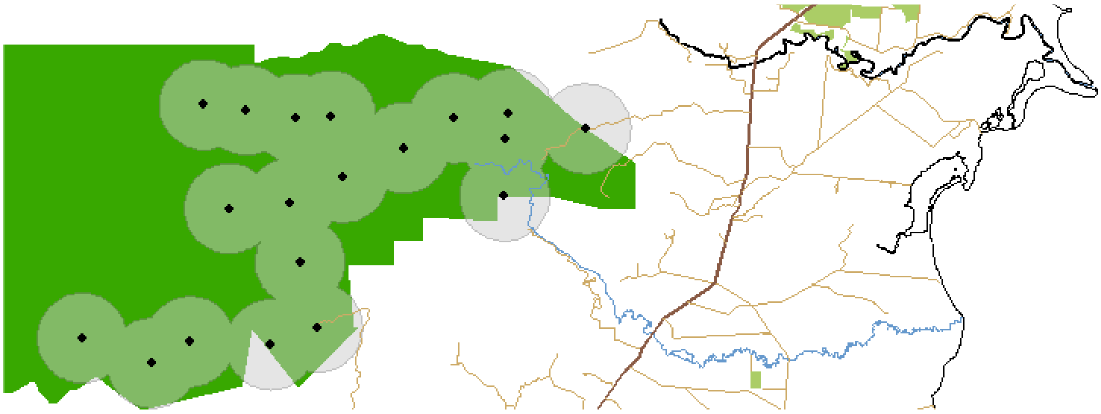


Figure 4.1b CBWS

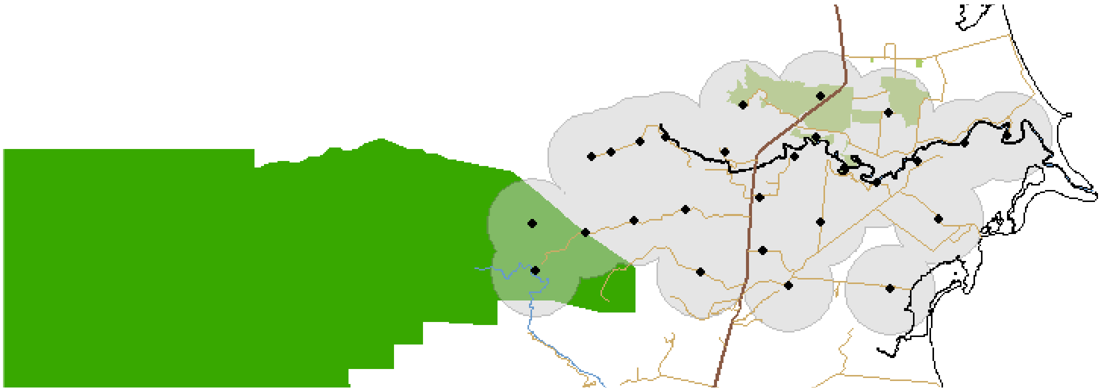


Figure 4.1c Sit05

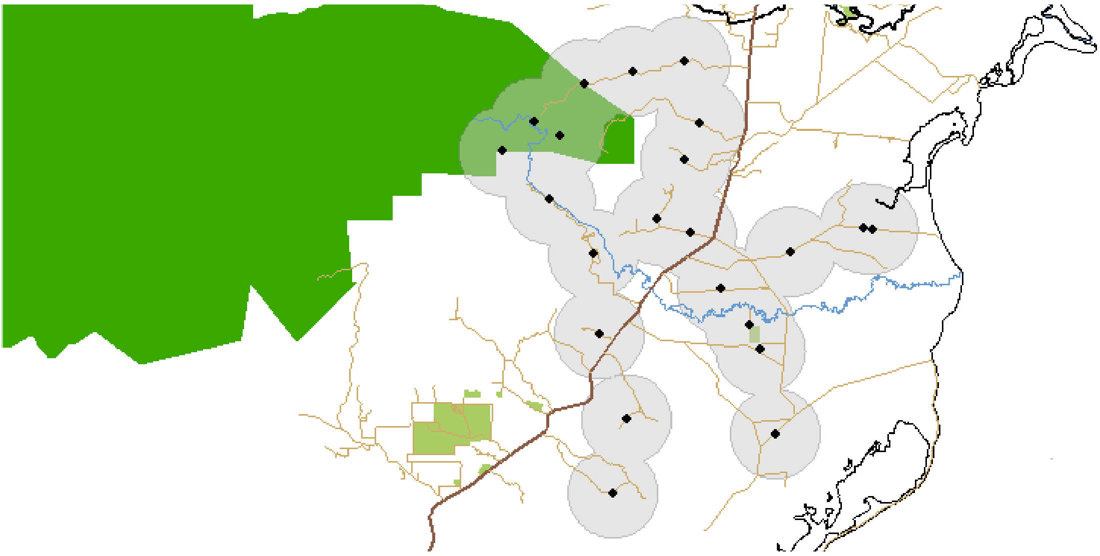


Figure 4.1d Arn06

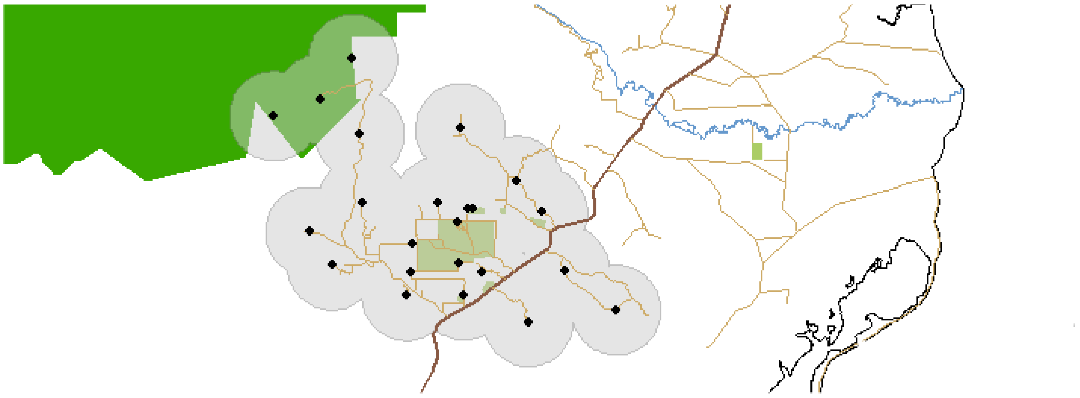


Figure 4.1e Zab05

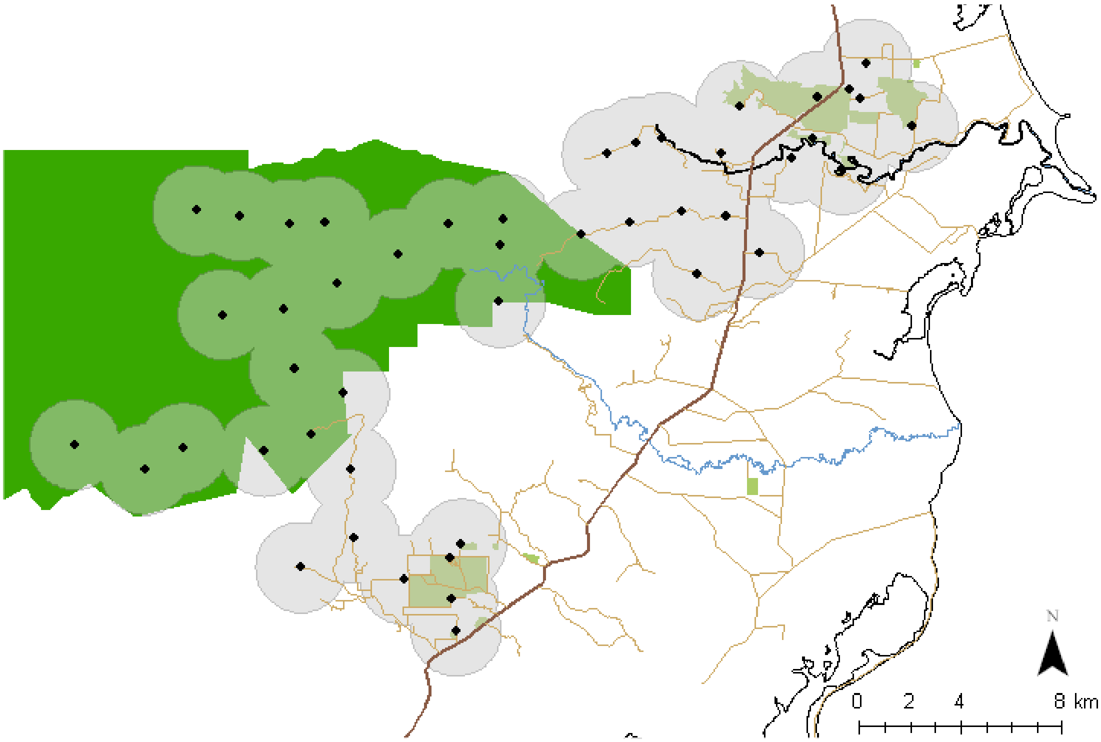


Figure 4.1f Ext06

🟩 CBWS ● camera station — Southern Highway
🟩 cattle pasture — river — roads & tracks

Figure 4.1a-f Camera locations during each survey: **a)** all camera locations 2004 to 2006 (All04-06; **b)** the protected area (CBWS); **c-f)** spanning the protected area boundary (Sit05, Arn06, Zab05, Ext06). Conservative effective trapping area of each survey is shown in grey as a merged buffer of 10 km^2 around each camera location (equivalent to a home range diameter of 3568 m)

Sex ratio

Adult jaguars with a reasonable trapping record can be sexed. Adult male jaguars are relatively easy to identify because they have prominent testicles (Figure 4.2). Females can be sexed if there are enough photographs with a clear view beneath the tail. Because it is easier to assign an adult jaguar as a male than as a female or immature male, individuals of unknown sex will be unevenly distributed between males and females. Individuals outside the reserve tended to have low capture histories and often not enough photographs with a clear view beneath the tail were available to confidently sex all individuals.

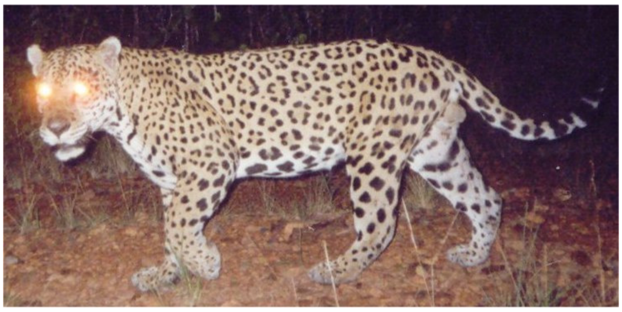


Figure 4.2 Male jaguar, M03-05; testicles can be seen clearly below the tail

Jaguar sex ratios were calculated for the subpopulations captured a) exclusively inside the forest block (the protected forest + buffer), b) exclusively outside the forest block (forest fragments or non-forest), and c) both inside and outside the forest block. Any individual captured only at the boundary was assumed to utilise both habitats.

Individuals were assigned to a subpopulation based on their entire capture histories between Jan-04 and Dec-06, the period during which cameras were present both inside and outside reserve. Estimation of the sex ratio was complicated by the presence of individuals of unknown sex and of single-side individuals within the dataset. Five sex categories were defined to account for the presence of unknown sex individuals: male (M), female (F), unknown (J), male plus unknown (MJ) and female plus unknown (FJ). Single-side individuals resulted from single cameras failing at stations such that only the right or left flank of an individual was photographed. Consequently if there are n single left flanks and m single right flanks within a dataset the maximum number of individuals is $n + m$ and the minimum number of individuals is n or m, whichever is the greatest. Maxima and minima individuals were calculated for sex categories which had multiple single-side individuals. This took into account the possibility that left sides captured exclusively within the forest block could match with right sides captured exclusively outside the forest block (and *vice versa*) such that the maxima individuals captured exclusively inside or outside the forest block were coincidental with the minima individuals utilising both habitats, and *vice versa* (Table 4.2). The procedure was repeated for the subpopulations captured a) exclusively inside the protected forest, b) exclusively outside protected forest, and c) both inside and outside the protected forest (Table 4.2).

Table 4.2 Number and sex of jaguars captured exclusively inside the forest block (or protected forest), exclusively outside the forest block (or protected forest) and both inside and outside the forest block (or protected forest), between Jan-04 and Dec-06. Any individual captured on the boundary was assumed to utilise both habitats. Minima and maxima are given if single left and right flanks were photographed. M is male, F is female, J is unknown sex, MJ is male plus unknown sex, FJ is female plus unknown sex. 88 camera stations were inside the reserve, 93 were outside the reserve and three stations were on the reserve boundary.

Sex		**Forest Block***				**Protected Forest†**			
		in	**both**	**out**	**total**	**in**	**both**	**out**	**total**
M	max	23	6	8	37	15	12	10	37
	min	22	7	7	36	14	13	9	36
F	-	7	1	6	14	3	4	7	14
J	max	12	1	10	23	7	2	14	23
	min	3	10	1	14	1	8	5	14
MJ	max	35	6	18	59	22	14	24	60
	min	25	17	8	50	15	21	17	53
FJ	max	19	2	16	37	10	6	21	37
	min	10	11	7	28	4	12	12	28
Total	max	42	8	24	**74**	25	18	31	**74**
	min	32	18	14	**64**	18	25	21	**64**

* 'Forest Block' refers to the protected forest plus unprotected forest buffer
† 'Protected Forest' refers to the reserve only

All possible combinations of sex ratio (eight in total, Table 4.3) were calculated for each subpopulation giving three ranges of ratios for each subpopulation: a) unknown sex excluded; b) unknown sex included as males; c) unknown sex included as females. The eight sex ratios for the subpopulation captured exclusively inside the forest block were compared with the eight sex ratios for the subpopulation captured exclusively outside the forest block using a Students paired t-test. The test was repeated for the subpopulations captured exclusively inside and outside the protected forest.

In addition, all combinations of sex ratio (as in Table 4.3) were calculated for all individuals captured in the forest block (regardless of whether they were also captured in the area outside the forest block) and for all individuals captured outside the forest block (regardless of whether they were also captured in the forest block) giving three ranges of sex ratio for either group. The procedure was repeated for inside/ outside the protected forest.

Table 4.3 Eight possible sex ratios: individuals of unknown sex are a) excluded (two ratios), b) assumed to be males (two ratios) and c) assumed to be females (four ratios).

	Ratios			
a)	M_{max} : F	M_{min} : F		
b)	MJ_{min} : F	MJ_{max} : F		
c)	M_{min} : FJ_{min}	M_{max} : FJ_{min}	M_{min} : FJ_{max}	M_{max} : FJ_{max}

MMDM as a proxy for home range diameter

The maximum distance moved (MDM) by each jaguar was calculated as the greatest distance between capture locations within each of the surveys. Individuals who were not recaptured, individuals who were only recaptured at the same location, and individuals of unknown sex were excluded. All statistical analyses were conducted using Minitab Version 14.

Variation in MDM with sex and habitat

It was expected that jaguar MDM varied with sex, with males having a higher MDM than females as shown by Harmsen (2006) for data collected in the protected forest between 2002 and 2005. It was unknown whether jaguar MDM also varied with the habitat utilised by different individuals or whether there was an interaction between sex and habitat. Variation in MDM with sex and with habitat was investigated using the entire dataset (All 04-06) because data from the single surveys did not provide sufficient sample sizes to test for interaction effects. Total trap effort varied from one trap-night to 47 trap-nights per day throughout 2004 to 2006 therefore the mean and maximum distance between functional stations varied from day to day. It was hypothesised that the probability of a jaguar being exposed to camera traps would depend on how long it had existed in the study area. Jaguars with a long trapping history ('age') would have potentially been exposed to a large number of cameras over a large area. Jaguars with a short trapping history may have been exposed to many or few camera stations depending on the point at which they appeared in the study period. As such it was hypothesised that MDM could vary with 'age' (time period between first and last capture) and so 'age' was included as a covariate in the analysis.

Each jaguar (with MDM > 0 and known sex) was classified according to its capture locations: 'Forest' refers to individuals who were only captured in the protected forest, or the unprotected forest buffer, or both (*n* = 25). 'Non-forest' refers to individuals who were only captured in locations that were non-forest or forest patches that were not contiguous with forest block ($n = 11$). Three locations, sited at the boundary of pasture and the forest block, were included in this category. Individuals who utilised both forest and non-forest were excluded from the analysis because the number of females within this category was only $n = 1$. The following general linear model (GLM) was fitted to the data, with age class as a covariate:

$MDM = sex \mid habitat \mid age + \varepsilon$ (GLM 4.1)

F-ratios were calculated using Type-II adjusted sums of squares (Doncaster and Davey 2007).

The GLM 4.1 revealed no significant variation in MDM with habitat therefore it was deemed appropriate to exclude habitat from the analysis and include individuals who utilised both forest and non-forest ($n = 6$) to improve the estimates of mean MDM by each sex. The ranges of ages for males and females were not balanced therefore ‘age’ was split into five classes (1-200 days, 201-400 days … up to 800-1001 days). Two males in the age class 1001-1200 days were excluded because there were no females in this age class. The mean MDM was calculated for each sex in each age class ($n = 5$) and the following GLM was fitted to the data, with age class as a covariate:

$MDM = sex \mid age\ class + \varepsilon$ (GLM 4.2)

F-ratios were calculated using Type-II adjusted sums of squares. The mean MDM for each sex adjusted for age class (least square means of MDM for each sex) were obtained from the model output. The associated SEs were calculated from the residual variance (error mean square) obtained by regressing the MDM of each sex against age class.

It was hypothesised that a dichotomy in MDM may exist among the individuals who utilised lands outside the protected forest such that individuals with a small MDM are associated with a high capture frequency on and around cattle farms (the high density of domestic animals negating the need to travel far in search of wild prey); whilst a low capture frequency on and around pastures is associated with a bigger MDM (reflecting the lower availability of prey away from farms and hence the need to range further). However, the sample sizes (female $n = 5$, male $n = 12$) were not considered large enough to fit a model of farm capture frequency, sex and age to the MDM data so MDM was plotted against capture frequency on farms for each sex separately for a simple visual inspection of the data, ignoring the any possible ‘age’ effect.

Comparison of MDM from camera trap survey data and telemetry

The mean MDM and 95%CI for each survey dataset (2004 to 2006) were compared with the maximum and minimum home range diameter obtained for male jaguars (via telemetry) and females (via tracking spoor) in the Cockscomb Basin (Rabinowitz and Nottingham 1986). A mean MDM of a similar magnitude to the home range diameters obtained via telemetry would suggest that the MDMs obtained via the camera surveys in the study area are a good proxy for home range diameter, and so can be used to estimate the effective trapping area of the surveys grids for density estimation.

Closed population abundance estimates

Closed population models were used to estimate jaguar abundance inside, outside and across the reserve boundary using data from six independent surveys. Where datasets were large enough abundance was also estimated for males and females separately. Before abundances were estimated, datasets were condensed to minimise the variation in trap effort between stations caused by camera failure.

Dealing with camera failure

Closed population estimators usually assume constant trap effort during the sampling period. Because all surveys with cameras located outside of the protected area suffered camera failure, the trap effort within surveys varied between stations. If trap effort is variable through the survey period, the probability of capture of some individuals may fall to zero if the only station that they ever pass within the study area is a failed camera. If trap effort is not constant it can be included as a covariate within maximum likelihood models in order to improve the estimate; however the low capture rates associated with jaguars give datasets that are often too sparse for such an analysis (Chapter 3). The only alternative is to minimise camera failure, by excluding stations with high failure rates, and to use an estimator that is reasonably robust. The jack-knife estimator for the M_h model seems to be fairly robust to failure up to ~ 10% of the trap-nights, based on data collected in the protected area (Chapter 3). For samples with many individuals with single captures, as may be expected outside the reserve because of the heterogeneous nature of the habitat and multiple travel routes available, we may tentatively expect trap failure to underestimate rather than overestimate the population abundance, however this is not conclusive (see Chapter 3).

In order to minimise the influence of trap-night failure on abundance estimates, data were only analysed from stations which did not fail for more than 10 nights during the survey. This lowered the trap-night failure to < 5% for all surveys (Table 4.4). Furthermore, capture histories were collapsed from 62 (or 40) occasions to nine (or 10) occasions, each occasion unit being 6 to 7 days (or 4 days) instead of one day. Only night captures were used in the analyses to allow an equal representation of all stations regardless of whether they sampled continuously or at night only. 'Night' was defined as those captures occurring between sunset and sunrise. Daily sunrise and sunset times (2004-2006) were acquired from the US Naval Observatory (2007).

It should be noted that removal of failed cameras from the edge of a survey area does not compromise the assumption that the stations are close enough together such that a jaguar with a home range ≥ 10 km^2 could not live between the two stations with zero probability of capture; it merely reduces the sampling area. However the removal of failed stations from within the centre of the survey area will break the assumption of capture probability greater than zero if the resultant distance between neighbouring cameras exceeds the MMDM by jaguars (Results section).

Table 4.4 Survey information after the removal of stations with >10 failed trap nights.

Survey	Nights	Occasions	Stations	% trap-night failure	Survey area (km^2)*
Sit05	62	9	17	4.4	10 + 120†
Zab05	62	9	13	1.9	79
Arn06	40	10	21	3.5	50 + 105†
Ext06	62	9	44	2.2	290

* Survey area calculated as a merged 10 km^2 circular buffer around each station.
† Survey area is discontinuous because of removal of failed camera stations.

Variation in abundance with habitat and sex

Abundance was estimated for each survey using the M_h jack-knife estimator with the program CAPTURE (Rexstad and Burnham 1991). The data from surveys which spanned the boundary of the protected area were partitioned according to habitat blocks for separate abundance estimates. Camera failure did not exceed 5% when the surveys were partitioned by habitat. The data of the large-scale survey in 2006 (Ext06) were sub-sampled according to the following schedules:

4.1 All stations inside and outside the reserve *(protected and unprotected forest and unprotected non-forest)*

4.2 Stations in the reserve or its buffer (*protected and unprotected forest)*

4.3 Stations in the reserve and on its boundary *(protected forest)*

4.4 Stations used historically for jaguar abundance estimates in CBWS (Silver *et al.* 2004, Harmsen 2006) includes all stations in the reserve and only two on the boundary (*protected forest)*

4.5 Stations in the reserve only (excludes those on the boundary) (*protected forest)*

The 2005 CBWS survey data (Harmsen 2006) were partitioned and re-analysed according to schedule 4.4 and 4.5. The 2004 protected area survey was not included here since no large-scale surveys were conducted outside the reserve during this year for direct comparison.

The data of each of the three surveys based primarily outside the reserve (Sit05, Zab05 and Arn06) and of the two components of the Ext06 survey which extended outside of the reserve (Sit06 and Zab06) were sub-sampled as appropriate according the following regime:

4.6 All stations inside and outside the reserve *(protected and unprotected forest and unprotected non-forest)*

4.7 Stations on and outside the reserve boundary *(protected and unprotected forest and unprotected non-forest)*

4.8 Stations outside the reserve boundary *(unprotected forest and unprotected non-forest)*

4.9 Stations outside the buffer boundary *(unprotected forest patches not contiguous with reserve and unprotected non-forest)*

For each survey and sub-sampled survey, the % cover of the following habitats was calculated: contiguous forest block (protected forest plus its unprotected forest buffer), fragmented forest, savannah, plantation (citrus and banana) and cattle pasture. The methods for deriving habitat cover are described in Chapter 5. The average distance of survey cameras from the protected forest and from the contiguous forest block were also calculated.

Survey Ext06 (schedule 4.1) was partitioned into males (n = 20 individuals) and females (n = 6) for separate sex abundance estimates. The total sample size (n = 28) included two of unknown sex. These were excluded and abundance estimated for the sample 'males + females' (*n* = 26) for direct comparison with the single sex estimates. The female estimate should be treated with caution since the sample size was low, although total female captures (pooled over nine occasions) was 14, which exceeded the minimum number of captures assumed for the model. Female samples sizes were too low (*n* = 2 to 4) in the other surveys to estimate female-only abundance, however male-only and 'male + female' abundances (excluding unknown sex) were estimated for the 2004, 2005 and 2006 CBWS surveys (schedule 4.4). Abundance estimates were used to estimate density (see next section).

Two study animals, one male and one female, which appeared in the trapping record during the large-scale survey in 2006 (Ext06), were killed outside the reserve before the survey ended. Therefore the population was not demographically closed and for part of the survey period the probability of capture of these two individuals fell to zero. It was recommended that the dead-animal data be removed before analysis, and then the number of dead individuals added to the final population estimate and 95% CI; the SE is unaffected (G. White, developer of program MARK, pers. comm., J. Nichols, expert of demographic estimation methods, pers. comm.). Such a method may be appropriate when dealing with large samples and high capture rates. However capture rates of jaguars tend to be low (Chapter 2) and this dataset was no exception. Removal of these data from the trapping record would lower overall capture probability and so lower the reliability of the estimate. The deaths occurred towards the end of the survey (during the 7th and 8th occasion of the nine occasion trapping record) therefore the capture histories of the two individuals were fairly complete and it was deemed appropriate to retain the individuals in the trapping record and estimate their final occasion(s) based on their previous capture history. Both cats had the same capture probability (0.286) whilst alive. This was used to predict the probability that they would have been captured during the 8th and 9th trapping occasions had they lived. A random number (*r*) was generated between 0.001 and 1.000 for each capture occasion that was missing data for these two cats. If $r \leq 0.286$, the individual was considered captured, and if $r > 0.286$ the individual was assumed not captured.

Density estimates

Jaguar density was estimated from each of the abundance estimates using estimates of the effective trapping area (ETA) of each survey. Estimates of the ETA were based on the most appropriate proxy of home range diameter (MMDM) derived from the trapping data (based on analysis in the previous section). Where single sex abundances were estimated, densities were estimated using single sex estimates of ETA based on sex-specific MMDM. The method of density estimation based on MMDM and ETA follows Nichols and Karanth (2002) and is described in fully Chapter 2.

Variation in the reliability of the density estimates with ETA was investigated; for survey areas considered large enough to give a reliable density estimate, variation in jaguar density with % forest cover was investigated.

Variation in density estimates with ETA

A plot of population density estimate against ETA suggested an inverse relationship existed between density estimate and the survey area. The data were modelled using a linear regression to determine whether there was a threshold ETA below which the sub-sampled survey areas were too small for reliable density estimation. Sub-sampled survey areas falling below the threshold were excluded from further analyses.

Variation in jaguar density with forest cover

For surveys (and sub-sampled surveys) above the minimum threshold survey area, density estimates were plotted against the mean distance of the survey camera stations from a) the protected forest, and b) the contiguous forest block. Linear regression was used to model the relationship between density and the % cover of contiguous forest.

Comparison of single sex and combined sex density estimates

It was hypothesised that density estimates based on abundance estimates and ETAs derived from the total sample (all individuals) may underestimate the female density component, and so underestimate the total density. Male and female (single-sex) density estimates were compared with each other and with ‘male + female’ (combined sex) density estimates to determine whether single-sex density estimates are more appropriate than total density estimates.

Results

During the study 64 to 74 jaguar individuals were photographed. A range is given because, due to camera failure, single-side individuals were present in the dataset. These are individuals for whom only one flank was photographed. In total there were 13 single right flanks and 10 single left flanks (representing 10 to 23 jaguars), and 51 double-sided individuals. In addition, cubs ≤ 6 months old (based on size) were photographed on three occasions, all outside the reserve; they are excluded from subsequent analyses. Eighteen double-sided individuals were captured exclusively inside the reserve, 15 double-sided individuals were photographed exclusively outside the reserve, and 18 double-sided individuals utilised land inside and outside of the reserve. Of the latter, 13 individuals were captured more than three times on alternate sides of the boundary of the protected forest (mean ± SD = 25 ± 38 alternate captures, range = 4 to 141, $n = 13$) equivalent to a rate of 0.1 to 6.6 boundary crosses per 28 days, suggesting that their home ranges spanned the reserve edge.

Sex ratio

During the study (Jan04 to Dec06) 36 to 37 males, 14 females, and 14 to 23 jaguars of unknown sex were detected by the camera traps. A further two females and two males were trapped and removed by farmers without photographic capture. The potential range of the sex ratio was consistently more skewed towards males within the subpopulation captured exclusively inside the forest block than within the subpopulation captured exclusively outside the forest block, regardless of whether or not individuals of unknown sex were included as females or as males or excluded (Figure 4.3). If individuals of unknown sex were all assumed to be female, the sex ratio became female-biased outside the forest block. The same patterns were observed when comparing sex ratio of subpopulations found exclusively inside and outside the protected forest.

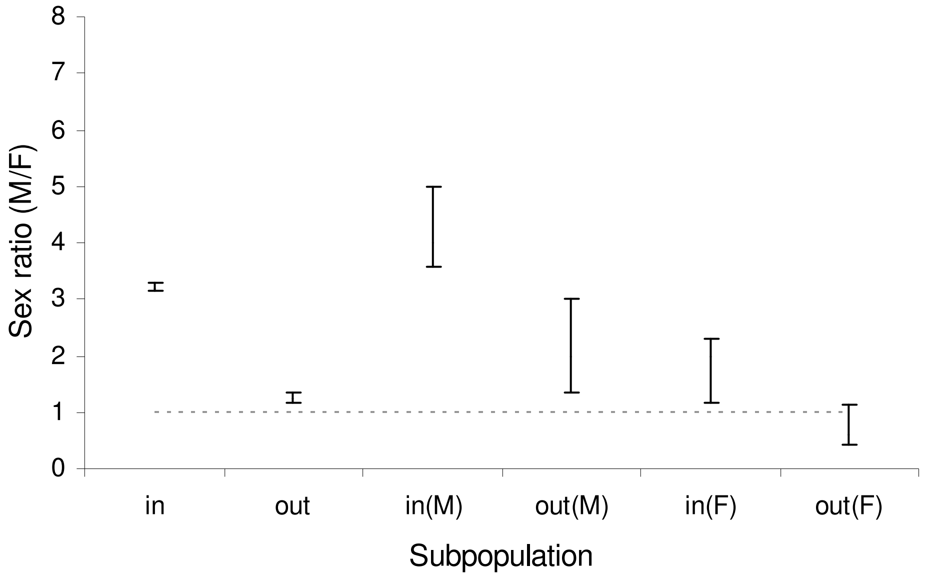


Figure 4.3 Maxima and minima jaguar sex ratios of subpopulations captured exclusively inside the forest block (in) and exclusively outside the forest block (out), between Jan-04 and Dec-06. Maxima and minima are shown by upper and lower bars. Three sets of ratios are calculated: individuals of unknown sex are excluded, individuals of unknown sex are assumed to be males (M), and individuals of unknown sex are assumed to be females (F). Grey dashed line shows 1:1 ratio.

The observed sex ratio of the subpopulation captured exclusively inside the forest block was significantly more male biased than was the subpopulation captured exclusively outside the forest block (mean difference = 1.494, 95%CI for mean difference = 0.979 to 2.010, $n = 8$, $t = 6.85$, $p < 0.001$, Appendix A: Table A4.1) regardless of whether or not individuals of unknown sex are included as females or as males or excluded. A similar result was observed for the subpopulation captured exclusively inside the protected forest versus exclusively on the unprotected lands (mean difference = 2.636, 95%CI for mean difference = 1.715 to 3.558, $n = 8$, $t = 6.76$, $p < 0.001$, Appendix A: Table A4.2).

Sex ratios calculated for the dataset of all individuals captured in the forest block (regardless of whether they were also detected outside the forest block) and for all individuals captured outside the forest block (regardless of whether they were also captured in the forest block) show a similar pattern of a more male-biased ratio inside the forest block than outside. The same pattern is also observed when comparing ratios between inside and outside the protected forest. Of note, if all individuals of unknown sex are assumed to be females, the sex ratio (male to female) outside the protected forest approximates 1:1 whilst it is ~ 2:1 inside the protected forest. These results support the hypothesis that the camera-trap detection rate of females is higher outside the protected area and the forest block. This may reflect the true distribution of sexes or a sampling bias between the protected /forested and unprotected /non-forested lands.

MMDM as a proxy for home range diameter

The effects of sex and habitat on estimates of MDM obtained from camera-trap data of jaguars collected over a 3-year period were investigated. The mean MDMs from several different surveys were compared with home range estimates derived from telemetry conducted in the same area 20 years ago.

Variation in MDM with sex and habitat

The MDM by jaguars varied significantly with age (period of time between first and last capture) and sex; it did not differ between jaguars that only moved through the forest block versus those that only moved through the non-forest or forest fragments (Table 4.5).

Table 4.5 Results of GLM 4.1 *MDM* = *sex* | *habitat* | *age* + ε. Interactions were non-significant ($p > 0.1$). *F-ratios* were calculated using Type-II adjusted sums of squares. Total DF = 35.

	DF	**MS**	***F-ratio***	***p-value***
Age	1	5339	5.62	<0.05
Sex	1	4310	4.54	<0.05
Habitat	1	1255	1.32	>0.1
Error	28	950		

The MDM by jaguars increased with the period of time between first and last capture (Figure 4.4). This was expected since the number of camera locations, hence maximum survey area, increased throughout the study period.

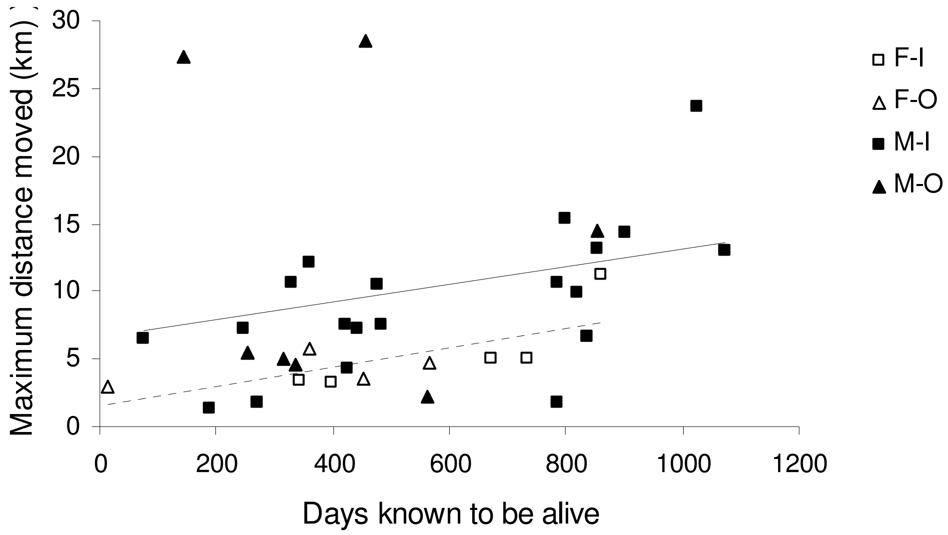


Figure 4.4 Variation in MDM of jaguars with ‘age’ (days known to be alive), sex and habitat; based on GLM 4.1. F-I = females inside forest block; F-O = females outside forest block; M-I = males inside forest block; M-O = males outside forest block; where ‘forest block’ is reserve + buffer. Solid line = males, dashed line = females.

The MDM by males was significantly higher than the MDM by females (male mean ± SE = 9491 ± 932 m, female = 5742 ± 1013 m, pooled *n* = 30 and 10 respectively; Table 4.6).

Table 4.6 Results of GLM 4.2 *MDM* = *sex* | *age class* + ε. Interactions were non-significant (*p* > 0.1). *F-ratios* were calculated using Type-II adjusted sums of squares. Total DF = 9.

	DF	MS	*F-ratio*	*p-value*
Sex	1	35130005	7.42	< 0.05
Age class	1	27429504	5.79	0.05
Error	6	4734123		

For individuals utilising habitat outside the protected area there are not sufficient data to determine whether those who tended to be captured around cattle farms ranged significantly less far than those who did not frequent cattle farms; however Figure 4.5 suggests that the individuals with the highest capture frequencies around cattle farms also tended to have the lowest MDM, regardless of sex.

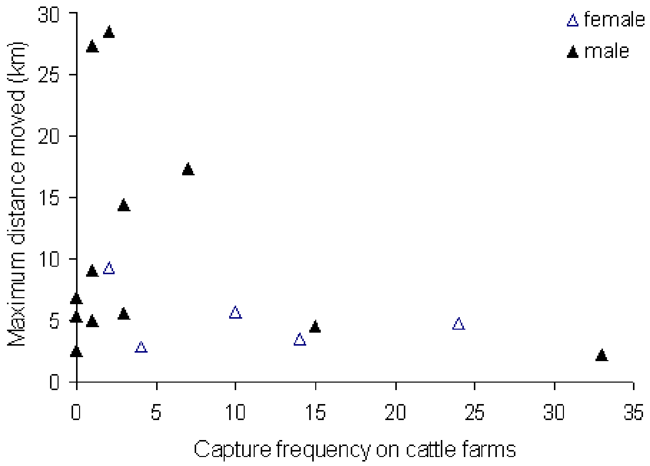


Figure 4.5 Variation in MDM by jaguars with individual capture frequency on cattle farms, 2004 to 2006. Females = white triangles; males = black triangles. Note that ‘age’ (days known to be alive) is not taken into account.

Deriving proxies for home range size from camera-trap data assumes that the methodology is not biased. It has been previously suggested that camera trapping of jaguars in dense secondary forest may be male-biased, as a consequence of researchers placing cameras on accessible roads which are dominated by males (Harmsen 2006). As such it could be argued that the difference detected between male and female MDM may be an artefact of camera location choice, i.e. males are observed to travel further because more of the cameras are in locations favoured by males. However many camera stations in this study were located in open habitat such as savannah and pasture edges; furthermore smaller female home ranges, compared to males, are consistent with telemetry studies of jaguars in some other areas of their range (Crawshaw *et al.* 2004, Scognamillo *et al.* 2003, Cullen *et al.* 2005, Azevdeo and Murray 2007).

The difference between the distances moved by females and by males is such that the effective trapping area of males is potentially larger than the effective trapping area of females, for the same survey grid. This may partly explain the overall male biased sex ratio: if females have smaller home ranges than males, fewer females will be detected than males simply because their effective trapping area is smaller. This may have important implications for the calculation of density based on the ETA method. An average MDM (based on males and females) could underestimate the female density, particularly if the estimate of the ETA is male-biased because more males contribute to the estimate of MMDM and ETA than do females. One option may be to calculate abundance and density of males and females separately, using ETAs appropriate for each sex.

Comparison of MDM from camera-trap survey data and telemetry

Rabinowitz and Nottingham (1986) reported the mean home range size of four radio-tracked male jaguars in the Cockscomb Basin and neighbouring lands as 33.4 km^2, ranging from 28 km^2 to 40 km^2 with SD of 5.5 km^2. Assuming a circular home range, this is equivalent to a home range diameter of 6512 m (±SE = 1323 m). The MDM by male jaguars measured within this study's surveys, and over the entire study period (2004-2006), range from 3007 m (±SE = 456 m) to 9491 m (±SE = 932 m), within the same order of magnitude as those determined by Rabinowitz and Nottingham (1986) in the same study area (Figure 4.6).

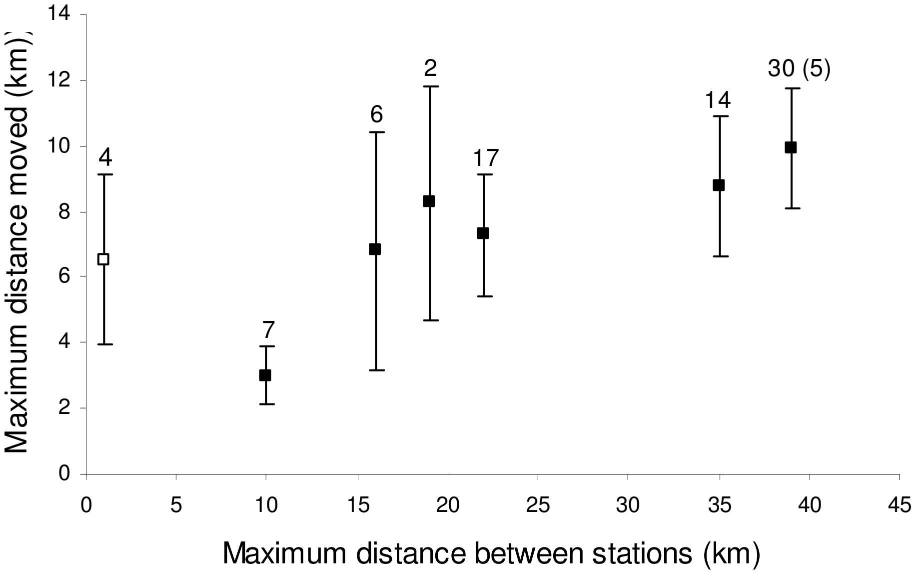


Figure 4.6 Maximum distance moved (MDM) by male jaguars during this study's camera surveys (black squares) and home range diameter based on historical telemetry data (white square, from Rabinowitz and Nottingham 1986).
X-axis shows the maximum distance between stations in each survey (10, 16, 19, 22 and 35 km). MDM for the survey with maximum distance between stations of 22 km is calculated over three repeated surveys in CBWS (2004, 2005 and 2006).
MDM is also shown as calculated over the entire study period Jan04-Dec06, adjusted for age (maximum distance between stations = 39 km).
Sample sizes and 95%CI are shown (sample size in parentheses is the pooled *n*).

Rabinowitz and Nottingham (1986) followed the pugmarks of three female jaguars in the Cockscomb Basin and neighbouring lands, and estimated a minimum home range size of ~10 km^2, equivalent to a home range diameter of ~ 3568 m. Determining home range size by following tracks is likely to underestimate the true home range size; however this is a similar order of magnitude as the MDM by females jaguars detected within the surveys, and over the entire study period (2004-2006) (Figure 4.7) which range from 2854 m (no SE, *n* = 1) to 5742 m (±SE = 1013 m).

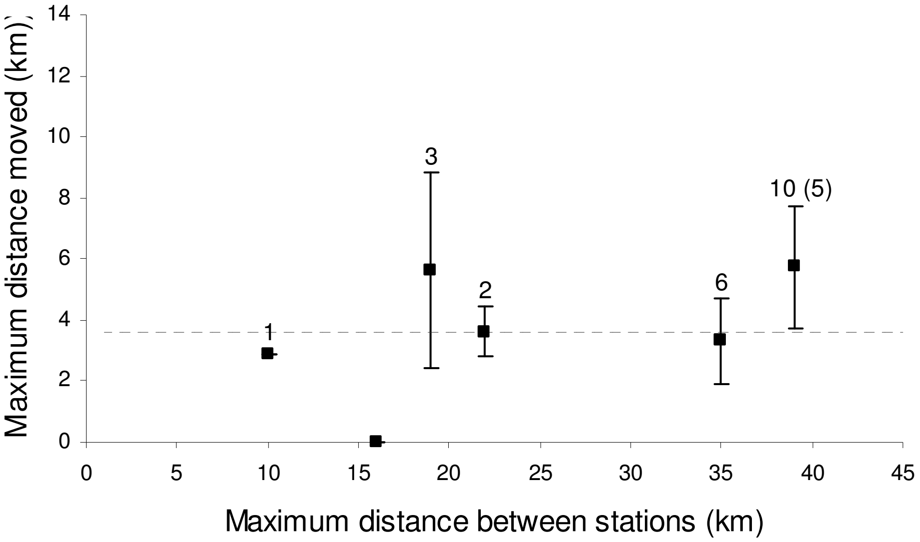


Figure 4.7 Maximum distance moved (MDM) by female jaguars during camera surveys (black squares) and home range diameter based on pugmark tracking data (dashed line, from Rabinowitz & Nottingham 1986, *n* = 3).
For explanation of X-axis see Figure 4.6 above.
Missing data points (*n* = 0) indicate that females were not caught at multiple locations therefore MDM cannot be estimated.
Sample sizes and 95%CI are shown (sample size in parentheses is the pooled *n*).

Choice of MMDM for density estimation

Yau (2007) studied the Ext06 dataset (Table 4.2) in more detail by analysing the affect of sequential removal of cameras from the trapping grid. Although sex differences were not taken into account Yau (2007) demonstrated that the mean MDM increased with survey area (based on a minimum convex polygon, MCP, connecting the outermost traps) and reached an asymptote at a survey area of ~ 139 km^2. Survey areas which are smaller than ~ 139 km^2 may underestimate the true MDM by individuals in the study area.

The use of the MCP with an irregular trapping grid for a study of the relationship between MDM and grid area (as in Yau 2007) is not satisfactory because the maximum distance between stations (i.e. the potential maximum distance that a jaguar can move) is not proportional to the MCP area of the grid. Perhaps a more appropriate analysis would have been to describe the relationship between MDM and maximum distance between trap locations as cameras are sequentially removed from the survey grid. The MDM detected for males tends to increase with the maximum distance between stations; larger surveys with high maximum distance between stations have

MDM estimates similar in size to those obtained over the entire study period (Figure 4.6). It may therefore be prudent to base male MDM on data from the larger survey areas or to base it on the MDM calculated over the entire study period (adjusted for age). In contrast, the MDM detected for females did not appear to be capped by the maximum distance between the stations (Figure 4.7) presumably because they did not tend to move further than the maximum distance between cameras in the smallest survey.

The problem with using movement data collected over 3 years is that home ranges may shift, regardless of their core size, through time, for example due to seasonal changes in prey availability or associated with changes in dominance. The output of GLM 4.1 (Figure 4.4) demonstrated that MDM increased with number of days that an individual was present in the survey. Such shifts in core home ranges will inflate the estimate of the instantaneous home range diameter. Although the MMDM calculated over the entire study period covers the largest area and allows for the greatest detectable movement (maximum distance between stations = 39 km) it may not be appropriate to apply this long-term movement data to short-term population data. Box 4.1 (at the end of this chapter) further discusses the influence of different proxies of home range diameter on density estimation.

For this study it was decided that the MMDM derived from the Ext06 dataset was the optimal available proxy for jaguar home range diameter and would be the most appropriate statistic for all estimates of ETA and density in the study area: the Ext06 survey covered the largest area (maximum distance between stations = 35 km) within a closed population period (62 days) and had the largest sample of individuals. The MMDM of both sexes combined was 6940 m (±SE = 939 m, $n = 21$: six females, 14 males and one unknown sex). The MMDM of males was 8776 (±SE = 1082 m) and that of females was 3312 m (±SE = 715 m). A MMDM of 3312 m approximates to a circular home range of ~ 8.6 km^2, smaller than the 10 km^2 home range on which the camera spacing was based (≤ 3568 m between neighbouring stations). The majority of neighbouring stations were < 3312 m apart; however some exceeded this spacing such that a female, assuming a home range of 8.6 km^2, could theoretically exist with zero probability of capture. As such, some of the surveys may have failed to fully sample the female component of the population. The extent of gaps or discontinuities in the female ETAs varied between the surveys and is illustrated in Appendix B.

Closed Population Abundance Estimates

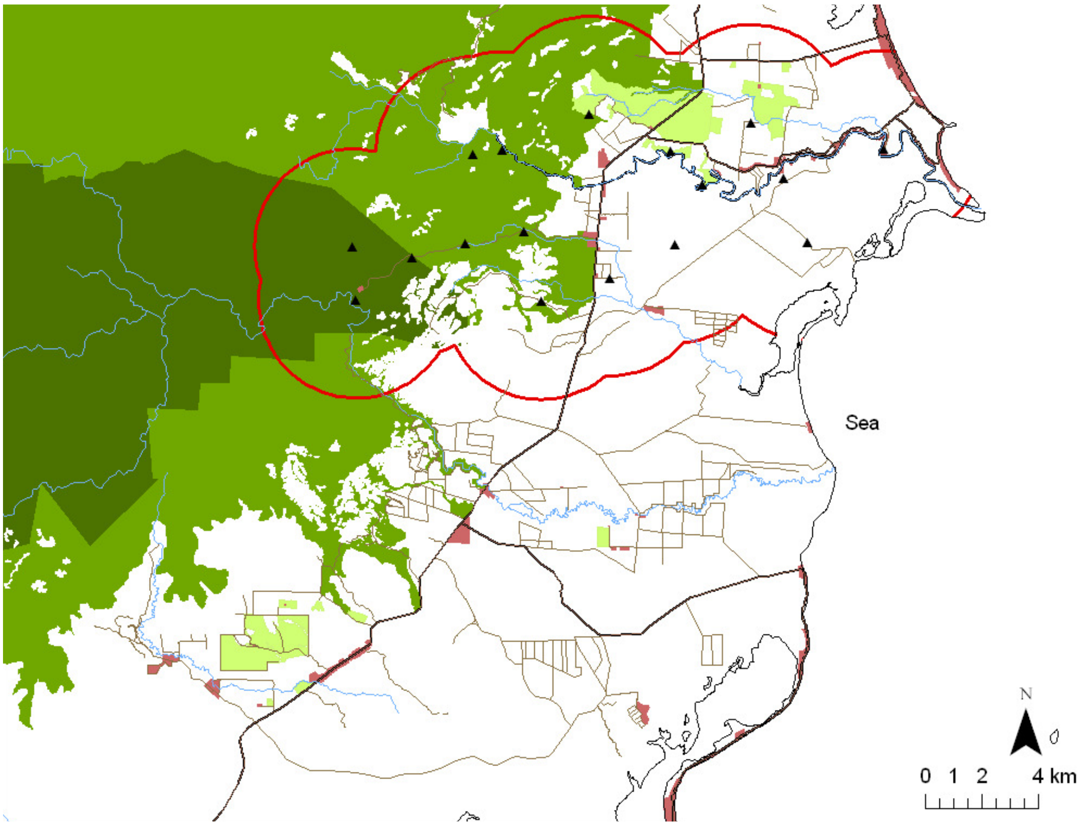
CAPTURE occasionally selected the null model (M_0) as more appropriate than M_h. When M_0 was identified as the most appropriate (model selection criteria 1.0), M_h was selected as next best (model selection criteria ≥ 0.8). Given the relatively high selection criteria for M_h and the fact that M_0 is unlikely to reflect the true situation, M_h was used in preference to M_0, although the M_h estimates are less precise (larger confidence intervals) than the M_0 estimates. Three estimates used the M_{th} model (Chao *et al*. 1992) as CAPTURE selected this over the simpler M_h model. Capture probability ($\hat{p}$) ranged from 0.062 to 0.366*,* above the 0.05 threshold advised by Harmsen (2006) for reliable estimates of jaguar abundance.

Density estimates

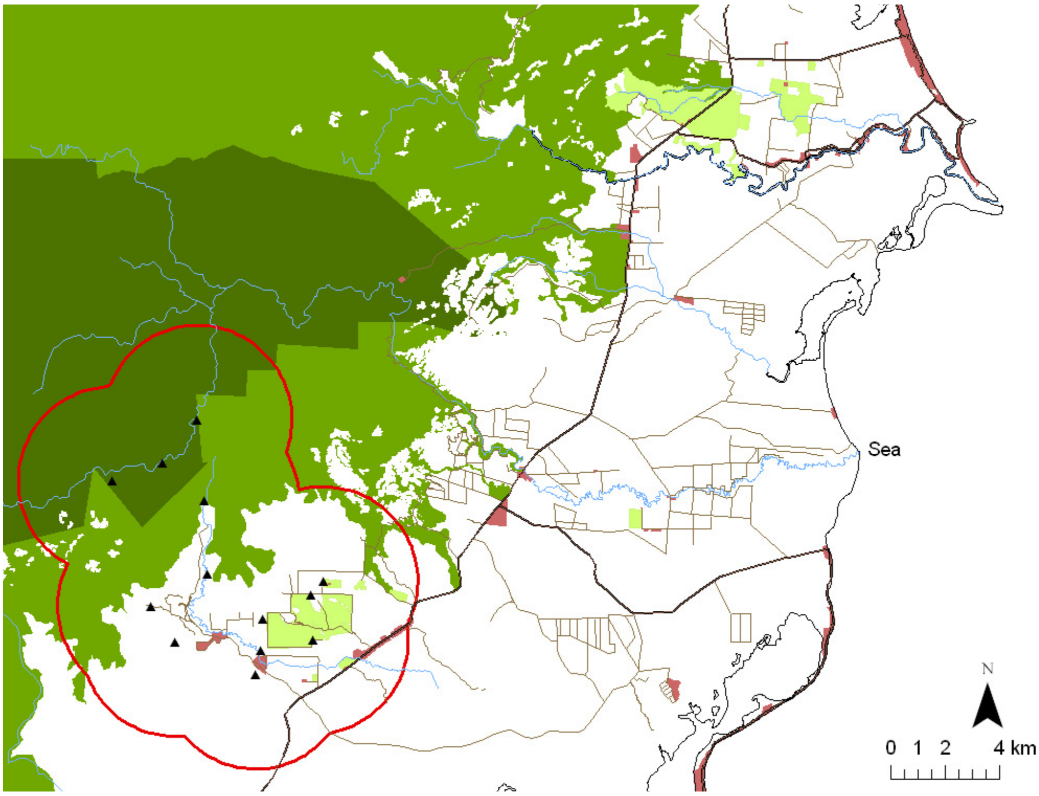
Jaguar density was estimated from the abundance estimates for each survey and sub-sampled survey, and the effective trapping area, ETA (Figure 4.8) based on the MMDM estimates derived and selected earlier in this Chapter.

Unreliable density estimates based on low ETAs were identified and excluded and the remaining densities were investigated with respect to habitat cover.

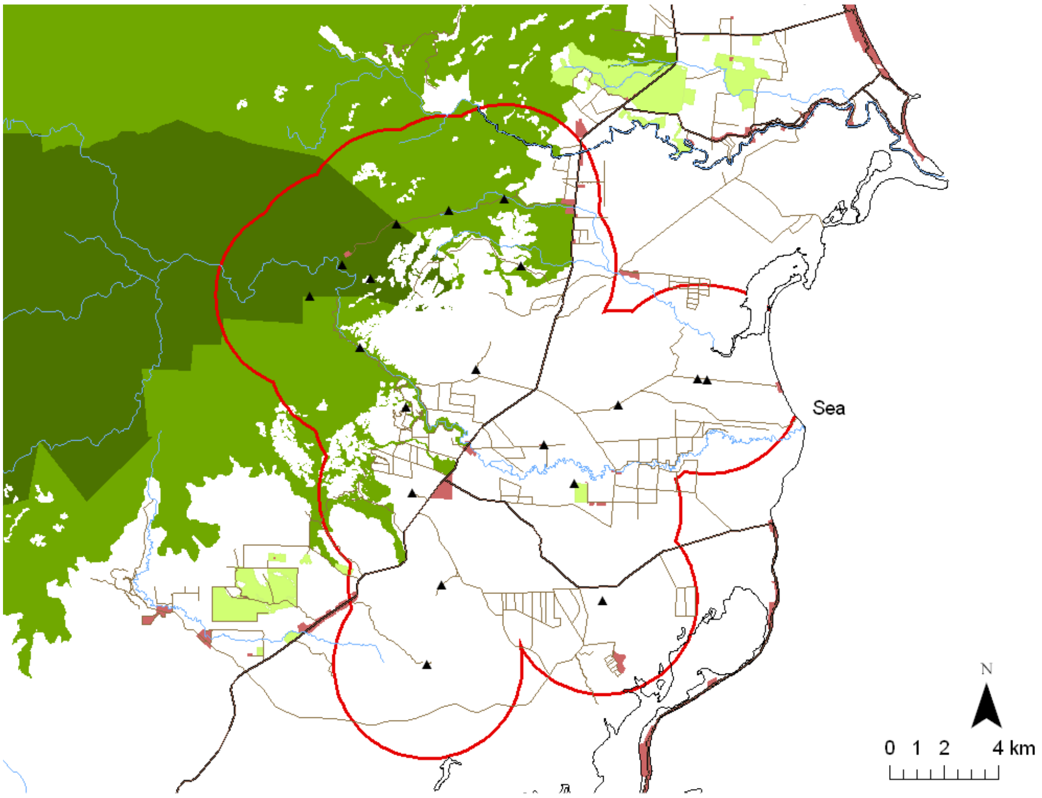
Single sex densities were estimated from single sex abundance estimates and single sex ETAs (i.e. based on sex-specific MMDM) and compared with combined sex (male and female) density estimated using combined sex ETA (i.e. based on population MMDM).



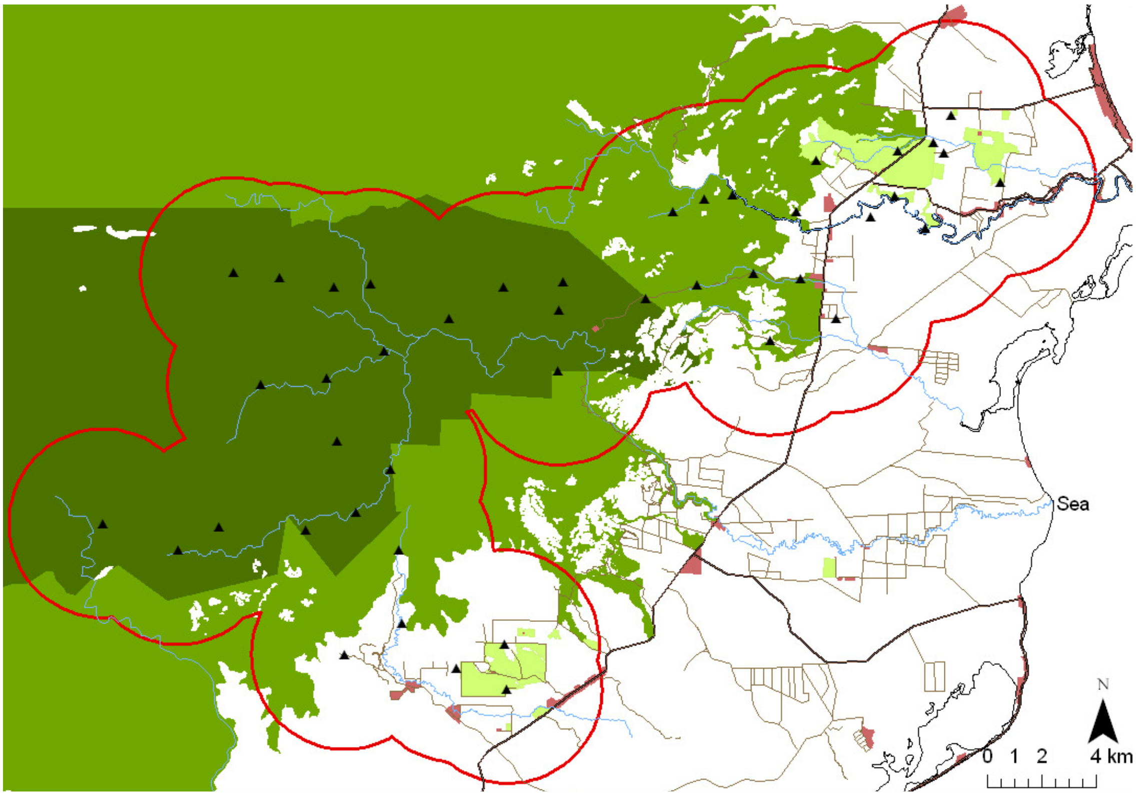
4.8 a) Sit05 ETA



4.8 b) Zab05 ETA



4.8 c) Arn06 ETA



4.8 d) Ext06 ETA

Figure 4.8 Effective trapping area during each survey: **a)** Sit05, **b)** Zab05, **c)** Arn06 and **d)** Ext06. ETA based on combined sex MMDM = 6940 m. Protected forest, unprotected forest buffer, pastures, settlements, roads and main rivers are shown.

Variation in density estimates with ETA

A plot of population density estimate against ETA suggested that small survey areas were associated with inflated density estimates with wide SEs (Figure 4.9).

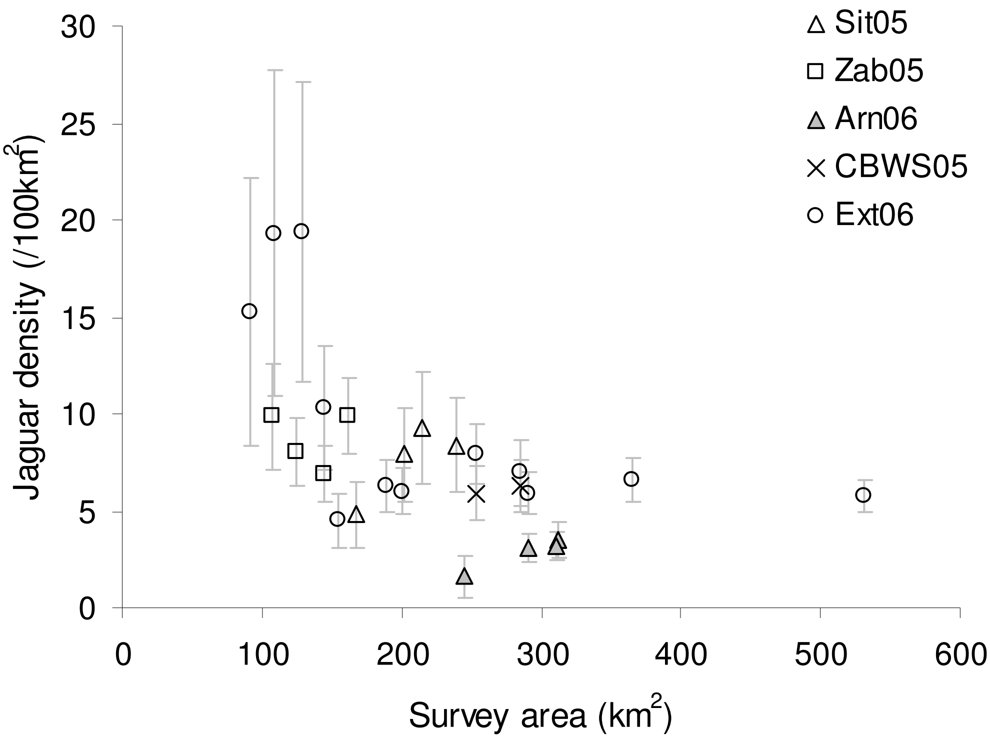


Figure 4.9 Variation in jaguar density estimate with effective trapping area. Data points are based on sub-sampled data from five separate surveys: white triangle (Sit05), white square (Zab05), grey triangle (Arn06†), black cross (CBWS05) and white circle (Ext06). Survey ETAs were based on MMDM = 6940m. Trap effort was night only. SE bars are shown. *n* = 26.
† Note that the lowest Arn06 estimate is based on only four individuals and nine captures. The model assumed at least ten captures so this estimate should be treated with caution.

Figure 4.9 suggests an inverse relationship of density to survey area. A linear model of density against 1/area fitted better than 1/density against area. It was unsatisfactory nevertheless, because the regression was influenced by three outliers and because it approaches the asymptote slowly resulting in an implausibly low prediction of asymptotic density, of 0.62 individuals /100 km^2 at infinite survey area (Figure 4.10).

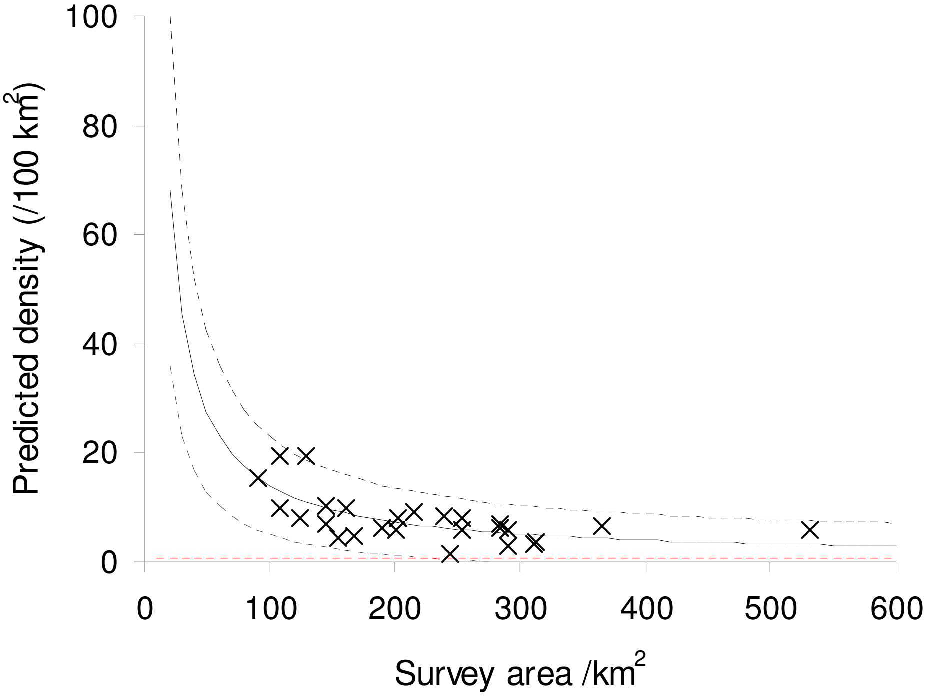


Figure 4.10 Predicted density based on the linear regression equation: density = 0.62 + 1348 1/area ($F_{1,24}$ = 23.5 $p < 0.0001$, adjusted r^2 = 47%, n = 26, density: /100km^2; area: km^2). Survey estimates shown by crosses, predicted density shown by continuous line. 95% CI shown as dashed lines. Asymptote (area independent density) of 0.62 /100 km^2 shown as red dashed line.

An alternative two-process model was fitted to the data by recognising that the area effect appeared to cease above survey areas of ~ 200 km^2. The break from the linear regression was chosen from the optimal combination of adjusted r^2, *p-value* and absence of outliers. This yielded a best-fitting model comprising a linear trend in density with area for the 10 smallest surveys ($F_{1,9} = 5.82$, $p < 0.05$, adjusted r^2 = 35%, n = 10):

$$density = 29.4 - (0.139 \times area) \qquad \text{(density /100km}^2\text{; area km}^2\text{)} \qquad \text{(Eqn 4.1)}$$

The mean density of the remaining 16 surveys, of 5.9 individuals / 100 km^2, was substituted into regression Eqn 4.1 to find the threshold above which density does not vary significantly with survey area, at 169 km^2. Figure 4.11 shows the model fit, which was deemed to better represent the data than the complete inverse model shown in Figure 4.10.

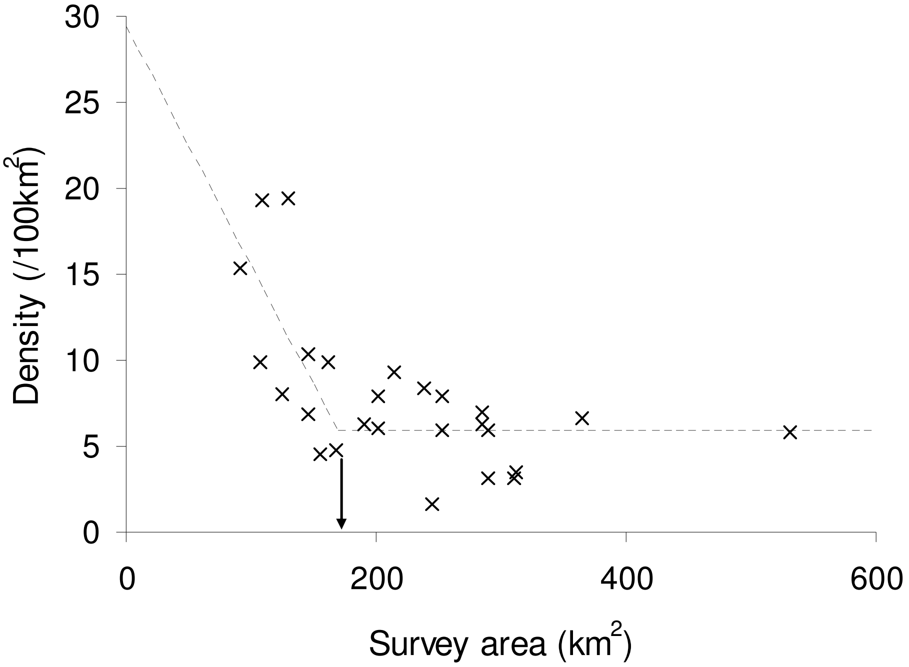


Figure 4.11 Variation in jaguar density estimate with effective trapping area. Arrow indicates survey area below which density varies significantly with survey area (< 169 km^2). Dashed line to left of arrow shows predicted density based on Eqn 4.1 (density = 29.4 – (0.139 × area). Dashed line to right of arrow is mean of 16 density estimates based on survey areas > 169 km^2 (mean = 5.9 individuals /100km^2).

Survey area was not significantly correlated with its percent cover of contiguous forest block, fragmented forest, savannah, or plantations (Pearson correlations r = 0.398, -0.181, 0.053 and 0.213 respectively, $p > 0.050$ and $n = 24$ for all), suggesting that the observed variation in density with small survey areas (Figure 4.11) was unlikely to be due to confounding effects of these habitat variables. The percent cover of cattle pasture was negatively correlated with survey area (Pearson correlation $r = -0.637$, $p < 0.01$, $n = 24$); however there was no significant relationship between density and the % pasture cover for survey areas < 169 km^2 (linear regression: $F_{1,8} = 0.25$, $p > 0.6$), again indicating that the positive trend of density with 1/area observed at low survey areas was due to an effect of survey area *per se* rather than habitat effects.

Based on these analyses, it was concluded that surveys with ETAs < 169 km^2 were too small and likely to inflate density estimates (Figure 4.11). This result accords with Harmsen (2006) who showed a similar relationship between ETA and density estimates inside CBWS; and with Maffei and Noss (2008) who suggested that the survey area should be at least four times the average home range area of the target species: in this study average home range diameter is 6940 m which approximates to a circular home range of 38 km^2 and a required survey area of at least 152 km^2. On the basis of these analyses, population density estimates based on combined sex ETAs < 169 km^2 were excluded from subsequent habitat analyses.

Variation in jaguar density with habitat

Jaguar density estimates showed no trend with mean distance of the survey cameras from the protected forest but did decline with mean distance of cameras from the contiguous forest block (Figure 4.12) suggesting that the availability of contiguous forest may limit density.

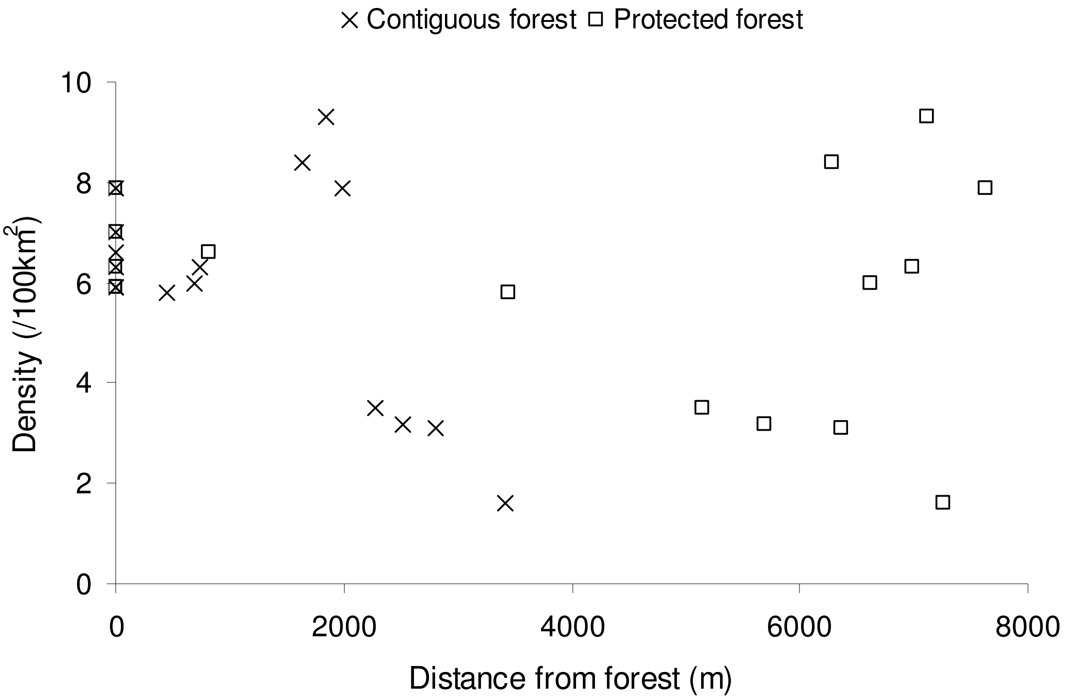


Figure 4.12 Variation in jaguar density estimate with mean distance of survey locations from the protected forest (squares) and contiguous forest block (crosses). Data points are based on data from four separate surveys. Survey ETAs were based on MMDM = 6940 m. All ETAS are >169 km^2 (190 to 532 km^2).Trap effort was night only.

Density increased at an accelerating rate with the % of survey area that was contiguous forest up to a plateau (Figure 4.13). This broken-stick response prompted exploration of two alternative models to explain the processes best fitting the observed variation in density.

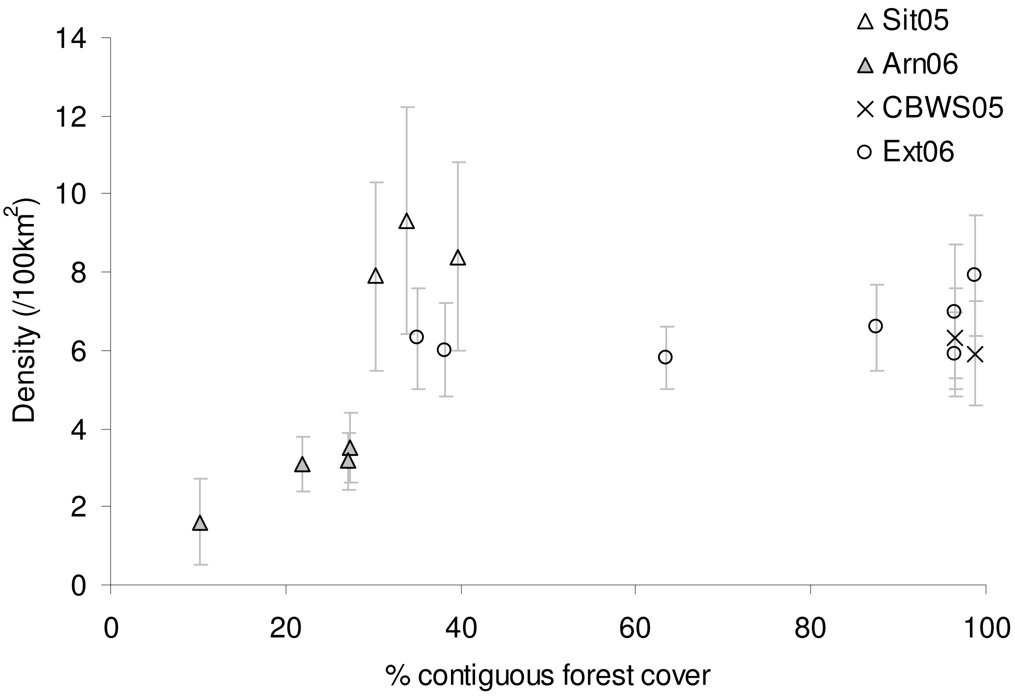


Figure 4.13 Variation in jaguar density estimate with % survey area that is part of the contiguous forest block. Data points are based on data from four separate surveys: white triangle (Sit05), grey triangle (Arn06), black cross (CBWS05), white circle (Ext06). Survey ETAs were based on MMDM = 6940 m. All ETAS are >169 km^2 (190 to 532 km^2).Trap effort was night only.

As a linear relationship between density and % contiguous forest cover was not suspected, density was inverted to give the available area per jaguar as a response to forest cover. This variable is not directly related to the mean jaguar home range (estimated earlier in this chapter as 38.7 km^2). Rather it reflects the amount of land that would be exclusively available to a jaguar if the whole survey area were divided equally between all members of the population with no range overlap. Area of exclusive use can be likened to a time-share in the sense that 10 km^2 exclusive use is equivalent to sharing 20 km^2 with one other individual, or 30 km^2 with two other individuals etc.

Two alternative linear models of area per jaguar were proposed and fitted to the data:

1. Constant forest area with decline in % forest cover: *As the % contiguous forest declines below a threshold, the available area per jaguar increases to maintain a constant area of forest.* This model is described by a linear relationship between area per jaguar and 1/ (%forest cover). Visual inspection of the data (Figure 4.14) revealed a decelerating rise rather than constant (linear) rise of area per jaguar with 1/ (%forest cover). The non-linearity was sufficient to reject this model. The deceleration suggests that the observed decline in density with reducing % contiguous forest is insufficient to sustain a constant absolute amount within the area per jaguar.

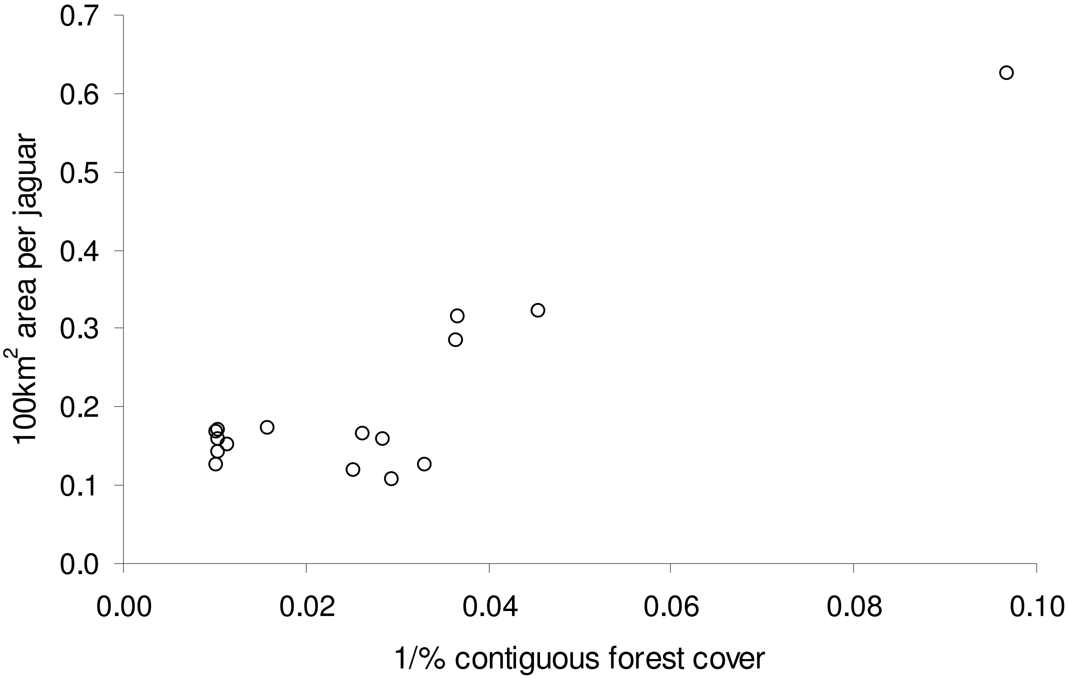


Figure 4.14 Variation in area per jaguar with 1 / % survey area that is part of the contiguous forest block. Data points are based on data from four separate surveys. Survey ETAs were based on MMDM = 6940 m. All ETAS are >169 km^2 (190 to 532 km^2).Trap effort was night only.

2. Constant increase in area per jaguar with decline in %forest cover: *As the % contiguous forest declines below a threshold, the available area per jaguar increases constantly.* This model is described by a linear response of area per jaguar to % contiguous forest. The best-fitting model had a linear trend in the six surveys with the least % cover of contiguous forest ($F_{1,4} = 33.1$, $p = 0.01$, adjusted $r^2 = 89\%$, $n = 5$):

$$100\text{-km}^2 \text{ area per jaguar} = 0.847 - (0.0218 \times \% \text{forest}) \quad \text{(Eqn 4.2)}$$

The mean area per jaguar of the remaining 10 surveys, of 14.7 km^2, was substituted into Eqn 4.2 to calculate the threshold of 32% contiguous forest below which area per jaguar increases with further forest fragmentation, and hence density decreases (Figure 4.15).

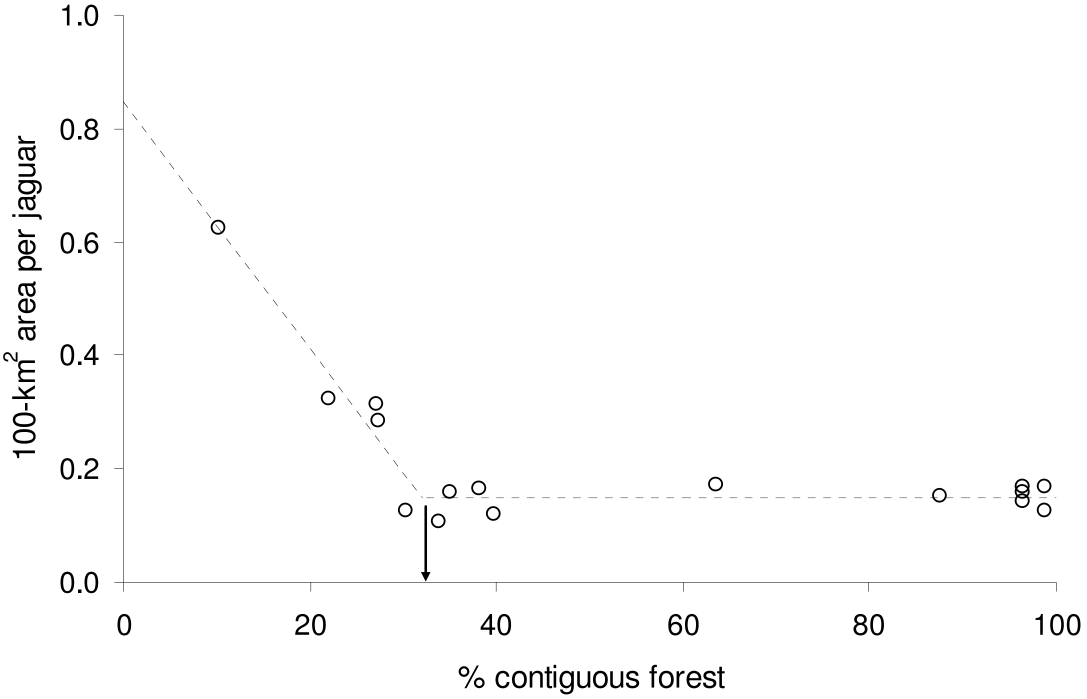


Figure 4.15 Variation in area per jaguar with % survey area that is part of the contiguous forest block. Data points are based on data from four separate surveys. Survey ETAs were based on MMDM = 6940 m. All ETAS are >169 km^2 (190 to 532 km^2).Trap effort was night only. Dashed line to left of arrow shows predicted area per jaguar based on Eqn 4.2. Dashed line to right of arrow is mean of 10 density estimates (mean = 0.147 x 100 km^2 per jaguar). Arrow indicates the % survey area that is contiguous forest above which area per jaguar stabilises.

The model shown in Figure 4.15 predicts that each 1 % increment in forest cover above zero causes a decline of ~ 2 km^2 in the area of exclusive use per jaguar until a threshold of about one-third contiguous forest cover. Above this threshold the area per jaguar remains constant at 14.7 km^2 (and thus density is constant at 6.8 /100 km^2). Given that there was no detectable variation in ranging behaviour between individuals that used the contiguous forest and those that did not, and that the average range was ~ 38.7 km^2 (see earlier Results) it can be concluded that above one-third contiguous forest cover the average jaguar shares its range with at least 2.6 (38.7 / 14.7) other jaguars. This agrees with Harmsen (2006) who found a tendency for range sharing amongst males in the protected forest with up to five individuals passing the same location in a given month, most commonly two per month. Below the threshold of one-third contiguous forest, the available area per jaguar increases by 2 km^2 for each further 1 % loss in forest cover. It is not possible to describe this decline in terms of changes in range overlap because a 2 km^2 increase in exclusive use could reflect a 4 km^2 increase in an area with double occupancy or an 8 km^2 increase in an area with four occupants and so on. However below 21 % contiguous forest cover the exclusive area per jaguar exceeds the average range of 38.7 km^2 so it can be assumed that the average jaguar no longer utilises all available land, for example they may avoid large settlements or busy plantations. This is investigated further in Chapter 5.

Although the results suggest that jaguar density may depend on the availability of contiguous forest, the % contiguous forest cover was not independent of the other habitat types within the surveys areas. More contiguous forest inevitably means less of other habitats, and indeed it was significantly negatively correlated with the % cover of fragmented forest, savannah, and plantation (Pearson correlations: $r = -0.985$, -0.904 and -0.978 respectively, $p < 0.0001$, $n = 14$). We cannot know whether jaguar density responds positively to the availability of contiguous forest or negatively to the availability of these other habitats, or to some function of all habitats. However it is reasonable to assume that jaguars will probably be limited by prey availability if the cover of contiguous forest is reduced. The % pasture cover was not significantly correlated with % contiguous forest cover within the survey areas (Pearson correlation: $r = -0.356$, $p > 0.2$, $n = 14$). Although these two habitat variables (like any that represent % cover) are not strictly independent it is notable that the high jaguar densities around 30% contiguous forest cover are associated with higher % pasture cover than are either the low densities at < 30% contiguous forest cover or the high densities at > 80% contiguous forest cover (Figure 4.16). This suggests that jaguar density increases as % cover of pasture and contiguous forest both increase from zero and the density then plateaus as % pasture declines again with increasing contiguous forest above ~ 30% cover.

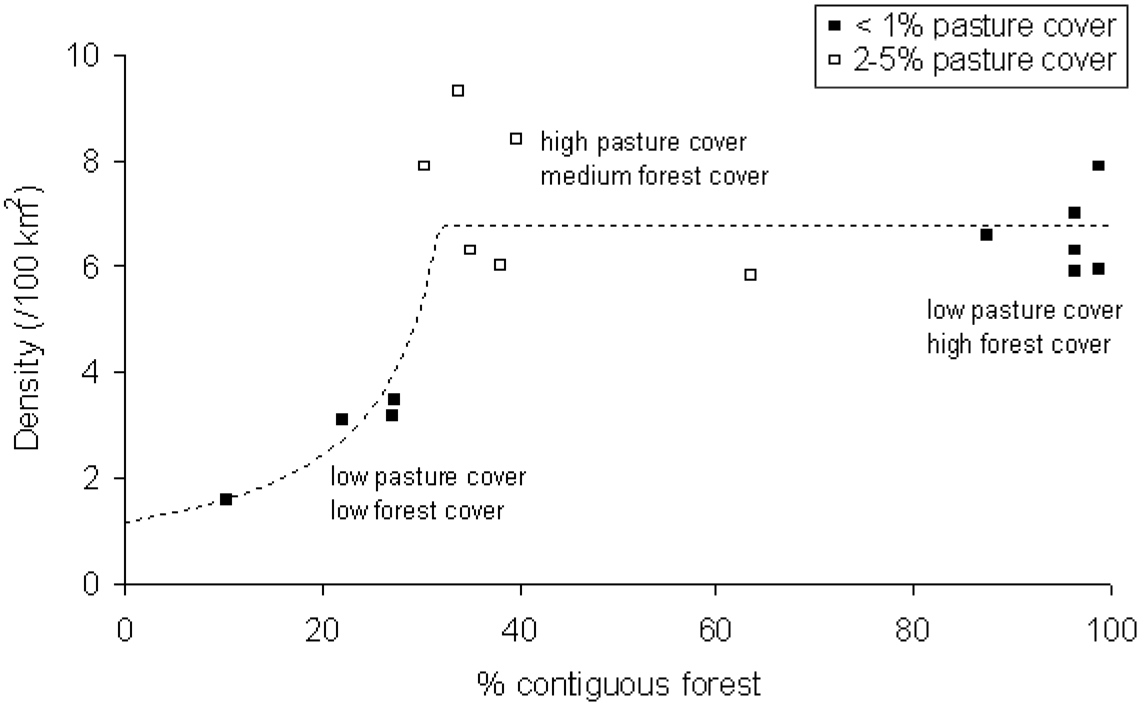


Figure 4.16 Variation in jaguar density estimate with % survey area that is part of the contiguous forest block, at two levels of % pasture cover. Black squares represent surveys with pasture cover < 1%, white squares represent surveys with pasture cover that is 2-5%. Dotted line shows predicted density back transformed from Eqn 4.2. Data points are based on data from four separate surveys. Survey ETAs were based on MMDM = 6940 m. All ETAs are > 169 km^2 (190 to 532 km^2).Trap effort was night only.

Comparison of single sex and combined sex density estimates

Male density estimates were equivalent to more than half (63 to 79%) of the total population density estimates for each of the surveys investigated (Figure 4.17). This suggests that either the population truly is male-biased or that the method of abundance estimation and/ or ETA estimation for the total population is biased.

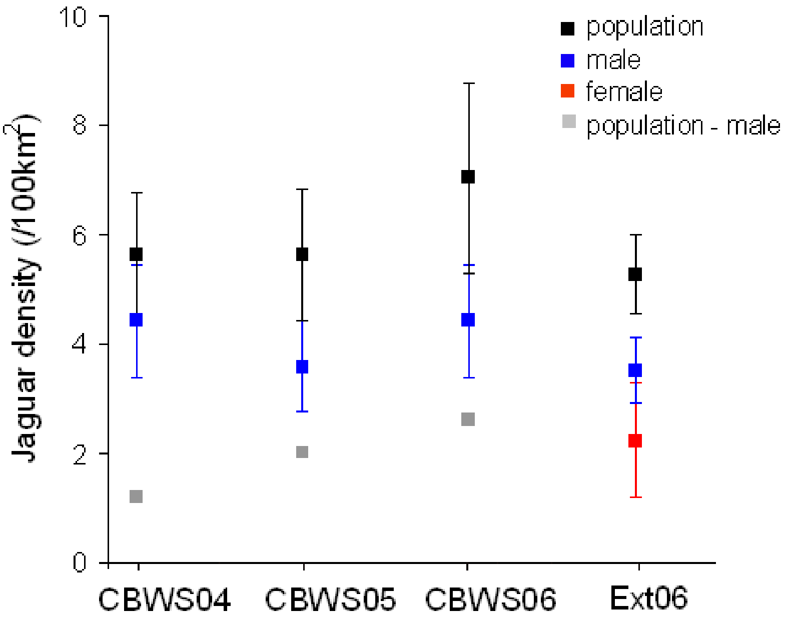


Figure 4.17 Single sex (male = blue, female = red) and total population (black) density estimates for three repeated surveys in the protected area (CBWS04, 05 and 06) and the large-scale survey spanning the protected area (Ext06). Densities are based on ETAs derived from sex-specific and combined sex MMDMs. Male MMDM = 8776 m, female MMDM = 3312 m and combined sex MMDM = 6940 m. SEs are shown. Gray data points show total population estimate minus the male estimate for surveys in which female sample size was too low for separate sex abundance estimate.

If density is estimated for the total population, using an ETA calculated over both sexes, a survey in which females are under-sampled will result in the total abundance being underestimated (too small) combined with a male-biased ETA (too large) such that the total population density estimate will be too low. The reverse situation, in which the density estimate is too high, may occur if both sexes are properly sampled but the male ranging behaviour is underestimated. It is likely that both biases exist: females are under-sampled and the ranging behaviour of males is underestimated. It may be argued that if both biases exist they may cancel out, but an accurate estimate of the density of each sex is preferred.

Discussion

This Chapter compares jaguar sex ratio, ranging behaviour and density across the protected and unprotected Cockscomb forest block and the neighbouring fragmented landscape in Belize, whilst also addressing methodological issues of density estimation using camera traps.

Methodological issues

The overall sex ratio of all sexed individuals photographed across the study area was male-biased (~2.6 males per female). Given that females are more difficult to sex than males it is likely that a higher proportion of the unsexed individuals were female. Under this assumption we may suppose that the observed ratio is the most extreme scenario for the area, and is expected to be less male-biased than this. Indeed, including all unsexed individuals as females gives an equal sex ratio of one male per female. Other jaguar studies have found a similar skew in camera-trap data, ranging from 1.2 males per female to males only, but if the unsexed individuals are included as females the sex ratio ranges from 0.8 to 4.5 males per female (Wallace *et al*. 2003, Maffei *et al*. 2004, Silver *et al*. 2004, Miller and Miller 2005, Miller 2006, Soisalo and Cavalcanti 2006).

A population sex ratio derived from camera-trap data may be expected to be skewed if the sexes differ in their ranging behaviour. Theoretically, a female bias in the derived sex ratio is expected under the classic cat social system in which the larger range of one male overlaps with the smaller ranges of multiple females (Harmsen 2006). However the detected ratio will be influenced by the number of male transients who are moving through the study area vying for a territory. High levels of male movement and overlap will shift the bias towards males (Harmsen 2006). The sex with the largest home range will also have the largest effective trapping area (ETA). Therefore, if male ranges are non-exclusive and larger than female ranges, fewer females will be detected than males simply because a smaller area is surveyed for females than for males by the same camera array. If the true population sex ratio is 1:1, and there are no other sampling biases in the methodology, then 1:1 ratio of male to female density, calculated from sex-specific ETAs, would be expected despite the observed skewed population ratio. Therefore, if a similar number of males and females are expected within a population, estimating densities separately for each sex may help to reveal whether there are other biases in the sampling methodology, for example that the survey area is too small, or the choice of trap spacing and location are favoured by a subsection of the population (Chapter 2).

Male jaguars in the study area have highly overlapping home ranges, with some locations visited by up to 5 males within a single month (Rabinowitz and Nottingham 1986, Harmsen *et al*. in press). In this study, estimates of ranging behaviour demonstrated that male jaguars ranged further than females, as previously documented in the Cockscomb forest (Harmsen 2006, Rabinowitz and Nottingham 1986). However, using sex-specific ETAs, a 1:1 density sex ratio was not detected; rather male density tended to be higher than female density, making up more than 50% of the observed jaguar density. This suggests a bias in the methodology other than that caused by sexual differences in ranging behaviour. Various studies have reported that small survey areas give inflated density estimates (see Chapter 2). Sub-sampling of the survey data revealed that density estimates were inflated and unreliable if derived from surveys below a threshold of ~170 km^2. The exclusion of these estimates from further analyses removed some of the positive bias associated with small survey size. Even so, male density may have been overestimated if the MMDM (mean maximum distance moved) derived from camera data as a proxy for home range diameter, and used to estimate the male ETA, was underestimated. This could occur if the survey grid is too small and males range beyond the camera array (Chapter 2). However, in this study the MMDM by males compared well with the home range diameters derived from long-term telemetry in the area (Rabinowitz and Nottingham 1986) so it is unlikely that the male jaguar density was positively biased by an underestimated ETA. Alternatively, and more likely, the female component of the population was underestimated. This could occur if cameras were too widely spaced, and/or because females avoided camera locations dominated by males. The home ranges of solitary female cats often contract when they have immobile cubs in a den (e.g. pumas, tigers, Sunquist and Sunquist 2002); and females with dependents may evade areas dominated by males to avoid the risk of infanticide (e.g. as observed in brown bears, *Ursus arctos*, Dahle and Swenson 2003). Traps which are spaced too widely or are preferentially placed in areas favoured by males may fail to detect this section of the female population, trapping only those which are without dependents. Indeed long-term camera surveys in the CBWS indicate that adult females reappear every 18-24 months for a brief period (B. Harmsen pers. comm.) suggesting that under the current methodology the capture probability of females may fall to zero when they are breeding.

In the current study, if density had only been estimated for the total population, using an abundance and ETA calculated over both sexes, these potential biases may not have been realised. This demonstrates that perfecting camera-trap methodology for accurate density estimation of the whole population will require accurate estimation of the home range diameter of each sex and improvements to ensure that both sexes are fully sampled.

There was detectable variation in sex ratio between different parts of the study area. The sex ratio was more male-biased inside the protected forest and its buffer, than in the forest patches and non-forest. However there was no detectable variation in ranging behaviour in either sex between those using the forest block and those using forest patches and non-forest (i.e. females who utilised the forest block ranged a similar distance as females who utilised the fragmented landscape, ditto for males). Therefore range size cannot explain the detected variation in sex ratios between these habitats. Rather it may be explained by a different sampling bias: that the choice of camera locations (primarily trails) within the forest block was favoured by males. Travelling routes through the dense vegetation of the Cockscomb Basin are potentially a limited resource for jaguars (Rabinowitz and Nottingham 1986), and are dominated by males (Harmsen 2006). Females may avoid these male-dominated trails, unless sexually receptive and in search of a mate. In contrast the fragmented habitat outside of the forest block is more open with numerous natural and man-made trails and roads. Accessible travelling routes are unlikely to be limited in this more heterogeneous environment and may explain the less male-biased sex ratio observed here compared to the forest. Alternatively, it is possible that there was no sampling bias and the ratio of females to males was in truth higher outside the forest block than inside. Such a situation could arise if, for example, females are attracted to areas rich in domestic prey around farms and villages outside the forest block. These two explanations may not be mutually exclusive, and it is not possible to distinguish between them in this study. This emphasizes the need to optimise methods to detect female jaguars off-trail within the forest block. Camera traps are not suitable as they depend on trails as funnels to direct the target species past the camera. One possibility currently being explored is the genetic analysis of scats which are collected off-trail using trained detector dogs. A recent pilot study has demonstrated a high rate of scat detection off-trail by the dogs, but methods to genotype scat samples to sex and to the individual are still being refined (A. Devlin, unpubl. data, B. Harmsen pers. comm.).

This study has highlighted inadequacies with the current method of density estimation which could potentially bias the estimates. If the biases are not consistent across the landscape then comparisons of density in different habitats will not be valid. Firstly, it could be argued that the overall higher densities observed in the forest may be an artefact of sampling mainly on trails. Because wide trails are limited in the forest, many individuals may overlap and exploit the same few access routes. Extrapolating to the rest of the forest, where there may be fewer trails, could overestimate the true density (Chapter 2). In contrast, outside of the forest block trails were not limited; they were abundant and spread more evenly throughout the landscape, therefore overestimation may be less likely. However, even if many individuals are exploiting trails within the forest, density would only be overestimated if the survey area was too small, and the proxy for home range diameter (MMDM) was underestimated. Both these potential biases were addressed in the study through the exclusion of small survey areas and the careful choice of home range proxy. Secondly, females may be under sampled in the forest, compared to the fragmented lands, if males dominate the forest trails. This bias is more likely, supported by the fact that the sex ratio was more male-biased in the forest, and implies that the true forest density may be higher than that estimated here.

Ecological issues

Most contemporary estimates of jaguar density in the Selva-Maya region are based on survey areas with complete forest cover and negligible human use (e.g. Ceballos *et al*. 2002, Novack 2003, Silver *et al*. 2004, Miller and Miller 2005, Harmsen 2006). In contrast, this study included areas that are not predominantly contiguous forest. The data clearly indicated that in southern Belize jaguars are not restricted to the protected forest. Rather, jaguars were living and breeding within the unprotected forest and the fragmented landscape, and thus should be incorporated into management plans. Density declined when contiguous forest cover fell below about one-third of the survey area. This has implications for the extrapolation of such density estimates through time or space to more fragmented landscapes, and could contribute to better predictions of the jaguar population at the regional level.

In areas where more than four-fifths of the forested landscape was fragmented, the average jaguar did not utilise all the available land. This may reflect avoidance of human activity around large settlements or plantations, or attraction to cattle pastures with a concentration of activity where there is an abundance of domestic prey. Habitat use is investigated further in Chapter 5. Home range may be expected to be larger, and density lower, in areas where prey are scarcer. Although density declined with reduced contiguous forest cover, home range size did not increase, suggesting that something other than, or in addition to, total prey availability (wild and domestic) may be limiting density outside the forest block. Thus low density further from the contiguous forest and closer to human habitation may be primarily due to direct conflict with people. Levels of human-induced mortality throughout the study area are investigated further in Chapter 7.

The constancy of jaguar density when contiguous forest cover declined from 100% to 30% was surprising for a cat often described as elusive and reluctant to utilise open areas (Schaller and Crawshaw 1980, Crawshaw and Quigley 1991, Silveira 2004, Cullen *et al*. 2005). Not until over two-thirds of the forested landscape was fragmented did density diminish. This is a positive sign for jaguar conservation and, at face value, suggests that the jaguar is remarkably adaptable and resilient to human development. A study of tiger distribution and habitat quality in Nepal and India found that when the ratio of good habitat (defined in terms of the level of horizontal cover, prey abundance and human use) to poor habitat fell below 50%, tigers failed to reproduce; and in areas where the ratio was < 30%, tigers were absent (Smith *et al*. 1998). In the current study we may broadly characterize the contiguous forest as good quality habitat, assuming that here wild prey are abundant and the negative impact of human activities are minimal. In reality the quality of the contiguous forest may decline from the protected area core to the outer edge of the unprotected buffer where the risk of direct conflict between jaguars and hunters may be greater, and wild prey may be depleted. For example, Chapter 6 shows that smaller wild prey species were taken by jaguars in the unprotected buffer than in the protected forest. This was largely due to the absence from the diet of white-lipped peccaries (*Dictolyes pecari*) in the unprotected forest, a favoured game species of both hunters and jaguars.

The 30% threshold observed here should not be interpreted as a universal rule throughout the jaguar range. Variance in the threshold is expected depending on the relative qualities of the contiguous forest and the fragmented landscape. For example, the benefit of extensive tracts of contiguous forest will be negligible if wild prey have been largely hunted out by people. Indeed the phenomenon of empty forests (Redford 1992) should not be overlooked if attempting to gauge predator density simply from the habitat availability. For example, the average jaguar density estimate from within the Rio Bravo forest block in the north of Belize is ~ 10 jaguar per 100 km^2 (Miller 2006); the forest extends into Guatemala, where the density falls to ~ 2 jaguars per 100 km^2 (Novack 2003). It is not clear whether this striking difference in jaguar density is related to variance in prey abundance or subtle environmental variation such as the level of precipitation. Nevertheless it is a reminder that multiple factors may influence population density and care should be taken if attempting to extrapolate from small survey areas to the regional level based on habitat variables alone.

The quality of the fragmented landscape (or poor habitat) will also vary across the region, depending on the extent of fragmentation and types of land use. In this study human density in the fragmented landscape was low, ~13 people per km^2, and forest patches were common, comprising up to 25% of the total land cover within the fragmented area of the surveys (mean ± SD =16 ± 10 % cover, n = 16 survey areas). Jaguars were widespread throughout the fragmented lands (see Chapter 5). This situation contrasts with, for example, the hyper-fragmented forest landscape of southern Brazil where jaguars are restricted to the larger forest patches only (Michalski and Peres 2005). In the current study the forest patches may facilitate jaguar reproduction and survival by supporting wild prey species and providing refuges for jaguars away from human activities during the day. Variation in jaguar density with the total % cover of forest patches was not detected (R. Foster unpubl. data); however the overall physiognomy of the fragmented landscape (size, shape and distance between patches) is probably influential and requires further investigation. The clearance of land for aquaculture or arable agriculture is likely to lower the quality of the human-influenced lands for jaguars. However, under some conditions, cattle pastures may contribute positively to the quality of the fragmented landscape, providing a source of large domestic prey where wild ungulates are lacking, potentially facilitating reproduction (Chapter 6). In this study the fragmented lands supported the equivalent of up to ~ 8 cattle per km^2, similar to the density of large wild ungulates such as white-lipped and collared peccaries (*Tayassu tajacu*) inhabiting un-hunted forests in Central and South America (e.g. Novack 2003, Peres 2005). In reality the densities of livestock were much higher (~ 200 km^{-2}), but localised to small areas (discrete pastures of 0.03 to 2 km^2) within the fragmented landscape (Chapter 5). Although domestic livestock may facilitate reproduction in an otherwise prey-poor environment, jaguar survival will be lowered if lethal control is practised to protect the livestock. Population dynamics and the influence of lethal control on population persistence are explored further in Chapter 7.

Summary

This study has raised, and attempted to address, some important methodological issues involving the density estimation of jaguars, which could be applied to other low density wide-ranging species. In particular, 1) ensuring that the survey area is large enough, 2) incorporating differences in range size, and 3) ensuring that trap-spacing is optimal and trap locations are unbiased, have been shown to be important. Jaguar density estimation using camera traps is far from perfect, and will greatly benefit from improved data on ranging behaviour, particularly of females. Alternatively the use of scat detection dogs may provide a complementary way to survey for individuals that elude the cameras. Within the acknowledged limitations, the method has permitted the first large-scale investigation of jaguar density in Belize beyond the boundaries of the tropical moist lowland forests of the Selva Maya. Superficially, the jaguar density in lands neighbouring the protected forest of the CBWS does not appear to be adversely affected by the current level of human development and associated deforestation and fragmentation. However it is unknown whether the unprotected section of the population can sustain current levels of lethal control in the long-term (see Chapter 7). Understanding the extent to which jaguars can persist in the fragmented human-influenced landscape outside protected areas such as CBWS will be crucial in identifying long-term viable connections between protected areas within the vision of the Mesoamerican Biological Corridor.

Box 4.1 The influence of home range diameter proxy on density estimate

Three male-only density estimates were calculated for each of the CBWS surveys (04, 05 and 06) using three different, yet equally valid, choices of home range proxies for ETA estimation (*n* refers to number of individuals with MDM > 0 m):

a) Survey-specific camera data based on movements made during the survey period and within the survey area only: 2004: 6429 m (±SE = 843, *n* = 9); 2005: 4593 m, (±SE = 956, *n* = 9); 2006: 8181 m (±SE = 1287, *n* = 9)

b) Long-term camera data based on accumulated movements made over the three repeated surveys: 7288 m (±SE = 950, *n* = 17)

c) Long-term telemetry data collected on from the same area: 6521 m (±SE = 1323, *n* = 4) (Rabinowitz and Nottingham 1986)

The three density estimates were compared within each survey year, demonstrating that lack of standardisation in choice of ETA estimation may make comparison between (or even within) studies invalid (Figure 1).

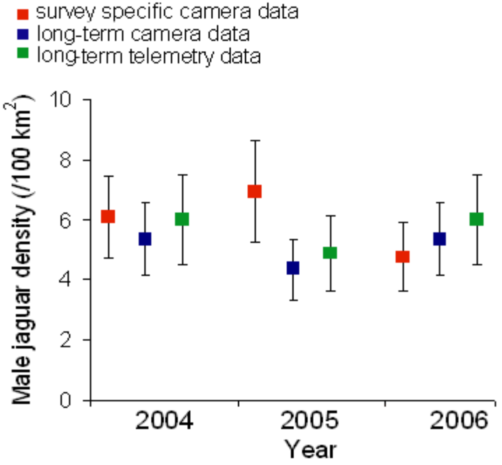


Figure 1 Male jaguar density estimates and SEs in the CBWS in 2004, 2005 and 2006 based on three different proxies of home range diameter for ETA estimation. Red: survey specific (2004 = 6429 m, 2005 = 4593 m, 2006 = 8181 m; blue: calculated over the three repeated surveys (7288 m), green: based on historical telemetry data from the area (6521 m).

Within 2004 and 2006 the density estimates are relatively consistent because the home range proxy is similar between survey-specific, long-term and telemetry data. In 2005 the survey-specific home range proxy was lower than that based on the long-term camera data or telemetry data, resulting in a density estimate that was almost twice as high than if long-term camera or telemetry data were used (an increase from four males /100km^2 to seven males /100km^2). Although the 2005 density estimates are not significantly different this example serves to highlight the fact that proxies for home range diameter, even if derived from the same dataset, can vary and so influence the final density estimate.

The extent to which MMDM is an appropriate proxy for home range diameter will depend on the survey area (Maffei and Noss 2008) and the spatial configuration of the trap locations (see Chapter 2 for details). If these requirements are not met then long-term data, if available, may be considered more appropriate than the short-term survey-specific data which may underestimate the home range diameter. Within a long-term camera study which comprises repeat surveys, preference may be given to long-term data if, during the shorter survey periods, several of the study animals were only ever captured at a single station such that their MDM = 0 and is excluded; for example during the three CBWS surveys only ~50% of the study animals were captured at >1 station and contributed to the estimate of the MMDM and ETA during each survey; this increased to 68% of the animals when their accumulated movement was calculated over the three survey periods. Similarly, telemetry data, although providing detailed information on ranging behaviour, are often limited to just a few individuals, who may or may not be representative of the population as a whole.

If long-term camera or telemetry data are used to estimate home range diameter, it must be assumed that home ranges are not shifting through time and that the resultant distance could be covered within the time constraint of the survey period i.e. the ETA that is calculated must be relevant to the sampling period.

These findings bring into question comparisons between different studies which have used alternative proxies of home range diameter for estimating ETA and density; for example to date researchers have used various combinations based on telemetry (which may or may not be from the same period or study area) and/or survey-specific camera data and/or long-term camera data from different survey periods e.g. Silver *et al.* (2004), Cullen *et al.* (2005), Harmsen (2006), Soisalo and Cavalcanti (2006), Salom-Pérez *et al.* (2007). It would seem prudent to standardise the methodology so that comparisons can be made with more confidence both within and between study sites.

Chapter 5

Habitat use by jaguars and pumas in a human-influenced landscape

Abstract

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are sympatric across the entire jaguar range. Where they occur together, both species exist in increasingly fragmented landscapes where they face direct persecution from people, mainly due to livestock predation. Pumas are known to inhabit a greater variety of natural habitats than jaguars, but the influence of anthropogenic factors on the co-existence of these two similar-sized cats is poorly known. This chapter uses camera-trap data to compare habitat use of jaguars and pumas in Belize, Central America. The cats did not differ in their use of a large block of relatively homogenous secondary rainforest. However, pumas were scarce outside of the forest block whilst jaguars were detected throughout the human-matrix. Reasons for this discrepancy are discussed, including differential tolerance to human disturbance and the absence of resources required for puma survival outside the forest block. Habitat correlates of jaguar activity and livestock predation around farms permit the first direct assessment of factors influencing depredation by cats in the region. These findings inform a discussion of potential site-specific techniques for reducing livestock predation within the context of Belizean livelihoods.

Introduction

Human activity impacts over three-quarters of the land on Earth (Sanderson *et al*. 2002a). Habitat transformation is the principal human threat facing all terrestrial mammals (Baillie *et al*. 2004). Degradation of natural habitats destroys forage, prey and refugia; fragmentation of the landscape further intensifies all other anthropogenic threats by bringing species into closer contact with humans and their activities. Habitat fragmentation is of particular concern for large carnivores because they often have large home ranges and so are forced into the human-matrix. Understanding how large carnivores use the human-matrix in comparison to the remaining contiguous natural habitat will be essential for predicting their long-term survival across an increasingly human-dominated landscape. In areas where multiple carnivores live sympatrically, such studies are valuable for predicting the interactive impact of human factors on co-existence: for example the vulnerability of competitively inferior species within carnivore guilds may increase under the pressure of human activity (e.g. Creel 2001, Woodroffe 2001).

This study focuses on the jaguar (*Panthera onca*) and the puma (*Puma concolor*), two similar-sized cats which co-exist throughout the neotropics, a region where current human population growth is second only to Africa (World Resources Institute, WRI, 2007). Both species are near-threatened (IUCN 2007) and both are known to prey on livestock with resulting persecution by people (e.g. Belize: Rabinowitz 1986a, Brechin and Buff 2005; Costa Rica: Sáenz and Carrillo 2002, Venezuela: Mondolfi and Hoogesteijn 1982, Polisar *et al.* 2003; Brazil: Mazzolli *et al.* 2002, Crawshaw 2002, Conforti and Azevedo 2003, Crawshaw *et al.* 2004, Zimmermann *et al.* 2005, Michalski *et al.* 2006, Azevedo and Murray 2007; Azevedo 2008, Palmeira *et al.* 2008). Little information is available, however, regarding the extent to which jaguars and pumas may favour human-influenced landscapes over wilderness, the impact of human disturbance on their behaviour, or how anthropogenic factors may influence the co-existence of these two species. Furthermore, although factors influencing livestock predation by these cats have been widely studied in South America (e.g. Hoogesteijn 2000, Polisar *et al.* 2003, Michalski *et al* 2006, Palmeira *et al.* 2008) data are lacking from Central America, a region with three times the density of humans (WRI, 2007) and distinctly different biomes and land-use practises than South America.

The aims of this chapter are to compare habitat use of both species between an undisturbed protected lowland rainforest and its neighbouring human-influenced landscape, in Belize, Central America, and to assess habitat factors associated with livestock predation in this region. The study tests particularly for a species-by-habitat interaction, and evaluates potential options for managing habitats to reduce livestock predation.

Habitat use by sympatric jaguars and pumas

Jaguars occupy a variety of lowland habitats (≤ 2000 m) including rainforest, wet grasslands, mangroves and even arid scrub, although they tend to be associated with water (Kitchener 1991, Emmons and Feer 1990, Nowell and Jackson 1996, Reid 1997). Pumas are found in a wider range of natural environments than are jaguars, covering every major habitat type of the Americas, including cold coniferous forest, tropical rain forest and desert, and live at altitudes up to 5,800 m (Emmons and Feer 1990, Nowell and Jackson 1996, Sunquist and Sunquist 2002). On this level and in the absence of human-factors, pumas may be considered to have more flexible habits than jaguars. A survey of jaguars and pumas in three protected areas in Brazil's endangered and increasingly fragmented Atlantic forest identified pumas in all habitats from the coast to mountain tops; whilst jaguars were only found at < 1000 m, and restricted to two of the protected forests (Leite and Galvão 2002). Indeed Hoogesteijn (2000) suggested that the jaguar has a more compromised future than the puma because it has a more restricted geographic range and exploits fewer habitat types. However this conjecture remains unverified until more data are available on the response of either species to human expansion.

Although the puma is relatively well-studied in North America (see Sunquist & Sunquist 2002), few studies have been published on habitat use of sympatric jaguars and pumas within the neotropics, and these are limited to the small sample sizes associated with telemetry, ranging from a single puma and two jaguars (Emmons 1987) to six pumas and five jaguars (Scognamillo *et al*. 2003). Although these studies have provided some insight into the simultaneous habitat use of both species, they are limited to natural and semi-natural environments: (1) the dry forests of Jalisco, Mexico (Núñez *et al*. 2002) and the rain forests of Manu, Peru (Emmons 1987), both homogenous, un-fragmented and relatively undisturbed; (2) the mosaic landscapes of the Brazilian Pantanal (Schaller and Crawshaw 1980) and the Venezuelan llanos (Scognamillo *et al*. 2003), both highly heterogeneous areas of floodplains, cerrado/savannah, forests and open cattle pastures. None of these studies assessed habitat use in relation to human activities *per se*, besides the rearing of cattle in the Pantanal and Venezuelan llanos where livestock generally exist at low densities in an almost feral state.

With the exception of Harmsen (2006) who used camera traps to compare jaguar and puma activity within a protected rainforest, there have been no published studies comparing jaguar and puma habitat use in Central America. This study has the benefit of comparing habitat use of jaguars and pumas within a large undisturbed area and within the neighbouring fragmented human-influenced landscape. Such comparisons are rare; carnivore studies are often limited to populations that have already been influenced by human activities and so require care when extrapolating evolutionary scenarios about habitat choice (Núñez *et al*. 2002). For example, a study of carnivores in the highly fragmented landscape of São Paulo, the most densely populated state of Brazil, detected pumas in fragments of natural vegetation (semi-deciduous forest and cerrado) and eucalyptus plantations. The jaguar was absent from all habitats, believed to have been locally extinct for 50 years; however whether this reflected an inability of the jaguar to adapt to habitat modification and human disturbance is uncertain as it was also historically persecuted in this area (Lyra-Jorge *et al*. 2008).

When considering habitat use of large predators, it is equally important to study broad habitat selection in heterogeneous landscapes and microhabitat differences within specific habitats. Even within otherwise homogenous environments, sympatric carnivores may have subtly different habitat requirements, perhaps related to their mode of hunting or preferred prey. Furthermore the use of a particular habitat may be influenced in part by the juxtaposition of other habitats and land-uses systems, such as the proximity of roads or settlements. Consideration should also be given to sexual differences in habitat use, particularly with respect to human activities. For example the preferential use by females of habitats where there is an increased risk of human-induced mortality (e.g. cattle farms, high traffic roads) or their avoidance of historic den sites or hunting grounds due to human disturbance may be detrimental to reproduction and long-term population survival. Accordingly, the main objective of this chapter is to compare habitat use by jaguars and pumas within an undisturbed forest and across a range of habitat types and land-use systems. Camera traps were used to monitor activity (as an index of habitat use) of both species simultaneously. This method allowed more individuals to be studied than is logistically possible with traditional telemetry studies, providing sufficient sample sizes for between-species and between-sex comparisons. Activity is compared between habitats, and with respect to the proximity of various natural features and anthropogenic factors.

Some species may avoid any kind of human activity, regardless of the natural habitat or land-use system. Species that are particularly sensitive to human disturbance will be less flexible even if they occur historically across a wide range of natural habitats. The second objective of this study is therefore to assess the relative tolerance of jaguars and pumas to human activity, by comparing their responses to ecotourism within an otherwise undisturbed protected forest.

Habitat determinants of cat activity and livestock predation

One of the most important tasks facing big cat conservation today is to reduce livestock predation in order to increase local tolerance of predators (Nowell and Jackson 1996, Hoogesteijn ad Hoogesteijn 2008). Habitat features and livestock husbandry practises are among a suite of interacting factors believed to influence livestock predation (Polisar *et al*. 2003). Understanding habitat use by jaguars and pumas around cattle farms and the local habitat correlates of depredation may help to improve farm management and so reduce losses of livestock to cats, and subsequently losses of cats to lethal control. Published studies of the determinants of jaguar and puma predation on livestock are limited to South America. There may be some similarities between the Central American situation and studies from southern Brazil (e.g. Michalski *et al*. 2006) in terms of average cattle density, ranch size and broad habitat types; however the majority of South American studies concern expansive ranches in seasonally flooded savannahs such as the Brazilian Pantanal and Venezuelan llanos (e.g. Polisar *et al*. 2003, Azevedo and Murray 2007). Ranches exceeding 100 km^2 with tens of thousands of cattle are common. Human population is low, livestock management is limited such that the cattle, which exist at relatively low densities, have become part of the natural ecosystem (Quigley and Crawshaw 1992), and the home ranges of several jaguars and pumas may fall within the ranch boundaries (e.g. Schaller and Crawshaw 1980, Scognamillo *et al*. 2003). Cattle farms in Belize, Central America, are small in comparison, averaging ~ 3.6 km^2 per property and the majority stocking fewer than 50 head (Brechin and Buff 2005). Multiple farms may fall within the home range of the same cat (R. Foster, pers. obs.). With forest still covering approximately 70% of Belize (WRI 2007), many farms and villages lie in close proximity to the forest, and almost every livestock holding is at risk of predation. The final objective of this study is to assess the habitat factors influencing jaguar and puma activity and livestock predation around Belizean cattle farms and, where possible, to make recommendations which may lower losses and the retaliatory killing of cats.

Methods

Camera-trap data were collected over three years (2004-2006) from habitats across the range of land-use systems in the region: the protected secondary rainforest of the CBWS, unprotected forest, shrubland, pine savannah, cattle pastures, citrus and banana plantations, shrimp farms, and villages. Camera locations and survey information are given in Chapter 4 (Figure 4.1 and Table 4.1). All cameras were set with an enforced delay of three minutes between consecutive exposures, in order to avoid wastage of film on herding species such as white-lipped peccaries (*Dicotyles pecari*) and cattle. At sites outside the reserve where high levels of non-target traffic were unavoidable (e.g. vehicles, cattle, people) the cameras were set to operate only at night. Only night captures were used in the analyses to allow an equal representation of all stations regardless of whether sampling was continuous or night-only. ‘Night’ was defined as those captures occurring between sunset and sunrise. Daily sunrise and sunset times (2004 to 2006) were acquired from the US Naval Observatory (2007).

Habitat use by jaguars and pumas

Jaguars were individually identified and sexed from the camera-trap photographs (Chapter 4). No attempt was made to individually identify or sex pumas. Individual recognition of pumas is difficult because they have a plain brown coat with no pattern. Harmsen (2006) attempted to individually identify pumas of the CBWS based on scars and temporary swellings beneath the skin caused by botfly larvae (*Dermatobia hominis*), and other identifiers such as tail kinks, black tail markings, residual juvenile markings, and overall body shape and size. Although pumas could be identified in certain areas for limited periods, photographs with distinguishing features were too infrequent for individual recognition over an entire survey period. Pumas are more difficult to sex from photographs than are jaguars (R. Foster pers. obs.). Given that they have a similar ratio of body weight to testes weight (Costa *el al*. 2006) this difference may be related to their posture and tail position whilst walking. Because pumas cannot be individually identified, assigning sex requires a good view beneath the tail in every photograph. In contrast once a jaguar has been sexed this can be linked to its individual identification such that further photographs do not require a view beneath the tail.

Measures of habitat utilisation

Three variables representing habitat utilisation by big cats were calculated for each camera location: presence-absence, absolute capture rate and total individual rate. Absolute capture rate (per 28 nights), an index of activity, was calculated for jaguars (males and females separately and combined) and for pumas as:

$$\frac{\text{Total number of captures}}{\text{Trap effort}} \times 28 \qquad \text{(Eqn 5.1)}$$

The total individual rate (per 28 nights), an index of how many individuals used the location, was calculated for jaguars (males and females separately and combined) as:

$$\frac{\text{Total number of individuals captured}}{\text{Trap effort}} \times 28 \qquad \text{(Eqn 5.2)}$$

Presence/absence and activity were calculated for camera locations that were functional throughout 3-year study period (Jan04 to Dec06). Individual rate was only calculated from short-term data derived from six large-scale surveys (Chapter 4). This is because the period between first and last functional trap night varied between camera stations such that trap effort was distributed over periods ranging from one month to 36 months. Limiting the analysis to short-term survey data (maximum 62-day survey period) ensured population closure such that individual rate was comparable between locations. For locations which were surveyed multiple times, the mean individual rate was calculated.

Over the 3-year period, the mean number of days that a camera was running until its first jaguar capture was larger inside the protected forest (mean ± SE = 22.8 ± 2.1 days, $n = 81$) than outside it (mean ± SE = 16.2 ± 2.7 days, $n = 57$). The presence-absence analysis therefore excluded camera stations without cat captures and < 28 days of uninterrupted trap effort. The rate analysis also excluded camera stations with < 28 days of uninterrupted trap effort, regardless of whether there was cat activity. Data from stations located < 100 m apart (e.g. those that were re-located because of risk of damage) were combined as the same location.

Because sex could not be determined for all jaguars with low capture histories, where possible, analyses of sex differences were conducted three times: unknown sex included as males, as females, and excluded.

Habitat and land-use map

A habitat and land-use map of the study area (Figure 5.1) was created manually in Arc Map (Arc GIS 2004) using a combination of resources: extensive ground-truth data collected by the author between 2004 and 2006, Ordnance Survey Maps of the region at a resolution of 1:50,000 (Ministry of Defence 1995), and Land Sat satellite images of the region for the years 2002, 2004, 2005 and 2006 which were of variable quality. Vegetation and land-use classification followed the UNESCO system of nomenclature adapted for the Central American Ecosystems Mapping Project (Meerman and Sabido 2001) as shown in Table 5.1. Bold text indicates the broad classification categories, with the vegetation types relevant to the study area below. In keeping with Meerman and Sabido (2001) woodland categories were clumped with lowland pine savannah habitats. Example photographs of each habitat type are shown in Appendix C.

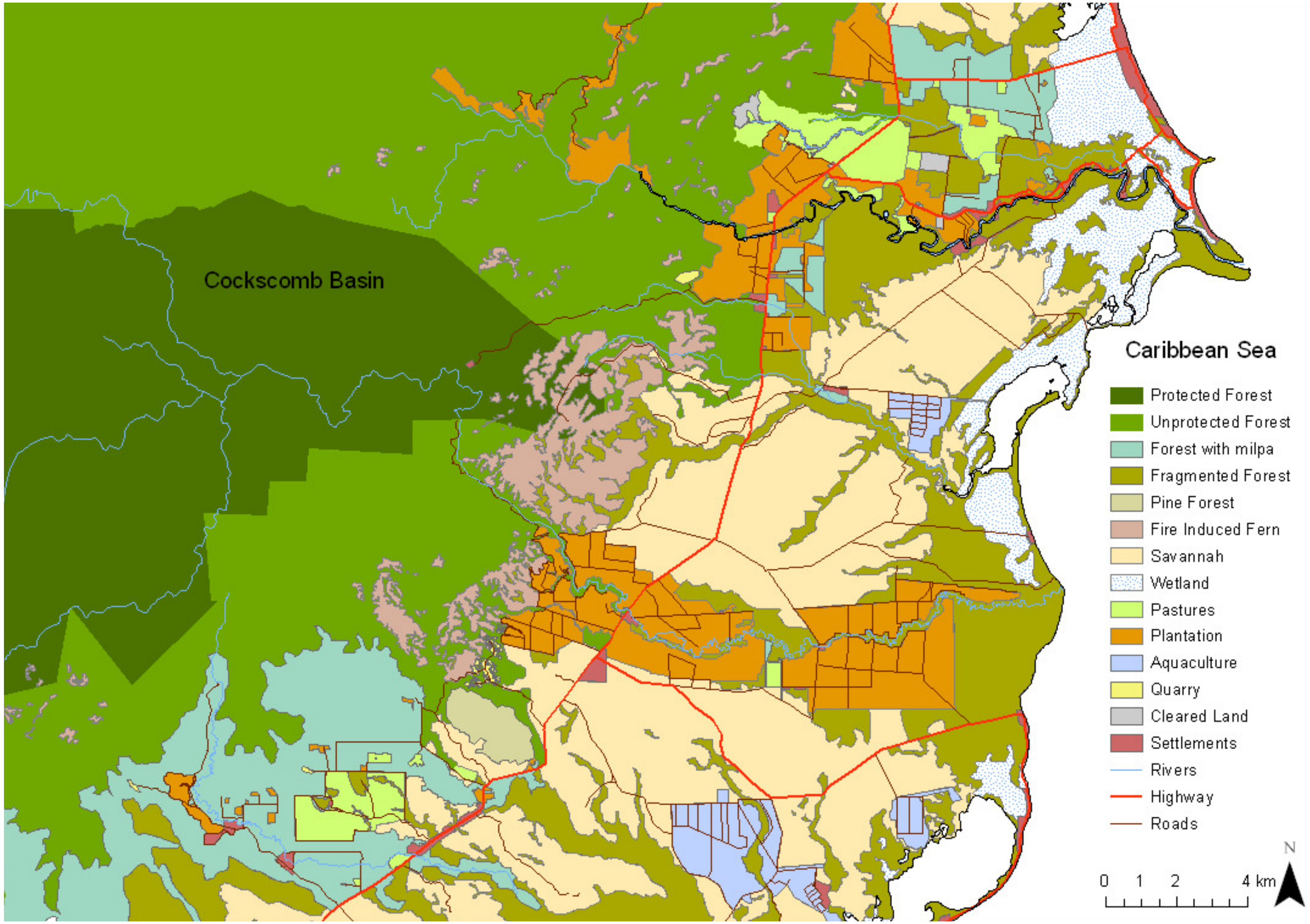


Figure 5.1 Habitat and land-use map of study area. Only major rivers are shown.

Table 5.1 Vegetation and land-use classification. Bold text indicates the broad classification categories following UNESCO, with the vegetation types relevant to the study area below each category

Category	Description
Closed Forest	trees ≥5 m tall with crowns interlocking, 65%(+) sky cover
- lowland broadleaf forest	*tropical evergreen seasonal broadleaf lowland forest*
- lowland pine forest	*tropical evergreen seasonal needle-leaved lowland forest*
Woodlands	open stands of trees, ≥ 5 m tall, most crowns not touching, cover 30%(+) sky
	not applicable
Shrublands	woody bushes or small trees 0.5-5.0 m tall; crowns maybe touching, cover 30%(+) sky
- lowland shrubland	*broadleaved lowland shrubland* *fire-induced lowland fern thicket*
Dwarf scrub	rarely > 0.5-m high
	not applicable to this study
Terrestrial herbs	grasses, graminoids and other herbaceous plants are predominant in the cover; woody plants (trees or shrubs) may be present but not covering > 30%
- lowland savannah (+/- pine)	*short grass savannah with needle leaved trees* *short grass savannah with shrubs*
Agriculture	agro-productive systems *shifting cultivation (milpa)* *pasture* *semi-woody perennial crops (e.g. banana, papaya)* *woody perennial crops (e.g. mango, citrus)* *aquaculture* *cacao*
Residential	Settlements

Classification of camera locations

Station locations were classified according to official protection status and hunting pressure; and forest connectivity and habitat. Cameras were either inside, on the boundary, or outside, the protected forest; however the true level of protection of the protected forest was variable throughout the reserve, as was the extent of hunting at different locations outside the reserve. Camera locations were therefore also categorised according to the evidence of hunting:

0 = ‘no hunting’ no evidence or local knowledge of hunting during study period

0.5 = ‘potential hunting’ evidence of camera theft or vandalism, no direct evidence of hunting during study period but anecdotes from local knowledge

1 = ‘hunters present’ camera-trap photographs of hunters with guns or spotlights, or gun cartridges found in the field.

With the reserve being bordered by unprotected forest, cameras were categorised according to whether they were located within or outside the single contiguous forest block (protected and unprotected forest). Some areas of the forest block adjoined milpa (‘forest-milpa’ in Figure 5.1, areas of forest dominated by milpa and cacao farms). Although essentially still a continuation of forest cover, the nature and structure of this habitat differed from that of the forest block ‘proper’ in that it was littered with trails and small-scale milpa and cacao farms, and had higher levels of human activity than the forest block. It was therefore classified separately from the contiguous forest block. Also, locations at the boundary of the forest block e.g. pasture-forest boundary were classified as outside the forest block.

The dominant habitat at each camera location was classified into one of five categories for analysis: protected forest, buffer (unprotected forest contiguous with protected forest), fragmented forest, savannah, and pasture. The category ‘fragmented forest’ combined dense shrublands, milpa, forest-milpa, and forest fragments. The category ‘savannah’ combined lowland savannah (+/- pine) and transitional zones between savannah and dense shrubland/ forest.

The proximities of every station were calculated to the following attributes: settlements, roads, flowing water (river or stream), cattle pastures, plantations, forest block, fragmented forest, and savannah. Settlements included permanent villages (population mean ± SE = 516 ± 121, $n = 9$); communities with temporally variable populations housing seasonal agricultural workers, both large-scale (population 120 to 650 workers, $n = 3$) and small-scale (population < 50 workers, $n = 3$); and single isolated houses located away from villages, for example on cattle farms ($n = 24$). Roads refer only to the major roads in the study area, represented by the main bus routes (‘Highways’ in Figure 5.1). Plantations included semi-woody and woody perennial crops (banana, papaya, mango, citrus). Forest block refers to the protected forest plus buffer. Fragmented forest and savannah are as defined above.

At the local scale, capture probability can be maximised if stations are located such that the target species is funnelled between the two cameras. For example the funnel may be a stream or trail which passes through dense vegetation. The width of the funnel may be important, for example Harmsen (2006) found that jaguars prefer wider trails in the protected forest of this study area. In this study funnels included permanent or seasonal man-made trails, streams, unpaved roads wide enough for motor vehicles, and buffers around the edge of pastures where natural vegetation had been cleared. Funnel width was calculated as the mean of three measurements: 0 m and ± 20 m from the station, following Harmsen (2006). Pasture cameras with no obvious funnel were located at the pasture edge usually bordered on one side by forest, milpa or plantation.

Statistical Analyses

Chi-square tests compared frequencies of locations with and without big cats across habitat/land-use (protected forest, buffer, fragmented forest, savannah and pasture), species (jaguar, puma), and sex (jaguars only) categories. A further chi-square test also compared the proportion of big cat scats collected opportunistically inside and outside the contiguous forest and identified as either jaguar or puma (see Chapter 6) during the same period (Jan 2004 to Dec 2006). Similarity between scat and camera data would indicate that the camera methodology is not biased in detecting presence/absence of jaguars and pumas.

The validity of comparisons of frequencies of locations with and without male (or female) jaguars in different habitats depended on whether variation in trap effort between the habitats could have influenced detected differences in the presence and absence of jaguars. Within each habitat, the trap effort until first capture was calculated for each location where jaguars were present and the total trap effort was calculated for each location from which jaguars were absent. For each habitat, if the trap effort at locations not detecting jaguars was equal to (or greater than) the trap effort until first capture at locations that did detect jaguars then it was assumed that variation in trap effort between habitats did not bias the data and comparison of presence/ absence of jaguars between the habitats was valid. The data were not normally distributed so were compared using a non-parametric Kruskal-Wallis test. The test was conducted for each sex separately and revealed in both cases that, for each habitat, trap effort at locations not capturing jaguars was greater than trap effort until first capture at locations where jaguars were detected (Kruskal-Wallis test: males $n = 161$, H = 65.9, df = 9, $p < 0.0001$; females $n = 153$, H = 21.5, df = 9, $p < 0.02$). This gave validity to comparisons of presence/ absence across the five habitats. Note that trap effort until first capture was unknown for males at three locations, so these were excluded from the analyses.

Jaguar activity and puma activity were compared at locations where both species were present using a paired *t*-test. Because pumas were present at so few sites in the human-matrix (compared to jaguars) this analysis was limited to locations within the forest block.

It should be noted that some of the cameras located in savannah or pastures were also associated with forest habitat, for example they were positioned at the boundary between pasture/forest or savannah/dense shrubland. Only 15 locations were not associated with forest (> 50 m from forest habitat). The mean distance from forest (if > 50 m) was calculated for locations at which jaguars were present and those from which they were absent, though the samples were too small to compare statistically. The proportions of locations associated with forest and those > 50 m from forest were compared using a chi-square test to determine whether jaguars were more likely to be present at locations associated with forest than those not associated with forest.

A two-factor model with repeated measures on one cross factor (Doncaster and Davey 2007) was used to investigate variation in jaguar activity with jaguar sex and habitat type (GLM 5.1).

Jaguar activity = *sex* | *habitat* + *sex* | *station´(habitat)* – *sex*station´(habitat)* (GLM 5.1)

Random factor ‘station’ (which refers to each camera location) is nested within fixed factor ‘habitat’ which is crossed with ‘sex’. Models with repeated measures, such as GLM 5.1, have no true residual variation. The highest order term (*sex*station´(habitat)*) therefore becomes the residual error term for calculation of the *F-ratios*, and the possibility of a *sex*station´(habitat)* interaction remains untested in this model. Locations with zero jaguar activity were excluded from the analysis. The data were square root transformed to fulfil model assumptions of homogeneity of variance and normal distribution of the response residuals. GLM 5.1 was also fitted to jaguar individual rate to investigate how the number of individuals utilising a location varied with sex and habitat.

Variation in jaguar activity with proximity to different habitats and land uses was investigated separately for each sex. Locations inside and outside the contiguous forest block were analysed independently. Inside the forest block, the following variables were investigated in relation to jaguar activity: trail width, distance to water, distance to human settlement, activity of jaguar of opposite sex, and level of hunting. Outside the forest block, seven additional variables were also investigated: distances to the forest block, fragmented forest, savannah, pasture, plantation and major roads. Spearman rank correlations were used to assess the strength and direction (positive or negative) of the relationship between activity and each habitat variable. The continuous habitat variables were then analysed in a stepwise regression to select the most parsimonious model of variation in jaguar activity. Data were square root transformed where required to normalise residuals for regression analyses. Variation in puma activity within the forest block in relation to trail width, distance to water, distance to human settlement, jaguar activity and level of hunting, was investigated following the same method.

Tolerance of jaguars and pumas to human disturbance

It was hypothesised that cat activity declines with increased human activity. This was tested by analysing the relationship between tourist visitation rates in the reserve, as a proxy for disturbance, and big cat activity at a camera station on the reserve access road. The road is unpaved and runs 10 km from the main highway through unprotected forest into the reserve. It is the only road available for tourists to access the park. The road terminates at the headquarters (HQ), approximately 2.5 km into the reserve. The majority of visitors arrive via taxi or minibus and usually travel in and out on the same day. There are basic over-night accommodation facilities for up to 50 people, plus a camp ground with space for approximately 30 people. Visitors are permitted to hike the maintained trail system which covers a radius of approximately 2 km around HQ. The peak tourist season has substantial traffic in and out of the reserve, and human activity within the vicinity of HQ. In contrast, during the low season tourist rates can fall to zero. This provided a unique opportunity to directly relate changes in human activity to shifts in cat activity.

The number of tourists visiting each month between January 2004 and May 2007 were made available from the CBWS records. Visitor rate was calculated for each calendar month as:

$$\frac{\textit{Visitors per month}}{\textit{Month length (in days)}} \times 28 \qquad \text{(Eqn 5.3)}$$

A camera station was maintained on the access road at the reserve boundary (2.5 km from HQ, 6.9 km from the nearest village) from Jan 2004 until May 2007. Data from Jan 2004 to Apr 2005 are from Harmsen (2006) and from Jan 2006 to May 2007 are from Harmsen and Higginbottom (unpubl. data). It was assumed that this location was far enough from the village not to be influenced by changes in human activity within the community, whilst close enough to the HQ to be affected by fluctuations in tourist activity. The camera was set to function only at night due to the high intensity of human traffic into and out of the reserve during the day. Jaguar and puma activity was calculated for each calendar month using Eqn 5.1.

The proportion of months during which jaguars and pumas utilised the road were compared using a chi-square test. A 2-sample *t*-test was used to compare activity between the species. Harmsen *et al*. (*in press*) demonstrated avoidance between jaguars and pumas in the reserve at a temporal scale similar to that used in this analysis. A negative association between jaguar and puma activity at this location could mask any relationship with human activity; therefore a correlation was tested between jaguar and puma activity. The activity of each species was regressed against tourist rate. Data were excluded for two months for which there were no visitor statistics available, and for months during which the trap effort was < 28 nights.

Visitor rates to CBWS are cyclical and tend to peak during the hotter, dry months and lessen in the wet season. It has been suggested that predator activity decreases with increased ambient temperature (e.g. Crawshaw and Quigley 1991). However Harmsen (2006) found that jaguar activity within the reserve did not vary with season, and it was therefore assumed that any correlation between tourist activity and jaguar activity reflected a true cause and effect relationship and was not a consequence of each co-varying with temperature or rainfall. To further substantiate this assumption, correlations between monthly rainfall and monthly jaguar or puma activity were tested at five other camera locations which had long-term data (12–18 months) and which were sited on forest trails or unpaved roads of similar width (mean width ± SD = 280 ± 137 cm, $n = 5$) as the target station (width = 392 cm). Two locations were on the access road in forest outside the reserve (4.3 km and 6.6 km from the HQ, 5.1 and 2.8 km from the nearest village); and three locations were within the reserve (one on an old logging trail and two on a wardens' patrol trail, all > 7 km from HQ) with no seasonal tourist activity and low human use. Rainfall data were obtained from a private biological research station 17 km from HQ (M. Shave, Possum Point Biological Station, unpubl. data).

Determinants of cat activity and livestock predation on farms

Eleven cattle farms were identified within the immediate study area. The farms ranged in size from 0.04 to 9.25 km^2 (~ six to 900 cattle). Camera traps were maintained on or near eight of the farms to monitor jaguar activity (Figures 5.2a-c). The cameras were maintained for varying periods from 2 to 30 months dependent on cooperation of the land owners and risk of damage/theft. Data were also collected on rates of predation on domestic animals on the farms, again dependent on the cooperation of stakeholders.

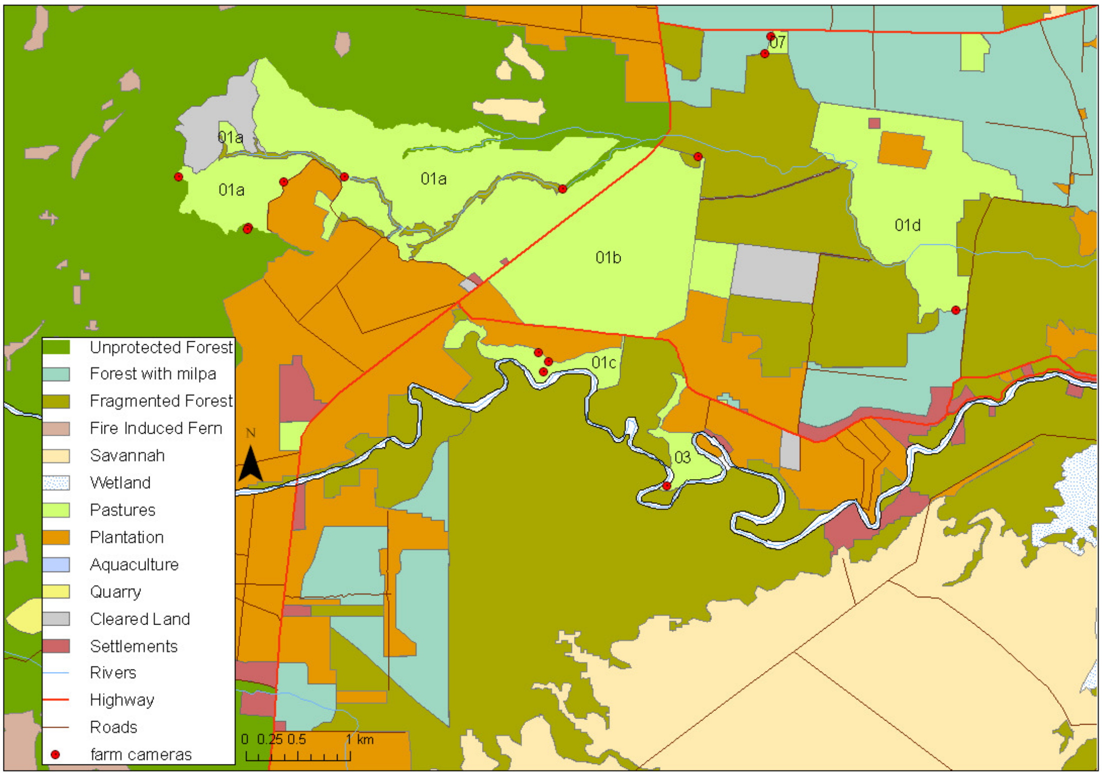


Figure 5.2 a) Farms #01a-d, #03a-b and #07

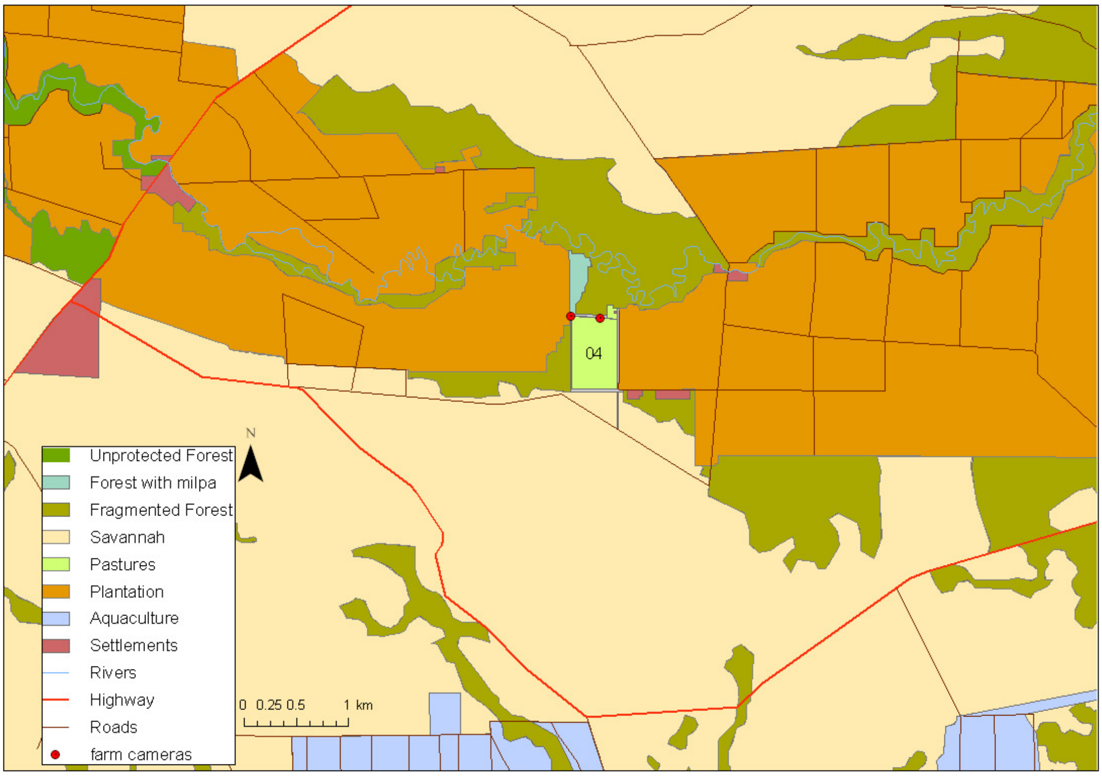


Figure 5.2 b) Farm #04

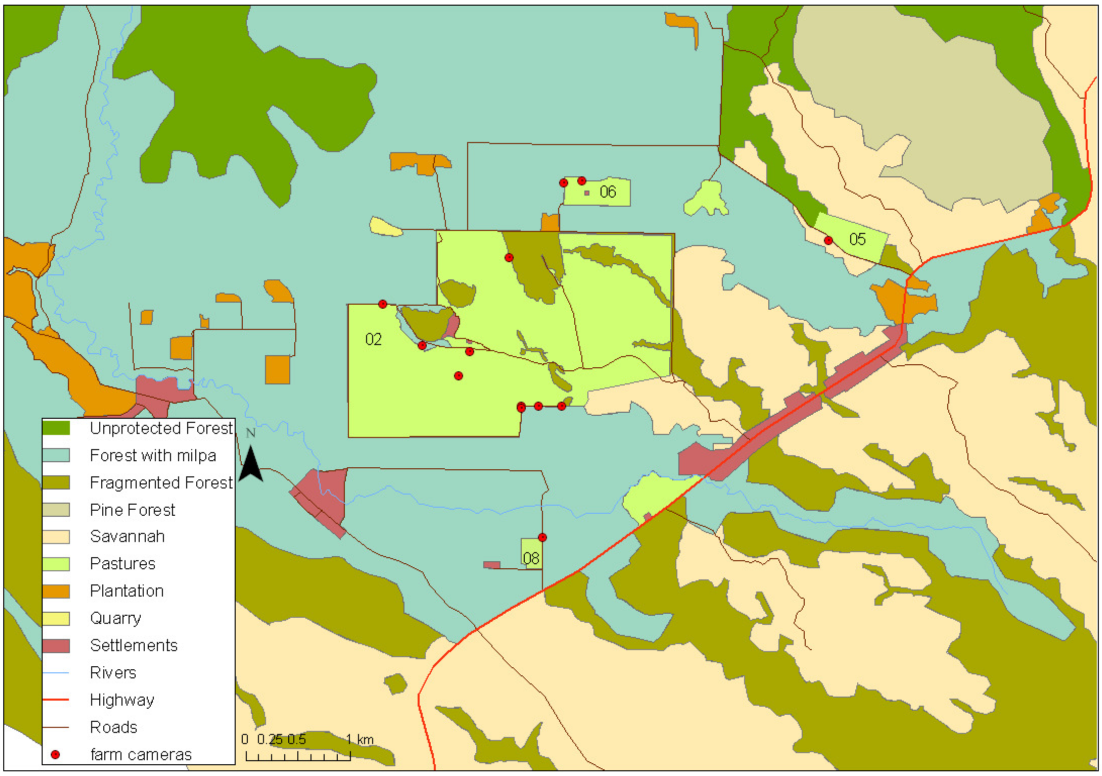


Figure 5.2 c) Farms #02, #05, #06 and #08

Figure 5.2a-c Location of cattle farms. Camera stations < 20 m from pasture shown.

It was rarely possible to verify reports of livestock predation, or the identity of the predator. Farm employees were often illiterate or reluctant to keep written records and found formal interviews intimidating (R. Foster pers. ob) so data were gathered during regular informal visits with livestock owners or their employees and opportunistically by talking with local people. Farm employees were provided with disposable cameras and encouraged to collect photographic evidence of livestock kills to ensure that data were not fabricated. Sometimes these photographs were also useful in identifying the predator, based on the nature of the attack (after Hoogesteijn 2000); for example see Figure 5.3. Often farm employees did not supply photographs and the attacks were reported too long after the event to examine the carcasses, which were disposed of or further damaged by scavengers. However most of the employees were knowledgeable about their livestock and potential predators. There was no evidence of them exaggerating the number of livestock kills, because they frequently reported no attacks. Also, jaguars were not routinely blamed; other causes of livestock death were also given as snake bite, cattle rustlers, crocodiles and feral dogs.

The available data were used to investigate farm characteristics that may influence jaguar and puma activity and levels of livestock predation on farms. It was recognised that sample sizes were limited thus qualitative assessments were sometimes deemed more appropriate than statistical analyses.

a) **b)**

Figure 5.3 a) Calf (150lb) believed to have been killed by a jaguar. The body was dragged ~600 m and the internal organs eaten. Note the canine punctures in the side of the head, width 50 mm, typical of jaguar attack. A jaguar was shot on site eight days later. **b)** Adult sheep believed to have been killed by a pack of feral dogs. Note the tears to the shoulder and ear ripped off; lacerations are typical of dog attack. A pack of feral dogs were chased from the premises five days later whilst attempting to attack an adult cow.

Factors influencing cat activity

The analysis of habitat utilisation by cats around farms was restricted to data from camera stations within 20 m of a pasture. Chi-square tests compared the proportions of locations with and without jaguars and pumas; and with and without male and female jaguars. Puma activity on farms was negligible (four captures over 4251 trap-nights) and so is not considered further. GLM 5.1 was used to compare the activity of male and female jaguars at pasture locations (see p.142) and jaguar activity was regressed against distance from the forest block.

It was hypothesised that jaguar activity may be influenced by the physiognomy of a farm, specifically the degree of exposed versus covered (forested, or forested + plantation) habitat at the pasture edges and the extent of covered patches within the property. Jaguar activity per farm was regressed against various farm habitat variables.

Jaguar activity per farm was calculated as the mean activity at locations with ≥ 28 days continuous trap effort and jaguar presence. Data from Farm #01 were analysed separately as #01a, #01b, #01c and #01d (Figure 5.2) since these four pasture blocks were separated from each other by extensive human development (highway, secondary roads and citrus plantations). Farm #05 was excluded from activity analyses because the single station at this farm did not function for at least 28 continuous nights, and Farm #07 was excluded because zero jaguar activity was recorded. Thus total sample size for these analyses was low ($n = 9$). Farm habitat variables were derived from the habitat and land-use map using Arc Map (Arc GIS 2004): the % of pasture edge that was clear (≥ 3.5 m wide strip of cleared land or road between pasture edge and adjacent habitat), the length of covered pasture edge per km^2 pasture, and the % of the property that had patches of cover. The two 'cover' variables were calculated twice, first as forest and then as forest + plantation. Accurate magnitudes of the 'cover' variables were unknown for Farm #01c therefore this data point was excluded from these analyses.

Jaguar activity per farm was also compared between farms with and without the following: forest patches, on-site human residence, streams or rivers, and some pasture edge cleared. Statistical comparisons were not appropriate for such small samples so means and standard deviations are presented only.

Factors influencing livestock predation

The primary livestock were cattle, but buffalo, horses, donkeys and sheep were also present on some of the farms. The farms had continuous breeding seasons with calves produced year round (although Farm #01 began restricted breeding in 2006). Therefore stocks can be assumed to have varied evenly throughout the year without a seasonal peak. Livestock density per km^2 per farm was calculated as (Eqn 5.4):

$$\frac{\textit{Total livestock}}{\textit{Property area}} \qquad \text{(Eqn. 5.4)}$$

where *total livestock* refers to the maximum number of livestock known to have been on the farm at one time during the study period.

Farm owners and staff provided information on livestock kills for periods ranging from 11 to 34 months. No predation data were available for Farm #01d so it was excluded from subsequent analyses. A measure of livestock predation, 'kill density', was calculated for each farm as the number of livestock kills per year per km^2 of the property (Eqn 5.5):

$$\frac{\text{Number of kills / total livestock / number of days monitored} \times 365}{\text{Property area}} \qquad \text{(Eqn. 5.5)}$$

Two competing hypotheses were tested by regressing kill density against stocking density. First, kill density increases with stocking density, as predator-prey encounter rate increases. Second, kill density declines with stocking density as herd vigilance increases and potential risk of injury to the predator from cattle increases. For this analysis, livestock density of Farm #01 was treated as a single data-point because the density in each pasture block varied as livestock were frequently divided between the pastures and moved according to herd management requirements.

It was hypothesised that kill density, like jaguar activity, may be influenced by the physiognomy of farm. Kill density was regressed against length of covered pasture edge per km^2 pasture, the % of the property that had covered patches, and the % exposed pasture edge. In addition a relationship between kill density and fence index was tested. Fence index was calculated as (Eqn 5.6):

$$\frac{\text{Fence height (cm)}}{\text{Bar width (cm)}} \qquad \text{(Eqn. 5.6)}$$

where *bar width* is the mean distance between barbed-wire strings. A high fence index indicates a fence that is high with narrow gaps between the strings, conversely a fence with a low index will be lower and/or with wider gaps between the strings.

Kill density was also compared between farms with and without the following: forest patches, on-site human residence, and streams or rivers. Statistical comparisons were not appropriate for such small samples so means and standard deviations are presented only.

It was hypothesised that levels of predation may vary seasonally in response to seasonal fluctuations in wild prey species. Livestock predation rate was regressed against monthly rainfall and against monthly rainfall from the previous month (in order to account for any lag in prey abundance in response to rainfall). The analysis was limited to the dataset for Farm #01 which provided suitable long-term data on monthly livestock kills for ~ 3 years. Rainfall data were obtained from a private biological research station <10 km from the farm (M. Shave unpubl. data).

Results

The utilisation of protected forest, unprotected forest buffer, fragmented forest patches, savannahs and pasture lands were compared between jaguars and pumas, and their tolerance of human disturbance was assessed. Determinants of cat activity and livestock predation on farms were investigated.

Habitat use by jaguars and pumas

Within the forest block (protected forest plus unprotected buffer) the relative frequencies of camera stations with and without big cat visits did not differ between jaguars and pumas ($\chi_1^2 = 0.175$, $p > 0.05$, of 106 locations 61 had jaguars and 64 had pumas, Appendix A: Table A5.1). Outside the forest block, in contrast, jaguars were present at more locations than were pumas (47/67 locations were visited by big cats, and all of these were visited by jaguars while only seven were visited by pumas, $\chi_1^2 = 49.6$, $p < 0.0001$, Appendix A: Table A5.1). The same trend was observed for inside / outside the protected forest, and inside / outside all forest habitats, with pumas rare on the outside (Appendix A: Tables A5.2-A5.3).

Relatively fewer puma than jaguar scats were found outside than inside the forest block (3:66 outside:inside for puma compared to 51:224 for jaguar, $\chi_1^2 = 8.4$, $p = 0.004$, Appendix A: Table A5.4). Comparison of the scat and camera data suggests that the uneven ratio (jaguar bias) outside the forest block observed using cameras probably reflects the true situation and is not an artefact of using night-only camera-trap data.

Despite the relative scarcity of pumas in the human-dominated matrix, at locations in the forest block where both jaguar and puma were captured they showed no significant differences in site usage (mean difference in visits per 28 days ± 95% CI = 0.580 ± 0.614, $n = 45$, paired-sample $t = 1.91$, $p > 0.05$). A particularly high jaguar activity was noted at one location in the forest block (11 visits per 28 days). This unusually high activity rate was attributed to a mating event which resulted in 17 captures of a courting pair over two nights. Exclusion of this data point from the analysis did not alter the conclusion that there is no significant difference between the activity rates of jaguars and pumas in the forest block (mean difference in visits per 28 days ± 95% = 0.379 ± 0.472, $n = 44$, paired-sample $t = 1.62$, $p > 0.10$). The mean jaguar activity ± SE was 1.7 ± 0.2 captures per 28 nights and mean puma activity was 1.3 ± 0.2 captures per 28 nights.

Both inside and outside the forest block male jaguars were present at significantly more locations than were females (males visited 58 of 104 forest block locations, whilst females visited only 18, $\chi_1^2 = 33.2$, $p < 0.0001$; males visited 37 of 63 locations outside forest block, whilst females only visited 18, $\chi_1^2 = 11.6, p < 0.0001$ Appendix A: Table A5.5). The same trend was observed for inside/outside the protected forest, and inside/outside all forest habitats; and if all individuals of unknown sex were included as females (Appendix A: Tables A5.6-A5.10).

The presence-absence of male jaguars at camera stations showed no broad-scale habitat associations ($\chi_4^2 = 9.0, p > 0.05$, Table 5.2). Male jaguars were nevertheless present at a high proportion of the pasture locations (17/21), relative to their presence at all other locations (72/140, $\chi_1^2 = 6.2, p < 0.015$, Appendix A: Table A5.11).

Table 5.2 Number of locations with and without male jaguars across five habitats. 'Buffer' refers to unprotected forest that is contiguous with the protected forest. 'Fragment' refers to fragmented forest patches plus milpa-forest (which may or may not be contiguous with the 'contiguous' forest).

	Protect	Buffer	Fragment	Savannah	Pasture	
Presence	42	10	12	8	17	89
Absence	40	6	17	5	4	72
	82	16	29	13	21	161

The presence-absence of female jaguars showed significant habitat associations with females present at a high proportion of fragmented forest locations and absent from many of the protected forest sites ($\chi_4^2 = 19.6, p < 0.002$, Table 5.3). Three cells had expected counts < 5 therefore the test was repeated comparing locations in protected forest against all other locations, showing that females were present at few protected forest (9/83) locations relative to their presence at all other locations (25/70, $\chi_1^2 = 13.2, p < 0.0001$, Appendix A: Table A5.12).

Table 5.3 Number of locations with and without female jaguars across five habitats. 'Buffer' refers to unprotected forest that is contiguous with the protected forest. 'Fragment' refers to fragmented forest patches plus milpa-forest (which may or may not be contiguous with the 'contiguous' forest).

	Protect	Buffer	Fragment	Savannah	Pasture	
Presence	9	7	12	1	5	34
Absence	74	9	16	10	10	119
	83	16	28	11	15	153

Non-forest locations that recorded male jaguars were a similar distance from forest as those that did not record males jaguars (mean ± SE where present = 235 ± 28 m, $n = 13$; absent = 282 ± 100 m, $n = 5$). Males were captured up to 438 m from forest (the second largest distance from forest available across the camera network), in savannah. Males were no more likely to be present at forest than non-forest locations (present at 82/151 sites < 50 m from forest and at 13/17 sites > 50 m from forest, χ_1^2 = 3.06, $p > 0.05$, Appendix A: Table A5.13). Similar trends were observed if jaguars of unknown sex were included as males (Appendix A: Table A5.14).

From the smaller sample of female captures, non-forest locations recording females tended to be closer to forest habitat than those without females (present: mean ± SE = 142 ± 36 m, $n = 2$; absent: mean ± SE = 302 ± 51 m, $n = 10$). Females were not detected at locations > 178 m from forest. Despite these stronger associations to forest than for males, there was no evidence that females were more likely to be present at forest than non-forest locations (present at 34/145 sites < 50 m from forest and at 2/10 sites > 50 m from forest, χ_1^2 = 0.29, $p > 0.5$, Appendix A: Table A5.15). Similar trends were observed if jaguars of unknown sex were included as females (Appendix A: Table A5.16).

GLM 5.1 of jaguar activity revealed sex-dependent habitat use (Sex*Habitat interaction in Table 5.4, Figure 5.4). Male activity was higher than female activity in the protected forest and the unprotected forest buffer, and in the savannah. Male and female activity did not differ in the fragmented forest or in the pastures. Male activity was higher in the protected forest than in the fragmented forest or pastures. Female activity was higher in the fragmented forest than in the savannah or protected forest. The same trends are observed if jaguars of unknown sex are included as males or included as females; with the exception that if unknowns are included as females, activity in the buffer does not differ between the sexes (Appendix A: Tables A5.17-18).

Table 5.4 GLM of jaguar activity with sex and habitat.
† Error variation for interaction is the highest order term in the model: sex*station'(habitat)

Source	**d.f.**	**Adj. MS**	***F***	***p***
Sex	1	10.09	57.62	< 0.0001
Habitat	4	0.32	1.44	> 0.2
Sex*Habitat	4	1.62	9.26	< 0.0001
Station'(Habitat)	84	0.22	1.26	> 0.1
Error†	84	0.18		
Total	**177**			

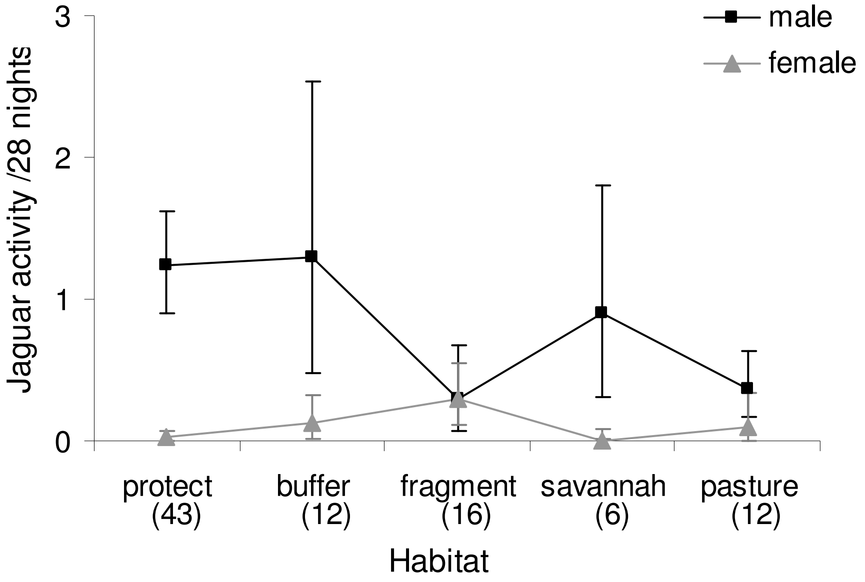


Figure 5.4 Jaguar activity in five habitats based on night captures from camera-trap data collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero jaguar activity (neither sex present) are excluded. Sample sizes indicate number of stations in each habitat. Means and 95%CI shown are back-transformed from square-root values. 'Protect' refers to protected forest; 'buffer' to unprotected forest contiguous with protected forest; 'fragment' to forest fragments and milpa-forest which may or may not be contiguous with the forest block.

The number of individual jaguars using a location per 28 days also revealed sex-dependent habitat use (Table 5.5, Figure 5.5). The patterns tended to replicate those for activity such that the high male activity observed in the protected forest and the low female activity observed in the protected forest and savannah (Figure 5.4) reflect the number of individuals using these habitats. Although male activity was higher in protected forest than in pastures, the number of individuals using locations in these habitats did not differ, suggesting that males utilise pasture less often than the protected forest. Similar trends are observed if unknown jaguars are included as males or included as females (Appendix A: Tables A5.19-20).

Table 5.5 GLM of jaguar individual rate with sex and habitat.
† Error variation for interaction is the highest order term in the model: sex*station'(habitat)

Source	d.f.	Adj. MS	*F*	*p*
Sex	1	3.98	29.21	< 0.0001
Habitat	4	0.06	0.60	> 0.6
Sex*Habitat	4	0.77	5.66	0.001
Station'(Habitat)	45	0.11	0.79	> 0.7
Error†	45	0.14		
Total	**99**			

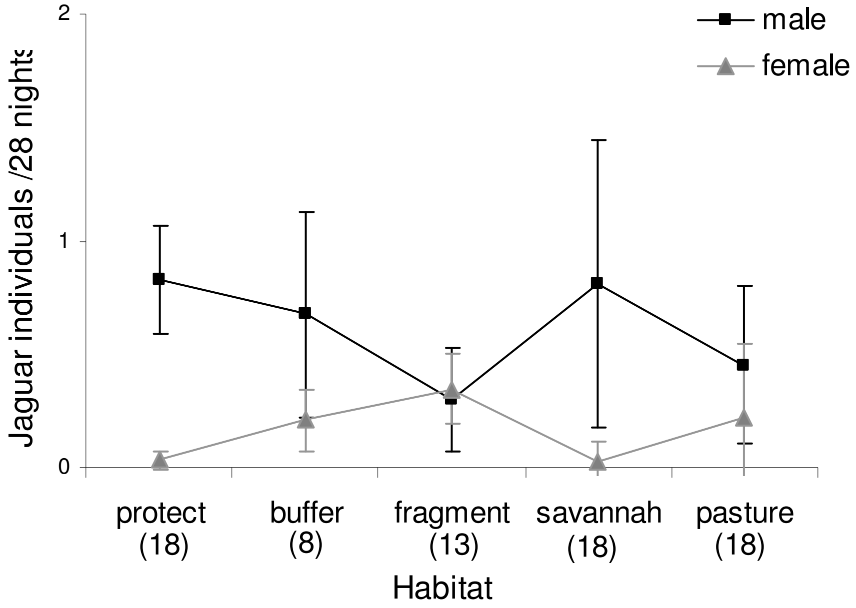


Figure 5.5 Number of individual jaguars per 28 nights using locations in five habitats, based on night captures from six large-scale camera-trap surveys Jan 2004 to Dec 2006. All cameras functioned ≥ 28 < 63 continuous nights. Locations with zero jaguar activity (neither sex present) are excluded. Sample sizes indicate number of stations in each habitat. Means and 95%CI are shown. 'Protect' refers to protected forest; 'buffer' to unprotected forest contiguous with protected forest; 'fragment' to forest fragments and milpa-forest which may or may not be contiguous with the forest block.

Within the forest block male jaguar activity positively correlated with trail width and with female activity, but not with distance from water or settlements or the level of hunting (Table 5.6). Note that a location with unusually high male and female jaguar activity known to be associated with a mating event (see p.151) was excluded from these analyses since it was coincidently on the widest trail. Stepwise regression of the continuous variables suggested that trail width best explained variation in male activity (Regression of square root transformed data: $F_{1, 50} = 23.80$, $p < 0.0001$, adjusted $r^2 = 31\%$, Figure 5.6). This concurs with Harmsen (2006) who found trail width to be the single most important factor influencing jaguar activity within the protected area of the contiguous forest block from 2002 to 2005. Trails provide accessible routes through the otherwise dense and homogenous secondary forest. The openness of wider trails may be favoured by males because they reduce travel times through otherwise dense secondary vegetation, but also because they may facilitate chemical communication via scats and scrape marking (Harmsen 2006).

Table 5.6 Spearman Rank Correlation matrix on activity of male jaguars in the contiguous forest block. Based on data from 55 camera stations collected Jan 2004 to Dec 2006 (*n* = 52 for trail width). **p* < 0.05; ** *p* < 0.01

	Dist to water	**Dist to settlements**	**Hunting**	**Female activity**	**Male activity**
Trail width	0.227	-0.445 (**)	0.133	0.278(*)	0.486(*)
Dist to water		-0.133	-0.095	-0.056	0.179
Dist to settlements			-0.043	-0.330(*)	-0.191
Hunting				0.190	0.116
Female activity					0.294(*)

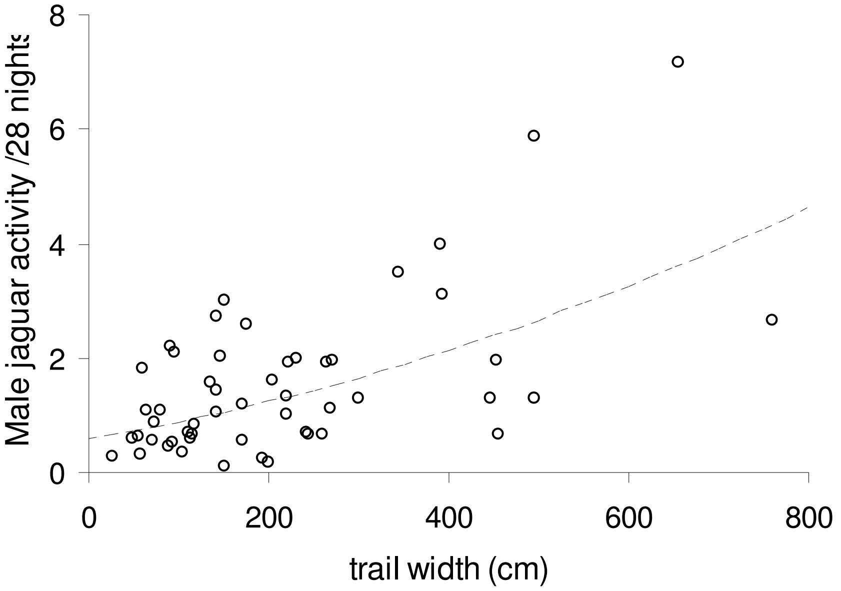


Figure 5.6 Variation in male jaguar activity with trail width within forest block. Based on data from 52 camera stations collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero activity are excluded.
Regression of square root transformed data: $F_{1, 50}$ = 23.80, $p < 0.0001$, adjusted r^2 = 31%, sqrt male activity = 0.769 +0.00173(trail width). Back-transformed (curved) regression line is shown

Within the forest block, female jaguar activity was negatively correlated with distance from water, but not with trail width, distance from settlements, hunting level, or male activity (Table 5.7). As in the analysis of male activity, the location with unusually high male and female jaguar activity known to be associated with a mating event was excluded. Stepwise regression of the continuous variables suggested that distance from water best explained variation in female activity (Regression of square root transformed data: $F_{1, 15}$ = 6.20, $p < 0.05$, adjusted r^2 = 25%, Figure 5.7). It is not clear why female activity associated with proximity to flowing water. These may be favoured areas for hunting; alternatively or additionally, females may use streams and rivers as travel routes, in contrast to the males who dominate the wider trails traversing the forest.

Table 5.7 Spearman Rank Correlation matrix on activity of female jaguars in the contiguous forest block. Based on data from 17 camera stations collected Jan 2004 to Dec 2006. *$p < 0.05$

	Dist to water	**Dist to settlements**	**Hunting**	**Male activity**	**Female activity**
Trail width	-0.125	-0.374	-0.239	0.402	0.316
Dist to water		0.098	-0.176	-0.129	-0.548(*)
Dist to settlements			0.327	0.148	-0.363
Hunting				-0.113	-0.089
Male activity					0.236

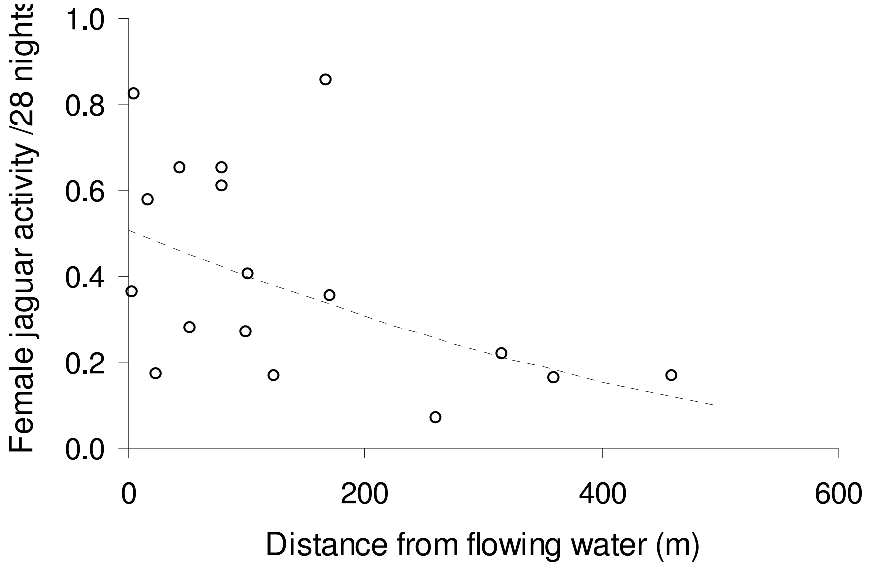


Figure 5.7 Variation in female jaguar activity with distance from water within forest block. Based on data from 17 camera stations collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero activity are excluded. Regression of square root transformed data: $F_{1,15} = 6.20$, $p < 0.05$, adjusted $r^2 = 25\%$ sqrt female activity = 0.713 – 0.000797(distance from water). Back-transformed (curved) regression line is shown

Outside the forest block, activity of male jaguars positively correlated with distance from pasture and from plantations. These two variables were positively correlated with each other, however, and with distance from settlements, such that camera locations which were further from pastures were also further from plantations and settlements (Table 5.8). Stepwise regression is inappropriate for correlated *x*-variables and it is not possible to determine which of the three may explain variation in male activity. However plots of the data do suggest that male activity declined with proximity to areas of human development such as settlements, major roads, pastures and plantations (Figure 5.8). In contrast to the forest block, male activity does not vary with trail width in the human matrix. This may be because outside the forest block the habitat is highly heterogeneous and more accessible, with a denser network of trails and roads.

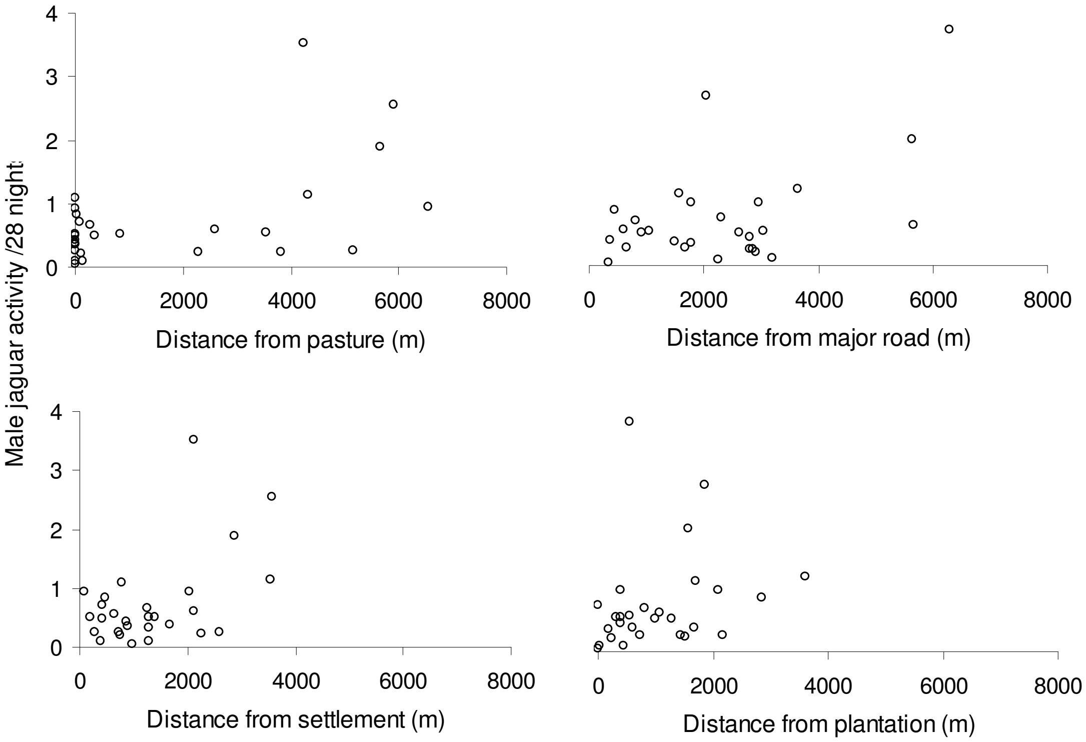


Figure 5.8 Variation in male jaguar activity outside forest block with distance from pastures, major roads, settlements and plantations. Based on data from 28 camera stations collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero activity are excluded.

Outside the forest block, female activity positively correlated with distance from contiguous forest (Spearman rank correlation: $\rho_s = 0.584$, $p < 0.02$, $n = 18$) and not with trail width, hunting level, male activity, or distances to: water, major roads, settlements, fragmented forest, pastures, plantations or savannahs. Stepwise regression of the continuous x-variables suggested that distance from the forest block best explained variation in female activity (Regression: $F_{1,16} = 12.27$, $p < 0.01$, adjusted $r^2 = 40\%$); however two outliers (a pair of locations ~ 500 m apart on the same road) had unusually high leverage because they were both far from the forest block. Spearman correlation and stepwise regression analyses re-run without this pair indicated a positive correlation of female activity with proximity to major roads (Table 5.9) and that variation in female activity was now best explained by proximity to major roads and distance from the contiguous forest (Table 5.10, Figure 5.9). This is difficult to interpret, but it implies that activity of female jaguars tended to be higher closer to areas of human development, further from the forest block and nearer the major roads. Although this contrasts with the activity patterns observed for male jaguars outside the forest block, it should be remembered that GLM 5.1 of jaguar activity demonstrated no significant difference between the sexes in pastures or fragmented forest habitats (both associated with human development) (Figure 5.4). That is, although male activity declines closer to human development and female activity increases, the net result that both sexes have similar rates of activity at these locations.

Table 5.10 Multiple regression of female jaguar activity against distance from contiguous forest block and major roads. Based on data from 16 camera stations collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero activity are excluded. Regression equation is:
Female activity = 0.598 – 0.000190(major road) + 0.000096(contiguous forest)
Adjusted r^2 = 50%

Predictor	**T**	***P-value***
Constant	5.70	< 0.0001
Major road	-3.60	< 0.01
Contiguous forest	2.43	< 0.05

Table 5.8 MALE	**Water**	**Major road**	**Settl.**	**Contig.**	**Fragment**	**Pasture**	**Plant.**	**Savannah**	**Hunting**	**Female activity**	**Male activity**
Trail width	0.328	0.146	0.019	0.004	0.180	0.214	0.221	-0.314	0.293	0.105	0.132
Water		0.121	-0.075	0.207	0.247	0.178	0.037	-0.559(**)	-0.150	-0.317	-0.001
Major road			0.227	0.077	-0.195	0.301	0.036	0.089	-0.248	-0.338	0.233
Settlement				-0.053	0.188	0.632(**)	0.466(*)	-0.129	0.030	0.256	0.250
Contiguous					-0.225	-0.054	0.256	-0.371	0.004	-0.037	-0.041
Fragment						0.116	0.058	-0.422(*)	0.084	-0.147	0.015
Pasture							0.489(**)	-0.411(*)	0.152	-0.050	0.396(*)
Plantation								-0.569(**)	-0.110	0.012	0.423(*)
Savannah									-0.019	0.184	-0.263
Hunting										0.237	0.209
Female activity											-0.075

Table 5.9 FEMALE	**Water**	**Major road**	**Settl.**	**Contig.**	**Fragment**	**Pasture**	**Plant.**	**Savannah**	**Hunting**	**Male activity**	**Female activity**
Trail width	0.352	0.169	0.103	-0.185	0.037	0.376	0.389	-0.286	0.150	0.142	-0.159
Water		0.329	-0.132	0.329	-0.428	0.555(*)	0.241	-0.443	-0.296	0.116	-0.126
Major road			0.209	0.106	-0.107	0.451	0.076	0.037	-0.134	0.158	-0.647(**)
Settlement				-0.447	0.382	0.185	0.100	0.116	-0.028	0.460	-0.412
Contiguous					-0.463	0.012	0.350	-0.237	0.050	0.015	0.359
Fragment						-0.227	-0.068	-0.122	0.128	-0.010	-0.075
Pasture							0.152	-0.257	-0.184	0.042	-0.257
Plantation								-0.653(**)	0.016	0.418	-0.068
Savannah									0.202	-0.272	0.099
Hunting										0.193	-0.233
Male activity											0.414

Tables 5.8 and 5.9 Spearman correlation matrix on jaguar activity (5.8 male, 5.9 female) outside the contiguous forest block. Data from 28 (Table 5.8, n =26 for trail width) and 16 (Table 5.9) camera stations, Jan 2004 to Dec 2006. *$p < 0.05$, ** $p < 0.01$.

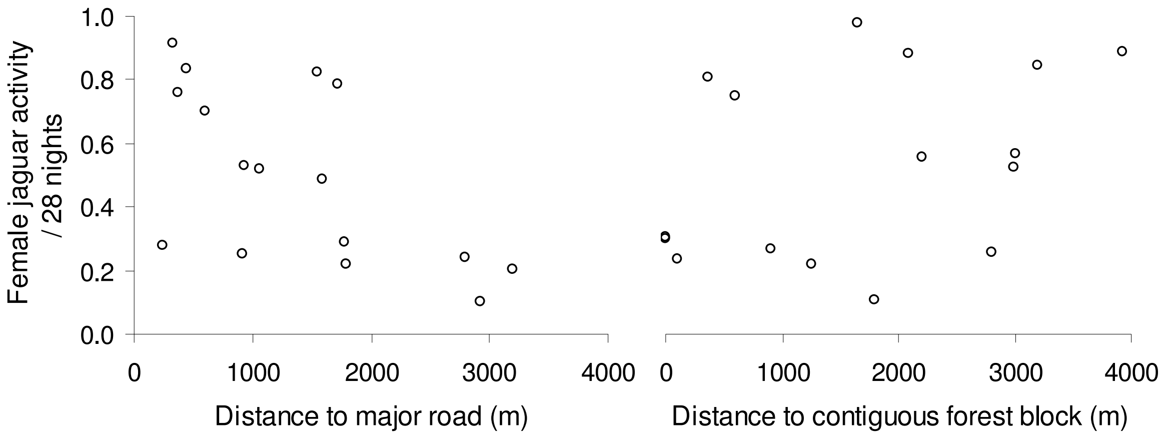


Figure 5.9 Variation in female jaguar activity outside forest block with distance from major roads and contiguous forest block. Based on data from 16 camera stations collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero activity are excluded.

Inside the forest block, puma activity positively correlated with jaguar activity (Table 5.11) suggesting that the two species utilise forest block locations with similar habitat attributes; indeed puma activity positively correlated with trail width (Table 5.11). Stepwise regression failed to show significant influences of the three continuous habitat variables ($\log_{10}$ transformed data: $F_{1,54} = 2.91$ $p > 0.05$, adjusted $r^2 = 3.4\%$).

Table 5.11 Spearman Rank Correlation matrix on activity of pumas in the contiguous forest block. Based on data from 55-59 camera stations collected Jan 2004 to Dec 2006. *$p < 0.05$ **$p < 0.01$

	Dist to water	**Dist to settlements**	**Hunting**	**Jaguar activity**	**Puma activity**
Trail width	0.036	-0.457(**)	0.111	0.536(**)	0.358(**)
Dist to water		0.007	0.034	0.075	0.133
Dist to settlements			-0.058	-0.116	-0.168
Hunting				0.256(*)	-0.192
Jaguar activity					0.364(**)

An earlier finding that pumas were active at significantly fewer unprotected sites than were jaguars (Table A5.2 in Appendix A) suggested that pumas may be particularly sensitive to factors associated with human activity, such that habitat use within the protected forest may differ from that in the unprotected contiguous forest. Following Harmsen (2006), the data were re-analysed, using locations limited to protected forest only and excluding all locations with vehicular traffic. Under these conditions puma activity correlated positively with trail width (Table 5.12), and negatively with distance to settlements, presumably because trail width correlated with settlement distance (narrower trails were further in the protected forest). Stepwise regression selected trail width as the single best predictor of puma activity (Regression of $\log_{10}$ transformed data: $F_{1,41} = 10.69$, $p = 0.002$, adjusted $r^2 = 19\%$, Figure 5.10). Given that male and female jaguars respond differently to habitat variables, variation in puma activity may be better explained if the data could be separated between the sexes.

Table 5.12 Spearman Rank Correlation matrix on activity of pumas in the protected forest and excluding locations with vehicular traffic. Based on data from 43-47 camera stations collected Jan 2004 to Dec 2006. *$p < 0.05$ **$p < 0.01$

	Dist to water	**Dist to settlements**	**Hunting**	**Jaguar activity**	**Puma activity**
Trail width	0.190	-0.392(**)	-0.080	0.412(**)	0.462(**)
Dist to water		0.016	-0.013	0.244	0.159
Dist to settlements			0.192	-0.041	-0.310(*)
Hunting				0.294(*)	-0.064
Jaguar activity					0.493(**)

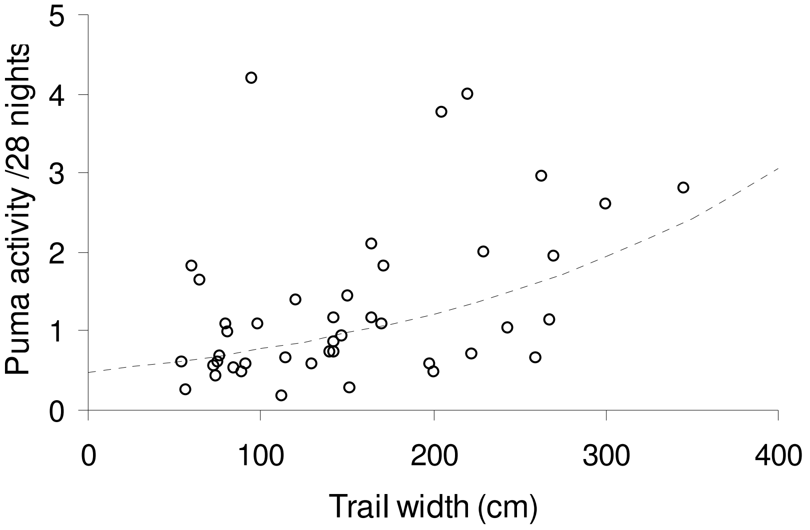


Figure 5.10 Variation in puma activity with trail width within protected forest, excluding locations with vehicular traffic. Based on data from 43 camera stations collected Jan 2004 to Dec 2006. All cameras functioned ≥ 28 continuous nights. Locations with zero activity are excluded.
Regression of $\log_{10}$ transformed data: $F_{1,41} = 10.69$, $p = 0.002$, adjusted $r^2 = 19\%$, $\log_{10}$ activity = -0.3083 +0.00198(trail width). Back-transformed (curved) regression line is shown

Tolerance of jaguars and pumas to human disturbance

The hypothesis that cat activity declines with increased human disturbance was tested by analysing the relationship between visitor rates to the reserve and jaguar or puma activity at the reserve boundary. The relationship between both species was also investigated to determine whether inter-specific avoidance could be masking relationships between activity of either cat and tourist activity. The relationship between cat activity and rainfall was investigated at this site and at five other locations to validate the assumption that any detected correlation between tourist activity and cat activity reflected a true cause and effect relationship and was not a consequence of each co-varying with rainfall.

Visitor rates to the reserve ranged from 88 to 787 people per month. Jaguars were present on the road during more months than were pumas (jaguars present 30/31 months, pumas present 16/31 months, $\chi_1^2 = 16.5$, $p < 0.0001$, Appendix A: Table A5.21) and were more active (2-sample *t*-test: $T = 4.27$, $p < 0.0001$, df = 43; jaguar mean ± SE = 4.74 ± 0.54 per 28 nights, puma 2.00 ± 0.34 per 28 nights), suggesting that jaguars had a higher tolerance for human activity than did pumas.

There was no significant negative correlation between jaguar activity and puma activity at any of the six sites, rejecting the hypothesis that inter-specific avoidance masked relationships between jaguar or puma activity and rainfall or tourist activity.

Jaguar activity and tourist activity were not constant throughout the year. Jaguar utilisation of the road decreased during peak tourist periods when vehicle intensity along the road and human activity at HQ were both high. Jaguar activity declined linearly with increasing visitor activity (Regression: $F_{1, 29} = 5.84$, $p < 0.05$, adjusted r^2 = 14%, Figure 5.11). Rainfall had a negative influence on visitor rate and a positive influence on jaguar activity at the reserve boundary (Spearmann rank correlations: visitor rate $\rho_s = -0.447$, $p < 0.01$, $n = 34$, jaguar activity $\rho_s = 0.491$, $p < 0.01$, $n = 31$). However there were no significant influences of rainfall on jaguar activity at the other five sites, suggesting that the variation in jaguar activity at the reserve boundary was a response to tourist activity rather than climatic factors associated with season.

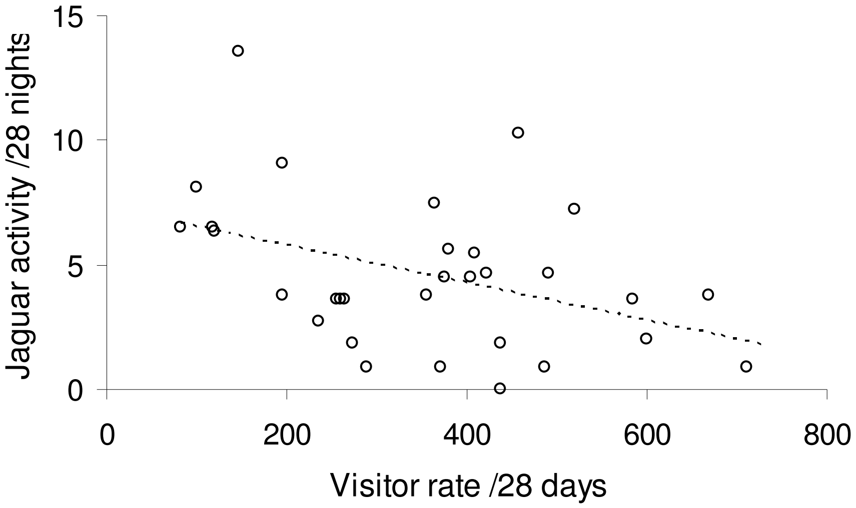


Figure 5.11 Variation in monthly jaguar activity with visitor rates in protected forest. Based on data from 31 months Jan 2004 to May 2007. All cameras functioned ≥ 28 continuous nights. Linear regression: $F_{1,29} = 5.84$, $p < 0.05$, adjusted $r^2 = 14\%$, jaguar activity = 7.24 – 0.00749(visitor rate)

Puma activity did not depend on visitor rate (Spearman $\rho_s = 0.100$, $p > 0.5$, $n = 31$), or rainfall at any of the six sites. Although there was no detectable decline in puma activity with human activity, the frequency of months during which pumas avoided the road, and the relatively low activity when present compared to jaguars suggests that pumas may be less tolerant of human disturbance than are jaguars.

Determinants of cat activity and livestock predation on farms

Relationships between jaguar activity, livestock predation and farm habitat attributes tended to be masked by jaguars frequently being removed from farms where predation occurred, forcibly lowering jaguar activity and predation compared to farms where action was not taken so quickly. Although the limited sample size precluded multivariate analyses, it is likely that a combination of factors influence both livestock predation and jaguar activity on farms. The results presented in this section should be interpreted with this in mind.

Factors influencing cat activity

Jaguars were present at more cattle-farm locations than were pumas: 21/24 farm locations were visited by big cats, all of which were visited by jaguars compared to only three by pumas ($\chi^2_1 = 27.0$, $p < 0.0001$, Appendix A: Table A5.22). Jaguar presence at farms was more likely to involve males than females (18/24 farm locations were visited by males and only 7 by females $\chi_1^2 = 10.1$, $p < 0.002$, Appendix A: Table A5.23). The same trend was observed if all individuals of unknown sex were included as females (Appendix A: Table A5.24).

As there was no sex difference in activity on pastures (see Figure 5.4), the sexes were pooled for analysis of variation in jaguar activity with farm habitat. There was no evidence that jaguar activity at locations on farms decreased with distance from the forest block, which ranged from 0 km (forest/pasture boundary) to 4.2 km (Regression, $F_{1,\,12} = 0.01$, $p > 0.9$, adjusted $r^2 = 0\%$). Nor did it vary with the % of property that had patches of cover, the length of covered edge per km^2 pasture, or the % of pasture edge that was clear (Regressions, adjusted $r^2 < 5\%$ and $p > 0.1$ for all, $n = 8$ or 9). There did not appear to be any difference in jaguar activity between farms with forest patches, or streams or river, compared to farms without; however the data do suggest that there may be a trend for lower jaguar activity to be associated with those farms which had on-site human residence (Table 5.13).

Table 5.13 Jaguar activity on farms with and without: forest patches, on-site human residence, and streams or rivers.

Farm Attribute		***n***	**Mean activity (/28 nights)**	**SD**
Forest patches	yes	6	0.70	0.33
	no	3	0.85	0.77
Residence	yes	5	0.48	0.27
	no	4	1.08	0.47
Streams or river	yes	6	0.63	0.25
	no	3	0.98	0.77

Factors influencing livestock predation

There was no evidence of higher livestock predation on farms with greater jaguar activity (Pearson correlation, $p > 0.8$, $n = 8$). However the periods during which jaguar activity was monitored on farms did not always coincide with periods of livestock attacks, making direct comparison of jaguar activity with the level of livestock predation questionable. One dataset (Farms #01a, b and c) provided simultaneous long-term data on both jaguar activity and predation rate on the livestock each month for ~ 3 years; this is investigated further in Chapter 7.

Kill density regressed inversely with livestock density ($F_{1,6} = 22.95$, $p = 0.002$, $r^2 = 49\%$, Figure 5.12) suggesting that the presence of high numbers of cattle within a small area may lessen successful attacks. Alternatively other farm characteristics associated with high livestock density may lower livestock predation, for example small farms with large herds may also have better fences.

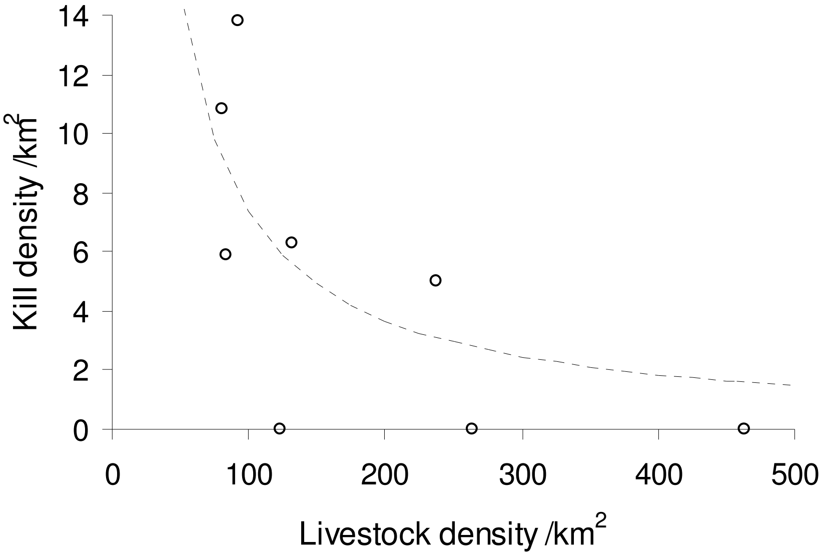


Figure 5.12 Predicted kill density based on linear regression equation (through origin): kill density = 736/ livestock density ($F_{1,6} = 22.95$, $p = 0.002$, $r^2 = 49\%$)

Kill density was not influenced by the length of covered pasture edge per km^2 pasture, or the % of the property that had patches of cover ($p > 0.5$, $n = 9$ for all). Kill density regressed negatively with the % pasture edge that was exposed (square root transformed data, $F_{1,8}$, $p < 0.05$, adjusted $r^2 = 39\%$), suggesting that kills may be fewer if there is a buffer between the pasture and the adjacent habitat. Kill density did not tend to differ between farms with and without human dwellings; however it tended to be higher on farms with forest patches or streams/rivers (Table 5.14).

All farms had barbed wire fencing which mainly functioned to keep livestock in, rather than cats out. The quality of fencing varied between the farms: smaller farms tended to have well-maintained fences, whilst the perimeters of three farms (Farms #01a, #01c and #03) lacked fencing in places, particularly where pasture bordered dense forest habitat or river banks. Farms that lacked complete fencing tended to have higher kill densities (Table 5.14), suggesting that fences are better deterrents than no fences. Rather than acting as a jaguar deterrent *per se*, the fences may simply prevent livestock from wondering into the adjacent forest where they are prone to ambush. Indeed, kill density was not influenced by the fence index on the eight properties (Regression, $F_{1, 7}$, $p > 0.7$, adjusted $r^2 = 0\%$). Fence width was more variable than fence height (mean width 31 cm, CV = 22%; mean height 143 cm, CV = 12% $n = 8$) and fence index varied by 30% between the farms. The two farms with the lowest and highest kill density (Farm #04 and Farm #06 respectively) both had the highest fence indices (6.5 and 7.0 respectively), suggesting that current fencing standards do little to prevent predation. A combination of factors may be important, which can only be assessed qualitatively here; for example Farm #04 not only had a high fence index but also 95% of its perimeter was clear; in contrast, although Farm #06 had a high fence index, 79% of its perimeter was forested.

Table 5.14 Kill density (livestock kills/ yr/ km^2) on farms with and without: forest patches, on-site human residence, streams/rivers, complete fencing.

Farm Attribute		*n*	Kill density	SD
Forest patches	yes	5	10.7	14.3
	no	5	4.9	6.8
Residence	yes	4	6.3	5.7
	no	6	8.8	14.0
Streams or river	yes	7	11.0	11.9
	no	3	0.3	0.5
Complete fence	yes	7	4.5	5.8
	no	3	15.5	17.8

There was no relationship between livestock losses on Farm #01 and monthly rainfall or lagged monthly rainfall (square root transformed data, Regressions, $p > 0.2$, adjusted $r^2 < 3\%$, $n = 34$ and 33) suggesting that if wild prey abundance does fluctuate seasonally with the rains, it does not influence predation rate on domestic prey.

Discussion

There are few published studies on the habitat use of sympatric populations of jaguars and pumas. They are known to coexist in homogenous forest environments, where there is little habitat variation and their daily activity patterns are similar (e.g. Núñez *et al*. 2002, Harmsen 2006). For example in the dry forests of Jalisco, Mexico, jaguar and puma ranges overlapped spatially and both species were associated with streams, which provided easy travel routes through the dense vegetation (Núñez *et al*. 2002). In contrast, Emmons (1987) detected subtle differences in habitat use between the two species in the lowland rainforest of Manu, Peru; here only jaguars were associated with rivers and this was linked to prey selection rather than accessibility through the forest. Harmsen *et al.* (in press) demonstrated that jaguars and pumas in the homogenous protected forest of the Cockscomb Basin, Belize, utilised the same locations, albeit not at the same time. Activity of both species increased with trail width, but no inter-specific habitat use differences were detected in relation to altitude, slope or proximity to water, although the validity of these analyses may be questionable given the limited ranges sampled (Harmsen 2006).

In the current study, jaguars and pumas were present at a similar number of locations and utilised the sites with similar intensity throughout the forest block, across both the protected sanctuary (previously studied by Harmsen 2006) and the contiguous unprotected forest buffer. This overall similarity emphasises the extraordinary ability of these morphologically similar predators to coexist. Neither species were influenced by the proximity of settlements bordering the buffer edge: activity levels in the protected core were similar to those at the forest periphery near settlements. The activity of both species (pumas, and male jaguars) increased on wider paths. Although for pumas this was only true on undisturbed roads. Wide trails and unpaved roads within forested habitats may not only facilitate movement through dense vegetation (e.g. Rabinowitz and Nottingham 1986, Dickson *et al.* 2005), but also may be preferentially used for hunting, particularly by pumas and for olfactory communication between conspecifics through the deposition and display of scrapes and scent marks (Harmsen 2006). Given that jaguars and pumas appear to have similar habitat requirements within the homogenous forest environment we may speculate that their co-existence is facilitated by differential food habits. This is investigated further in Chapter 6.

Heterogeneous landscapes provide opportunities for habitat partitioning between sympatric species. Where jaguars and pumas are sympatric in mosaic landscapes, pumas have been reported to utilise more open habitats than jaguars, including disturbed areas such as croplands and pasture (Scognamillo *et al.* 2003, Silveira 2004). In contrast jaguars tend to utilise forested areas and avoid more exposed areas such as open pasture (Schaller and Crawshaw1980, Crawshaw and Quigley 1991, Silveira 2004, Cullen *et al.* 2005). However during this study jaguars were common and pumas were scarce outside the forest block. This was unexpected, given the greater range of habitats associated with pumas than jaguars (Sunquist and Sunquist 2002); we may have expected the puma to use the human-matrix equally, if not more, than did the jaguar.

Four hypotheses, which are not necessarily mutually exclusive, may explain why pumas did not utilise lands outside the forest block:

1) Pumas are heavily hunted by humans outside the forest block
2) Pumas have a low tolerance of human disturbance (avoid human activity)
3) An essential resource, present in forest block, is lacking in the human-matrix
4) Pumas are excluded by jaguars outside the forest block

It is unlikely that the rarity of pumas outside the forest block is related to direct persecution by humans. Pumas were rarely detected on cattle farms and were seldom held responsible for livestock predation; and there were no verified reports of lethal control of pumas in the study area (Chapters 6 and 7). Furthermore, historically the international fur trade focused on spotted cats (e.g. Smith 1976, McMahan 1982, Nowell and Jackson 1996, Payán and Trujillo 2006) so it is unlikely that pumas are hunted in preference to jaguars for illegal markets.

Numerous studies indicate that carnivores, particularly felids, avoid areas with human activity and/or become more nocturnal in areas with high human-use, including tigers (*Panthera tigris*) in a Sumatran rainforest (Griffiths and van Shaik 1993), and bobcats (*Lynx rufus*) in a Californian urban nature reserve (George and Crooks 2006). Even leopards (*Panthera pardus*), which are considered the large felid least sensitive to disturbance (Sunquist & Sunquist 2002), are more nocturnal in areas more heavily used by people, and their activity declines with proximity to settlements (Ngorprasert *et al.* 2007). There is no *a priori* reason to suppose that pumas are less tolerant than jaguars of human activities *per se*. There are no published data on the response of jaguars to human disturbance. Various studies have demonstrated temporal and/or spatial avoidance of areas with human activity by pumas (e.g., van Dyke *et al.* 1986, Janis and Clark 2002, Dickson *et al.* 2005 and Sweanor *et al.* 2008). However behavioural responses in these studies were variable: it was not always clear whether prey avoided human activity, resulting in reduced use of areas by pumas, versus a direct effect of human disturbance on puma behaviour (e.g. Sweanor *et al.* 2008). The rarity with which the author saw either species during four years in the field (12 jaguars, one puma) is testament to the elusive behaviour of both species around people. This study found that jaguar activity declined during months when tourist activity increased. Although pumas showed no detectable response to tourist activity, they completely avoided the disturbed site for half of the study period; in contrast puma activity rivalled that of jaguar activity at other sites throughout the protected forest. Although inconclusive, these results suggest that, in this area at least, pumas were less tolerant than jaguars of human disturbance.

Pumas may have been absent from the human-matrix because it lacked an essential resource, for example specific microhabitat features or prey species. Pumas are adaptable to a wide range of vegetative and environmental conditions, living in a variety of habitats from arid scrub to tropical rainforests (Sunquist & Sunquist 2002), including disturbed habitats (e.g. Silveira 2004), and it therefore seems unlikely that specific microhabitat requirements prevented their survival outside the forest block in this study. More feasible is the hypothesis that puma utilisation of the human-matrix is restricted by prey availability, which may be limited by competition with human hunters and potentially exacerbated by competition with jaguars. Testing this hypothesis requires knowledge of the food habits of both species, and the extent to which their diets overlap. This is explored further in Chapter 6.

Jaguar habitat use

Jaguars utilised the entire study area, and were present in all habitat types surveyed: savannah, fragmented forest patches (including shrubland) and the contiguous secondary forest block, and were also recorded around all land-use systems: villages, plantations, aquaculture, pastureland and forest-milpa. Habitat use nevertheless differed between the sexes. Males were present at more locations than females across the study area. This is expected since males had larger home ranges than females thus also had a higher probability of encountering a camera station (Chapter 4). Males dominated the protected forest, both in terms of the number of individuals utilising a given location, and the intensity of use. As described above, in the forest block male activity increased on wider trails; however female activity did not, rather higher activity was associated with proximity to flowing water. This disparity in microhabitat use may be a strategy for females with young to avoid infanticide by males attempting to gain mating opportunities. Infanticide is common in carnivores, and females with dependents may avoid areas dominated by males, as reported in brown bears (*Ursus arctos*) by Dahle and Swenson (2003). Infanticide has been recorded in the Felidae (e.g. caracal (*Caracal caracal*), domestic cat (*Felis silvestris catus*), leopard, lion (*Panthera leo*), tiger, Sunquist & Sunquist 2002) including jaguars (Soares *et al*. 2006). In this study, whilst males dominated the wider trails to traverse the forest, females may have used streams and rivers as alternative safe travel ways through the dense habitat. CBWS has a high density of rivers and streams, with approximately 2.5 km of waterways per km^2. The potential number of access ways through the forest is thus high, and detection rate of females by researchers will be correspondingly low. Consequently the apparent scarcity and low activity of females within the protected forest compared to males, and compared other females in habitats outside CBWS, may be an artefact of the methodology: cameras located on trail systems (man-made or game trails) are potentially avoided by females unless in oestrus, and cameras located on streams have a low probability of detection given the high number of alternate waterways available. Whilst preferential use of streams over trails by females is speculative, increasing trap effort in such locations may go someway to correct the observed sampling bias within the protected forest surveys and improve density estimates (Chapter 4) and warrants further investigation. Research addressing these questions in CBWS is currently underway (B. Harmsen, Panthera Belize, pers. comm.).

Overall male jaguars were present at more sites in the human-matrix than were females; however the high activity of males observed in the protected forest was not observed in disturbed areas such as fragmented forest and pastures, and habitat use outside the forest block declined with proximity to areas of human development. Intra-specific variation in use of developed areas by carnivores has been documented, for example in California male bobcats used areas near or in urban sites more than did females (Riley *et al*. 2003, Riley 2006). Indeed male carnivores are often described as the more risk-prone sex however it is not clear whether this phenomenon arises from intrinsic risk-taking behaviour *per se* versus their wider ranges causing more encounters with people (Linnell *et al*. 1999). In this study there was no evidence that female jaguars were less tolerant of lands with human activity than were males. In fact, outside the forest block female activity increased closer to areas of human development, and both sexes were equally active on disturbed lands (pastures and fragmented forests).

Chapter 4 demonstrated that where more than four-fifths of the forested landscape was fragmented the average jaguar did not utilise all the available land, and it was suggested that this may reflect habitat preferences within the mosaic landscape, and/or vacant territories arising from direct conflict with people. With regards the latter hypothesis, the extent and implications of human-induced mortality are considered further in Chapter 7. With regards the former, the results of this study cannot reject the hypothesis that jaguars preferred or avoided certain habitats in the human-matrix; however the interpretation is not clear. The decline in male activity with proximity to settlements and plantations suggests some degree of avoidance of human activity. Also, males were present at more pasture locations than expected suggesting an attraction to ranches where there is an abundance of domestic prey; however it should be noted the number of males present at any location in the human-matrix did not vary between habitats, thus it does not seem to be the case that more males used pastures than, for example, forest fragments or savannahs. Females were less common in savannahs than were males. It is possible that this habitat is simply not productive enough to support the energetic needs of females with dependents. The energetic needs of jaguars are investigated further in Chapter 6.

Determinants of cat activity and livestock predation on farms

The study of factors associated with livestock predation aims to seek methods to reduce losses without the need for lethal control. Both jaguars and pumas attack livestock; studies from different locations cite different levels of predation by either species. For example jaguars were reported to attack livestock more heavily than pumas in fragmented forest habitats of the Brazilian Amazon, southern Brazil and Belize (Michalski *et al*. 2006, Conforti & Azevedo 2003, Azevdeo 2008, Brechin and Buff 2005) and in the Brazilian Pantanal (Azevedo and Murray 2007). The reverse was reported in the Venezuela llanos (Polisar *et al*. 2003) and the cerrado/forest transition zone of central-western Brazil (Palmeira *et al*. 2008). In this study it was not often possible to assess livestock carcasses and identify predator species; however pumas were rarely detected on farms and the majority of cat attacks were usually attributed to jaguars. Indeed when asked about jaguars and pumas it was common for local people to be unfamiliar with the ‘red tiger’. This is reflected across the country; in a nationwide survey Brechin and Buff (2005) found that the majority of predation events were blamed on jaguars and retaliatory killings of cats were of jaguars rather than pumas. Characteristics of cats associated with depredation and thus at risk of lethal control are discussed further in Chapter 7.

Given the result that pumas were rarely present on farms in the study area, the following discussion of habitat factors associated with livestock predation is limited to jaguars only. Although males were present at relatively more pasture than non-pasture locations, and females at fewer, they both had similar activity on pasture. Neither jaguar activity nor predation was influenced by the extent of canopy cover (forested or plantation) within the property or along its perimeter. Jaguar activity did not vary with the extent to which the pasture edge was clear, however predation declined as the proportion of exposed edge (≥ 3.5 m wide) increased. These findings suggest that although jaguar movement through farmlands was uninhibited by physiognomy, successful predation of livestock required some level of cover for stalking prey. Indeed several studies indicate that higher predation rates are associated with proximity to forest cover (e.g. Polisar *et al*. 2003, Michalski *et al*. 2006, Azevedo and Murray 2007).

Jaguar activity on the farms was not limited by distance from the forest block. However, no location was further than 4.2 km, a distance smaller than the average home range diameters estimated for male and female jaguars in the area (Chapter 4). Indeed in Costa Rica, Sáenz and Carrillo (2002) reported that 87% of attacked cattle farms were up to 15 km from protected areas, much further from the forest block than in this study. Given that 72% of the Belize is still forested (WRI 2007), most farms and villages lie in close proximity to the forest so we may expect them to be at high risk of depredation if methods to protect livestock are not employed.

In this study annual livestock (cattle) predation on the farms varied from 0% to 15% of the total stock, with an average of 5% loss across all eight properties. This is higher than reports for South America, most of which come from Brazil. In the Brazilian Pantanal losses due to cat predation range from 0.2 to 2.3% (Dalponte 2002, Zimmermann *et al*. 2005, Azevedo and Murray 2007); in the Atlantic forest and Amazonian regions of southern Brazil, where habitat and ranch size is more comparable to that seen in Belize, losses range from 0.3% to 1.2% (Mazzoli *et al*. 2002, Conforti and Azvedo 2003, Michalski *et al*. 2006, Azevedo 2008). However, annual losses from individual farms may be high. For example Mazzolli *et al*. (2002) report cattle losses of 16% of the stock at one of the ranches in their study site. Indeed, although it is frequently cited that '*wild felids are only responsible for the loss less than 3% of annual domestic stock'* (Nowell and Jackson 1996), the losses to individual farmers may be much higher. Thus the problem needs to be assessed and addressed at the local level. Attempts to mitigate conflict must be site specific, and take into account local constraints such as culture, attitudes and economy, as well as the spatial scale of properties involved and physiognomy of the landscape. Some potential methods to reduce depredation, relevant to the situation observed in Belize, are discussed below.

Methods to lower livestock predation in Belize

Farms that lacked complete fencing tended to suffer more predation, suggesting that fences are better than no fences. However the quality of fencing was generally poor: low, widely spaced and poorly constructed. Farmers often showed the author where the jaguar had passed through the fence. Improving fences such that they are higher with taut strings and narrow spacing may deter predators; however it seems that economics prevent sufficient investment from the outset, with a tendency to first purchase cattle, and suffer predation, then to gradually improve fencing when money is available (R. Foster pers. obs.). Although there is some evidence that electric fencing may prevent attacks (Schiaffino *et al*. 2002, R. Foster pers. obs.) this option is again limited by high costs, as well as high maintenance because vegetation must be regularly cleared from the fence line to prevent short-circuit. Corrals may provide an alternative solution, in which livestock are brought into a small well-protected area at night. Costs of ~ US$2,000 are estimated to build and maintain an electrified 1-ha enclosure, and ~ US$4,600 per year required for staff to round up and release 100 cattle every day; a barbed wire corral and a night watchman would cost approximately the same (S. Juan, Farm Manager, pers. comm.). The loss of productivity from corralling cattle at night is estimated at US $45/year per animal; whilst the cost of losing an animal to a predator is approximately US$500 (S. Juan pers. comm.). Thus lost productivity due to corralling is estimated at ~ 9% per year (S. Juan pers. comm.). Investment in a corral (with either night watch or electrified fencing) is probably only appropriate and affordable for large-scale operations, and only if enough deaths are prevented so as to offset both the cost of installing and maintaining the corral, staff wages, and the lost productivity associated with corralling at night.

Depredation tended to be higher on farms which had forest patches or streams/ rivers. Forest patches potentially provide good stalking cover within a pasture, as do streams with riparian vegetation as cover, enabling the predator to ambush cattle while they are drinking. Furthermore, streams in the study area were often unfenced, providing predators with easy access on to the property. In a nationwide survey, Brechin and Buff (2005) found that only 28% of ranchers interviewed exclusively used artificial water sources on their farms; the majority relied to some extent on natural water bodies, and in 74% of properties these were forested also. Encouraging cattle to utilise artificial watering troughs, and fencing off streams may help to reduce attacks. Farmers may also lower risk of predation by clearing the natural vegetation adjacent to the pastures. Farmers may be tempted to graze cattle right up to the edges of their property such that the pasture boundary abuts forested habitats, in order to maximise the space available. Bringing in the fence line, or clearing a buffer between a fenced pasture edge and the adjacent vegetation, may help to reduce attacks as predators may be reluctant to cross an exposed area with no livestock before reaching the grazing lands.

Although this study detected no difference in predation between farms with and without human dwellings, jaguar activity was lower where people were permanently present and we may expect that human activity on small holdings could help to reduce predator attacks. For larger properties it may be advisable to bring herds with vulnerable calves closer to human dwellings, particularly when sign of predators are detected. This practise was common on the two largest farms in the study. However it is not unheard of for jaguars to approach dwellings, with two cases of jaguars attempting to snatch dogs from doorsteps reported from settlements during the study.

Recent research from Venezuela has highlighted the benefits of incorporating water buffalo (*Bubalus bubalis*) into cattle herds, or switching entirely to buffalo, as a means to reduce losses to predators (Hoogesteijn and Hoogesteijn 2008). Buffalo were less likely to be attacked and displayed defensive behaviours not observed in the *Bos* species; as well as being more productive and more resistance to disease. Buffalo are well-suited to the expansive ranches in the seasonally flooded savannahs of the Venezuelan llanos and Brazilian Pantanal (Hoogesteijn and Hoogesteijn 2008), and their suitability to Belizean pastures, or to the Central American meat market, remains to be established. Presumably only the larger ranches which have waterholes for wallowing are appropriate. Given that the majority of cattle owners are small-scale farmers managing < 50 head (Brechin and Buff 2005) it seems unlikely that buffalo will provide a universal solution in Belize. Furthermore the market value of buffalo meat tends to be low (Hoogesteijn and Hoogesteijn 2008). Cultural tastes in Guatemala and Mexico (the main market for Belizean beef) may not adapt easily and few farmers may see the economic benefit of switching from beef. An alternative may be to mix some buffalo with cattle purely for protection, not for meat production. Currently 25 Belizean holdings do have buffalo, albeit in low numbers (Belize Government 2007). The two largest farms in this study stocked buffalo. These totalled < 5% of the total stock, however, with the result that not all the cattle herds shared pastures with buffalo, and it is not yet clear whether they have reduced overall predation rates.

Livestock guard dogs (LGDs) have been used successfully in Africa, Europe, Australia, Canada, USA, India and the Middle East to protect livestock (usually sheep, but also cattle and horses) from a suite of predators including bears, wolves, pumas, leopards, cheetahs and hyaenas, in both rangeland and pasture situations (Smith *et al.* 2000a, Dawydiak and Sims 2004). To date LGDs have not been used to protect cattle from jaguars in the neotropics. They would not be suited to the expansive and often poorly managed ranch operations in Venezuela and the Brazilian Pantanal; however they may be appropriate in the small-scale pastures of Belize. Whether or not LGDs would be effective against jaguars is debatable. Indeed jaguars are reported as a major main cause of dog mortality in Belize (Brechin and Buff 2005). Furthermore the relatively high cost associated with rearing and training LGDs (Smith *et al.* 2000a) makes this option unviable for most Belizean farmers.

A growing trend in Belize is to incorporate donkeys into herds. Anecdotal reports suggest that donkeys work well as guard animals against big cats in the north of the country. They are less expensive, require less maintenance and have a higher life expectancy than livestock guarding dogs; however their effectiveness at deterring predators remains to be formally evaluated (Smith *et al.* 2000a).

Repellents may offer a means to lower livestock predation, particularly on small holdings. They rely on novel stimuli to immediately disrupt the action of a predator. Examples include capsaicin sprays, strobes, flares, propane exploders, high frequency and intensity sounds, rubber bullets and jets of water, some of which can be trigged automatically by motion detectors. To date there has been relatively little research on felid repellents. They have been shown to offer immediate results in other predators (e.g. ursids, canids, mustelids) however the effect is usually only temporary due to habituation to the stimulus, and does not create an aversion to the food source (Smith *et al.* 2000b, Shivik *et al.* 2003). Thus, repellents may not offer a long-term solution on a large-scale, but they may be sufficient to protect a small focal pasture for a critical period e.g. during calving. A pilot-study on the response of captive jaguars and pumas to commercially available ‘ultrasonic cat deterrents’ detected no effect (R. Foster unpubl. data). Certainly the potential for felid repellents requires further investigation.

The majority of losses reported during this study were of calves, rather than adults, as has been observed elsewhere (e.g. Polisar *et al.* 2003, Michalski *et al.* 2006, Azevedo and Murray 2007, Palmeira *et al.* 2008). Thus methods to reduce losses need to focus on protecting young animals. If money is limited, efforts should ensure that priority is given to females with young, locating them in the 'safest' pastures (e.g. best fencing, away from forest edges etc). This can be facilitated by establishing short breeding seasons of 3-4 months rather than year-round breeding (Hoogesteijn 2000). Furthermore it has been suggested that synchronised reproduction can reduce overall losses to predators: in the case of cattle, swamping the predator with vulnerable prey within a short period may result in fewer losses than if calves are available, albeit in lower numbers, throughout the year (Palmeira *et al*. 2008). This strategy may be appropriate for large-scale operations with hundreds of head cattle, in which the predator truly is 'swamped' with calves, but is unlikely to benefit small-holdings. In fact, if the herd is small, asynchronous breeding may be preferential. With jaguars and pumas being generalist predators, if wild prey are available in numbers greater than one or two calves in a pasture, they may not perceive the pasture as a reliable resource patch to which they will return.

Research suggests that a low abundance of wild prey is associated with a high level of predation on domestic animals: in Brazil the overexploitation of wild species by man has coincided with an increase in cattle predation e.g. white-lipped peccary (Conforti and Azevedo 2003, Crawshaw *et al*. 2004, Azevedo 2008) and caiman (*Caiman crocodilus*, Hoogesteijn 2000). In contrast, ranches rich in wild prey may suffer little or no depredation, suggesting a preference for wild prey when it is available (e.g. Miller 2002). It is likely that there is an interaction between the availability of wild versus domestic prey. In Venezuela the frequency of cattle depredation was inversely related to availability and vulnerability of natural prey and directly related to availability and vulnerability of livestock (Polisar *et al*. 2003). Promoting wild prey populations may provide part of the solution to lowering livestock predation. Although this study did not assess wild prey abundance, hunting was common throughout the study area. Evidence of hunting was detected across the landscape including savannahs, farms, the forest block and extending into the protected area. In areas where farms are bordered by several communities it may be impossible to reduce levels of local hunting; however in some cases the owners of larger ranches could ban staff from hunting. Alternatively, the ranchers or communities (as collectives) may consider augmenting the wild prey on their land with species such peccaries and allow controlled levels of hunting from which they may get economic returns. Knowledge of the relative abundance of both wild and domestic prey, and the food habits and preferences of the predators, is required to assess whether wild prey augmentation or reduced hunting may help to lower livestock predation within a given area. There is little value in bolstering wild prey if this merely supports more predators which continue to attack domestic stock as well. Food habits of jaguars and pumas are investigated further in Chapter 6.

Chapter 6

Food habits of jaguars and pumas in a human-influenced landscape

Abstract

Jaguars (*Panthera onca*) co-exist with pumas (*Puma concolor*) across their entire range. In areas where they occur together their coexistence may be facilitated by differences in diet. This study describes a comparison of the food habits of jaguars and pumas in Belize, Central America, between a protected lowland rainforest and the neighbouring human-influenced landscape. Diets were determined from 362 jaguar scats and 135 puma scats that were genotyped to species level, representing the largest analysis to date of the species in sympatry. It was estimated that at least 100 scats are required to adequately represent diet in this region. The diet breadths of jaguars and pumas in the protected forest were low and showed little overlap. In this habitat each relied heavily on a single small (5-10 kg) prey species: jaguars mainly ate nine-banded armadillos (*Dasypus novemcinctus*) and pumas principally ate pacas (*Agouti paca*). It is suggested that jaguars were exploiting a super-abundant prey resource, whilst pumas may have been selecting pacas over armadillos. Both cats also took larger prey (>10 kg), mainly white-lipped peccaries (*Dictolyes pecari*) by jaguars and red brocket deer (*Mazama americana*) by pumas; it is proposed that jaguar and puma reproduction may be limited if large prey are unavailable for females with dependents. In unprotected fragmented lands, jaguar scats rarely contained large wild prey species; rather, a diet of relatively small wild prey was supplemented with larger domestic species. The augmentation of populations of large ungulates such as collared peccaries may provide an alternative prey source and so reduce jaguar predation on cattle. Pumas were scarce outside the protected forest. This may reflect a reluctance to utilise domestic species near human development and/ or competition with humans for their preferred prey species, paca and deer, which are also prized game species in the region.

Introduction

The coexistence of similar sympatric species may be facilitated by ecological separation along trophic, spatial and temporal dimensions of their environment (e.g. Pianka 1969); most commonly through the partitioning of food resources and differential habitat use (Schoener 1974). The extent to which sympatric species compete will depend on their level of niche overlap and the availability of resources, thus ecological separation can reduce exploitative and interference competition between similar species (e.g. Durant 1998). Changes in the resource spectrum and availability of resources may alter the degree of inter-specific competition and the balance of coexistence (e.g. Bonesi and Macdonald 2004). If alternative exploitable resources are available phenotypic plasticity may facilitate a shift in resource use so reducing competition; conversely if alternative resources cannot be exploited the subordinate species may be competitively excluded (Pfennig *et al.* 2006). Human population growth is placing increasing pressure on natural resources; particularly across the tropics where the recent increase in hunting of wildlife for meat is considered unsustainable in many areas (Milner-Gulland *et al.* 2003), and people may compete with large carnivores not only for space but also for prey (e.g. Leite and Galvão 2002). Reductions in prey availability, either through direct competition with man or indirectly through habitat loss, may reduce carnivore survival (Fuller and Sievert 2001); for example wild prey depletion is considered a principal cause of tiger (*Panthera tigris*) population decline (Karanth *et al.* 2004). It has been suggested that when prey become scarce, the long-term persistence of large felids may depend on diet flexibility and their ability to use human-disturbed areas (Azevedo 2008). Thus changes to habitat and the availability of different prey species may alter patterns of co-existence of sympatric species (Núñez *et al.* 2000a). This study focuses on the jaguar (*Panthera onca*) and the puma (*Puma concolor*), two similar-sized cats that co-occur throughout the neotropics. The aim of this chapter is to compare the food habits of jaguars and pumas inhabiting an undisturbed protected lowland rainforest with those utilising the neighbouring human-influenced landscape, in Belize, Central America. Evidence of dietary overlap will be interpreted in relation to implications for the persistence of these two sympatric felids and options for conservation management. Until now diet studies of sympatric jaguars and pumas have been limited by sample size and/or reliable techniques to distinguish between predator species (Chapter 1). In this study diets are described using scats that have been genotyped to species level. The scat collection represents the largest dataset available to date for a comparative study of jaguar and puma feeding ecology.

The Neotropics is one of the most biodiverse ecozones in the world; Mesoamerica alone supports 2,859 species of terrestrial vertebrates (Myers *et al.* 2000), providing a high number of potential prey for neotropical predators such as jaguars and pumas. At single rainforest sites, as many as 24 different taxa have been detected in jaguar diet, and 20 in puma diet, (Garla *et al.* 2001, Leite and Galvão 2002, Moreno *et al.* 2006). When describing carnivore food habits, researchers in this region should consider the potential number of prey taxa available for top predators and evaluate whether the scat sample size will adequately represent the true richness of prey taken and the level of plasticity in the feeding ecology of the target species. This is rarely done. As a prerequisite to achieving the main aim of this chapter, the first objective was set as an analysis of prey taxa identified in relation to scat sample size, using published studies of jaguar and puma diets and new data from this study.

Similar-sized carnivores may coexist by hunting in different areas (e.g. cheetahs (*Acinonyx jubutas*) with hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*), Durant 1998), at different times (e.g. red foxes (*Vulpes vulpes*), Iberian lynxes (*Lynx pardinus*) and Eurasian badgers (*Meles meles*), Fedriana *et al.* 1999; dholes (*Cuon alpinus*) with leopards (*Panthera pardus*) and tigers, Karanth and Sunquist 2000) or by employing different hunting strategies and using different habitats (e.g. tigers and leopards, Seidensticker 1976; badgers and lynx, Fedriana *et al.* 1999), but perhaps most commonly by using prey of different size-class or taxa (e.g. lions and leopards, Bertram 1982; aardwolves (*Proteles cristatus*), bat-eared foxes (*Otocyon megalotis*), black-backed jackals (*Canis mesomelas*) and Cape foxes (*Vulpes chama*), Bothma *et al.* 1984; ocelots (*Felis pardalis*), hog-nosed skunk (*Conepatus semistriatus*), tayra (*Eira barbara*), grison (*Galictis vittata*) and crab-eating fox (*Cerdocon thous*) Sunquist *et al.* 1989; dholes, leopards and tigers, Karanth and Sunquist 2000; Andean mountain cats (*Leopardus jacobitus*), colocolos (*Leopardus colocolo*) and culpeos (*Lycalopex culpaeus*), Walker *et al.* 2007). Where jaguars and pumas occur together they often use the same habitats and follow similar activity patterns (e.g. Núñez *et al.* 2002, Scognamillo *et al.* 2003, Harmsen 2006). It is therefore reasonable to hypothesise that in such areas their coexistence may be facilitated by selecting different prey species. The second objective of this chapter is to describe the diets of jaguars and pumas inhabiting a protected secondary rainforest, and to evaluate the level of dietary overlap between the two cats. Prey availability is a prerequisite for determining whether prey species are taken opportunistically or selectively. One of the intractable problems with dietary studies of top predators inhabiting densely forested habitats is evaluating prey availability against which to compare prey consumption. Although relative abundances of wild prey species were unknown in this study, differences between the relative occurrence of a given prey species within the diets of sympatric jaguars and pumas would imply that one or both cats were taking prey selectively.

Optimal foraging theories predict that when prey are abundant predators should select large prey in order to maximize energy intake, but when prey are scarce they should be taken opportunistically according to their availability (Griffiths 1975). The high proportion of small prey in the diet of jaguars and pumas in the Paraguayan Chaco has been attributed to a reduction in the availability of larger prey caused by intensive commercial hunting by people (Taber *et al.* 1997). It has been suggested that pumas have a superior ability to exploit smaller prey than jaguars and that this may give them a competitive advantage in human-influenced landscapes (Núñez *et al.* 2000a). In the Atlantic forests of Brazil, jaguars are in decline because local people hunt the same species (Leite and Galvão 2002), but in some areas jaguars move outside protected forests and use livestock as an alternative prey resource (e.g. Azevedo 2008). The utilisation of livestock may allow large predators to supplement their diet with larger prey where wild animals are otherwise scarce, but it will also bring them into direct conflict with people. In Belize, although illegal incursions into protected areas to hunt prized game species occur, it is likely that wild prey abundance and species richness are lower outside the protected forests where the habitat is fragmented by cattle ranches and monocultures, and unregulated hunting is common (R. Foster pers. ob., G. Hansom, Belize Forestry Officer, pers. comm.). Although the hunting of wild game is not permitted without a valid hunting license (Belize Wildlife Protection Act 2000), monitoring and enforcement are difficult (G. Hansom pers. comm.). Fire-arms are legal and landowners are permitted to kill any wildlife that threatens crops or domestic animals on their property (Belize Wildlife Protection Act 2000). This is often used as a pretext to hunt game, not only on their property but also beyond. Hunting trips into forest may last one or two nights, either on foot or by boat. A successful trip will bag three pacas (*Agouti paca*) and up to three white-lipped peccaries (*Dicotyles pecari*) (R. Foster pers. obs.) White-tailed deer (*Odocioleus virginianus*) are often hunted in the savannah areas. Although the use of artificial lights to shoot any animal is prohibited, spotting for deer is common, even within the closed season (Belize Wildlife Protection Act 2003, R. Foster pers. obs.). Pacas can sell for ~US$25 each, whilst white-lipped peccaries and white-tailed deer can each fetch up to ~US$150. The average wage in Belize is just US$3,740 (World Bank 2008), so for many there is good economic incentive for hunting, and they may make several trips each month. In this chapter, we hypothesise that the persistence of jaguars and pumas is facilitated in these unprotected regions by diet shifts leading to subsistence on smaller prey than those taken by individuals inhabiting the protected areas, and/or on domestic prey. Since pumas were rarely detected outside the protected forest in this study (Chapter 5), the third objective of this chapter is to focus solely on jaguars in a comparison of diet within a protected rainforest to diet in the neighbouring human-influenced habitats.

Prey depletion threatens nearly all cat species and has been attributed to population decline in 92% of cat species (IUCN 2007). Lowered prey availability may reduce neonatal, juvenile and adult survival (Fuller and Sievert 2001). For big cats, pregnancy and the long period of association during which the mother is lactating and hunting to feed both herself and her off-spring, is energetically demanding; and the availability of large prey may be particularly important to fulfil the high energetic requirements of rearing young. For example, although an adult tiger could satisfy its own energy requirements by hunting only small deer, off-take rate would need to increase to unsustainable levels to support reproduction; the inclusion of some larger prey in the diet appears necessary for reproduction (Sunquist *et al.* 1999). The final objective of this chapter is to investigate the energy requirements of jaguars and pumas in the study area to asses whether absence of pumas from the fragmented landscape (Chapter 5) may be linked to prey preferences and availability, and whether jaguars could persist outside the protected area in the absence of livestock.

Methods

A total of 645 scats (n = 229 this study and n = 416 Harmsen 2006) were collected opportunistically between 2003 and 2006 throughout the study area from a range of habitats: protected and unprotected secondary rainforest, shrubland, pine savannah, and cattle pastures. Local people were also encouraged to collect scats for a US$2.50 / bag reward. UTM locations of scats were recorded in the field using a GPS unit or retrospectively using field notes and OS maps. For scats collected by local people only approximate locations are available within a radius of up to ~ 5 km. Locations of 96% of the scats were accurately known to be either in the protected forest, the forest buffer or the fragmented lands. Approximate scat locations are shown in Figure 6.1.

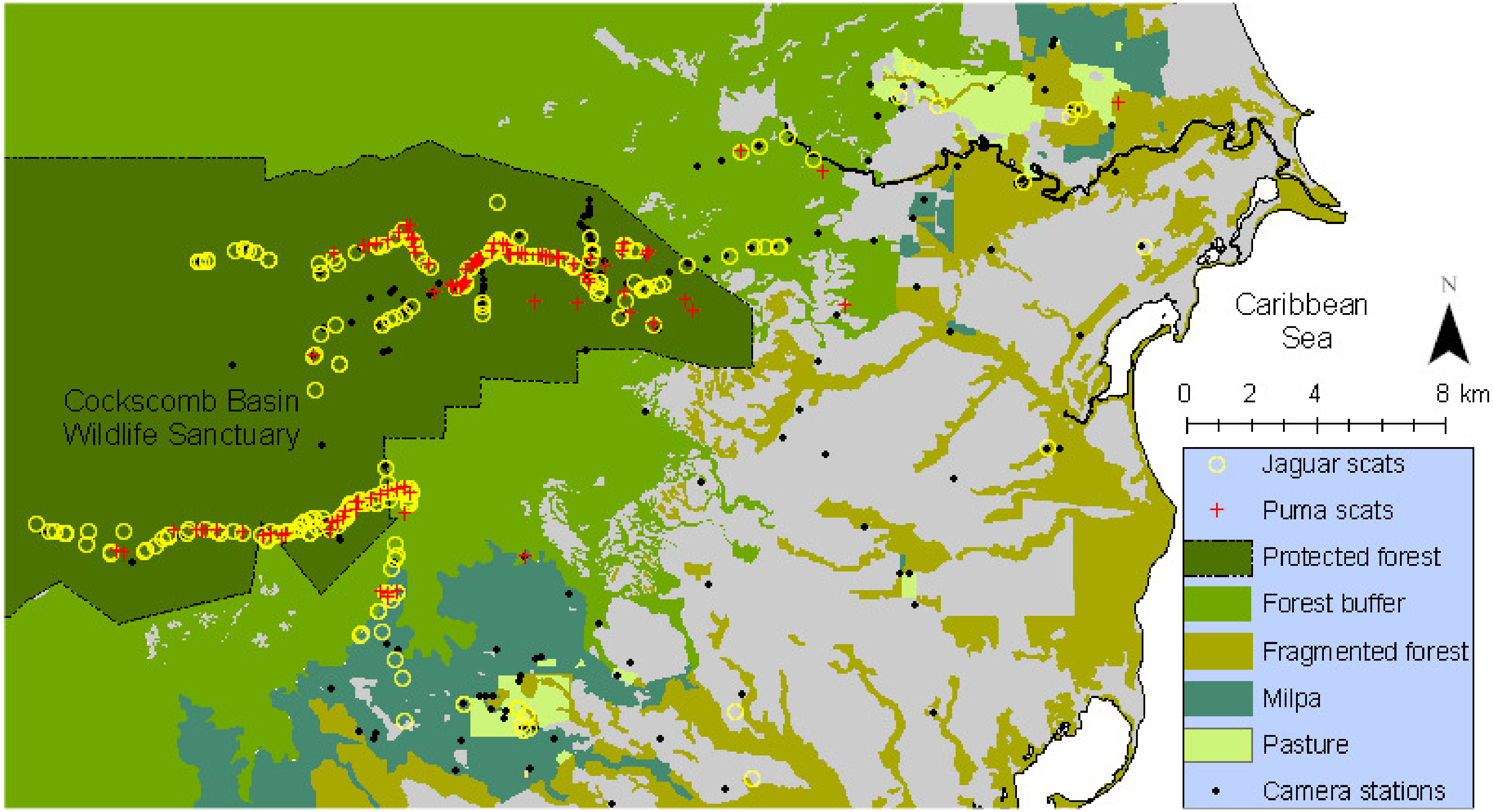


Figure 6.1 Locations of scats collected opportunistically throughout the study area from Jan 2003 to Oct 2006. Point locations may include multiple scats within a radius of up to ~5 km. Camera stations are shown to indicate areas where researchers conducted fieldwork.

Each scat was stored with silica granules in a paper bag at room temperature for a maximum of 9 months until transport to the UK where the scats were stored at 4 ºC prior to genetic and diet analyses. Genetic analysis of the faecal samples was conducted by the WCS and the American Museum of Natural History Global Felid Genetics Program. Total DNA was extracted using the QIAamp DNA Stool Mini Kit (Qiagen, Valencia, CA, USA) with minor modifications. Primers were adapted from Hoelzel and Green (1992) to amplify the 16S region of the mitochondrial genome and identify the species of the extracted DNA (C. Pomilla unpubl. data). DNA was extracted from 588 samples and species of origin was identified for 532 samples (Table 6.1, C. Pomilla unpubl. data).

Table 6.1 Number and species of origin of scats, collected 2003 to 2006

Species		Number of scats
Jaguar	*Panthera onca*	362
Puma	*Puma concolor*	135
Ocelot or margay	*Leopardus pardalis or wiedii*	31
Margay	*Leopardus wiedii*	2
Domestic dog	*Canis familiaris*	2

Prey species eaten by a carnivore can be identified from the remains in the scat. Hairs from different species differ in colour, pattern, length, width and texture. At the microscopic level, the medulla width and pattern, and the scale pattern of cells may differ. Valdes (2006) and Harmsen (2006) created a reference collection and key from hair and body parts (teeth, claws, hooves, scutes and bone fragments) of Belizean mammals for use in diet studies from the region. Since many of the scats in this study originated from areas with livestock, an additional reference collection was created for hair from common domestic animals (cattle, horse, donkey, sheep, pig and dog). The two reference collections were used to identify the contents of the scats to species level. Where species identification from hair remains was ambiguous, inferences were made about the size class based on bone size and morphology. A total of 27 jaguar scats and six puma scats did not contain enough remains to identify any prey items. Note, prior to species-specific genotyping, the prey contents of 329 of the scats were analyzed by Valdes (2006) for a discussion of the diet of big cats in the protected forest (Harmsen 2006). The prey contents of the remaining 168 scats were analyzed by the author and following genetic analysis the two diet datasets were combined (this study).

The % relative occurrence of each prey species in the diet of each cat species was calculated using Equation 6.1, where '*prey item*' refers to an identifiable taxon within a scat.

$$\frac{\textit{Number of prey items that are species X}}{\textit{Number of all prey items identified}} \times 100 \qquad \text{(Eqn 6.1)}$$

Eqn 6.1 is often used in to describe diet (e.g. Rabinowitz and Nottingham 1986, Crawshaw et *al*. 2004); however smaller species will tend to be over-estimated relative to larger species by this fraction because they contribute a higher ratio of hair:meat to each scat. Ackerman *et al*. (1984) derived a linear relationship between body weight of prey and collectible scats produced by pumas during feeding trials. This relationship can be used as a correction factor. Following Ackerman *et al*. (1984) the biomass of species X consumed per scat was calculated as:

$$1.98 + 0.035 \times \textit{mean live mass of prey species X} \qquad \text{(Eqn 6.2)}$$

The correction factor was not used for prey species < 2 kg as it was assumed that each occurrence in a scat represented a whole individual (Ackermann *et al*. 1984).
The relative biomass of species X consumed was then calculated as:

$$\frac{\textit{\% relative occurrence of species X} \times \textit{biomass of species X consumed per scat}}{\sum \textit{(\% relative occurrence of species)}_i \times \textit{(biomass of species consumed per scat)}_i} \qquad \text{(Eqn 6.3)}$$

where i = species 1, 2, 3, … x

Table 6.2 shows the potential wild mammalian prey species available in the study area, and their mean live masses adapted from Reid (1997). As it was possible to distinguish between adult and juvenile peccary remains based on hoof size and coarseness of hair, all analyses involving peccary mass discriminated between adults and young. A juvenile peccary was estimated to weigh 7.5 kg. The live masses of domestic species were obtained from local knowledge. Cattle range in size from 37 kg (newborn) to 900 kg (bull) (S. Juan, Farm Manager, pers. comm.). Because the majority of cattle predations reported during the study with size estimates were of calves (up to ~ 250 kg), the live mass used for the correction factor of cattle was 125 kg.

Table 6.2 Potential mammalian prey species in study area, ordered by average mass, based on Reid (1997).

Average mass (kg)	**Latin name**	**Common name**	**Mass (kg)**		**Biomass consumed per scat (kg)**[†]
			range	**average***	
> 10 kg					
	Bos taurus	Domestic cow	900.0	125.0[‡]	6.36
	Tapirus bairdii	Baird's tapir	180.0 - 300.0	240.0	10.38
	Panthera onca	Jaguar	30.0 - 100.0	65.0	4.26
	Puma concolor	Puma	24.0 - 65.0	44.5	3.54
	Odocioleus virginianus	White-tailed deer	25.0 - 43.0	34.0	3.17
	Dictoyles pecari	White-lipped peccary	27.0 - 40.0	33.5	3.15
	Ovis aries	Domestic sheep	30.0	30.0	3.03
	Mazama americana	Red brocket deer	12.0 - 32.0	22.0	2.75
	Tayassu tajacu	Collared peccary	12.0 - 26.0	19.0	2.65
	Canis lupus familiaris	Domestic dog	15.0	15.0	2.51
	Leopardus pardalis	Ocelot	7.0 - 14.5	10.8	2.36
5 to10 kg					
	Agouti paca	Paca	5.0 - 12.0	8.5	2.28
	Lutra longicaudis	Neotropical river otter	5.0 - 9.5	7.3	2.24
	Ateles geoffroyi	Central American spider monkey	5.0 - 9.0	7.0	2.23
	Alouatta pigra	Yucatan black howler monkey	5.7 - 8.0	6.9	2.22
	Felis yaguarondi	Jaguarundi	4.0 - 9.0	6.5	2.21
	Tamandua mexicana	Northern tamandua	3.8 - 8.5	6.2	2.20
	Procyon lotor	Northern raccoon	3.3 - 7.8	5.6	2.18
	Dasypus novemcinctus	Nine-banded armadillo	3.0 - 7.0	5.0	2.16
2 to 5 kg					
	Nasua narica	White-nosed coati	2.7 - 6.5	4.6	2.14
	Eira barbara	Tayra	3.0 - 6.0	4.5	2.14
	Leopardus wiedii	Margay	2.6 - 5.0	3.8	2.11
	Potos flavus	Kinkajou	2.0 - 4.6	3.3	2.10
	Dasyprocta punctata	Central American agouti	3.0 - 4.0	3.5	2.10

/cont next page

Table 6.2/cont Potential mammalian prey species

Class	**Latin name**	**Common name**	**Mass (kg)** range		**average***	**Biomass consumed per scat (kg)** †
	Conepatus sp	Hog-nosed skunk	1.4 -	4.0	2.7	2.07
	Urocyon cinereoargenteus	Grey fox	1.8 -	3.5	2.7	2.07
	Galictis vittata	Greater grison	1.5 -	3.2	2.4	2.06
	Coendou mexicanus	Mexican porcupine	1.4 -	2.6	2.0	2.05
< 2 kg						
	Various opossums and rodents including:					
	Didelphis virginiana	Virginia opossum	1.1 -	2.5	1.8	n/a
	Didelphis marsupialis	Common opossum	0.6 -	2.4	1.5	n/a
	Philander opossum	Gray four-eyed opossum	0.3 -	1.4	0.9	n/a
	Chironectes minimus	Water opossum	0.6 -	0.8	0.7	n/a
	Rattus sp	Old World rats	0.1 -	0.5	0.3	n/a
	Heteromys sp	Spiny pocket mouse	0.04 -	0.09	0.07	n/a

* Average mass is taken as the mid-point of the range; used to calculate the biomass of each species consumed per scat

†1.98 + 0.035 × average live weight of species (Ackerman *et al*. 1984); only calculated for prey ≥ 2 kg

‡Calf weight

Note, non-mammalian prey species included birds (unknown size) and iguanas (*Iguana iguana*), estimated to be ~ 5 kg

Scat sample size required to represent diet

The influence of scat sample size on the number of taxa identified in big cat diets was investigated using data from 23 published studies of neotropical jaguar and pumas. Where published studies compared diet in multiple samples from the same region, for example between habitats or seasons, each sample was treated as a single data point (jaguar $n = 21$, puma $n = 26$, plus data from this study). Data points were classed as 'forest' or 'grassland, savannah and shrublands' to account for potential differences in the number of available prey taxa between ecoregions (Table 6.3).

Table 6.3 Ecoregion classification of the data points derived from 23 published studies of diets of neotropical jaguar and pumas

Ecoregions	**Number of data points**	
	Jaguar	**Puma**
1) Forests		
- tropical and subtropical moist broadleaf forest[1]	13	9
- tropical and subtropical dry broadleaf forest[2]	2	2
- temperate broadleaf and mixed forests[3]	-	6
2) Grassland, savannah and shrubland		
- deserts and xeric shrublands[4]	1	1
- tropical and subtropical grassland, savannahs and shrublands[5]	1	1
- flooded grasslands and savannahs[6]	4	-
- montane grasslands and shrublands[7]	-	1
- temperate grasslands, savannahs and shrublands[8]	-	6

Forest: **1** - Aranda and Sánchez-Cordero 1996, Mexico; Azevedo 2008, Brazil; Chinchilla 1997, Costa Rica; Crawshaw *et al.* 2004, Brazil; Emmons 1987, Peru; Facure and Giaretta 1996, Brazil; Garla *et al.* 2001, Brazil; Kuriowa and Ascorra 2002, Peru; Leite and Galvão 2002, Brazil; Moreno *et al.* 2006, Panama; Novack *et al.* 2005, Guatemala; Rabinowitz and Nottingham 1986, Belize; Weckel *et al.* 2006b, Belize; **2** - Núñez *et al.* 2000a, Mexico; Taber *et al.* 1997, Paraguay; **3** - Rau *et al.* 1991, Chile; Rau and Jiménez 2002, Chile; Yáñez *et al.* 1996, Chile.
Grasslands, savannahs & shrubland: **4** - Olmos, 1993, Brazil; **5** - Polisar *et al.* 2003, Venezuela; **6** - Azevedo and Murray 2007, Brazil; Dalponte *et al.* 2002, Brazil; **7** - Romo 1995, Peru; **8** - Branch *et al.* 1996, Argentina; Yáñez *et al.* 1996, Chile.

Because the range of potential prey species in this study area was wide (Table 6.2), it was deemed appropriate to estimate the number of scats required to adequately represent diet. The total numbers of species consumed, and the relative occurrence of each prey species, were calculated for ten randomly selected jaguar scats. Scats were then added to the sample in groups of five (up to 100 scats), each time recalculating the species total and the relative occurrence. This was repeated 25 times. The decelerating regressions of mean species total and mean occurrence of each prey species against the cumulative numbers of scats (10, 15, 20 … 100 scats) were used to estimate the asymptotic scat count. This process was repeated for puma scats.

Food habits of jaguars and pumas

Relative prey consumption of the most commonly eaten prey species ($\geq 5\%$ occurrence), were compared between jaguars and pumas, and between locations (protected forest, unprotected forest buffer contiguous with protected forest, unprotected fragmented habitat), using chi-square tests. Although it is impossible to determine where the contents of the scats were hunted and eaten it is assumed that scat location equates to the hunting area.

Food niche breadth

Food niche breadth was calculated in terms of dietary diversity for jaguars and pumas following Levins (1968):

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2} \qquad \text{(Eqn 6.4)}$$

where p_i is the relative occurrence of a prey taxon in the diet. B ranges from one (minimum niche breadth, maximum specialization) to n, where n is the total number of prey taxa (Krebs 1999); for example, $B = 5$ if the diet consisted of five taxa that were consumed in equal proportions. The index was standardized following Colwell and Futuyma (1971) to allow comparisons of diet breadth between predator species and between locations:

$$B_{sta} = \frac{(B_{obs} - B_{\min})}{(B_{\max} - B_{\min})} \qquad \text{(Eqn 6.5)}$$

where B_{obs} is the observed niche breadth, B_{min} is the minimum niche breadth (1) and B_{max} is the maximum niche breadth (n). B_{sta}, the standardized niche breadth, ranges between zero and one.

Food niche overlap

The overlap in prey use between jaguars and pumas was calculated using the Pianka (1973) measure of niche overlap:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^{2} \sum_{i}^{n} p_{ik}^{2}}} \qquad \text{(Eqn 6.6)}$$

O_{jk} = Pianka's measure of niche overlap between species j and species k

p_{ij} = proportion resource i is of the total resources used by species j

p_{ik} = proportion resource i is of the total resources used by species k

n = total number of resource states

A value of 0 indicates complete dissimilarity, and a value of 1 indicates complete similarity. Monte Carlo simulations (1000) were run using the program EcoSim 7 (Gotelli and Entsminger 2008) to determine whether the observed overlap was greater or lower than that expected from random, following Walker *et al.* (2007). The randomisation algorithm was constrained to retain zero states (i.e. prey that are never taken in the actual dataset are also never taken in the simulations) but relax the diet breadth (i.e. values of relative prey occurrence which are > 0 are replaced with random prey proportions in the simulations). All prey species were assumed to be equally available to both cat species.

Mean weight of vertebrate prey

The mean weight of the vertebrate prey items consumed (MWVP) is frequently reported in diet studies as a method of comparing diet between carnivores. Since body weight of prey taken is likely to have a skewed frequency distribution, most studies follow Jacksic and Brakker (1983) and calculate the geometric mean by computing the arithmetic mean of the $\log_e$-transformed values then use exponentiation to return the computation to the original scale. Walker *et al.* (2007) suggest that this method underestimates the mean weights and they recommend using the arithmetic mean for which asymmetric confidence intervals can be calculated. For this study MWVP was calculated as a geometric mean for comparison with contemporary studies of jaguar and puma diet.

Jaguar and puma energetics

The numbers of individuals of each prey species killed per year by adult jaguars and pumas were estimated from the relative biomass consumed (Eqn 6.3), and estimates of jaguar and puma energetic requirements were derived from the literature and field data. Simple harvest models were used to determine the prey density necessary to maintain sustainable off-take.

Estimates of prey off-take

The cats were assumed to require 34-43 g of meat per day per kg of body mass (after Emmons 1987; following Polisar *et al.* 2003, Novack *et al.* 2005, Azevedo and Murray 2007). Body mass of jaguars and pumas varies by a factor of two across their geographic range (Chapter 1), with Belizean populations being amongst the smallest (e.g. Iriate *et al.* 1990). Mean body masses were estimated from adult cats trapped in Belize: male jaguar 51 kg (n = 8), female jaguar 44 kg (n = 3), male puma 35 kg (n = 3) and female puma 21 kg (n = 1) (Rabinowitz and Nottingham 1986, R. Foster this study, O. Figueroa unpubl. data); and used to calculate the annual intake of meat per cat in each sex/species category. Energetic requirements of females increase during pregnancy, nursing and when with dependents, for example in domestic cats energy intake can increase three-fold during peak lactation (Loveridge 1986). Estimates of female reproductive energy requirements of wild jaguars and pumas either follow Sunquist (1981) who estimated that a tiger cub requires 25% of its mothers requirements during its first year and thereafter consumption is equivalent to that of its mother (e.g. Polisar *et al.* 2003, Azevedo and Murray 2007), or they assume that female requirements approximately double when she has kittens (e.g. Núñez *et al.* 2000a). In this study reproductive correction factors were derived from Laundré (2005) who used an allometric equation to calculate energy demand of wild pumas based on movement data from telemetry. His estimates indicate that the daily intake of meat of a solitary female puma increases by a factor of 1.1 during gestation, 1.5 during nursing and 3.2 during dependence (cubs taking solid food) when raising an average litter of 2.6 young. These correction factors were applied to estimates of solitary female requirements, in order to calculate the amount of meat required during pregnancy, lactation and dependency. The estimates were then adjusted by the average lengths of pregnancy, lactation and dependency (Table 6.4) and combined to give the average annual requirements of a reproductively active female of each cat species.

Table 6.4 Reproductive periods of jaguars and pumas derived from Kitchener (1991) and Sunquist and Sunquist (2002)

	Jaguar (days)	Puma (days)
Gestation	96	93
Nursing (full-time)*	74	60
Dependents (solid food)	556	480

* Note that jaguars may continue partial nursing for 5-6 months, but this is excluded from estimates

The mass of each prey species consumed per year for each cat sex/species category was calculated as the product of the relative biomass consumed and the annual intake. Note that for prey >15 kg, 30% of the carcass was assumed to be inedible (e.g. skulls, large bones) following Emmons (1987) and Polisar *et al.* (2003).The same assumption was also applied to armadillo which are covered by a hard carapace (following Novack *et al.* 2005). In addition, large cats may not fully utilise the edible parts of a carcass; for example it may be abandoned if it spoils, if there is a high availability of alternative prey or if they are disturbed. Rates of decomposition and the tolerance for perished meat are difficult to estimate, making it difficult to estimate the extent to which the edible parts of a large carcass are utilised by the predator. However, in this study scats containing remains of white-lipped peccary frequently included hooves of adults (R. Foster pers. obs., B. Harmsen, Panthera Belize, pers. comm.). The feet are likely the last part of a carcass consumed, if at all, with priority given to internal organs and soft tissue. The fact that cats in the protected forest consumed the feet of white-lipped peccary, the largest wild prey taken, implies that they did not abandon carcasses, but consumed them fully. Within the protected forest it is assumed that disturbance at feeding sites is negligible, and decomposition based on field observations is estimated to be ~ 5 days (B. Harmsen pers. comm.). It can thus be assumed that a white-lipped peccary (~ 33.5 kg) can be eaten within 5 days. Accounting for 30% wastage, this would require an average consumption of ~ 4.7 kg per day over the 5-day period. This is higher than the daily requirements of a jaguar, and allows for a feast-famine cycle in which they may not succeed in catching prey every day. These figures can be used to estimate the extent to which carcasses of large domestic species may be utilised, given that disturbance rates by livestock owners may be high. A solitary undisturbed jaguar could consume 23.5 kg of a 125-kg calf before decomposition. If disturbed after two days, as was common, (cow boys frequently moved carcases, R.

Foster pers. obs.) then a solitary jaguar can only consume ~ 9.4 kg of the 125-kg calf, whilst a female with two dependents could jointly eat three times this amount.

The number of each prey species killed per year was thus calculated by dividing the mass of each prey species consumed per year by the mean prey mass (Table 6.2) or, for domestic species, by the mass of prey assumed to be eaten per carcass (under different levels of disturbance). The number of kills per year was compared between cat species, sex, reproductive status (females only) and habitat (protected forest, fragmented landscape).

Sustainability of prey off-take

Simple models have been developed within the bush meat and fisheries literature to determine whether hunting is sustainable in the absence of detailed demographic data (e.g. Robinson and Redford 1991, Wade 1998). Basic life history parameters and density estimates are used to estimate the maximum number of prey animals available for off-take per unit area (P_{max}). Hunting is considered unsustainable if extraction exceeds this threshold. Unless the stochastic nature of reproduction and survival are incorporated into the model the sustainable harvest will tend to be overestimated; as such these models are used to determine whether hunting is unsustainable, rather than if it is sustainable (Slade *et al.* 1998, Salas and Kim 2002). In this study, a harvest model of P_{max} (Robinson and Bodmer 1999, Eqn 6.7) was rearranged to estimate the threshold prey population (D) below which the observed harvest would be unsustainable. For the purposes of this study D was interpreted as the minimum prey abundance that is required to sustain the observed levels of off-take by jaguars and pumas, recognising the fact that this may be an underestimate.

$$P_{max} = 0.5\, D\, \varphi\, F \qquad \text{Eqn. 6.7}$$

where φ is the prey fecundity and F is a prey 'mortality factor'. The value of D is multiplied by 0.5, assuming a 1:1 sex ratio, to give the female density. The value of φ is derived from field data of average numbers of litters per year and young per litter. The parameter F attempts to account for natural mortality. It is assumed that natural mortality depends on average lifespan, and F is approximated to 0.2 for species with lifespan >10 yrs, 0.4 for 5-10 yrs and 0.6 for < 5 yrs (Robinson and Redford 1991). However given that the survival of juvenile mammals is usually lower than in subsequent years, the term 'φ F' will overestimate survival. If pre-reproductive survival is known it can be substituted for the mortality factor to improve the estimate. In this study no attempt was made to incorporate levels of pre-reproductive survival into the models. Estimates of φ and F for the main wild prey species were derived from the literature (Table 6.5) and used to estimate the population sizes (D) required to sustain the levels of off-take by jaguars and pumas (P_{max}). Estimates were compared between species and habitats and used to make inferences about jaguar and puma reproduction and co-existence in the study area.

Table 6.5 Estimates of φ and F for the main wild prey species

Species	**φ** (offspring per female per year)	***F*** (mortality factor)
Nine-banded armadillo[1]	4.0	0.4
White-lipped peccary[2]	1.5	0.2
White-nosed coati[3]	4.0	0.4
Paca[4]	2.5	0.2
Red brocket deer[5]	1.2	0.4
Kinkajou[6]	1.0	0.2

[1]Loughry and McDonough 2001; [2]Gottdenker and Bodmer 1998, [3]Robinson and Redford 1986, Marceau 2001, Hass and Valenzuela 2002; [4]Dubost *et al.* 2005; [5]Hurtado-Gonzales and Bodmer 2006; [6]Kays and Gittleman (2001), Rehder and Olson (2007)

Results

A total of 362 jaguar scats were collected between January 2003 and October 2006. Of these, 27 did not contain prey remains, and a further 13 contained only unidentifiable remains. The 322 scats with identifiable prey items contained 378 distinct items, of which 348 were identified to species level, six to genus, two to family, five to sub-order, seven to order, and 10 to class. An average of 1.2 prey items (maximum = 3) were identified per scat (260 scats only contained one prey item). A size class was assigned to 372 of the prey items (from 320 scats).

A total of 135 puma scats were collected between February 2003 and September 2006. Of these, six scats did not contain prey remains, and a further two contained only unidentifiable remains. The 127 scats with identifiable prey contained 140 prey items, of which 133 were identified to species level, five to sub-order and two to order. An average of 1.1 prey items (maximum = 3) were identified per scat (114 scats only contained one prey item). A size class was assigned to 141 prey items (from 128 scats).

Scat sample size required to represent diet

The sample sizes of scats presented in 23 published studies of jaguar and puma diet across the neotropics rarely exceeded 75 scats (jaguar mean ± SE = 52 ± 12, *n* = 21, puma = 69 ± 17, *n* = 26). Figure 6.2 shows a trend for the number of taxa detected in the diet to increase and then plateau with increasing sample size, both for forested and grassland ecoregions. Given the generally high biodiversity of habitats across the neotropical geographical ranges of these cats (e.g. Myers *et al*. 2000), it is unlikely that smaller sample sizes were coincidentally collected in areas with a lower diversity of prey. However it is noted that the number of taxa in puma diet plateaus at a smaller sample size in grasslands than for the other ecoregion/species classes. This is probably because the majority of data points for this class originate from temperate grasslands of Argentina and Chile (Table 6.3) where the diversity of terrestrial vertebrates may be lower than, for example, the moist tropical forests of Central America and Amazonia or the grasslands of the Pantanal in Brazil. Overall Figure 6.2 suggests that within the neotropics, particularly the tropical ecoregions, samples with less than approximately 100 scats may fail to detect all taxa present in the diet, and that researchers should consider the potential prey diversity of the habitat in which they are working when assessing a suitable sample size to represent diet.

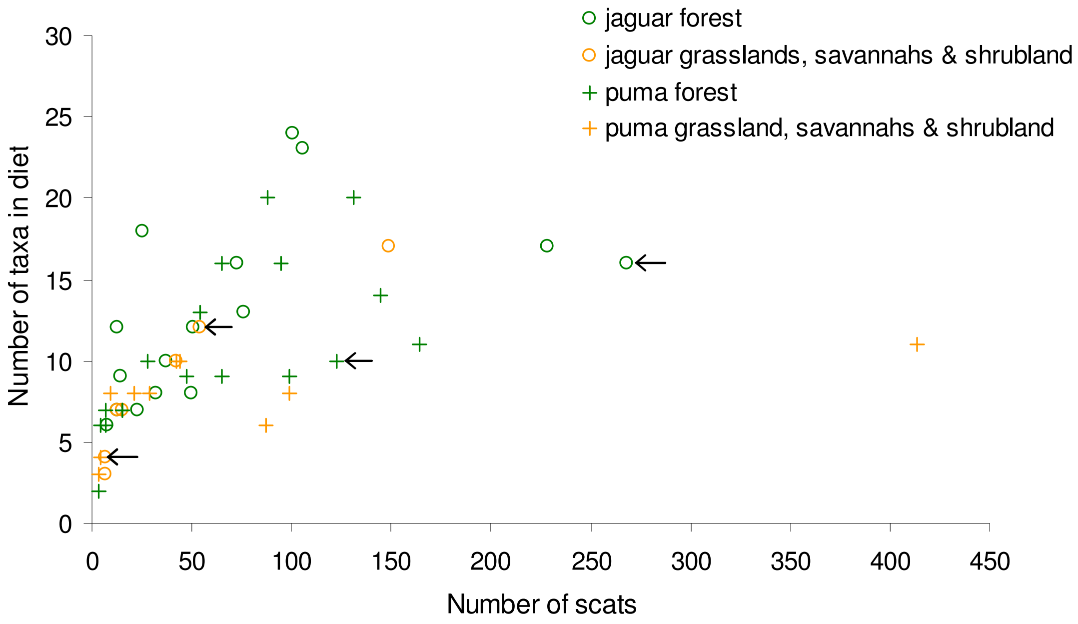


Figure 6.2 Variation in number of taxa detected in jaguar and puma diets with sample size from 23 published studies (listed in Table 6.3) from the neotropics. Data points are categorized according to ecoregion as ‘forest’ (green symbols) or ‘grasslands, savannahs and shrublands’ (orange symbols). Arrows indicate data from this study.

The sample size required to reliably represent diet in this study was investigated by randomly selecting samples of scats and comparing the species total and relative occurrence of different prey to those obtained from the entire dataset. Prey items that could not be identified to an acceptable level were excluded from this analysis (e.g. ‘unknown mammal’, ‘carnivore’ etc), leaving 312 jaguar scats (363 prey items) and 126 puma scats (139 prey items) available for random selection of samples.

The species accumulation curves indicated that even 100 randomly selected scats were insufficient to detect all 20 taxa known to be present in the 312 jaguar scats; however as few as 45 scats were sufficient to detect the six most common prey (≥ 5% relative occurrence) (Figure 6.3). This suggests that analyses based on < 100 samples may underestimate the true richness of the jaguars’ diet, shown previously in Figure 6.2. Although the most important prey will be detected, their relative occurrence will tend to be overestimated as the occurrence of rare prey may not be detected at all. Similarly, 100 randomly selected scats failed to detect all 11 taxa previously identified in the puma diet with 126 scats; however 40 scats were sufficient to detect the five most common prey species (Figure 6.4).

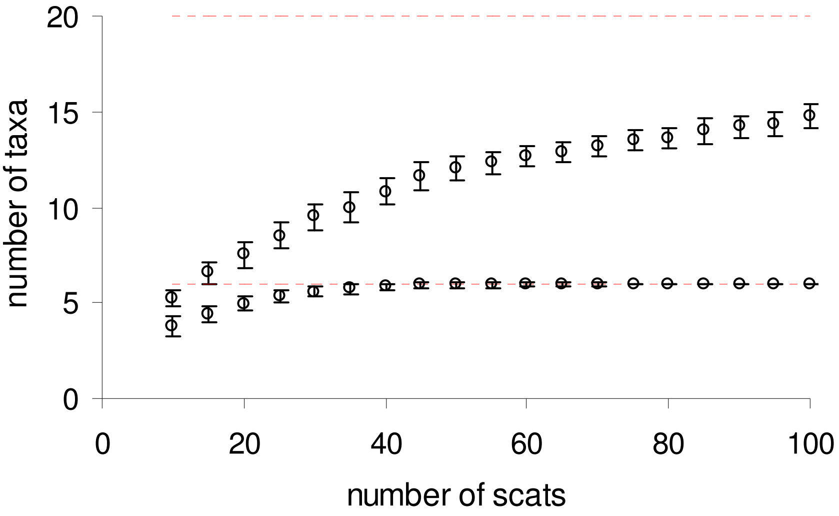


Figure 6.3 Species accumulation curves for jaguar diet. Mean and 95%CI shown for 25 trials. Red dashed line indicates number of species detected with 312 jaguar scats **upper** - all taxa, **lower** - six most common species (≥ 5% relative occurrence).

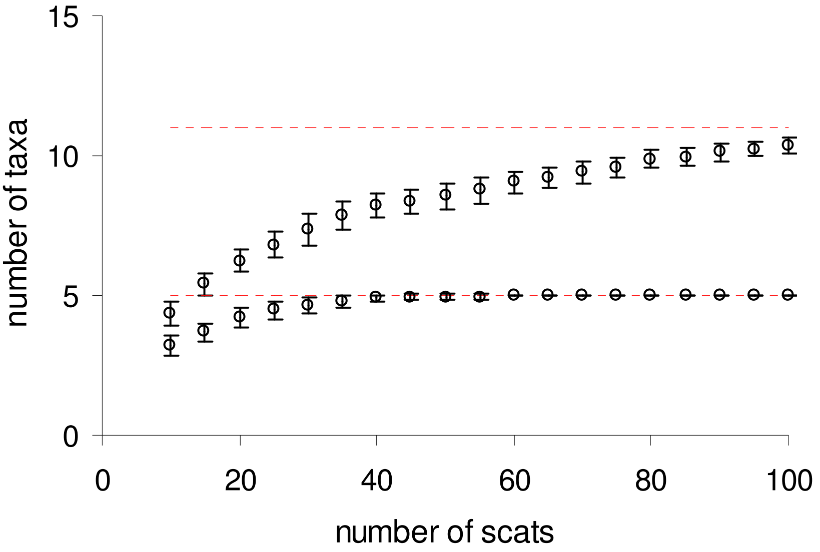
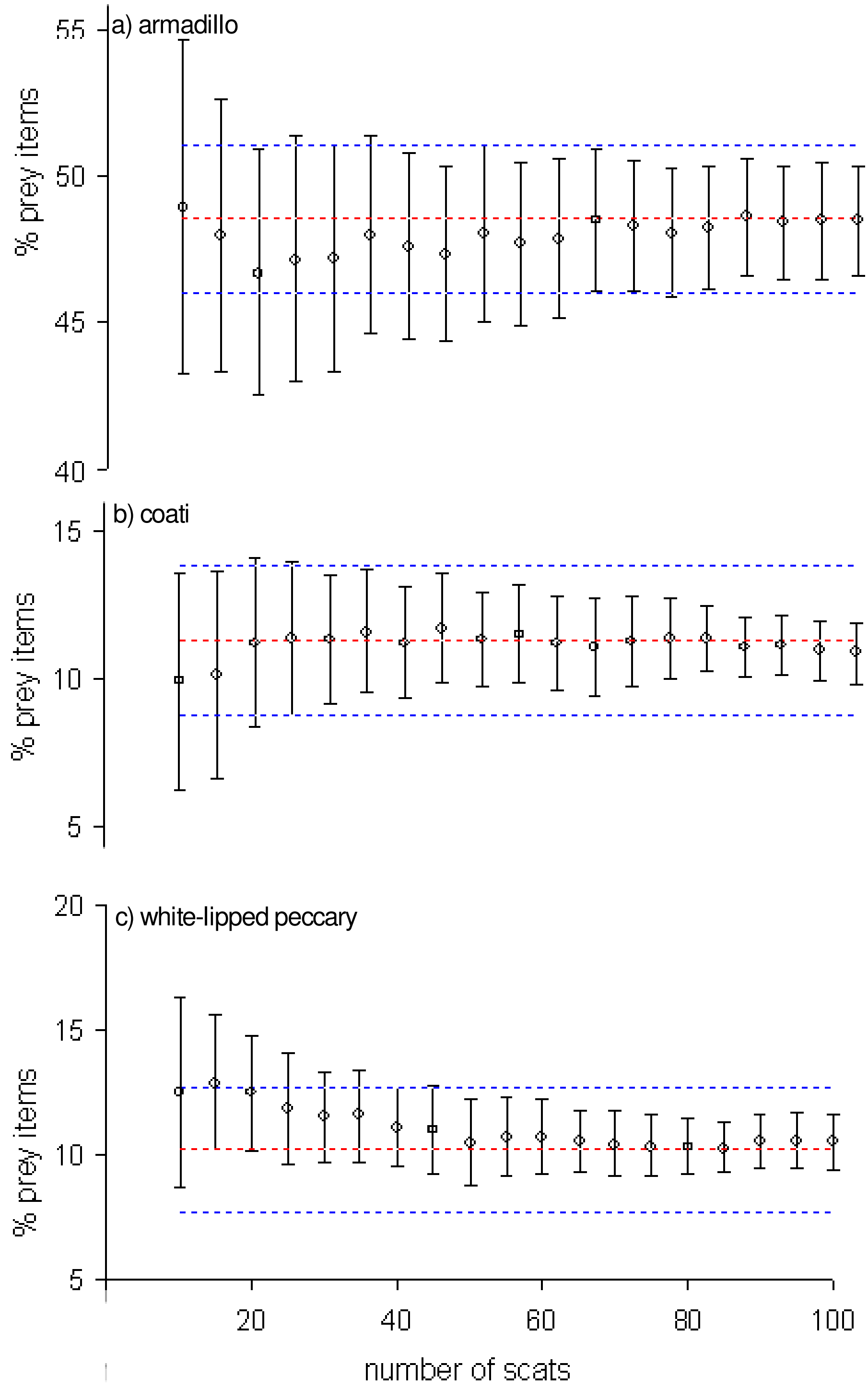


Figure 6.4 Species accumulation curves for puma diet. Mean and 95%CI shown for 25 trials. Red dashed line indicates number of species detected with 126 puma scats **upper** - all taxa, **lower** - five most common species (≥ 5% relative occurrence).

The minimum number of jaguar scats required to estimate relative occurrence of the most common prey within ± 2 % varied between the six main species, from ~ 65 scats for armadillo to 15 scats for paca (Figure 6.5a-f). For pumas the minimum number of scats required varied from ~ 65 for paca to 25 for kinkajou (Figure 6.6a-e). It is not clear why mean relative occurrence is consistently underestimated for some species (e.g. armadillo and paca, Figure 6.5a and e) but overestimated for others (e.g. white-lipped peccary and sheep, Figure 6.5c and f). It does not appear to depend on the frequency with which the target species occurs with other species within the same scat (e.g. 38% of scats which contained white-lipped peccary also contained other species, compared to only 12% for scats containing sheep).


a) armadillo
% prey items
55
50
45
40
b) coati
% prey items
15
10
5
c) white-lipped peccary
% prey items
20
15
10
5
20
40
60
80
100
number of scats

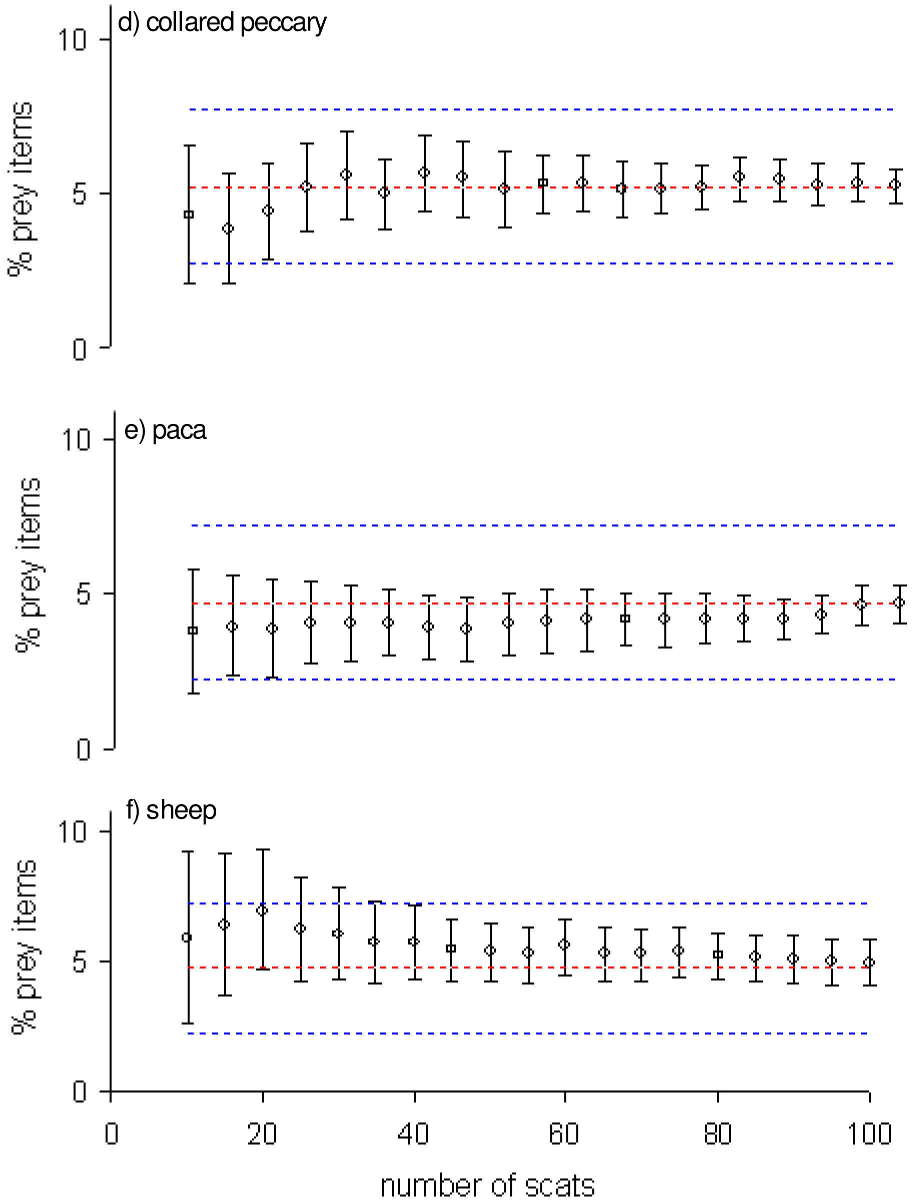
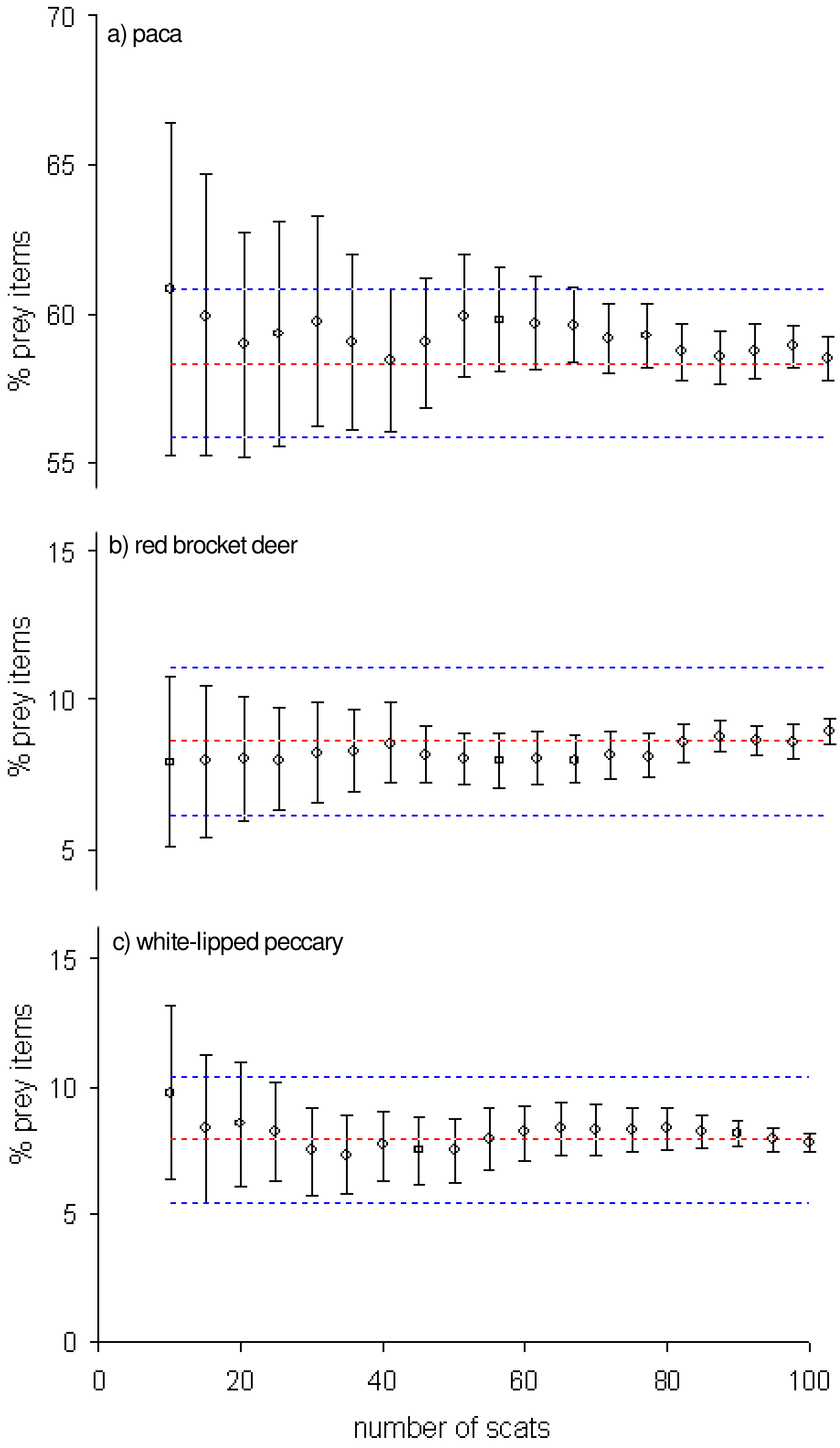


Figure 6.5 Relative occurrences of six principal species in jaguar diet against number of randomly-selected scats. Mean and 95%CI shown for 25 trials. Dashed lines indicate % occurrence (and ± 2) estimated with all 312 jaguar scats.
a) armadillo, **b)** coati, **c)** wari, **d)** collared peccary, **e)** paca, **f)** sheep


a) paca
70
65
60
55
% prey items
b) red brocket deer
15
10
5
% prey items
c) white-lipped peccary
15
10
5
0
% prey items
0
20
40
60
80
100
number of scats

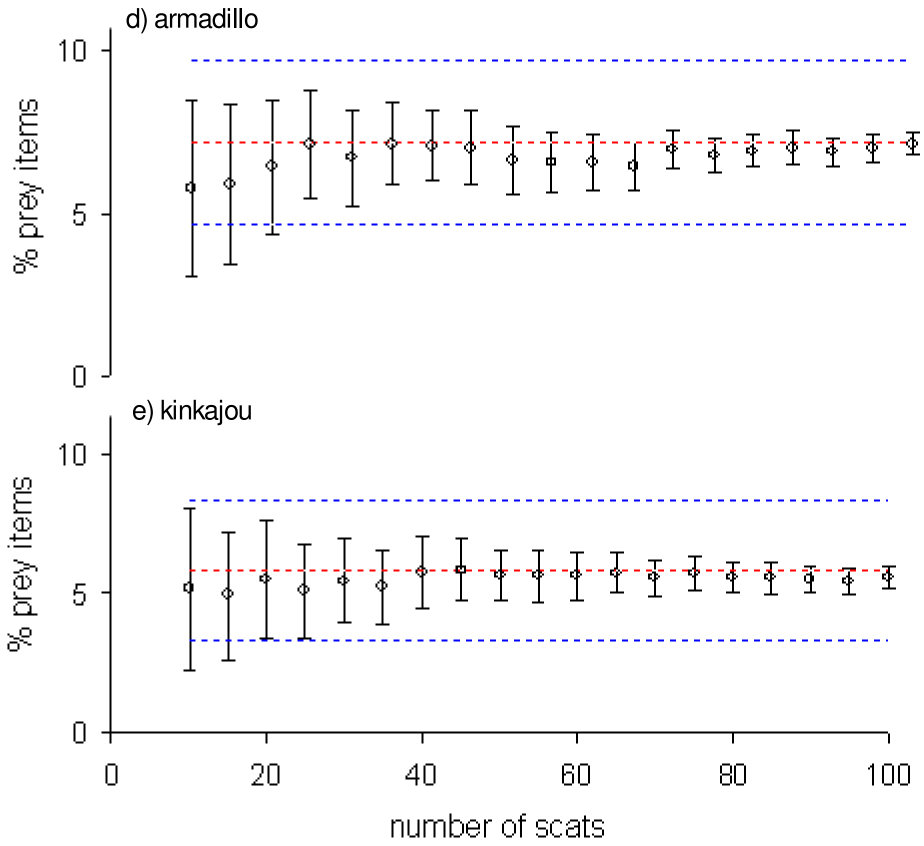


Figure 6.6 Relative occurrences of five principal species in puma diet against number of randomly-selected scats. Mean and 95%CI shown for 25 trials. Dashed lines indicate % occurrence (and ± 2) estimated with all 126 puma scats.
a) paca, **b)** red brocket deer, **c)** wari, **d)** armadillo, **e)** kinkajou

Diet of jaguars and pumas

Across the entire study region of protected and unprotected areas, jaguar diet included at least 20 species: 15 wild mammals, three domestic mammals, one reptile and one bird (Table 6.6). Although the diet had a high species richness, it was not diverse, with $B_{sta} = 0.143$. Four species were frequently used (≥ 5% relative occurrence).The prey most often consumed by jaguars were armadillos, which made up 47% of the prey items and constituted 42% of the total biomass eaten. The next most frequent prey item were coatis, accounting for 11% of the prey items, then white-lipped peccaries at 10% (9% adults, 1% juvenile), and collared peccaries at 5% (4% adults, 1% young). The remaining species each comprised < 5% of the diet. MWVP was 7.6 kg (*n* = 372 prey items).

Table 6.6 Relative occurrences and consumed biomasses of prey species (ordered by mass) in 322 jaguar scats collected across the study area Jan 2003 to Oct 2006. *n* = 378 prey items

Prey Species	Relative occurrence (%)	Relative biomass† (%)
> 10 kg		
Cow	2.9	7.7
White-lipped peccary (adult)	8.7	11.5
Sheep	4.5	5.7
Red brocket deer	2.9	3.3
Collared peccary (adult)	3.7	4.1
Dog	0.3	0.3
Unknown peccary (adult)	0.3	0.3
5-10 kg		
Paca	4.5	4.3
Northern tamandua	0.8	0.7
Northern raccoon	0.3	0.2
Nine-banded armadillo	46.4	41.9
White-lipped peccary (juvenile)	1.1	1.0
Collared peccary (juvenile)	1.3	1.2
Iguana	1.3	1.2
Unknown peccary (juvenile)	0.3	0.3
Paca/armadillo	0.3	‡
Unknown mammal	0.8	1.0
2-5 kg		
White-nosed coati	10.8	9.7
Kinkajou	2.6	2.3
Skunk	0.3	0.2
Grey fox	0.3	0.2
Greater grison	0.8	0.7
Unknown carnivore	1.3	1.2
< 2 kg		
Virginia/common opossum	1.3	0.9
Rodent	0.3	<0.1
Spiny pocket mouse	0.3	<0.1
Unknown size		
Unknown mammal	1.1	-
Unknown bird	0.5	-

† *n* = 372 because sizes of six prey items are unknown (320 scats)
‡ Combined with unknown mammal category for biomass calculation

Puma diet contained at least 11 species: eight wild mammals, two reptiles and one decapod (freshwater crustacean) (Table 6.7). Unlike jaguars, there was no evidence that pumas took domestic species. Four species were frequently used. The species most frequently consumed by pumas were pacas, which made up 58% of the prey items and constituted 57% of the total biomass eaten. The next most frequent was red brocket deer, accounting for 9% of the prey items, then armadillos at 7%, and kinkajous at 6%. The remaining species each comprised < 5% of the diet. Although puma diet was less species-rich than jaguar diet, it was slightly more diverse, with $B_{sta} = 0.174$. MWVP was 8.5 kg ($n = 138$).

Table 6.7 Relative occurrences and consumed biomasses of prey species (ordered by mass) in 127 puma scats collected across the study area Feb 2003 to Sep 2006. n = 140 prey items

Prey Species	Relative occurrence (%)	Relative biomass† (%)
> 10 kg		
White-tailed deer	0.7	1.0
White-lipped peccary (adult)	3.6	4.9
Red brocket deer	8.6	10.2
Collared peccary (adult)	2.9	3.3
5-10 kg		
Paca	57.9	57.3
Nine-banded armadillo	7.1	6.7
White-lipped peccary (juvenile)	4.3	4.2
Collared peccary (juvenile)	0.7	0.7
Iguana	4.3	4.0
2-5 kg		
Kinkajou	5.7	5.2
Mexican porcupine	2.1	1.9
Unknown carnivore	0.7	0.7
< 2 kg		
Decapod (FW crustacean)	0.7	<0.1
Unknown size		
Snake	0.7	-

† n = 139 because size of one prey item is unknown

Comparison of jaguar and puma diets

Puma scats were not found everywhere across the study area: 97% were located within the forest block, of which 89% were within the protected forest (Table 6.8). For this reason direct comparisons between jaguar and puma diet are restricted to the protected forest.

Table 6.8 Location and number of scats with identifiable prey remains

Location	Jaguar	Puma
Contiguous forest block	268	123
- *protected*	*204*	*110*
- *unprotected buffer*	*38*	*11*
- *protected status unknown*	*26*	*2*
Fragmented landscape	54	4
Total	**322**	**127**

Inside the protected forest jaguar diet was richer than puma diet (14 versus nine prey species); however puma diet was more diverse (jaguar: B_{sta} = 0.113, three frequently used prey; puma B_{sta} = 0.169, five frequently used prey). The same pattern was observed across the entire forest block of protected forest and buffer areas (jaguar: 16 prey species, B_{sta} = 0.108, four frequently used prey; puma: 10 prey species, B_{sta} = 0.162, five frequently used prey).

Inside the protected forest, jaguar and puma diets were not similar (Table 6.9). Diet overlap was 0.246 (Pianka index). This was less than expected by chance: the simulated mean overlap obtained from 1000 randomisations was 0.479 (variance 0.013), significantly higher than the observed overlap ($p < 0.05$). Other studies have also found low dietary overlap between jaguars and pumas in closed forest habitats (reviewed in Harmsen 2006). Significantly low niche overlap, as observed here, is conventionally interpreted as inter-specific competition and resource partitioning (Gotelli and Entsminger 2008). Competition is best shown by a shifted realised niche in sympatry compared to the fundamental niche in allopatry, however experimental manipulations would be required to test for these processes. The same pattern was observed for scats pooled across the entire forest block with a Pianka index of 0.236, significantly lower than expected by chance (1000 randomisations, p < 0.05).

Within the protected forest the dominant size class taken by both cats was 5-10 kg. The MWVP taken by jaguars was 7.1 kg (n = 236), and 8.6 kg (n = 121) by pumas. Jaguars ate more armadillos and coatis compared to pumas (armadillo $\chi_1^2 = 68.9$, $p <$ 0.0001; coati $\chi_1^2 = 12.5$, $p < 0.0001$, Appendix A: Tables A6.1-2). Pumas ate more paca and red brocket deer compared to jaguars (paca $\chi_1^2 = 132.7$, $p < 0.0001$; red brocket deer $\chi_1^2 = 5.3$, $p < 0.05$, Appendix A: Tables A6.3-4). Jaguars and pumas did not differ in the frequencies of white-lipped peccaries or kinkajous taken (white-lipped peccary $\chi_1^2 = 2.6$, $p > 0.1$; kinkajou $\chi_1^2 = 0.5$, $p > 0.5$, Appendix A: Tables A6.5-6). However jaguars tended to take adult white-lipped peccary more frequently than did pumas: 85% of jaguar scats containing white-lipped peccary remains were identified as adult remains, compared to only 45% for puma. The same patterns were observed for scats pooled across the entire forest block (Appendix A: Tables A6.7-12). Across the entire forest block MWVP of pumas was the same as in the protected forest (8.6 kg, n = 133), but jaguar MWVP was 6.8 kg (n = 308), lower than the protected forest.

Table 6.9 Relative occurrences and consumed biomasses of prey species (ordered by mass) in jaguar and puma scats collected in the protected forest Jan 2003 to Oct 2006.

Prey Species	**Relative occurrence (%)**		**Relative biomass (%)**	
	Jaguar	**Puma**	**Jaguar**	**Puma**
> 10 kg				
White-lipped peccary (adult)	13.8	4.1	18.9	5.6
Red brocket deer	3.3	9.0	4.0	10.7
Collared peccary (adult)	2.9	3.3	3.4	3.7
Unknown peccary (adult)	0.4	-	0.5	-
5-10 kg				
Paca	4.6	58.2	4.6	57.2
Northern tamandua	1.3	-	1.2	-
Nine-banded armadillo	50.8	6.6	47.9	6.1
White-lipped peccary (juvenile)	1.3	4.9	1.2	4.8
Collared peccary (juvenile)	1.3	0.8	1.2	0.8
Iguana	1.3	3.3	1.2	3.0
Unknown peccary (juvenile)	0.4	-	0.4	-
Unknown mammal	0.4	-	0.4	-
2-5 kg				
White-nosed coati	9.6	-	9.0	-
Kinkajou	4.2	5.7	3.8	5.2
Grey fox	0.4	-	0.4	-
Greater grison	0.8	-	0.8	-
Mexican porcupine	-	2.5	-	2.2
Unknown carnivore	0.8	0.8	0.8	0.7
< 2 kg				
Virginia/common opossum	0.4	-	0.4	-
Spiny pocket mouse	0.4	-	<0.1	-
Decapod (FW crustacean)	-	0.8	-	<0.1
Unknown size				
Unknown mammal	1.3	-	-	-
Unknown bird	0.4	-	-	-
Total prey items	240	122	236	122
Total scats	204	110	202	110
MWVP (kg)	-	-	7.1	8.6

Variation in jaguar diet across the landscape

Outside the protected forest, jaguar diet contained at least 15 species, including three domestic mammals (Table 6.10). Five species were frequently taken (including cattle and sheep) and jaguar diet was more diverse than inside the protected forest (B_{sta} = 0.427 outside compared to 0.113 inside). Unlike the protected forest, where almost 50% of the diet depended on armadillo (Table 6.9), the biomass consumed in the unprotected lands was more evenly distributed between armadillo, cattle, sheep and coati (Table 6.10). The high reliance of jaguar on domestic species (43% of biomass consumed) is of concern for conservation management. However, scats from farms may have been over represented in the dataset: 45% (41/92) scats collected outside the protected forest were from farms, but these pastures constituted only ~5 % of the available lands (Chapter 4) and jaguars were known to be equally or more active in other unprotected habitats (Chapter 5). It was not considered appropriate to measure the dietary overlap because the availability of different prey species almost certainly differed substantially between the areas, given their differences in habitat.

Table 6.10 Relative occurrences and consumed biomasses of prey species (ordered by mass) in 92 jaguar scats collected outside the protected forest Jan 2003 to Oct 2006. *n* = 108 prey items.

Prey Species	**Relative occurrence (%)**	**Relative biomass† (%)**
> 10 kg		
Cow	10.2	24.2
Sheep	15.7	17.8
Red brocket deer	0.9	1.0
Collared peccary (adult)	4.6	4.6
Dog	0.9	0.9
5-10 kg		
Paca	3.7	3.1
Northern raccoon	0.9	0.8
Nine-banded armadillo	33.3	26.8
Collared peccary (juvenile)	1.9	1.6
Iguana	1.9	1.5
Unknown mammal	0.9	0.8
2-5 kg		
White-nosed coati	14.8	11.8
Skunk	0.9	0.7
Greater grison	0.9	0.7
Unknown carnivore	1.9	01.5
< 2 kg		
Virginia/common opossum	3.7	2.3
Rodent	0.9	0.1
Unknown size		
Unknown mammal	0.9	-
Unknown bird	0.9	-

† *n* = 106 because size of two prey items are unknown (92 scats)

Outside the protected forest, jaguar MWVP was 9.5 kg (*n* = 106), greater than inside the reserve (7.1 kg, Table 6.9); however this falls to 5.1 kg (*n* = 77) if domestic species are excluded. Partitioning the data further, in the unprotected forest buffer jaguar MWVP was 5.7 kg (*n* = 42) (or 5.6 kg, *n* = 41, excluding single domestic prey item), and 13.2 kg (*n* = 64) in the unprotected fragmented landscape (or 4.5 kg, *n* = 36 excluding domestic species). Although the puma sample is small it is worth noting that puma MWVP outside the protected forest was 8.4 kg ($n = 15$) and contained no domestic species.

Jaguars ate more white-lipped peccaries inside the protected forest than outside (white-lipped peccary $\chi_1^2 = 18.1$, $p < 0.0001$, Figure 6.7, Appendix A: Table A6.13). No scats found outside the protected forest contained white-lipped peccaries, suggesting that, as a favoured game species by hunters, they may be scarce or absent in the unprotected lands. Jaguars ate more domestic livestock outside the protected area than inside (cow Fisher's exact test odds ratio= 0.02, $p < 0.0001$; sheep $\chi_1^2 = 39.7$, $p < 0.0001$, Figure 6.7, Appendix A: Tables A6.14-15). No scats found inside the protected forest contained domestic species; this is expected as there are no livestock holdings within the protected area, or contiguous forest buffer. Jaguars ate the same amount of armadillos inside unprotected forest buffer as in the protected forest (armadillo $\chi_1^2 = 0.1$, $p > 0.8$, Figure 6.7, Appendix A: Table A6.16), but more coatis and collared peccaries (coati $\chi_1^2 = 6.6$, $p < 0.05$; collared peccary Fisher's exact test odds ratio = 0.27, $p < 0.05$, Figure 6.7, Appendix A; Tables A.17-18). Outside the protected forest, jaguars ate more armadillos, coatis and collared peccaries in the forest buffer than in the unprotected fragmented landscape (armadillo $\chi_1^2 = 7.7$, $p < 0.01$; coati $\chi_1^2 = 4.0$, $p < 0.05$; collared peccary Fisher's exact test odds ratio = 10.4, $p < 0.02$, Figure 6.7, Appendix A: Tables A.6.19-21).

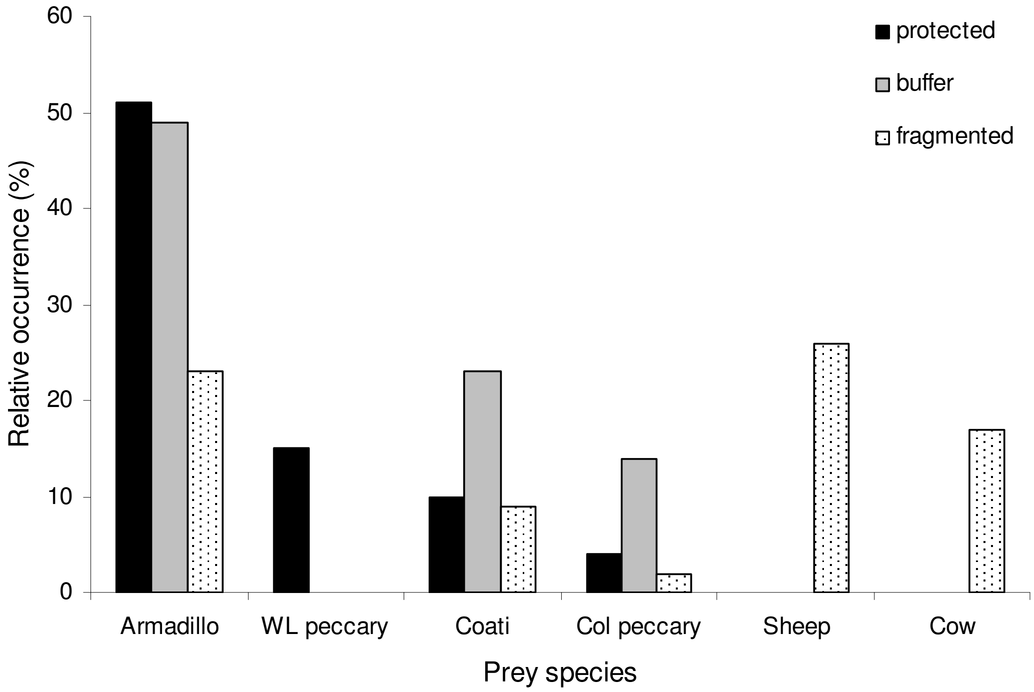


Figure 6.7 Variation in relative occurrence of main† prey species in jaguar diet in the protected forest (*n* = 204 scats), unprotected contiguous forest buffer (*n* = 38 scats) and unprotected fragmented landscape (*n* = 54 scats).
† ≥ 5% relative occurrence

Variation in jaguar diet through time

Within the protected forest, jaguar diet was relatively stable between the four years (Figure 6.8). Armadillos, white-lipped peccaries and coatis each comprised ≥ 5% of the diet every year. The relative occurrences of armadillos and coatis were moderately consistent between the years and negatively correlated (Spearman rank correlation: $\rho_S = -1.0$, $p < 0.0001$, $n = 4$). These were the only two prey species whose occurrences in the diet were correlated over the years. White-lipped peccaries showed high annual variation, ranging from 8% in 2006 to 22% in 2003. Although this may reflect inter-annual variation in sampling effort in different parts of the protected forest, it is consistent with the large ranges of white-lipped peccary herds which moved in and out of the focal study area during the study period (B. Harmsen pers. comm.) and have been recorded to range ~ 40 km^2 in Costa Rica and up to 109 km^2 in the Brazilian Amazon (Carillo *et al.* 2002, Fragoso 1998). Kinkajous, collared peccaries, pacas and red brocket deer all dropped below 5% occurrence in the diet during some years, and showed high annual variation.

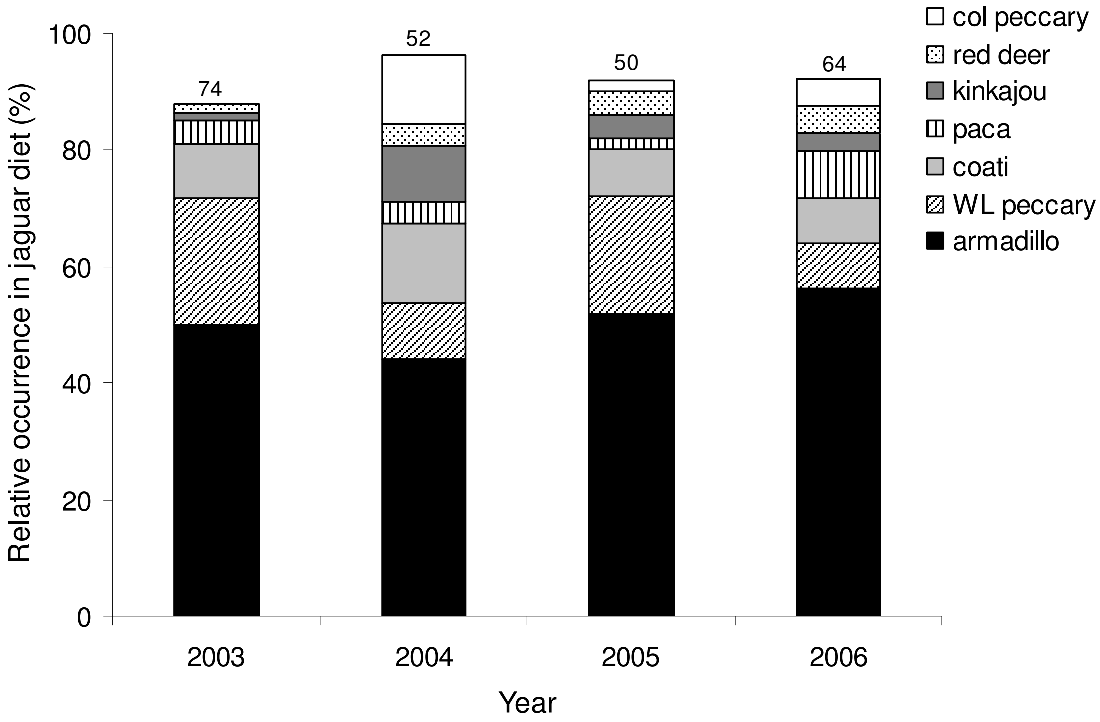


Figure 6.8 Relative occurrences of principal† prey species in jaguar diet in the protected forest over four years (2003 to 2006). Number of prey items shown; number of scats ranged from 42 to 62 per year.
† refers to species with ≥ 5% relative occurrence during any year

Jaguar and puma energetics

The number of each prey species killed per year by adult jaguars and pumas were estimated (Table 6.11) and simple harvest models were used to determine the prey populations necessary to maintain sustainable off-take at these levels (Tables 6.12, 6.13 and 6.14).

Jaguars in the protected forest have a higher kill rate than pumas (Table 6.11). This reflects the smaller MWVP prey taken by jaguars (predominately armadillos) than by pumas (predominantly pacas, Table 6.8) and the higher energy demands of jaguars, which are approximately 50% heavier than pumas in this region. If jaguars in the protected forest only ate armadillos (or any small species providing a similar biomass per individual) their kill rate would have to increase by ~ 40%; in contrast if pumas solely consumed pacas (or any similar-sized species) their kill rate could decrease by ~ 15% (Table 6.11). That pumas do not appear to be maximising energy intake by selecting more pacas in their diet may suggest that local paca densities are lower than those required to sustain a puma population; in contrast the fact that jaguars are able to find and consume so many armadillos suggests that they may be super-abundant in the area. The prey densities required for sustainable off-take by jaguar and puma populations in the protected forest (Tables 6.12 and 6.13) are discussed in relation to expected prey densities in the region (see Discussion).

Table 6.11 Estimates of the total number of prey kills made per year by a big cat inside the protected forest, and in the unprotected fragmented landscape, under different scenarios.

	Jaguar protected		**Jaguar fragmented**			**Puma protected**	
	all prey[1]	only armadillo[2]	undisturbed (5 nights)[3]	disturbed (2 nights)[4]	no livestock[5]	all prey[1]	only paca[6]
Solitary male	129-163	182-230	82-104	107-136	178-225	60- 76	52- 65
Solitary female	111-141	157-198	71- 89	92-117	153-194	36- 46	31- 39
Breeding female	270-344	383-484	159-199	190-238	376-474	98-126	85-107
pregnant†	122-155	172-218	84-107	119-150	169-213	40- 50	34- 43
nursing†	167-211	235-297	115-146	162-205	230-291	54- 69	47- 59
dependents	356-450	502-634	202-255	235-297	491-620	116-146	100-216

[1] prey biomass consumed in ratios observed in this study
[2] hypothetical scenario: only armadillo are consumed
[3] livestock carcasses undisturbed, consumed until decomposition (five nights)
[4] livestock carcasses abandoned after two nights due to human disturbance
[5] hypothetical scenario: livestock kills are replaced with armadillo kills
[6] hypothetical scenario: only paca are consumed
† although annual rates are given, gestation and lactation are < 365 days

Table 6.12 Estimates of prey population sizes required to sustain off-take by a single jaguar in the protected forest; and prey densities required to sustain off-take by a population of jaguars* numbering 10 per 100 km^2; five adult males, five adult females, four of which are breeding.

	Armadillo	**Armadillo (2)†**	**WL peccary**	**Coati**	**Paca**
Solitary male	109-138	227-288	34-43	16-20	14-17
Solitary female	94-119	196-248	30-37	13-17	12-15
Breeding female	229-290	479-605	72-91	32-41	27-37
Density /km^2	16- 20	32- 41	5- 6	2- 3	2- 2

* In the absence of off-take by pumas
† Population required if all biomass consumed was armadillo

Table 6.13 Estimates of prey population sizes required to sustain off-take by a single puma in the protected forest; and prey densities required to sustain off-take by a population of pumas* numbering 10 per 100 km^2; five adult males, five adult females, four of which are breeding.

	Paca	**Paca (2)†**	**Brocket deer**	**Armadillo**	**WL peccary**	**Kinkajou**
Solitary male	118-150	207-261	13-16	10-12	7- 9	69- 87
Solitary female	71- 90	124-157	8-10	6- 7	4- 5	42- 53
Breeding female	195-246	341-430	21-23	16-20	12-17	112-145
Density /km^2	14- 18	25- 32	2- 2	1- 1	1- 1	8- 11

* In the absence of off-take by jaguars
† Population required if all biomass consumed was paca

Breeding females have higher energy demands than males or solitary females and so must kill more frequently (Table 6.11). A female jaguar with dependents in the protected forest may have to make up to 1.2 kills per day in order to fulfil her own needs and those of her off-spring. If she fed only on armadillos this would increase to 1.7 kills per day (Table 6.11). Such high kill rates may prevent ‘armadillo-only’ diets and necessitate predation on larger prey also.

The MWVP of jaguars in the fragmented landscape was greater than in the protected forest, and this is reflected in lower kill rates in the human matrix (Table 6.11). This is facilitated by the presence of livestock; if jaguars did not have access to cattle and sheep, and instead had to increase predation on armadillos, kill rates would need to more than double (Table 6.11) and the armadillo density would need to be similar in magnitude to that required in the protected forest (Tables 6.12 and 6.14). Of note, the densities of coati and paca putatively required to support a jaguar population do not differ greatly between the protected forest and the fragmented landscape and are relatively low (Table 6.14). Assuming that pacas are more abundant in the protected forest than the human matrix, this suggests that jaguars may be selecting against them in the protected forest.

Jaguars may compensate for disturbance at livestock carcasses by increasing kill rate (Table 6.11). If a female and her young are forced to abandon livestock carcasses after 2 nights, rather than feeding for 5 nights, she will have to make an additional 33-42 kills per year (Table 6.11), which increases the number of cattle and sheep deaths from 13-16 and 9-12 respectively, to 32-40 and 23-29 per year.

Table 6.14 Estimates of prey population sizes required to sustain off-take by a single jaguar in the fragmented landscape; and prey densities required to sustain off-take by a population of jaguars numbering **a)** 4 per 100 km^2 (two reproductively active females and two adult males), and **b)** 10 per 100 km^2 (four reproductively active females plus one other, and five adult males).

	Armadillo	Armadillo (2)†	Coati	Paca
Solitary male	37-47	178-226	11-14	14-18
Solitary female	32-41	154-194	10-12	12-15
Breeding female	79-99	375-475	24-31	30-37
a) Density /km^2	2- 3	11- 14	1- 1	1- 1
b) Density /km^2	5- 7	25- 32	2- 2	2- 3

† Population required if consumed livestock biomass was replaced by armadillo

Discussion

Diet studies of jaguars and pumas in areas with a wide range of potential prey species may underestimate the true richness of the diet. If sample sizes are too small, the importance of the more commonly taken prey taxa may be overestimated as the rarer prey species remain undetected. This study suggests that studies of big cats from biodiverse regions such as tropical rainforests should aim for samples of ~ 100 scats to adequately describe diet. Samples half this size will likely detect the principal prey species, but measures of relative occurrence may be inaccurate. It would help interpretation of findings from small-sample studies if dietary components were presented with an accompanying list of potential prey species occurring in the area and a species accumulation curve. It is noted that felid scats are often difficult to find, particularly in hot humid climates where fecal material rapidly decomposes or is washed away in heavy rains. However, often scats are collected opportunistically by scientists who are simultaneously conducting other research on the target species. As such the effort put into finding scats may be low priority. The use of scat detector dogs is becoming more widespread in a range of studies monitoring carnivore diversity and abundance (e.g. Harrison 2006, Long *et al.* 2007), and could potentially improve scat collection rates for diet studies.

In this study jaguar diet was found to be richer than puma diet, reflecting the greater diversity of habitats utilised by jaguars across the study area (Chapter 5) which provide a greater range of potential prey than the forest block alone. Even within the protected forest, however, more species were recorded in jaguar than puma diet, though this probably reflects the larger sample of jaguar versus puma scats. Indeed the number of species detected per scat collected in the protected forest was similar between the two cats (jaguar 0.07 species per scat; puma 0.08).

Food habits within the protected forest

Across their ranges, the average sizes of prey taken by jaguars and pumas are positively correlated with their body weights (Iriate *et al.* 1990, de Oliveira 2002). In areas where jaguars and pumas are sympatric, pumas tend to be smaller and it has been suggested that they also take smaller prey species; particularly in closed environments such as dense forest where jaguars may be more efficient at hunting (Iriate *et al.* 1990, Taber *et al.* 1997). However in a review of eight studies of the diets of sympatric jaguars and pumas, de Oliveira (2002) found no difference in the average size of prey between the two cats. Emmons (1987) suggested that solitary predators such as jaguars and pumas hunt opportunistically in rainforest environments because encounters with prey are unpredictable and vision is limited by the dense vegetation. In open environments with abundant prey, predators can be more selective and are predicted to take larger prey in order to maximise energy intake. Indeed a review of 16 jaguar studies and 17 puma studies found that average prey size differed with habitat type, with larger prey taken in open floodplain areas (de Oliveira 2002); however this did not account for variation in the relative abundance of prey of different sizes across the different habitats. More recently, studies in the open habitats of the Venezuelan llanos and Brazilian Pantanal assessed prey availability in relation to diet, finding that jaguars showed a general preference for large-bodied prey, and pumas took most large prey in proportion to availability (Polisar *et al.* 2003, Azevedo and Murray 2007).

Published estimates of MWVP in neotropical forests range from 6.2 kg to 15.6 kg for jaguars and 7.2 kg to 12.7 kg for pumas (Núñez *et al.* 2000a, Novack *et al.* 2005), and are comparable to estimates in this study. It is possible that high decomposition rates associated with hot and humid conditions may limit the preferred prey size taken in the closed environments of tropical rainforests. Given the choice, a solitary cat may not risk attacking a 240 kg tapir over a 22 kg brocket deer if the spoilage rate prevents any additional energetic gain. This may help to explain the absence of tapir in the diet in this study, and from other forests in the Central America region: Belize (Rabinowitz and Nottingham 1986), Mexico (Aranda and Sánchez-Cordero 1996), Guatemala (Novack *et al.* 2005), Costa Rica (Chinchilla 1997). However, the small surface area to volume ratio of tapirs, coupled with the paucity of hair on their bodies, may also explain why so few studies detect tapir remains in jaguar and puma scats.

Diet overlap within the protected forest

Aranda and Sánchez-Cordero (1996) postulated that the co-existence of jaguars and pumas is facilitated by specialisation on different prey, with jaguars selecting peccary, and pumas selecting deer. These conclusions were based on their own study in a Mexican rainforest, and that of Chinchilla (1997) in a rainforest of Costa Rica; however sample sizes were small, particularly for pumas (n = 11-15 scats). In contrast, in the tropical dry forests of Mexico, white-tailed deer were the most important prey in the diet of both cats, consisting 54% and 66% biomass consumed by jaguar and pumas respectively (Núñez *et al.* 2000a).

In this study, jaguars of the protected forest took more armadillos than did pumas, whilst pumas took more paca and brocket deer, in accordance with findings in nearby Guatemalan rainforest within the Selva Maya region (Novack *et al.* 2005). Coatis were absent from puma diet yet contributed 9% of the total biomass taken by jaguars. It is not clear why pumas did not prey on coati, but a similar pattern is seen in the forests of both Guatemala and Mexico, with low coati predation by pumas compared to jaguars (Núñez *et al.* 2000a, Novack *et al.* 2005).

No differences were detected between the two cats in overall use of either peccary species; however jaguars seemed to focus on adult white-lipped peccary whilst pumas took mainly juveniles. This may reflect the size difference between the two cats and the risks associated with preying on adult white-lipped peccaries which will attack defensively using their large canines. Polisar *et al.* (2003) also noted that whilst jaguars and pumas both took collared peccaries, pumas mainly took juveniles. Fatal injuries sustained by solitary felids when attacking large prey are not uncommon; for example Ross *et al.* (1995) estimated that 27% of mortality in an un-hunted puma population in Alberta resulted from failed predation attempts.

White-lipped peccaries were found more frequently in the diet of both cats than were collared peccaries. Garla *et al.* (2001) also noted higher predation by jaguars on white-lipped peccaries than collared peccaries in the Atlantic forest of eastern Brazil, and suggested that this is because white-lipped peccaries are more conspicuous than collared peccaries, forming larger herds, vocalising and producing strong odours.

Diet breadth within the protected forest

Within the protected forest, the diets of both cat species each greatly depended on a single prey species, with armadillos comprising 48% of the biomass consumed by jaguar, and pacas comprising 57% of puma diet. Consequently the diversity of prey taken by jaguars and pumas in CBWS (B_{sta} = 0.11 and 0.17 respectively) was considerably lower than the diet breadth recorded in seven studies where jaguars and pumas co-exist (mean B_{sta} ± SD: jaguar 0.45 ± 0.14, puma 0.51 ± 0.21; from de Oliveira, 2002). Intense use of a single prey species could reflect a highly selective predator with a preference for a specific prey, or a more opportunistic predator surviving in a community where there is one highly abundant species and a low abundance of alternative prey species. In this study, both cat species inhabiting the protected forest had similar MWVP and took prey ranging from <1 kg to 34 kg, demonstrating that both were capable of handling prey of the same size; yet their diet overlapped little, as has been noted in other densely forested neotropical habitats (Harmsen 2006). Such a low level of niche overlap suggests resource partitioning between the jaguars and pumas, which may facilitate their co-existence. It also implies that one, or both, of the cats may be hunting selectively to some extent, rather than being limited to opportunistic predation as proposed by Emmons (1987). Experimental manipulations would be required to test for these processes.

The role of armadillos and pacas

Activity patterns of jaguars vary across their range: they may be equally active day and night, diurnal, crepuscular or nocturnal (e.g. Emmons 1987, Crawshaw and Quigley 1991, Núñez *et al.* 2002, Scognamillo *et al.* 2003, Maffei *et al.* 2004, Rabinowitz and Nottingham 1986, Harmsen 2006, Weckel *et al.* 2006a). In the CBWS, activities of jaguars and pumas mirrored the nocturnal activities of their main prey, armadillos and pacas respectively (Harmsen 2006). When inactive, pacas and armadillos rest in burrows (Reid 1997). Hunting them when they are active is therefore likely to maximise the rate of chance encounter. It may also improve the detection rate, as both species rustle leaves when they move through the undergrowth; and armadillos in particular are noisy foragers as they rummage in the leaf litter for arthropods. That cat activity patterns were so finely tuned to those of armadillo and paca, combined with the high level of predation on these distinct yet similar-sized species, suggest that jaguars and /or pumas may have been hunting selectively.

A dietary preference for armadillos by jaguars is difficult to explain because if hunting were selective we would expect jaguars to exploit larger prey, for example pacas, which are on average 3 kg heavier than armadillos and represent a more energy-rich prey source. If hunting is in fact opportunistic, jaguars may be utilising armadillos either because they are exceptionally abundant, and /or because other prey species are unusually scarce. It has been suggested that armadillos may be superabundant within CBWS and a recent pilot study may support this (Harmsen 2006, B. Harmsen pers. comm.). Although there are no current data on the abundance of any prey species in the area, historical data from the area may help. In 1983, before the forest was officially protected, sign of armadillo within the Cockscomb basin were encountered 100 times more frequently than were sign of peccaries (Rabinowitz and Nottingham 1986). The relative occurrence of armadillos in jaguar diet in the area has not altered since that time (54% Rabinowitz and Nottingham 1986, 51% this study), despite 20 years of protection. Although the protected forest suffers incursions by poachers seeking game species at the edges (R. Foster pers. obs.), it is likely that prey populations within the Cockscomb basin have improved since it became formally protected and the logging camps were disbanded. Before protection, only 5% of jaguar prey items were white-lipped and collared peccaries (Rabinowitz and Nottingham 1986) compared to 19% in this study, suggesting that protection may at least have aided peccary recovery. The continued high predation on armadillos despite this dramatic increase in use of larger prey supports the hypothesis that armadillos are indeed abundant in the area and are exploited opportunistically by jaguars.

Even if armadillos are superabundant in the area, and are easy to detect because they are noisy foragers, their tough carapace may deter pumas from predating on them (e.g. Novack *et al*. 2005). It may be hypothesised that the handling time associated with killing and eating an armadillo will be relatively high for the energy return (~ 3.5 kg edible material), compared to a paca which is larger (8 kg edible material) and does not have protective armour. Jaguars have the strongest bite (for their size) of all the big cats (Sunquist and Sunquist 2002). Indeed it has been suggested that they evolved taking large armoured reptiles (Emmons 1987). As such the handling time of an armadillo will likely be minimal for a jaguar. In contrast, the pumas of CBWS may have more difficulty, making intense predation on armadillos energetically unviable, and selection of pacas more profitable. Their reduced handling effort on pacas compared to armadillos is probably offset against a higher search effort for the relatively agile paca.

A paca has some probability of escaping an attack, whereas an armadillo is almost invariably condemned once detected by a jaguar unless it can quickly find refuge in a burrow or sufficiently thick undergrowth.

In an analysis of camera-trap data collected within the CBWS, Harmsen (2006) found no differences in habitat use between pacas and armadillos. Both species had similar capture rates at the edge of streams, and neither were trail walkers, with the majority of trail footprints detected crossing rather than following trails (57% armadillo tracks and 69% paca tracks crossed trails). Although Chapter 5 detected no fine-scale differences in habitat use between jaguars and pumas within the forest, Harmsen (2006) found that pumas spent more time travelling on trails than did jaguars and suggested that pumas mainly hunt on trail, whilst jaguars hunt off-trail. It is possible that when armadillos are in the undergrowth they are less easy to detect from a trail than are pacas, which are larger (standing up to 0.3 m high, Reid 1997) thus more conspicuous, and so armadillos may be less likely to be preyed on by pumas than jaguars.

An armadillo density of ~16-20 km^{-2} would be required to sustain off-take by a jaguar density of 10 individuals per 100-km^2 at the levels of off-take observed in this study. With their occurrence in jaguar diet remaining unchanged since 1983, we may suspect that off-take has also remained sustainable (assuming that jaguar densities have not increased). If armadillos were the only prey of jaguars in the protected forest an armadillo density of ~32-41 km^{-2} would be required to allow sustainable off-take. Published estimates of nine-banded armadillo densities in the neotropics are scarce and limited to burrow counts, from which it is difficult infer population size, for example in the Atlantic rainforest of Brazil armadillo burrow density was estimated at 173 ha^{-1}, though the majority were inactive (McDonough *et al.* 2000). A study in the pine forests of northern Belize detected 27 burrows per hectare, of which at least 23% were active (Platt *et al.* 2004) which equates to ~ 600 active burrows per km^2. Burrow use per armadillo is likely to vary with habitat and predation level (e.g. McDonough *et al.* 2000). If each armadillo used as many as 10 burrows, we may expect a population density of ~60 individuals per km^2 in the Belizean pine forests. We might therefore hypothesise that armadillo density within CBWS could be realistically high enough to support the jaguar population in the absence of alternative prey. That jaguars do not take more armadillos suggests a need for at least some larger prey in their diet. The simple models investigated in this study suggest that it may be energetically preferable to occasionally take larger prey, particularly for a female with dependents. If armadillos were the only available prey a female jaguar would need to double her kill rate to ~1.7 kills per day in order to raise two juveniles. It is unknown whether the foraging effort required to achieve the necessary armadillo encounter rate would be possible. Although jaguar feeding behaviour may be adaptable to a wide range of prey, reproduction may depend on a minimum availability of larger prey, below which the long-term persistence of jaguars may be in jeopardy. Based on the food habits observed in CBWS we can tentatively predict that jaguar population turnover requires at least 27% of the biomass taken to be prey larger than 10 kg. This requirement may be more or less strongly sex dependent, however. The estimate is derived from scats that are probably mostly from male jaguars (the majority having been found on trails), and females may require a higher proportion of larger prey particularly when breeding.

Unlike jaguars, whose use of armadillos appears to be limited by the high kill rates that would be necessary if larger prey were not also taken, kill rate by pumas in the protected forest could be lowered if they increased their intake of paca in place of smaller species such as kinkajou. That they do not do this suggests they are limited by paca availability and encounter rates. Indeed the occurrence of paca in jaguar diet has almost halved since 1983, from 9.3% to 4.6% (Rabinowitz and Nottingham 1986, this study). Without long-term monitoring of prey abundance we can only speculate as to whether this reflects a true decline in paca availability or an increase in the relative abundance of alternative prey. The estimated intrinsic rate of increase of paca is less than that of other game species such as peccary (Robinson and Redford 1986). Thus, whilst peccary populations may have improved with reduced hunting pressure following establishment of the protected area, the paca population may be kept below carrying capacity by continued poaching (albeit at a lower level) within the park. If pacas were the sole prey taken, the estimated density required to sustain a puma population of 10 per 100 km^2 within the protected forest is only 25-32 km^{-2}. Paca densities of up to 93 km^{-2} have been recorded in non-hunted forest in Costa Rica (Beck-King *et al.* 1999) indicating that pacas can reach high densities if undisturbed. However in a hunted forest in Guatemala paca density was just 3.7 km^{-2} (Novack *et al.*2005). These findings highlight an urgent need for estimates of both prey and puma densities in the area.

Food habits outside the protected forest

The MWVP taken by jaguars was smaller, and diet was less species-rich, in the forest buffer than in either the protected forest or the fragmented habitat, presumably because hunters deplete the unprotected forest buffer of larger game species such as deer and peccary and there are no livestock here to supplement jaguar diet. Note that sample sizes in the forest buffer and fragmented habitat were 38 and 54 respectively, and so may underestimate the true number of species taken in these areas.

The higher prevalence of coati and collared peccary in jaguar diet in the buffer than in the protected forest may reflect either the scarcity of prized game species such as brocket deer and white-lipped peccary and/or potentially a higher abundance of coati and collared peccary in this 'edge' habitat. Novack *et al.* (2005) detected higher coati densities in a hunted site closer to a settlement (53 km^{-2}) than a non-hunted site (23 km^{-2}) in a Guatemalan rainforest. In the same study, although the non-hunted area had similar densities of collared and white-lipped peccaries (8.1 and 9.6 km^{-2} respectively), the hunted site had no white-lipped peccary whilst collared peccary persisted albeit at lower density (2.4 km^{-2}). Unlike the white-lipped peccary, which requires extensive tracts of undisturbed forest, the collared peccary appears to adapt well to disturbed habitats (e.g. Peres 1996, Reyna-Hurtado and Tanner 2007). The persistence of collared peccary in areas where other large prey are more quickly depleted by humans may play an important role in sustaining jaguar populations outside protected areas.

The role of livestock in jaguar diet

Livestock constituted an important part of jaguar diet in the fragmented landscape, replacing armadillos to some extent and supplementing a diet of otherwise small prey (MWVP = 4.5 kg without domestic species). This probably reflects the scarcity of large game species and a lower armadillo density in the human-matrix than in the protected forest, as well as the presence of farms which provide resource-rich patches with high densities of livestock (Chapter 5). Although not all jaguars in the fragmented landscape may feed on livestock, those whose home ranges encompass pastures have potentially high encounter rates with domestic prey, which may be exploited by opportunistic predators, particularly if alternative wild prey species are scarce. Azevedo (2008) found that livestock contributed most to jaguar diet (26% of biomass consumed) in and around Iguaçu, a national park of subtropical forest bordered by livestock farms in Brazil. An increase in livestock predation in this area has been linked to a decline in white-lipped peccaries (Conforti and Azevedo 2003, Crawshaw *et al.* 2004, Azevedo 2008). Indeed the utilisation of domestic prey is often inversely associated with the availability of wild prey (e.g. Hoogesteijn, 2000, Miller 2002, Polisar *et al*. 2003), a fact that is recognised by researchers and livestock owners alike. For example during a survey of 72 Belizean livestock owners who had lost animals to big cats, many interviewees believed that the over-hunting of wild game species was responsible for increased depredation (Brechin and Buff 2005).

Jaguars bred outside the protected forest of this study area, as indicated by camera-trap photographs of at least two different females with cubs (one in the buffer and one on a cattle farm), during the study period (Chapter 4), and by frequent sightings of a female with cubs on a different ranch within the study area during 2007 (S. Juan pers. comm.). It is unknown whether these females were preying on livestock, as jaguars of both sexes were detected on farms concurrently (Chapters 5 and 7). The scats are in the process of being gentoyped to distinguish males from females (C. Pomilla, WCS geneticist, pers. comm.) and these data will be available for further analyses. An important question to answer is whether female jaguars could afford to reproduce in the human-influenced landscape in the absence of cattle and sheep. Certainly a female with sub-adult dependents would benefit from taking down large prey. If undisturbed during feeding, a calf of 125 kg could provide three times more food to a mother with two cubs than that provided by an adult white-tailed deer, and 20 times more than from an armadillo. Estimates based on jaguar diet observed outside the forest block indicate that breeding females would have to increase kill rate by an additional 150% if armadillos were substituted for livestock within their diet. Even if a female could achieve the required foraging effort it is unknown whether the armadillo population could sustain this level of off-take. The harvest models presented in this study suggest that an armadillo population of 79 to 99 within the home range of the breeding female would be required for sustainable off-take. If her home range is approximately 8.6 km^2 (Chapter 4) and exclusive, a local armadillo density of at least 9-12 km^{-2} is required. Armadillos may not achieve these densities in the fragmented landscape, which is dominated by citrus plantations. For example, in Brazil armadillo burrow density in grasslands was less than one third of that that observed in the rainforest (McDonough *et al*. 2000). Although armadillos are not a prized game species in Belize, a firearm is not required to hunt them as they are easy to kill with dogs or machete (R. Foster pers. obs.). As such, local attitudes towards armadillos perhaps also reflect the response of jaguars: if you see one, kill it (R. Foster pers. obs.) It may be expected therefore that armadillo densities are substantially lower in the human-matrix than inside the forest block.

Any disturbance to livestock kills may increase depredation and subsequent losses, as jaguars that are forced to abandon livestock carcasses early will need to kill again sooner. Estimates from the study area suggest that losses to sheep and cattle could decrease by 60% if people leave the carcass to be fully utilised rather than moving it after 2 nights. These estimates are speculative and do not consider the potential benefits of disturbance which may drive the jaguar from the area, and halt depredation altogether.

Diet and the absence of pumas from unprotected lands

Núñez *et al.* (2000a) proposed that the broader prey niche of pumas and their ability to take smaller prey may give an advantage over jaguars in human-altered landscapes, and suggested that persistence of pumas appears more likely than jaguars in disturbed environments. This does not appear to be true for this study: pumas took larger prey and fewer species than did jaguars, and their feeding habits, combined with wild prey availability, may partly explain the scarcity of pumas compared to jaguars outside the protected forest (Chapter 5). The three most important prey species in puma diet within the protected forest were paca, white-lipped peccary and brocket deer. Locally these are also popular game species and it is likely hunting prevents them from reaching similar densities outside the protected forest to those within it (R. Foster pers. obs.). The food habits of big cats observed inside the protected forest suggest that the pumas may be more selective than jaguars, avoiding armadillos in favour of pacas. Such a feeding strategy will limit their success in the fragmented landscape where pacas are also favoured by man.

Unlike jaguars, which supplemented their intake of otherwise small prey with cattle and sheep, there was no evidence that pumas ate livestock. The same phenomenon was observed in Iguaçu, Brazil, where jaguars killed both wild and domestic animals, but pumas utilised only wild prey (Conforti and Azevedo 2003, Azevdeo 2008). In the Venezuelan llanos and Brazilian Pantanal where jaguars and pumas coexist and both are documented to kill livestock, pumas tend to focus on the smaller age classes (e.g. González-Fernández 1995, Crawshaw and Quigley 2002, Scognamillo *et al.* 2002, Azevedo and Murray 2007). Across Belize, reports of pumas predating on livestock are relatively few compared to jaguar (Brechin and Buff 2005).Here pumas are among the smallest in their range (e.g. Iriate *et al.* 1990) and are smaller than the sympatric jaguar; thus their size may deter them from attacking large cattle. However this does not explain why they do not utilise the human matrix and eat sheep, pigs, dogs or small calves. Chapter 5 provided evidence that pumas in Belize tend to be less tolerant of human activity than jaguars. It seems likely that a combination of food habits, prey availability and their wariness of people prevents pumas from exploiting the human-matrix. In contrast, jaguars appear to be living and breeding across the landscape, both inside and outside the protected forest, albeit at lower densities in the human matrix than in the reserve (Chapter 4). They persist despite utilising relatively small prey species, although it is possible that in areas where large wild species have been depleted, livestock may become an increasingly important supplement in their diet, particularly for breeding females.

Further work

The discussion presented here is limited by lack of information on the abundance of wild prey species. Obtaining such data from the protected forest will improve interpretation of the observed differences between jaguar and puma feeding habits, and the extent to which these behaviours influence or facilitate their co-existence. Estimates of wild prey abundance in dense secondary forest using techniques such as distance sampling may be hindered by the low visibility (Appendix D); however pilot studies are currently underway to assess the relative abundance of pacas and armadillos in the CBWS using a number of independent methods that can be cross-validated, and there are plans to begin monitoring the larger prey species also (B. Harmsen pers. comm.). Outside the protected lands, data are also needed on the abundance of wild prey species, including estimates of the intensity and impact of hunting by humans on wild prey populations. Improved parameter estimates are also needed for modelling the energy requirements of jaguars and pumas; these will benefit from sex-specific descriptions of food habits in order to assess whether wild prey abundance is sufficient for female reproduction. A better understanding of the effect of the availability of domestic versus wild prey on the food habits of jaguars is also required, particularly for assessing whether wild prey augmentation, especially large ungulates, could reduce levels of livestock predation.

Chapter 7

Lethal control and population persistence of jaguars

Abstract

Although jaguars (*Panthera onca*) are well known to suffer persecution for killing livestock, the intensity of this human-induced mortality and its impact on long-term population persistence is poorly known. Belize is thought to support one of the last jaguar strongholds in Central America. Jaguars are common throughout the country, in the two main protected forest blocks and in the unprotected human-influenced landscape. Many farms and villages border forested habitat, and with an abundance of livestock as prey, they are potentially resource-rich areas for cats, resulting in high rates of conflict between humans and jaguars. This chapter combines field data and individual-based population simulations to investigate the impact of current levels of human-induced mortality on the population dynamics and long-term persistence of the Belizean jaguar population. The study found that human-induced mortality of jaguars was most common in the unprotected lands, estimated at ~ 45% annually. Male and female jaguars were equally susceptible to human-induced mortality. Young individuals in good body condition were frequently killed, indicating high turnover rates potentially facilitated by immigration. Population simulations indicated that in the absence of immigration from the two protected populations, and under the current level of human-induced mortality, the hunted population had zero probability of persisting for more than 20 years. The two protected populations were large enough to withstand demographic and environmental stochasticity, assuming no catastrophes, edge-effects or the negative influence of genetic stochasticity; and could sustain low levels of migration into the hunted population. However the probability of all three populations persisting for 100 years fell to ~ 50% if the migration of natal dispersers (2-4 year olds) from the protected to unprotected population was ≥ 13% per year. If farms and villages do attract dispersers from the protected forest at this rate, and levels of human-induced mortality remain high, then the long-term persistence of the jaguar population in Belize may be in doubt.

Introduction

Human activities may impact on the population dynamics of large carnivores existing at low densities indirectly through their influence on habitat and prey availability and directly as human-induced mortality. Habitat loss and prey depletion will lower the carrying capacity of a population, and a scarcity of prey may additionally lower reproductive rates within the population (Fuller and Sievert 2001). Intentional or accidental deaths caused by people will impact directly on survival (e.g. grizzly bears (*Ursus arctos horibilis*), Knight *et al.* 1988, Iberian lynx (*Lynx pardinus*), Ferreras *et al.* 1992). Frequently, populations of large carnivores are limited by human-induced mortality; even those existing within protected areas may be influenced, as wide-ranging individuals that move beyond reserve boundaries are killed by people (Woodroffe and Ginsberg 1998). It has been suggested that this strong 'edge effect' may be just as important as stochastic effects on long-term persistence of isolated carnivore populations (Woodroffe and Ginsberg 1998). Under such circumstances the most appropriate conservation strategy may be to focus on ways to lower human-induced mortality of the population rather than attempt to restore habitat or prey abundances outside the protected area. In studies of jaguar (*Panthera onca*) ecology, direct conflict with people has been identified as the most common cause of death (Sunquist 2002), yet few researchers have attempted to quantify levels of human-induced mortality, and those that do make no assessment of the likely impact on the local jaguar population (e.g. Crawshaw 2002, Conforti and Azvedo 2003, Brechin and Buff 2005, Michalski *et al.* 2006). Consequently there is a need for a better understanding of the potential impact of jaguar persecution on population dynamics, and an assessment of whether it is feasible or desirable to lessen death rates. The aim of this study is to quantify human-induced mortality of jaguars outside protected areas in Belize, with particular reference to retaliatory killings in response to livestock loss, evaluating whether lethal control is an effective method of preventing depredation and the whether the current level is likely to be sustainable for the country's jaguar population in the long term.

Causes and rates of human-induced mortality

Many large carnivore species are persecuted for the harvest and trade of body parts, recreational sport hunting, and in response to real or perceived threats to human life or livelihood (Frank and Woodroffe 2001, Sillero-Zuibiri and Laurenson 2001, Thirgood *et al.* 2005, Dinerstein *et al.* 2007). Additionally, they may be killed 'accidentally' by human activities, for example in road traffic accidents or through the poisoning or trapping of non-target species (Ferreras *et al.* 1992, Nielsen and Woolf 2002, Taylor *et al.* 2002, Haines *et al.* 2005, Riley *et al.* 2007). For big cats, livestock predation is considered the principal source of conflict with people, and a major reason for their disappearance from considerable areas of their former range (Nowell and Jackson 1996, Mazzolli *et al.* 2002). Most large cats will occasionally kill accessible livestock (Linnell *et al.* 1999) depending on extrinsic variables such as the availability of wild versus domestic prey and specific livestock husbandry practises (Linnell *et al.* 1999, Hoogesteijn 2000, Miller 2002, Mazzolli *et al.* 2002, Conforti and Azevedo 2003, Polisar *et al.* 2003, Crawshaw *et al.* 2004). The extent to which big cats prey on domestic animals is also influenced by the individual's sex, status and health, as well as hunting behaviours learned with their mother (Rabinowitz 1986a, Hoogesteijn 2000, Polisar *et al.* 2003). Understanding which individuals within a population are most likely to attack livestock and thus are most at risk from persecution can contribute to predictions about the consequences of lethal control, for example the removal of adult females will directly lower the breeding potential of the population whilst the removal of males may have more subtle effects through the disruption of social dynamics, for example increased infanticide following the removal of resident males, as has been observed in lions (*Panthera leo*) and leopards (*Panthera pardus*) (Loveridge *et al.* 2007, Balme *et al.* 2007).

In developing regions that still retain a high proportion of forest cover, such as Belize (72% forest, World Resource Institute, WRI, 2007), the contact zone between people and wildlife is extensive, and increasing as the forests are further fragmented. In Belize the close proximity of many farms and villages to forest means that almost every livestock holding may be at risk of jaguar predation. This can be particularly damaging to small-scale farmers unless preventative action is taken when depredation begins; usually lethal control is seen as the cheapest and quickest solution (R. Foster pers. obs.). Furthermore, multiple farms may fall within the home range of the same cat or cats (Chapter 5) which often leads to the misconception by locals that jaguar abundance may be higher than reality (R. Foster, pers. obs.). For example, erroneous beliefs by some livestock owners neighbouring the Cockscomb Basin Wildlife Sanctuary (CBWS), a protected forest of 425 km^2 in southern Belize, that the reserve sustains a population of 1000 jaguars encourages a gung-ho approach to lethal control at the periphery (R. Foster pers. obs.). In reality the CBWS is estimated to support around 40 jaguars (Harmsen 2006) and the impact of continuing lethal-control at its border has not been estimated to date.

Management of jaguars in Belize is hindered not only by the difficulties of accurately estimating the density of this elusive species outside protected areas

(Chapters 3 and 4), but also by lack of information on rates of lethal control resulting from rather grey laws surrounding the hunting of jaguars and the reluctance of people to report these deaths to the Government. The Belize Wildlife Protection Act (2000) states *'it is not unlawful for any person to take such measures as maybe reasonably necessary to defend self or property'*; thus it is not an offense to kill a jaguar that is threatening life or livelihood. However the death must be reported within 1 month and the remains are strictly the property of the Government; trade in jaguar body parts carries a fine of US$250 for the first offence, rising to US$500 for a second offence and imprisonment for a third offence (Belize Wildlife Protection Act 2000). Unfortunately the wildlife law is neither well publicised nor understood within Belize, with many people believing that it is illegal to kill a jaguar under any circumstances (R Foster pers. obs.). Consequently informal lethal control of jaguars, although widespread, is covert and rarely reported to the Government (R. Foster pers. obs., Brechin and Buff 2005). The problem is further exacerbated because the Government lacks the necessary resources to respond to reports of depredation in farms and villages, and disillusioned livestock owners and communities often feel forced to take matters into their own hands (R. Foster pers. obs.). The first objective of this chapter is to report and discuss causes and rates of human-induced mortality of jaguars, and the characteristics of those culled jaguars, on agricultural lands neighbouring a protected forest (the CBWS) in southern Belize. Jaguar activity on farms and differences in the intensity of livestock loss before and after lethal control are used to assess whether lethal control of jaguars correctly targets the livestock predators and effectively lowers losses.

Impact of human-induced mortality on population dynamics

Rates of human-induced mortality of carnivores can be expected to vary across the landscape, for example they may peak close to highways or livestock holdings (e.g. Knight *et al.* 1988) and decline with distance into a protected area (e.g. Revilla *et al.* 2001). Spatial heterogeneity or gradients in mortality can result in source-sink dynamics (Pulliam 1988), in which hunted local populations (sinks) are sustained by immigrants dispersing from neighbouring un-hunted populations (sources). Source-sink like dynamics arising from spatial variation in hunting have been observed in bobcats (*Felis rufus*) (Knick 1990); Canadian and Iberian lynx (*Lynx sp.*) (Slough and Mowat 1996, Gaona *et al.* 1998); pumas (*Puma concolor*) (Stoner *et al.* 2006, Robinson *et al.* 2008; grizzly bears (Knight *et al.* 1988, Schwartz *et al.* 2006); and culpeo foxes (*Pseudalopex* *culpaeus*) (Novaro *et al.* 2005). Although demographic sinks cannot persist independently, theoretical models demonstrate that they may contribute positively to meta-population longevity (e.g. Howe *et al.* 1991). However this assumes that individuals disperse from source to sink only if the source population exceeds carrying capacity, i.e. sinks are maintained by the surplus reproduction of the source population. In contrast, if sinks are 'attractive' they can potentially drain individuals from source populations leading to regional population declines. These so-called 'ecological traps' may be common in human-landscapes, particularly where rapid anthropogenic change has taken place such that behaviours governing habitat choices are no longer optimal (Pulliam 1996, Remeš 2000, Delibes *et al.* 2001, Kristan 2003, Battin 2004). Livestock farms may potentially function in this way, attracting carnivores to resource-rich patches where the probability of mortality resulting from conflict with people is high.

Jaguars are common throughout Belize, both in protected forests and in the human-influenced landscape (Silver *et al.* 2004, Harmsen 2006, Miller 2006, this study Chapter 4), and it is likely that they form a single connected population (e.g. Eizirik *et al.* 2001, Rabinowitz 2006). Two separate blocks of protected forest, the 'Maya Mountain' block to the south and the 'Rio Bravo' block to the north, make up ~ 35% and ~ 13% of the country's broadleaf forest respectively (from Meerman and Sabido 2001). Both forest blocks are buffered by unprotected forest, and the remaining landscape is a matrix of human development and forest fragments (Figure 1.4, Chapter 1). The two protected blocks have been identified as important jaguar strongholds in Belize, but concern has been raised that these two local populations may not be large enough to persist if they become isolated (Meerman 2004). Future isolation of the two blocks is not an unrealistic prediction as the natural habitat is increasingly being cleared for human development in the unprotected lands, and they are already separated by a highway running east-west across the country (R. Foster pers. obs.). Once isolated the populations may not be large enough to withstand the effects of demographic, environmental and genetic stochasticity, and/or edge effects, which may lead to the decline and extirpation of small populations (Schaffer 1981, Woodroffe and Ginsberg 1998). Even if connectivity is retained between the populations, livestock production is increasing throughout Belize to meet export demand to Mexico (J. Carr, Belize Livestock Producers Association, pers. comm., WRI 2007), and the human population is growing with increasingly more vehicles on the roads (WRI 2007, UN Stat Division 2008). Consequently the risk to jaguars both from persecution and accidental deaths such as vehicle collisions is likely to increase in future years, potentially facilitating a population sink in the unprotected lands. Under the circumstances described we may envisage four simple hypothetical scenarios: 1) human-induced mortality in the unprotected lands has no significant impact on local or regional population persistence, the jaguars of Belize exist as a single, connected population; 2) mortality in the unprotected lands exceeds reproduction and there is no immigration from the protected forests (alternatively development in the human-landscape reduces the carrying capacity to zero), the jaguars of the protected blocks exist as two isolated populations at risk from stochastic decline; 3) mortality in the unprotected lands exceeds reproduction (sink), but the population is sustained by random immigration from the protected forest blocks (sources); 4) individuals are ‘attracted’ from the protected forest blocks to resource-rich livestock farms in the unprotected lands where mortality exceeds reproduction (ecological trap). Understanding whether any of these scenarios could be applicable now, or in the future, to the Belizean jaguar population, and the long-term consequences they would bring, will help to guide management strategies. Thus the second objective of this chapter is to simulate the dynamics of the jaguar population of Belize as a meta-population comprising two un-hunted populations (one in each protected forest block), and a single hunted population in the remaining lands, using simple individual-based stochastic demographic models. The models explore the probability of long-term persistence of the Belizean jaguar population under alternative scenarios of population isolation/ connectivity (dispersal) and human-induced mortality to 1) examine whether the protected populations are large enough to persist in isolation; 2) evaluate the level of human-induced mortality that the unprotected population can sustain in the absence of immigration and compare this with observed levels of human-induced mortality from the region; 3) evaluate the level of immigration required to maintain the unprotected population under current rates of human-induced mortality and identify the threshold above which it becomes an ecological trap with a negative effect on the protected populations.

Methods

Eleven cattle farms were identified within the immediate study area (see Figure 5.2, Chapter 5). The farms ranged in size from 0.04 to 9.25 km^2 (~ six to 900 cattle). Camera traps were maintained on or near eight of these farms for varying periods (two to 30 months), depending on the cooperation of the land owners, in order to create a database of cats utilising the farm habitat. Data about cat deaths or removals from the wild were collected opportunistically from local people. Large-scale camera-trap surveys conducted between 2004 and 2006 were used to estimate jaguar density across the study area, both in the protected forest and in the neighbouring unprotected lands, incorporating eight of the cattle farms (Chapter 4). Stochastic demographic models incorporating observed hunting rates and density estimates were used to assess the sustainability of human-induced mortality of jaguars in Belize.

Causes and rates of human-induced mortality

One of the most important stages of the research involved gaining the confidence of the local people to facilitate information exchange and allow collection of reliable data. The responses of all livestock owners and employees were positive even though the informal hunting of cats is a sensitive subject. No judgement was made when pro-lethal control or anti-jaguar attitudes were displayed. Emphasis was placed on the non-authoritarian role of the researcher, who was there purely for information collection and dissemination, with the ultimate goal of long-term conflict resolution between farmers and jaguars. Livestock owners were generally more willing to provide information if they were offered camera traps on their property. Typically they already knew if big cats were present, from spoor and predation events; however the dissemination of camera data was carefully controlled to prevent the possibility of livestock owners reacting negatively to information about jaguars on their land. Photographs of cats and other wild animals, when shared appropriately, greatly increased the interest of local people. The establishment of amicable relationships with all stakeholders made possible the collection of data on the lethal control of jaguars in the study area. Despite this, any estimate of lethal control will likely be conservative.

Reports of any human-induced mortality of big cats in the study area were collected opportunistically (traffic deaths, poaching for trade in body parts, poaching for live animal trade, ‘incidental’ shootings whilst hunting game, retaliation for livestock predation). Methods of lethal control across the study area were recorded, along with long-term data on attempt and success rates of lethal control over a 3-year period on the largest farm in the area. Jaguar activity on farms and rates of livestock predation (Chapter 5) were used to determine whether more than one individual frequented the same farm during the same spate of attacks. Differences in rates of livestock loss before and after lethal control were calculated in order to assess the likelihood that the correct individual was killed. The final destination of the valuable body parts (pelt, canines and skull) were also recorded where possible (kept, sold or discarded).

Characteristics of ‘problem’ jaguars

Data on the demographics and physical features of jaguars killed by people were combined with camera-trap data to investigate the relationships between the probability of human-induced mortality and characteristics such as sex, age, body condition and habitat use. Characteristics of ‘problem’ jaguars (those that are livestock killers) cannot be defined *per se* because it is rarely possible to link an individual to specific livestock predation events. Rather, characteristics of jaguars that are susceptible to persecution were investigated, regardless of whether they actually kill livestock.

Demographics and health

Details of any big cat that was killed and reported to the researcher during the study period were recorded. Historic anecdotes (up to five years prior) were also offered from some livestock owners and recorded. Whenever possible, reports were verified and data were collected on: species, sex, weight, dental condition, age (estimate based on cranial suture closure and tooth development and tooth wear, and camera-trap data where available), body condition, stomach contents and cause of death. The collection of these data depended on the condition and availability of the remains once the event had been reported. Usually the body was skinned immediately, the canines pulled out and the carcass dumped and scavenged by vultures. Therefore the farm employees were given cameras and encouraged to photograph the body before skinning the cat. This allowed individual identification if already present in the database of jaguars photographed in the study area (Chapter 4), and sometimes also provided data on the general body condition, depending on the quality of the photographs. Estimates of body weight were often provided by the farm employees but were probably exaggerated in accordance with the macho image of killing a big cat.

Habitat use

It was hypothesised that jaguars which predominately inhabit human-dominated habitats were more likely to suffer human-induced mortality than those which also use forest buffer contiguous with the protected area. Jaguars photographed more than once were classified according to their capture locations and whether they were killed by people during the study period. A Fishers exact test compared the proportion of survivors and mortalities between individuals which only used the fragmented landscape and those which used both the fragmented landscape and the forest block.

Impact of human-induced mortality on population dynamics

The potential impact of human-induced mortality on the jaguar population of Belize was investigated under different scenarios using individual-based models built within the software program Vortex (Lacy and Pollak 2005). Although such programs may not accurately predict the future status of wild populations, they can be used to explore model assumptions on population dynamics and to compare alternative scenarios or management strategies (Coulson *et al*. 2001). Vortex was designed for long-lived vertebrate populations with relatively low fecundity and it is therefore suitable to model big cat populations (O'Regan *et al*. 2002). It models the effects of deterministic processes (such as density-dependent reproduction and survival, age/sex specific mortality, and the harvesting of individuals), and the effects of stochastic processes (demographic and environmental stochasticity, catastrophic events, and genetic factors) on population dynamics. It can also simulate migration between populations. The model tracks individuals and is run over a series of time steps (e.g. years) to predict the future population size. Because of the stochastic component of the model it is run many times with the same input parameters, each iteration following a different course. The results are therefore probabilistic, giving a distribution of final population sizes (Miller and Lacy 2005).

Modelling stochastic and deterministic processes

Demographic parameters such as birth rates, litter size, sex ratio and death rates derived from field data can be used to estimate the deterministic growth rate of a population. In reality these life events are probabilistic, fluctuating randomly from year to year. This demographic stochasticity is modelled by simulating a binomial process in which the probability of the event (e.g. birth, death) is drawn randomly from a binomial distribution around the mean. In this study estimates of jaguar life history parameters were derived from the available literature on jaguars and other big cats**.** The model parameters are summarised in Table 7.1 (next section).

In addition to demographic stochasticity, random fluctuations in the environment such as the weather, disease, the abundance of predators or prey, or the availability of nest sites, may cause births and deaths to vary from year to year (Miller and Lacy 2005). This environmental stochasticity is modelled by assigning a variance to each demographic parameter (Miller and Lacy 2005). The field data necessary to estimate environmental variation in demographic rates requires at least 1-2 generations of study, which may equate to > 20 years of research for long-lived species such as big cats (Beissinger and Westphal 1998). As no such data are available for jaguars, a coefficient of variation of 0.3 was chosen following Mills and Smouse (1994) who derived this value from long-term studies of other mammal populations in order to model a generic 'felid' population. This seems reasonable given that the coefficients of variation of survival of different age/sex groups of pumas in a hunted population in Washington state ranged from 0.17 (adult females) to 0.6 (adult males) (Robinson *et al.* 2008). Environmental variation in reproduction and survival were assumed to be concordant, i.e. years that were favourable for reproduction were also favourable for survival.

Sometimes it may be appropriate to model rare and extreme environmental events or 'catastrophes' separately from the environmental variation, for example the effects of hurricanes, floods, droughts and forest fires. Although Belize is occasionally hit by devastating hurricanes (e.g. Hurricane Hattie in 1961) it is not possible to accurately predict their occurrence or their effect on reproduction and survival of jaguars. For this reason catastrophic events were not included in the model.

Genetic factors may become important in the population dynamics of small populations through inbreeding, the loss of genetic diversity and the accumulation of deleterious alleles (Frankham 2005). Models of inbreeding require estimates of the number of 'lethal equivalents' per diploid genome, the average number of lethal alleles per individual if all the negative effects of inbreeding were due to recessive lethal alleles (Miller and Lacy 2005). Although there is evidence of inbreeding depression in a number of captive and wild species (Frankham 2005), there are few data on genetic loads in wild populations (Beissinger and Westpahl 1998). In a review of 38 mammal species in 40 captive populations, Ralls *et al.* (1988) found that lethal equivalents ranged from -1.4 to 30.3 (median 3.14) and showed no obvious phylogenetic relationships. When unknown, a default value of 3.14 lethal equivalents is often used in population models (e.g. Eizirik *et al.* 2002, Wilkinson and O'Regan 2003, van Pelt *et al.* 2006). Given the wide variation in lethal equivalents between species, however, this value seems somewhat arbitrary. Although there is evidence that mammalian carnivore populations can be negatively affected by inbreeding (for example the reduction litter size in captive brown bears, Laikre *et al.* 1996, and the reduction of fecundity and juvenile survivorship in captive South China tigers, Xu *et al.* 2007); the magnitude of inbreeding depression in carnivores may be small relative to other mammals (Xu *et al.* 2007, Ralls *et al.* 1988). For these reasons genetic effects were not included in the model, in accordance with Beier (1993) and Karanth and Stith (1999) who ignored inbreeding depression in their models of puma and tiger populations.

Density dependence can be incorporated into the model by enforcing a population ceiling (K, the carrying capacity) above which the population is truncated across all age classes, and/or by modifying demographic rates as a function of the population size. The exact form of density dependence modelled may strongly affect the population dynamics (thus the model predictions) and so should be used with care (Mills *et al.* 1996); however it was assumed that the inclusion of density dependence was more realistic than its exclusion. This seems reasonable for a big cat population. For example, Kissui and Packer (2004) detected density dependence in lions, with higher cub recruitment at low population densities. Long-lived large mammals generally show non-linearity in density dependence, with changes most pronounced at high population levels (Fowler 1981). Accordingly, the reproductive rate was modelled so that it declined at high populations close to K, but remained stable at low populations, following van Pelt *et al.* (2006). For simplicity the model ignored Allee effects, in the form of disproportionately low reproductive rates in small populations arising from the low probability of prospective mates meeting each other. This seems reasonable in a population of big cats such as jaguars which have the ability to range widely. In addition density-dependent mortality was modelled by enforcing a population ceiling. This method results in the equilibrium population remaining below K (Mills *et al.* 1996). The initial population sizes (N_0) and K were derived from density estimates from the study area (Chapter 4).

Model parameters and sensitivity analysis

The model input parameter values shown in Table 7.1 were derived from the available literature on jaguars (Mondolfi and Hoogesteijn 1982, Seymour 1989, Nowell and Jackson 1996, Sunquist and Sunquist 2002) and, where necessary, pumas, leopards, tigers and lions (Mazák 1981, van Orsdol *et al.* 1985, Logan *et al.* 1986, Lindzey *et al.*

1988, Packer *et al.* 1988, Smith and McDougal 1991,Lindzey *et al.* 1992, Lindzey *et al.* 1994, Nowell and Jackson 1996, Sunquist and Sunquist 2002, Kerley *et al.* 2003, Stoner *et al.* 2006, Robinson *et al.* 2008); see Appendix E for more details. A base model was run with 100 iterations over 100 years with these parameters and a starting population of 2000 individuals. This represents a jaguar population of Belize prior to deforestation and human development based on density estimates from the protected forest (Chapter 4) and estimates of original forest cover (WRI 2007). The characteristics of this large population were examined in order to determine whether the chosen input values were realistic for the species. The mean stochastic per capita growth rate, $r\text{-}_{stoch}$, over 100 iterations and 100 years, and prior to carrying capacity truncation, was 0.037 (SE = 0.0016) individuals per individual per year. There are few datasets of big cat population growth rates with which to compare this estimate. A recent field study based on long-term camera-trap data estimated a mean annual multiplicative growth rate (λ) of 1.03 (i.e. 3% increase per year) within a wild tiger population (Karanth *et al.* 2006). This is equivalent to a per capita growth rate of 0.03, comparable with that estimated for jaguars in this base model. This suggests that the base model population behaves as we may expect for a population of big cats. In the absence of stochastic effects the sex ratio of adults was 50%, and approximately 2% of individuals survived to be 10 years old. This is comparable to the observations of Rabinowitz (unpubl. data in Nowell and Jackson 1996) that few wild jaguars in Belize survived more than 11 years, and of Harmsen (unpubl. data) who found that jaguars first captured as adults on camera (at least 3-4 years old) disappeared from the camera record within ~7 years.

Table 7.1 Model input parameter values for the base jaguar population

Parameter		
	Female	**Male**
First age of reproduction	3 y	4 y
Maximum breeding age	10 y	10 y
Sex ratio at birth	1	1
% adult males in breeding pool	-	75
% adult females breeding each year (SD)	30-50 (12.5) density dependent†	-
% cub mortality (SD) age 0 -1 y	30 (10.0)	30 (10.0)
% juvenile mortality (SD) ages 1 - 2 y	10 (3.3)	10 (3.3)
% sub-adult mortality (SD) ages 2 – 3 y	15 (5.0)	25 (8.3)
% sub-adult mortality (SD) ages 3 – 4 y	-	25 (8.3)
% adult mortality (SD) age > 3 y	10-80 age specific‡	-
% adult mortality (SD) age > 4 y	-	15-80 age specific‡
	Other input	
Initial population size	2000	
Carrying capacity (SD)	2000 (100)	
Breeding system	Polygynous	
Maximum litter size	4	
% breeding females producing 1 cub per y	20	
% breeding females producing 2 cubs per y	45	
% breeding females producing 3 cubs per y	20	
% breeding females producing 4 cubs per y	15	

† Density-dependent reproduction. Modelled in Vortex as: (50-((50-20)*((N/K)^16))) following van Pelt *et al.* (2006)
‡ Age-specific mortality, stable until age 8 years (10% females, 15% males) then increasing linearly to 80% at age15 years due to tooth wear and injuries. Modelled in Vortex as: a) females 10+((A>8)*10*(A-8)) and b) males 15+((A>8)*9.29*(A-8)) following van Pelt *et al.* (2006)

Because data on the life history parameters of some species of big cats are relatively sparse, estimation of their vital rates for population models are often based on biological intuition or on the life histories of similar species, as in this study and others (e.g. Karanth and Stith 1999, Eizirik *et al*. 2002, Wilkinson and O'Regan 2003, Linke *et al*. 2006). It is necessary to fully explore uncertainty in these rates (Beissinger *et al*. 1998). Therefore a sensitivity analysis was conducted to investigate which parameters may have greatest influence on the long-term population performance by varying each parameter in turn through a range of values and re-running the base model.

Scenarios: Initial population sizes and carrying capacities

The jaguar population of Belize was modelled as three sub-populations comprising two un-hunted populations, one in each protected forest block (the Maya Mountains, 'MM' and the Rio Bravo 'RB'), and a single hunted population in the remaining 'unprotected' lands ('UP'). It was assumed that the MM and RB populations were at carrying capacity and suffered no human-induced mortality, whilst UP was below carrying capacity due to lethal control. Density estimates based on camera-trap data from these three areas were used to estimate each population size.

The population of MM was estimated to be between 277 and 496 individuals based on density estimates from three of its 13 contiguous protected areas (Mountain Pine Ridge Forest Reserve and Chiquibul Forest Reserve, M. Kelly, unpubl. data; CBWS, Harmsen 2006, Chapter 4 this study). Recently concern has been raised regarding the increase in Guatemalans crossing the border to illegally collect xaté palm (*Chamaerdorea sp.*) in the west of MM. These 'xateros' may remain in the forest for many weeks, subsisting on game (G. Hansom, Belize Forestry Officer, pers. comm.), and may drastically lower the availability of wild prey for jaguars. In addition it has been suggested that some areas of the MM may be too mountainous and rugged to support jaguars (Harmsen 2006). For these reasons the population and carrying capacity of MM was estimated at 350 individuals.

The population and carrying capacity of RB was estimated at 170 individuals, based on density estimates from one of its three contiguous protected areas (Gallon Jug Private Reserve, Miller 2006). The RB borders Guatemala, but, unlike MM which has no forest buffer on the Guatemalan side, the RB is contiguous with the forest of the Guatemalan Biosphere Reserve Petén which may provide some degree of protection from foreign hunters and xateros.

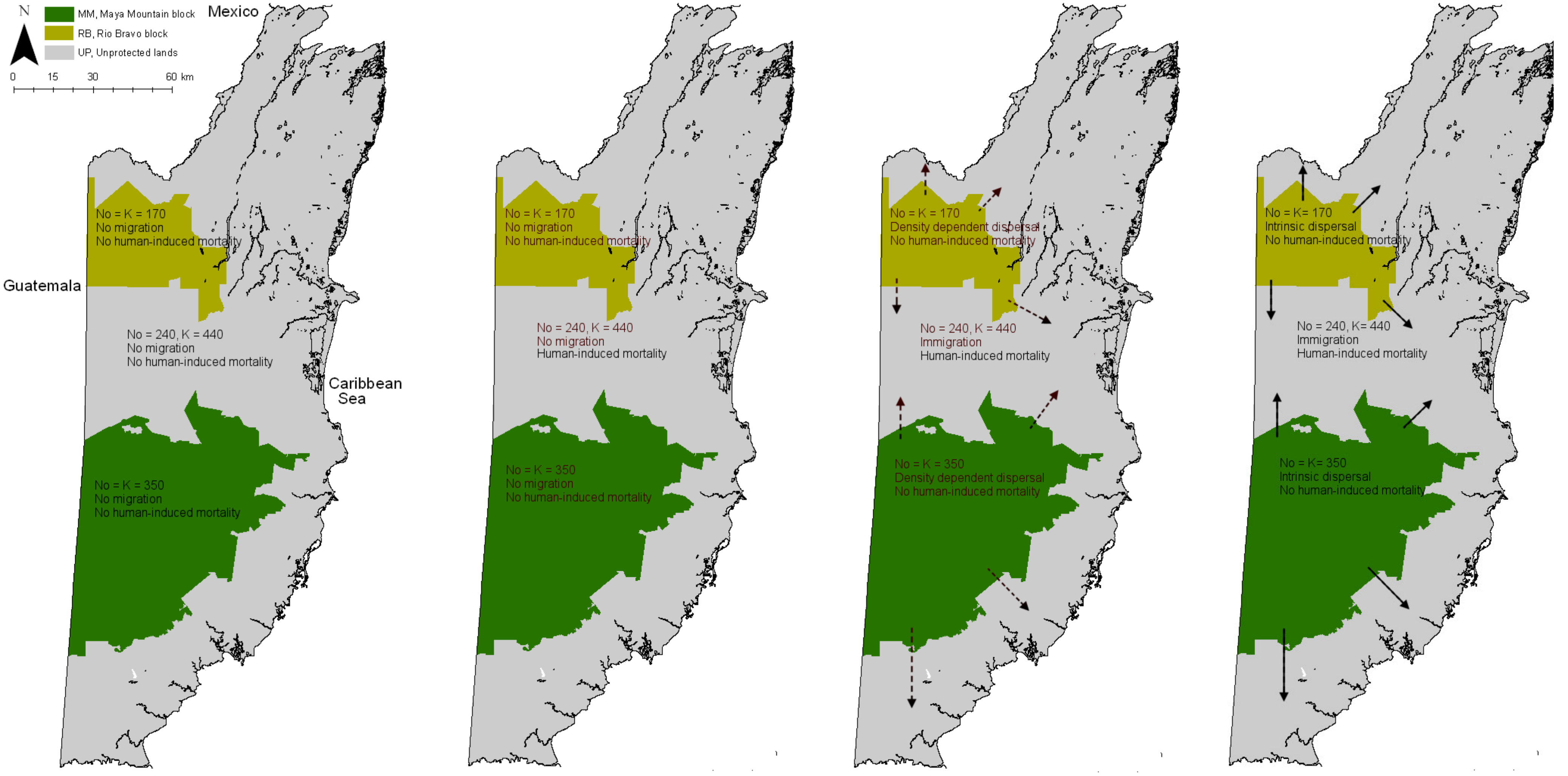
The population of UP was based on the author's own density estimates from the unprotected lands neighbouring the MM in southern Belize (Chapter 4). Jaguar density on these lands declines with distance from the forest block, tending to be higher in the west (closer to the forest block) and lower to the east (near the coast). A conservative density estimate of 1.6 jaguars/100 km^2 was used giving a population of 240 individuals living outside the two protected forest blocks across the entire country. The carrying capacity of UP was set at 440 jaguars based on field estimates of human-induced mortality in the unprotected lands (see Results) and the assumption that natural and human-induced mortality was additive. This is a reasonable assumption, given that density-independent natural mortality of big cats is expected due to intra-specific killings and injuries sustained when attacking prey (e.g. as observed in a hunted puma population, Lindzey *et al*. 1988, 1992). Further explanation of the three population estimates are described in Appendix E.

Apart from N_0 and K, demographic parameters were assumed to be the same in all three sub-populations. In reality there may be more nutritional stress in the UP population than in MM or RB, because jaguars are more likely to have to compete with humans for wild prey, potentially lowering the reproductive rates of females. However the scarcity of wild prey in the unprotected forests may be countered by the abundance of domestic prey on farms (Chapter 6). Environmental variation in demographic rates was assumed to be fully correlated between the three subpopulations. This is reasonable given the small size of Belize.

Scenarios: Dispersal and human-induced mortality

Models were run for each subpopulation in isolation (no migration between populations) over 100 years and for 500 iterations, and repeated for the UP population under increasing levels of human-induced mortality. Human-induced mortality was modelled as an annual % off-take from each age/sex group. Thus an annual off-take of 10% simulated the removal of 10% of each of the following groups every year: juveniles (age 2y), subadult males (age 3y), subadult males (age 4y), subadult females (age 3y), adult males (age 5y+), and adult females (age 4y+). Field data suggested that adults and subadults of both sexes were equally vulnerable to lethal control (see Results section) thus it was reasonable to apply the same level of human-induced mortality to all within a given simulation. Juveniles were included also under the assumption that the removal of a breeding female would result in the death of her dependent off-spring. Cubs were not included because the annual off-take was applied to the population before breeding in any given year, i.e. cubs could only be born to adult females who survived that year’s lethal control, becoming juveniles in the subsequent year and thereon susceptible to human-induced mortality.

Movement between the subpopulations was modelled as both density-dependent and density-independent migration. Jaguars are usually independent by the age of 24 months, however the age of dispersal or the social circumstances associated with it are poorly known (Sunquist and Sunquist 2002). Relatively good dispersal data are available for other large solitary cats. Often young males are obligate dispersers, dispersing regardless of the local population density, whilst females tend to be philopatric and their dispersal may be more related to habitat saturation (pumas, Logan *et al.* 1986, Ross and Jalkotzy 1992, Laing and Lindzey 1993, Sweanor *et al.* 2000, Stoner *et al.* 2006; tigers, Smith 1993). Migration between subpopulations was modelled as the 'natal' dispersal of 2-4 year olds only, although it is recognised that range shifts in adult jaguars do occur (e.g. Rabinowitz and Nottingham 1986, Harmsen 2006). Density-independent dispersal was modelled as a fixed % of 2-4 year olds migrating from one population to another each year. This was multiplied by N/K in order to model linear density-dependent dispersal. For simplicity both sexes were assumed to disperse equally, although it is recognised that a male-bias may exist in reality. Increasing the basic level of dispersal from one population to another can be interpreted as increasing the level of attractiveness of the destination population (an increasing proportion of individuals disperse to another population rather than within their own population). In these models, under density-dependence, individuals only move to a different population if local conditions force them out, i.e. they always 'choose' their own population first. In contrast, under density-independent (intrinsic) dispersal, a certain proportion of the individuals are 'attracted' to another population regardless of the local conditions. Figure 7.1 shows a spatial representation of the models. For simplicity, movement of jaguars between Belize and its neighbours (Guatemala and Mexico) were not included in the model. The implications of this are considered in the Discussion. All models were repeated varying those demographic parameters deemed influential in the sensitivity analyses



a) Three isolated populations

b) Lethal control in UP

c) Density-dependent dispersal from MM & RB to UP, lethal control in UP

d) Density-independent dispersal from MM & RB to UP, lethal control in UP

Figure 7.1 Spatial representation of models

Results

Given the sensitive nature of lethal control of jaguars, the quality of data varied with the number and turnover of farm employees. Stronger relationships were formed with long-term employees and this aided reliable data collection.

Causes and rates of human-induced mortality

The majority of reported deaths were retaliatory following livestock predation (Table 7.2). However it is likely that other human-caused deaths were under-reported, particularly those considered criminal such as poaching specifically for trade in animal parts. Only one (unverified) puma death was reported from the study area; it was shot, with no reason given, prior to the study period (*circa* 2000). More jaguar deaths were reported than pumas or ocelots.

Table 7.2 Reports of human-caused deaths of wild cats April 2004 to November 2006 (31 months) across a study area of ~360 km^2 unprotected land.
V = verified (evidence seen by researcher) and Unv = unverified.

	Ocelot		**Puma**		**Jaguar**	
	V.	Unv.	V.	Unv.	V.	Unv.
traffic death	-	-	-	-	-	-
trade in animal parts	-	-	-	-	-	1
trade in live animals	-	-	-	-	-	2†
‘incidental’ shooting	1	-	-	-	-	1
retaliation for livestock predation	1	-	-	-	12	3
no reason given	1	-	-	-	-	2
Total	**3**	**0**	**0**	**0**	**12**	**9**

†Two cubs stolen from mother

Across ~ 360 km^2 of unprotected lands, 12 jaguar deaths were verified over 31 months, giving a conservative estimate of 4.6 jaguars killed per year (8.1 per year including the unverified deaths, Table 7.2). This equates to 1.3 deaths per year per 100 km^2. The 360 km^2 study area is considered representative of UP throughout Belize, consisting of a mosaic of pastures, plantations, settlements, forest, shrublands and savannah. Extrapolation to the entire UP (~ 15,068 km^2) gives an annual off-take of ~ 200 jaguars nationwide. Although this seems remarkably high (45% of the UP population if natural and human-induced mortality is assumed to be additive), it is similar to estimates of unverified lethal control based on interviews conducted by Brechin and Buff (2005) with livestock owners who had lost animals to jaguars nationwide. In their study, 54 ranchers and 28 communities, all with cat problems, killed a total of 64 jaguars and 10 pumas from 2002 to 2004. 46% of the ranchers with problems admitted to killing cats (39 jaguars) and 48% of the communities with problems admitted killing cats (25 jaguars). This equates to ~ 20 jaguars per year over 25 ranches that had problems and took action, and ~ 12 jaguars per year over 13 communities that had problems and took action. There are at least 1,600 livestock owners in Belize (Brechin and Buff 2005). If only 25% of them had problems in a given year, and 50% of those with problems took action, 200 farms would take action each year. Using the estimate of 20 jaguars killed per year per 25 farms who take action, this equates to ~160 jaguars killed per year by ranchers alone. Therefore, the estimate of ~200 jaguars killed per year nationwide may indeed be realistic.

Jaguar death rates on the study farms ranged from zero to three verified deaths per year. Farm #01, the largest farm (~ 9.25 km^2), had the highest death rate (~3 /year). This death rate resulted from ~14 separate attempts (over ~19 nights) to kill jaguars each year. Methods of lethal control reported across the study area included: trap and shoot, trap and take to the zoo, wait at bait and shoot, wait at kill site and shoot, poison remains of livestock carcass, hunt with dogs. Waiting at the kill site for the jaguar to return for a second feed was the most commonly used method. All reported cases of lethal control on farms in the study area were reactive (in response to livestock predation), rather than pro-active (actively hunting jaguars in the absence of livestock predation). However evidence suggested that the individual responsible for depredation was not always the one killed, particularly when traps were baited.

On the largest farm, lethal control of jaguars was followed by a halt to livestock predation in only three out of eight jaguar deaths (Table 7.3, Figure 7.2). In the other control attempts, either multiple cats were predating on livestock at the same time or the methods employed to kill jaguars were not targeting the correct individual, or the cowboys were wrongly presuming jaguars were responsible for cattle deaths. During the study period 12-13 jaguars were recorded on the farm, and there was frequently more than one cat using the farm during a spate of attacks.

Table 7.3 Cattle losses before and after lethal control of jaguars on Farm #01 between Jan 2004 and Nov 2006. Minimum numbers of big cats detected < 20 m from pasture during the period of losses are shown if camera traps were present.

Sex	**Cattle loss (/week) prior to action**	**Weeks until losses resumed**	**Control method**	**Minimum number of cats using farm**	
				jaguars	pumas
Male	0.7 for 12 weeks	0 (immediate)	Shoot at kill site	1	0
Male	3.5 for 2 weeks	23	Bait and shoot	unknown	unknown
Female	1.1 for 4 weeks	0 (immediate)	Trap and shoot	2-3	0
Male	1.0 for 45 weeks	~6	Shoot at kill site	5	1
Female	1.5 for 3 weeks	0 (immediate)	Shoot at kill site	1	1
Male	1.1 for 6 weeks	8	Shoot at kill site	3	0
Female	2.2 for 5 weeks	0 (immediate)	Shoot at kill site	3	0
Male	n/a (as above)	0 (immediate)	Shoot at kill site/bait	2	0
n/a	1.2 for 24 weeks	n/a	n/a	3	0

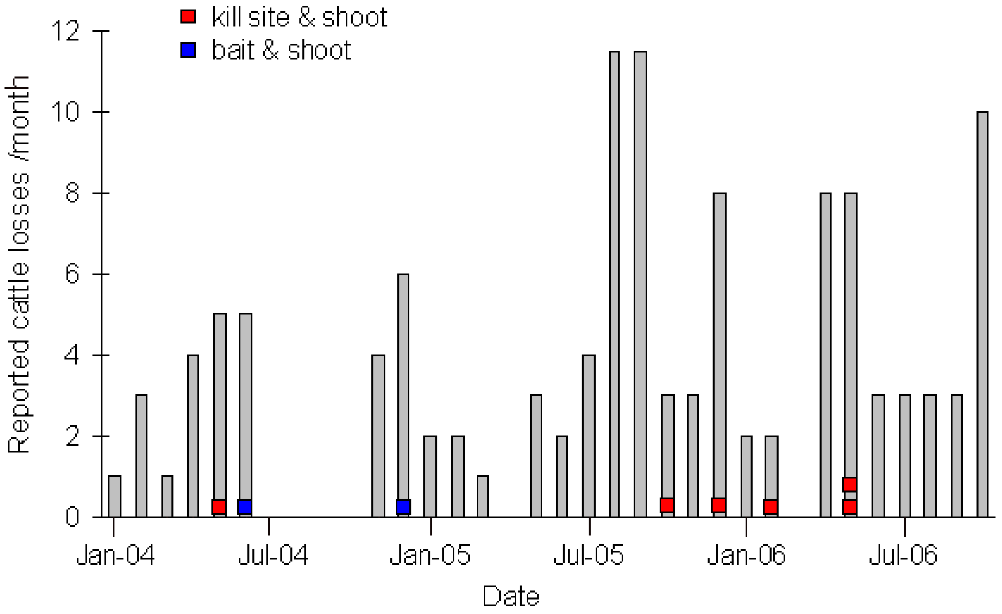


Figure 7.2 Cattle losses before and after lethal control of jaguars on Farm #01 from January 2004 to November 2006. Events of lethal control of jaguars are shown as coloured boxes: red = shot at kill site, blue = shot at bait.

Data from the other farms were less detailed, and are briefly summarised here. Farm #03 was only ~ 2 km from Farm #01 and both the jaguars (two females) recorded there were shot on Farm #01. The presence of one coincides with two calf attacks but there were also periods when both females were present and no livestock were killed. Two farms reported no livestock losses during the study period (Farms #04 and #08), despite the presence of up to three jaguars, indicating that livestock predation is not inevitable if jaguars are in the area. Prior to the establishment of camera traps at Farm #04, a local resident living within 500 m of the pastures reported attacks on his unfenced sheep and ducks. He lost nine sheep, four dogs and 19 ducks before baiting and shooting a female jaguar. Following her death he reported two small jaguars, presumably her cubs, in the area, and this was verified by other residents. No cats were detected at Farm #07, and the owner attributed their only losses (sheep) to feral dogs. The four remaining farms all suffered livestock predation and jaguars were present. Farm #05 lost two calves over a three-day period before shooting a male jaguar at the kill site. The male had first been recorded at the pasture boundary 4 months previously. Attacks immediately stopped following his death. The cowboy claimed that two jaguars were feeding at the carcass when he shot the male, and this fits with photo records of a female jaguar in the local area, albeit not at that farm. She was photographed two months later with a cub (< 6 months old) on Farm #02. Farm #06 lost two calves, and another was injured, over a 6-week period. Two male jaguars were photographed on the farm during that time. Attacks ceased for ~ 4 months after one of them was shot on a neighbouring farm (Farm #02). Thereafter one calf was lost, coinciding with the appearance of a third male. Farm #02 lost cattle and sheep throughout the study period, during which time 9-10 jaguars (and 1-2 cubs) were recorded on the farm. The data from this farm are not sufficiently detailed to determine whether the removal of a female in 2004 and a male in 2006 influenced the predation rates.

Although the majority of reported jaguar deaths were reactions to livestock predation, the thrill of owning, or the prospect of selling, trophies such as the pelt or canines may be an added incentive. During the study period the author heard reports of up to 18 skins, eight skulls with canines, five additional sets of canines, and one entire carcass, in the possession of local people; this included body parts derived from 11 of the study animals known to have been killed. However, these tended to be trophies kept by the hunter, as opposed to items sold on an illegal market. Nevertheless, during the study period two cubs were reportedly taken from their mother for the live trade, and the author heard of at least four additional attempts to capture jaguars or pumas for captivity. In addition the author saw evidence of a local hunter selling canines, and heard of an attempt to sell two skulls and pelts. Although local trade in body parts is unlikely to be the main incentive for killing a jaguar, the increasing number of rich foreign tourists and immigrants to Belize may change market forces. For example, one village was offered US$7,500 for a dead jaguar by a visiting American. The villagers collectively refused and the man was later arrested (N. Coc, CBWS Park Director, pers. comm.).

Characteristics of 'problem' jaguars

The 12 jaguars killed during the study period (Table 7.2) were all killed between April 2004 and July 2006 outside the protected forest, on and around farmland. One was removed to the zoo, not killed, but her removal still represents a death from the wild population. No jaguars were reported killed between July 2006 and November 2006. However, one of the few females recorded in the study area, a young adult, was killed in February 2007 in a road traffic accident on the highway 10 km from the protected area.

Demographics and health

Of the 12 jaguars killed, seven were male and five female (Table 7.4). This sex ratio is similar to that derived from camera trapping in the area (Chapter 4), which suggests that one sex is not more susceptible lethal control than the other. Previous work has suggested that injured or infirm jaguars unable to hunt wild prey may turn to easier domestic animals (Rabinowitz 1986a, Hoogsteijn 2000). Although true, in this study at least one-third of the individuals killed were subadults or young adults ($\leq$ 5y), perhaps suggesting high turnover rates as young animals disperse from their natal range into human contact zones and thus into conflict. Furthermore, for those deaths yielding data on body condition, ~ 80% were considered to be in good condition (Figure 7.3a), and at least two-thirds of the females were breeding. Nonetheless, at least 20% of the jaguars removed for killing domestic animals bore injuries, most of which were old gun shot wounds. Figure 7.3b shows the teeth of a jaguar that was shot for attacking dogs in a village. His canines are clearly reduced to nubs, having been destroyed by a previous encounter with a hunter. Indeed his skull was found to be filled with old gunshot. It is hypothesised that these injuries forced the cat to begin preying on dogs. Over 40 dogs were reported taken from the community during one year before villagers took action. When shot, the cat released the dog it had snatched unharmed, indicating its incapacity to kill prey efficiently.

Table 7.4 Characteristics of jaguars killed in the study area April 2004 to November 2006 (*n* =12). Bodyweights are approximate estimates by cowboys (except 4 and 6 who were both weighed). Age estimates are based on tooth wear, tooth and cranial development and trapping records.

ID	Sex	Age	Mass (kg)	Dentition	Body condition
1	F	young adult	36	good	good
2	F	-	32	good	good, pregnant/lactating
3	F	young adult	54	good	no data
4†	F	young adult	46	no data	good
5	F	adult	-	good	good, with cubs
6	F	young adult	43	canines broken*	broken femur, gunshot pellet behind knee
7†	M	old adult	-	no lower incisors, all canines broken	good; old gunshot wounds to face, pellets embedded in skull, arthritis in hind feet
8	M	adult	68	no data	blind in one eye, possibly dislodged retina from trauma
9	M	adult	-	good	good, old gunshot pellets in flesh
10	M	young adult	79	good	good
11	M	adult	63	good	good
12	M	adult	90	canines broken*	good
13	M	young adult	45	good	no data
14	M	adult	104	no data	good
15†	U	adult	no data	no data	no data

† Killed prior and subsequent to the official study period (2003 *n* = 2 and 2007 *n* = 1).
*Canines broken, unclear whether broken prior to death or as a consequence of trapping/ shooting

a) Adult male jaguar shot at bait in forest bordering cattle farm, good body condition

b) Damaged canines of adult male jaguar shot whilst attacking a dog in a village

Figure 7.3 Photographs showing condition of jaguars shot for killing domestic animals

Habitat use

The proportion of jaguars that were killed by humans was significantly higher in the subpopulation that used only fragmented habitats compared to those that used both fragmented habitat and the forest block (Fishers exact: odds ratio = 0.05, $p < 0.02$, Table 7.5). None of the jaguars inhabiting the protected forest were reported killed; therefore the protected area density (Chapter 4) is a fair estimate of an un-hunted carrying capacity for the population models.

Table 7.5 Frequency of human-induced mortality of jaguars and their habitat use.

	Survivor	**Mortality**†	
Fragmented habitat only	7	8	**15**
Fragmented habitat and forest block	8	0	**8**
	15	**8**	**22**

†Note that the number of jaguars deaths is *n* =8, not *n* =12 (as in Table 7.2), because photo location records were not available for four of the 12 jaguars that were killed.

Impact of human-induced mortality on population dynamics

The potential impact of human-induced mortality on the jaguar population of Belize was investigated under different scenarios using individual-based models.

Model parameters and sensitivity analysis

Because of the uncertainty in some of the estimates of demographic rates used in the model, the sensitivities of the base model parameters were investigated to identify those which had greatest influence on the population dynamics by assessing the change in mean stochastic growth rate ($r\text{-}_{stoch}$) as each parameter was varied through a range of values within the base model. Those parameters considered uncertain and identified as important could then be compared at different levels within the specific model scenarios of human-induced mortality.

The maximum age of reproduction, estimated at 10 years, caused $r\text{-}_{stoch}$ to decline if lowered to 8 years, but had little effect if increased to 12 years, because so few individuals survived to this age (Figure 7.4a). There are few data on longevity and age of last reproduction in wild big cat populations but captive data suggest that many species can continue reproducing into old age (Nowell and Jackson 1996). In the wild, however, it is suspected that old individuals may be less successful, particularly males, who may fail to secure mating rights over healthy younger males. For this reason it was concluded that a maximum age of reproduction of 10 years was a suitable parameter estimate for the models. The model was not sensitive to the % of adult males in the breeding pool (Figure 7.4b), because neither genetic effects nor Allee effects were included in the model.

Litter size strongly influenced $r_{\text{-}stoch}$ (Figure 7.4c). If all litters comprised just one offspring the population would decline, whilst litters of two or more would ensure population growth. Jaguar litter sizes range from 1-4 with a mean of ~2 (Seymour 1989). This was best approximated in a distribution of litter sizes which gave a mean litter size of 2.2 cubs (Table 7.1, Methods section).

The model was differently sensitive to natural mortality depending on the specific age/sex class (Figure 7.4d-i). Altering juvenile mortality, subadult male mortality or adult male mortality had little effect on $r_{\text{-}stoch}$. In contrast female and cub mortality were more important. Doubling adult female mortality (from 10% to 20%) caused the population growth rate to fall to 25% of its original value, whilst halving it (from 10% to 5%) caused $r_{\text{-}stoch}$ to increase by 30%. This indicates that inaccurate estimates of adult female mortality could significantly influence the model predictions. Field estimates of the natural mortality of adults of other big cats fall within a range of ~ 5-20%, with pumas at 11-16% (although may be as low as 5% in some populations), Asiatic lions 8-10%, leopards 10-17% (Nowell and Jackson 1996, Robinson *et al.* 2008). For these reasons the specific scenarios modelling the potential impact of human-induced mortality on the jaguar population (next section) were repeated with ×2 and ×0.5 of the base model value of adult female natural mortality (10%, Table 7.1, Methods section). Halving cub mortality (from 30% to 15%) had the same effect on $r_{\text{-}stoch}$ as halving the adult female mortality; however doubling cub mortality (from 30% to 60%) caused population decline. Assuming that the other base model parameters were realistic, this indicates that cub mortality of 60% is unrealistic in a stable or growing jaguar population (the desired starting point for the base model and un-hunted populations in subsequent scenarios in this study). Indeed natural mortality of jaguar cubs may not be as high as that observed in group-living cats such as lions (14-73%, Nowell and Jackson 1996), where multiple cubs may compete with adults for an opportunity to feed (Sunquist and Sunquist 2002) and in which disease may spread rapidly through prides; or in subordinate cats, such a leopards (41-50%, Nowell and Jackson 1996), which may lose their cubs to other predators (Sunquist and Sunquist 2002). Cub mortality of 34% has been reported in tigers, mainly due to the high level of infanticide in this species (Smith and McDougal 1991). Certainly infanticide occurs in jaguars (Soares *et al.* 2006) however its prevalence is unknown. Based on this information it was not deemed appropriate to vary jaguar cub mortality above 30% in subsequent model scenarios.

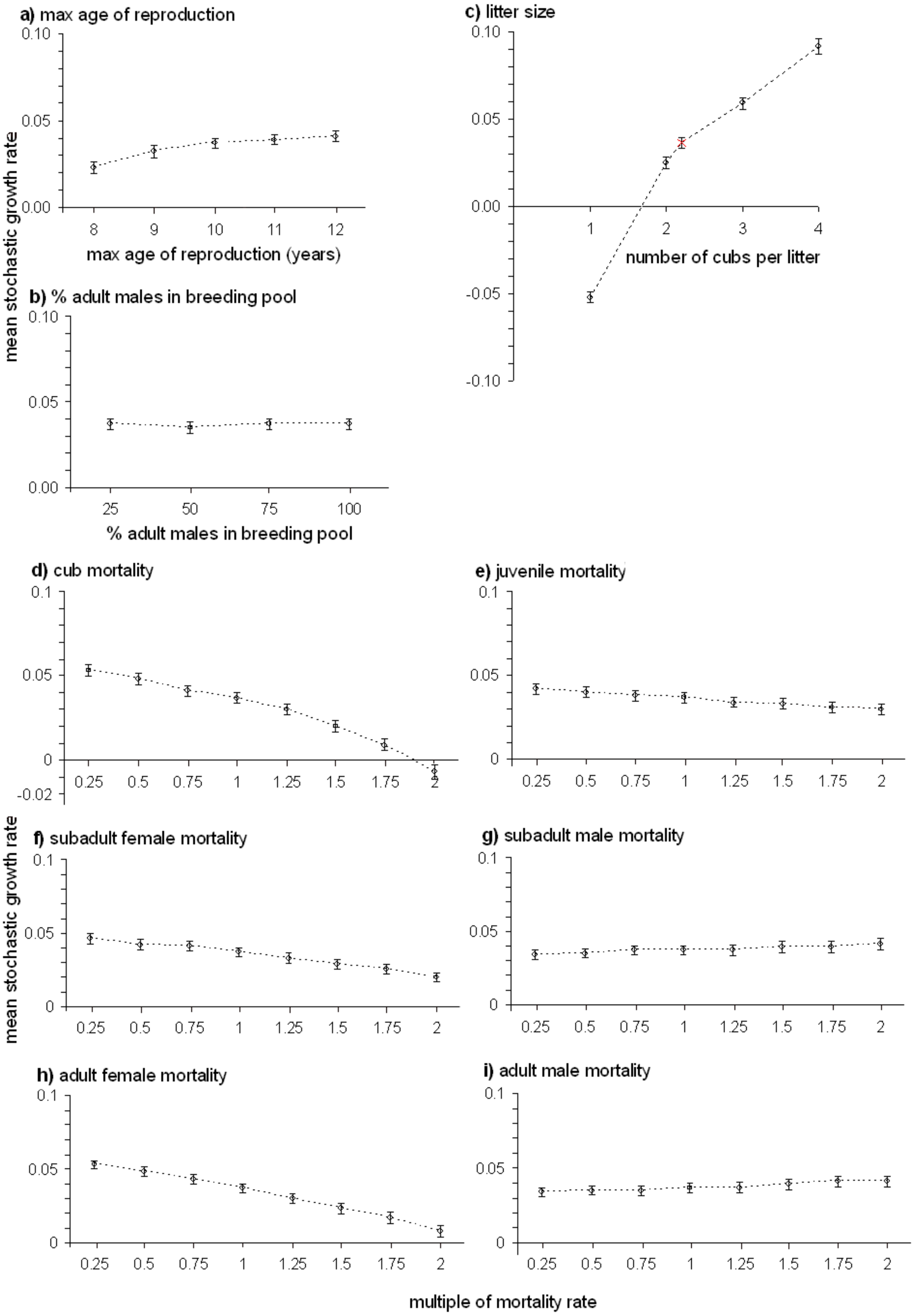


Figure 7.4 Sensitivity of mean stochastic growth rate (r_{-stoch}) to base model parameters varied through a range of values **a)** maximum age of reproduction, **b)** % males in breeding pool, **c)** litter size (red cross indicates distribution of litter sizes of mean 2.2), **d-i)** natural mortality of specific age/sex groups. The model was run for100 years with100 iterations, N_0= K= 2000, for each sensitivity analysis. 95% CI are shown.

Dispersal and human-induced mortality

Simulations of the population dynamics of the two protected populations (MM and RB) as isolated units over 100 years indicated that both are large enough to withstand demographic and environmental stochasticity (under the model assumptions), having a mean $r\text{-}_{stoch}$ of 0.037 and 0.036 respectively (Figure 7.5a, b). The probability of extinction of either population over 500 simulations was zero, if extinction is defined as only one sex remaining. The two populations were stable even if adult female mortality was doubled, although the probability of extinction in 100 years increased to 0.026 in MM and 0.084 in RB. In isolation and in the absence of human-induced mortality, the unprotected population (UP) was also stable, first increasing to a constant size as determined by the carrying capacity, having a mean $r\text{-}_{stoch}$ of 0.41 (Figure 7.5c).

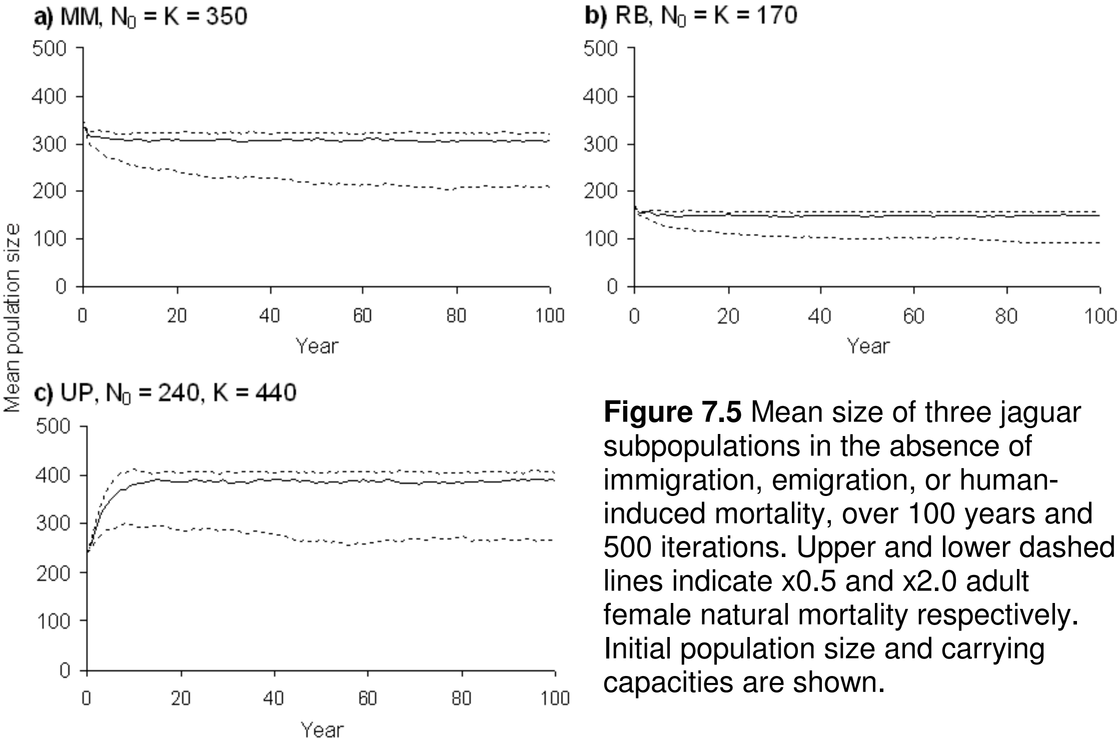


Figure 7.5 Mean size of three jaguar subpopulations in the absence of immigration, emigration, or human-induced mortality, over 100 years and 500 iterations. Upper and lower dashed lines indicate x0.5 and x2.0 adult female natural mortality respectively. Initial population size and carrying capacities are shown.

In the absence of immigration from the protected populations, the UP population was able to sustain low levels of human-induced mortality (Figure 7.6). The probability of population persistence over 100 years fell dramatically if off-take exceeded ~ 12% of the population each year. Halving the natural mortality of adult females made little difference to this threshold, and if their natural mortality was doubled the threshold fell to ~ 6%.

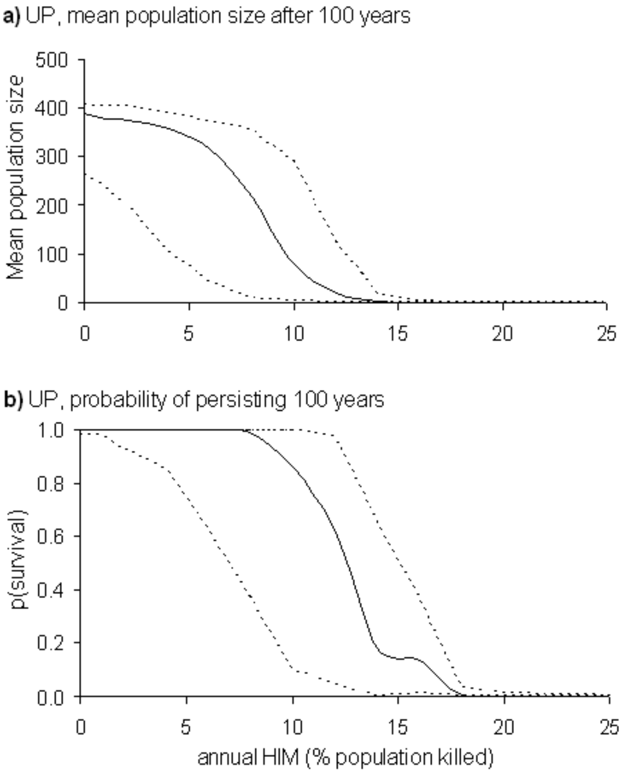


Figure 7.6 Influence of the level of human-induced mortality (HIM) on **a)** the mean population size and **b)** the probability of persistence, of the unprotected jaguar population, UP, after 100 years. Populations were simulated 500 times. $N_0 = 240$, $K = 440$. Upper and lower dashed lines indicate x0.5 and x2.0 the natural mortality of adult females respectively. Persistence is defined as both sexes remaining in the population.

Closer inspection of the temporal dynamics of the simulated unprotected populations showed that the mean $r\text{-}_{stoch}$ of populations exposed to > 8% human-induced mortality per year for 100 years was negative and an average population was unlikely to stabilise in 100 years (Figure 7.7). The sustainable threshold for human-induced mortality appears to be much lower than the 45% annual off-take estimated for the unprotected lands. Human-induced mortality of 45% per year was unsustainable (Figure 7.7); all 500 simulated populations went extinct within 20 years under such conditions, even if natural mortality of adult females was halved. This suggests that the current UP population has sink-like properties and its persistence depends on high levels of immigration.

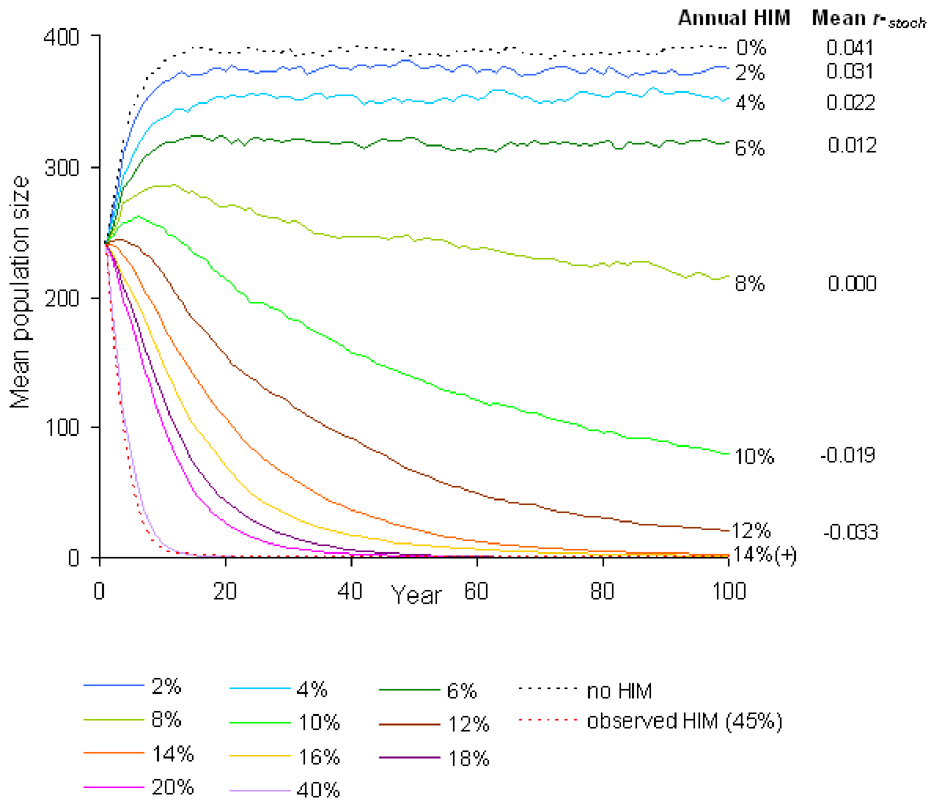
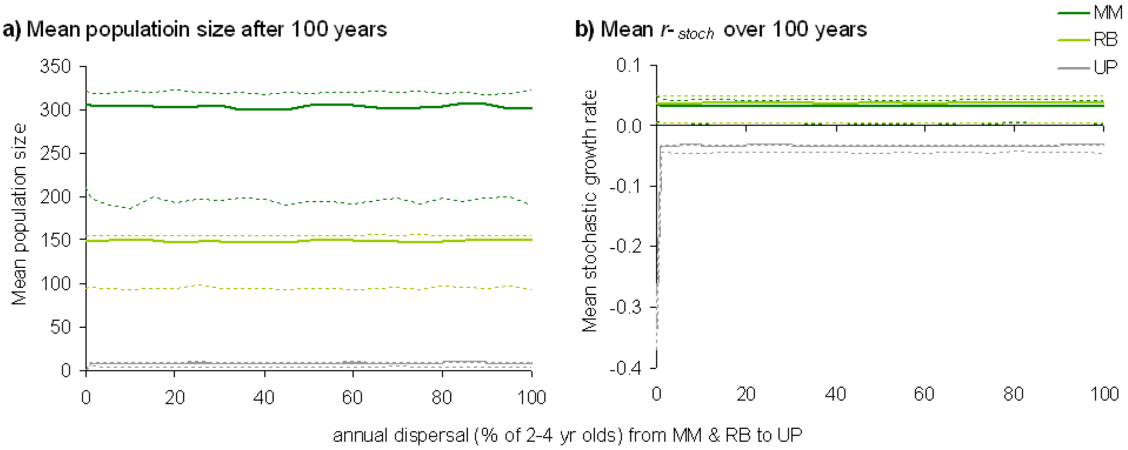
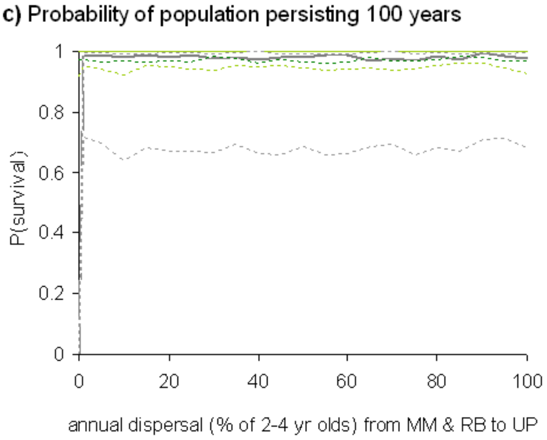


Figure 7.7 Influence of the level of annual human-induced mortality (HIM) on the mean population size of the unprotected jaguar population, UP, over 100 years. Populations were simulated 500 times. Mean stochastic growth rates ($r_{\text{-}stoch}$) are shown. N_0 = 240, K = 440. Level of HIM observed in current study (45%) is shown as dashed red line.

Simulation of density-dependent dispersal from the two protected source populations (MM and RB) to the unprotected sink population (UP), where annual loss to human-induced mortality was 45%, indicated that immigration of 2-4 year olds could maintain a population, albeit of minimal size, within the unprotected lands even though the mean growth rate there was negative (Figure 7.8a, b). However, even with an annual immigration rate of 100% (=100N/K), intense human-induced mortality for 100 years resulted in a small and probably unviable unprotected population, equivalent to a density of ~ 1 jaguar per 1750 km^2 (mean N_{100} ± SD = 8.7 ± 3.6 jaguars, n = 500 simulations, Figure 7.8a). The protected populations were able to sustain high rates of emigration because dispersal was density-dependent (a function of N/K). Thus the annual dispersal rate did not influence final mean population sizes of MM and RB (e.g. no dispersal: MM mean N_{100} ± SD = 307 ± 42; 100% dispersal: MM mean N_{100} ± SD = 302 ± 42; n = 500 simulations), or their probability of persistence over 100 years (1 for both populations) (Figure 7.8a, c). Including density-dependent dispersal from the unprotected to the protected populations did not alter the findings because the unprotected population was below carrying capacity therefore the number of natal dispersers available to leave this population was very low.





Note that actual dispersal rate is x *N*/*K* e.g. '20% dispersal' refers to (0.2*N*/*K*)

Figure 7.8 Influence of the level of density-dependent dispersal on **a)** the mean population size **b)** the mean stochastic growth rate, and **c)** the probability of persistence, of the protected populations (MM and RB) and unprotected population (UP), after 100 years. Dispersal is from the protected populations to the unprotected population. Human-induced mortality was set at 45% per year in UP. Populations were simulated 500 times. Upper and lower dashed lines indicate x0.5 and x2.0 the natural mortality of adult females respectively. Persistence is defined as both sexes remaining in the population.

Attraction of natal dispersers (2-4 year olds) from protected lands to unprotected lands (where human-induced mortality was fixed at 45% per year), independent of the local density, had negative consequences for all three subpopulations if intrinsic dispersal rate exceeded ~ 8% annually (Figure 7.9). After 100 years in which 10% of 2-4 year olds dispersed each year, the mean populations of MM and RB fell to approximately half their initial sizes, and became effectively zero if dispersal was 20% annually (Figure 7.9a). MM and RB appeared to be able to sustain dispersal rates ≤ 8%, at least over 100 years, and in doing so could maintain a population of up to 50 individuals in the unprotected lands (Figure 7.10). Above 8% annual dispersal, reproduction within the protected populations did not exceed losses due to natural mortality and emigration and so the mean stochastic growth rate fell below zero (Figure 7.9b). Consequently the unprotected population could no longer be sustained as fewer individuals were available to re-populate from MM and RB.

The number of 2-4 year olds present in MM and RB at year zero was approximately 113 and 55 respectively based on a stable age distribution. The probability of long-term persistence of the all three populations fell to ~ 0.5 if dispersal was ~ 13% annually (Figure 7.9c). Thus, under the model assumptions, if as few as 15 ‘MM’ and seven ‘RB’ natal dispersers were attracted to the unprotected lands each year (where 45% of the population is killed annually by people) then the long-term consequences for all three subpopulations could be bleak.

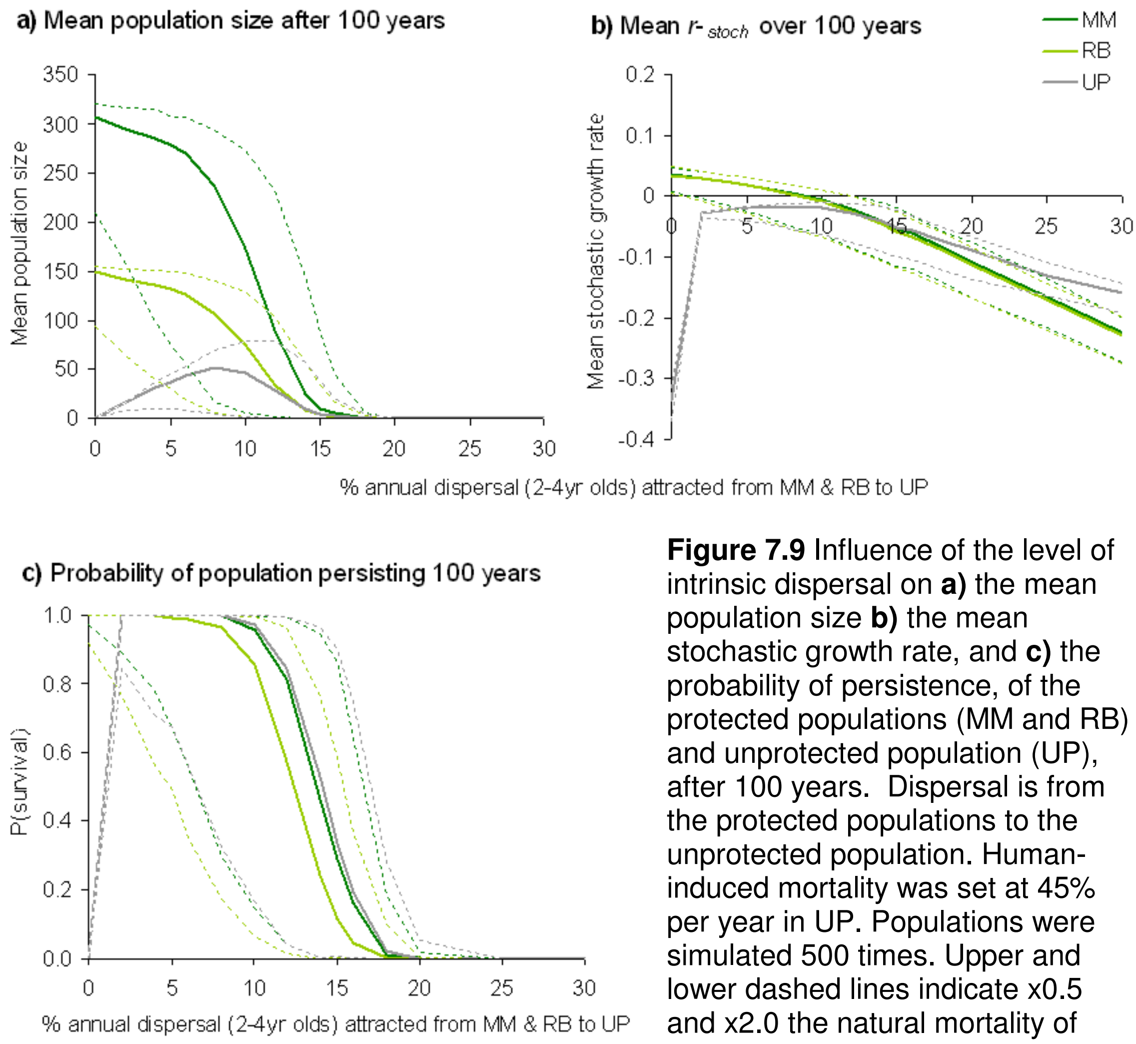


Figure 7.9 Influence of the level of intrinsic dispersal on **a)** the mean population size **b)** the mean stochastic growth rate, and **c)** the probability of persistence, of the protected populations (MM and RB) and unprotected population (UP), after 100 years. Dispersal is from the protected populations to the unprotected population. Human-induced mortality was set at 45% per year in UP. Populations were simulated 500 times. Upper and lower dashed lines indicate x0.5 and x2.0 the natural mortality of adult females respectively. Persistence is defined as both sexes remaining in the population.

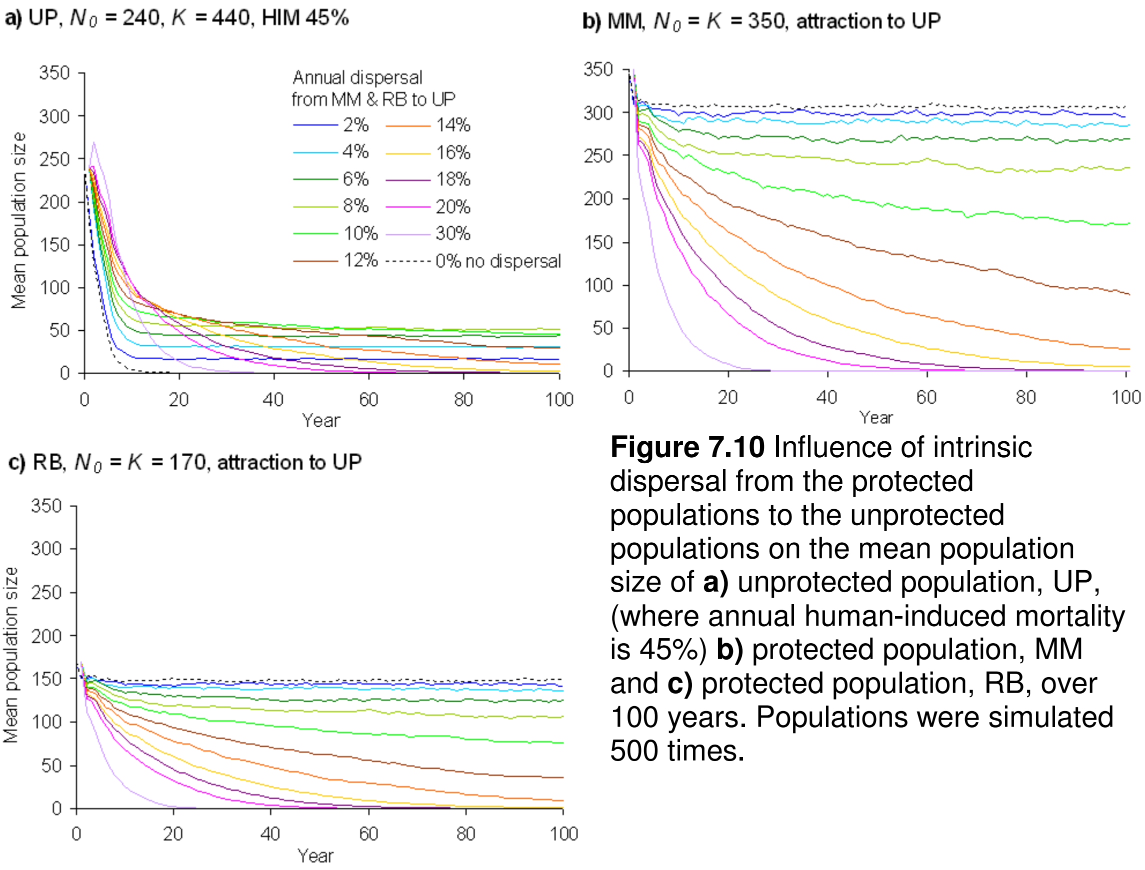


Figure 7.10 Influence of intrinsic dispersal from the protected populations to the unprotected populations on the mean population size of **a)** unprotected population, UP, (where annual human-induced mortality is 45%) **b)** protected population, MM and **c)** protected population, RB, over 100 years. Populations were simulated 500 times.

Note that 'two-way' intrinsic dispersal (movement from UP to MM and RB as well as from the MM and RB to UP) was not simulated, as the aim was to specifically model attraction from protected to unprotected lands. It is acknowledged that the inclusion of obligate dispersal from UP to MM and RB could potentially increase longevity of the protected populations and warrants further research.

Discussion

Historically jaguar populations suffered intense exploitation for the commercial skin trade (McMahan 1982, Rabinowitz 2006). With the implementation of CITES in the 1970s demand for pelts diminished; however the cattle industry has grown, and today one of the main threats faced by jaguars is direct persecution from livestock owners. Indeed in this study the majority of verified jaguar deaths were associated with livestock predation. However, unlike some areas where jaguars are not tolerated on ranches under any circumstances (e.g. Pantanal, Brazil: Zimmermann *et al*. 2005) most people in this study accepted jaguars frequenting village vicinities and farms in the absence of depredation (R. Foster pers. obs.). Camera-trap data revealed that attacks on livestock were not inevitable if jaguars were in the area, with 25% of the cattle farms having no problems despite jaguar presence. Specific habitat and livestock management characteristics of the farms with no attacks are discussed in detail in Chapter 5. Reports from other parts of Belize, particularly in Mennonite communities, indicate that jaguars are less tolerated, and pro-active rather than reactive culling is practised (B. Harmsen, Belize Jaguar Program, pers. comm.). Such behaviour may be counter-productive because the removal of well-behaved residents through indiscriminate culling may aggravate the situation if replaced by naïve individuals who have not learned to avoid human activity and livestock. In this study all reported cases of lethal control were reactive; however livestock losses did not necessarily cease following a jaguar death, suggesting that the problem individual was not always the one removed. The chosen method of lethal control may improve the chances of removing the right cat. Methods that involve the use of bait will always run the risk of drawing in non-livestock killers, and potentially may give them a taste for livestock. Lacing bait with poison may additionally kill scavengers. Waiting at the site of a livestock kill and shooting the cat when it returns for a second feed would seem the most favourable option and was most commonly practised in the study area. Nevertheless, on the largest farm predation rates did not always decline when this method was employed. It is not clear whether multiple cats were attacking livestock or whether the cowboy occasionally blamed jaguars wrongly. Cattle rustling is a problem in Belize (G. Hanson pers. comm.) and could be responsible for some otherwise unexplained losses. Attacks are usually obvious (e.g. machete wounds to cattle, signs that calves were butchered on site, R. Foster pers. ob.) and it is unlikely that the experienced cowboy mistook rustling events for depredation. However, well-planned attacks that leave little evidence could be misinterpreted as depredation by less experienced cattle owners, leading to unnecessary persecution of jaguars. Alternatives to lethal control are discussed in Chapters 5 and 8.

Characteristics of 'problem' jaguars

In general across the carnivores, adult males tend to be responsible for more depredation events than any other age or gender class, perhaps due to greater risk-taking behaviour and/or greater encounter rates with livestock due to their larger home range (Linnell *et al.* 1999). We may therefore anticipate that more males would be killed on farms than females. In this study, however, males and females used pastures in similar numbers and at a similar rate (Chapter 5) and there was no apparent sex bias in the susceptibility to lethal control, with males and females killed in roughly equal numbers for attacking livestock. This is concerning because, as shown by the sensitivity models, in a polygynous species such as jaguars the loss of adult resident females will impact more on the local population productivity than the deaths of males.

Injured or infirm jaguars unable to hunt wild prey may turn to domestic animals, and they often make up a high proportion of the animals killed for livestock predation (Rabinowitz 1986a, Hoogsteijn 2000). Although a few killed jaguars in this study were infirm, the majority were young and/or in good condition. Debilitating injuries were mostly human-induced. Indeed the injuring of healthy jaguars through indiscriminate shooting is likely to encourage livestock predation rather than prevent it (Rabinowitz 1986a).

All jaguars deaths verified in this study were limited to lands outside the protected forest. The protected area was buffered from the farms and villages of the fragmented landscape by unprotected forest with which it was contiguous (Chapter 5). Although the buffer may be less rich in wild prey than the protected forest (Chapter 6) it appeared to provide an important refuge for those jaguars which also used the fragmented habitat. In contrast jaguars that used only the fragmented habitat suffered high human-induced mortality. Clearance of this forest buffer for other uses would clearly increase the contact rate between jaguars and humans and ultimately intensify conflict.

Impact of human-induced mortality on population dynamics

Population models such as those used in this study allow the exploration of hypotheses about the influence of hunting intensity on big cat populations, which would be difficult to study in the field. Nevertheless, an increasing body of field research is being published on the dynamics of hunted populations of pumas in North America, as good data are becoming available on levels of sport-hunting. For example, Lindzey *et al*. (1992) found that a population that suffered a harvest of 27% during one year failed to attain its pre-removal size two years after the removal. Stoner *et al*. (2006) found that an annual removal > 40% for ≥ 4 years resulted in a smaller, younger, less productive and socially unstable population. Robinson *et al*. (2008) found that ~27% removal over 5 years resulted in compensatory immigration and a shift in the age/sex class to younger males and a decline in females. In this study, extrapolation of the field data implied an annual off-take of ~ 200 jaguars nationwide, estimated to be ~ 45% of the population that resides outside the two main protected forest blocks of Belize. Based on the puma field studies, sustained off-take at such a level could profoundly influence big cat population dynamics.

The population simulations suggested that, even if lethal control only occurred outside the two main protected blocks, it could still cause the regional population to crash under certain conditions. Within the model assumptions, the unprotected population functioned as a sink, unable to sustain an annual off-take > 8% for 100 years without high levels of immigration. With continued off-take above this rate, and in the absence of immigration, the unprotected population had zero probability of surviving more than 20 years. Density-dependent movement of natal dispersers from the protected blocks could theoretically sustain current rates of human-induced mortality in the unprotected lands for 100 years, but the population there would become effectively unviable (~ 1 jaguar per 1750 km^2). However, even if the protected populations became technically isolated under such a scenario, they seemed resilient to demographic and environmental stochasticity and had a high probability of persistence in isolation, assuming no catastrophes, edge-effects or the negative influence of genetic factors. Intrinsic dispersal, the attraction of natal dispersers from the protected forest to the unprotected lands, presented less optimistic consequences for the regional population. Low levels of intrinsic dispersal could be sustained by the protected populations, and could maintain a population of up to ~ 50 jaguars (~1 jaguar per 300 km^2) in the unprotected lands; although not modelled, in theory this sink population could feedback at a low rate into the two protected populations allowing genetic mixing and extended longevity of the regional population (e.g. Howe *et al.* 1991). At higher rates of intrinsic dispersal the unprotected population functioned as an ecological trap, the probability of long-term persistence of the three populations decreased, falling to 50% if as few as 15 and seven 2-4 year olds dispersed from the two protected populations annually into the unprotected population. If farms do attract dispersers from the protected forest at this rate, and levels of human-induced mortality remain consistently high in the unprotected lands, then the long-term persistence of the jaguar population in Belize may be in doubt. There is some evidence from the study area to suggest that jaguars may be attracted to the resource-rich pastures. For example jaguars which were most active around cattle farms also tended to have the smallest ranges, regardless of sex, suggesting a contraction of their range around the pastures; and jaguar density was higher in survey areas with ≥ 2% pasture cover than those with < 1% pasture cover (Chapter 4). Although these observations do not explicitly demonstrate attraction from protected forest to pasture they do suggest that cattle farms may be become a focal point of activity for some individuals. More field data are need on jaguar dispersal, particularly at the boundary between a protected population and a potential sink.

The population simulations discussed here must be interpreted within the context of the model assumptions; in particular the following restriction are assumed: 1) no catastrophes, 2) no genetic factors, 3) no difference in demographic parameters between populations, 4) no social dynamics, 5) constant level of human-induced mortality, 6) limited migration between populations, 7) no spatially explicit factors. Catastrophes, such as hurricanes or floods, and genetic factors (the effects of inbreeding and loss of genetic heterozygosity), are expected to have negative consequence in small populations. Thus one may assume that their occurrence in the jaguar population would either have no effect or lower the probability of long-term persistence. Restrictions 4-7 could have negative or positive impacts.

The mean values of the demographic parameters used in the simulations were assumed to be the same in all three subpopulations and temporally-independent. In reality reproduction and survival, particularly of cubs and juveniles, will be influenced by prey availability. For example if prey are depleted, fewer females may be able to raise young, particularly if large prey are limited (Chapter 6). Although there are currently no data on the abundances of prey species in Belize, it is likely that as the human population grows (20% increase predicted by 2018, WRI 2007), the game species will decline, particularly in the unprotected lands. Similarly the carrying capacity of the jaguar population in the unprotected lands will probably decline as forest is increasingly cleared for settlements and plantations (Chapter 4). Such factors will lower the population resilience and the probability of long-term persistence.

No attempt was made to incorporate the effect of social structure and dynamics into the population simulations. Hunted populations with high rates of immigration of young individuals may be socially unstable (e.g. Stoner *et al*. 2006) and may, in turn, impact on the population dynamics. For example the frequent removal and replacement of males may elevate levels of infanticide (e.g. Loveridge *et al*. 2007, Balme *et al*. 2007) or increase territorial disputes and intra-specific aggression. Intra-specific aggression may also intensify in isolated populations in which habitat is severely limited, for example a 21-year study of the causes of mortality in the Florida panther, an isolated population of ~30-50 pumas in south-eastern USA, found that aggression between individuals accounted for the deaths of 41% of 47 radio-collared cats, and most of the deaths were young males (Taylor *et al*. 2002). Although infanticide has been reported in wild jaguars (Soares *et al*. 2006) nothing is known of its prevalence. The level of aggression between adults is also poorly known, although rates of serious flesh wounds detected on camera-trap photographs were considered low in the study area. Camera-trap photographs of jaguars inside and outside the protected forest collected over 4 years (~1,200 captures of 68-78 individuals, comprising at least 16 females and 38 males) showed four separate occurrences of flesh wounds on just three individuals, all male (Harmsen *et al*. in press, R. Foster unpubl. data). It is unknown whether the wounds resulted from conflict with conspecifics or were received whilst attacking prey. However the male bias in injuries may indicate intra-specific aggression as the cause. As such we may suspect that in a real jaguar population, human-induced mortality will impact on the long-term persistence not only through the direct removal of individuals but also through its disruption of social dynamics.

Lethal control was modelled very simply by assuming that the population inhabiting the two main protected forest blocks suffer no human-induced mortality. In reality some jaguar deaths caused by humans within the protected forests are inevitable, mainly from incidental shootings by poachers hunting for game who accidentally stumble across a cat. This may be particularly common in the Maya Mountain forest block near the border where Guatemalan xateros illegally set up camps and hunt game (B. Harmsen, pers. comm.). In the models, human-induced mortality was restricted to the 15,068 km^2 of lands outside the two protected forest blocks. It ignored the additional protected areas which are scattered throughout the country ranging in size from 0.09 km^2 to 420 km^2, and totalling 1,924 km^2. These areas may function as important refuges for jaguars outside the two main protected blocks, and thus the level of human-induced mortality modelled in this population may be too high. However, the estimate of current levels of human-induced mortality used in the models was based on an area where lethal control of jaguars is largely reactive; this may underestimate the true value because pro-active lethal control is practised in some areas of the country. Thus, although the model of one unprotected and two protected populations is greatly simplified it is probably a reasonable approximation of the true situation.

The percentage of human-induced mortality modelled in the population simulations was held constant through time, assuming that a fixed fraction of the jaguar population would come into contact with humans each year. It is plausible that the rate of contact, and consequently lethal control, is density-dependent. It might become increasingly smaller as the population declines, as more territories are freed up and jaguars do not need to roam so close to areas with human activity. Alternatively the rate of lethal control might increase as the population declines, as resource-rich territories on cattle farms become vacant and individuals preferentially establish ranges near livestock rather than around milpa-farms, plantations or savannahs where prey availability may be lower.

Movement of jaguars between Guatemala and Belize was not incorporated into the models. To the north-west, Belize is bordered by the forest of the Guatemalan Biosphere Reserve Petén. Drug trafficking is rife throughout this region (R. McNab, WCS Guatemala, pers. comm.) and associated with high levels of illegal hunting of wild prey. Accordingly the only jaguar density estimate from the region is low (1.7 individuals per 100 km^2, Novack 2003). The rate of movement of jaguars from Belize into this area of Guatemala is unknown; however, a camera survey spanning the border found no overlap in individuals (Miller 2005). To the south-west, the Belizean side of the Maya Mountains is thickly forested, but across the border the forest has been extensively converted to agriculture. It is suspected that the emigration of jaguars from this degraded area, if it still contains any, would have negligible influence on the Belizean population. However this area could have sink- or trap-like properties. Guatemalan xateros crossing the border into Belize may locally deplete wild prey, so increasing the attractiveness of the Guatemalan cattle as alternative prey for jaguars. Such an ecological trap extending along the Belize-Guatemala border could greatly increase the pressure on the Belizean jaguar population and warrants further research.

Sexual differences in dispersal type or ability were not included in the model. Little is known about jaguar dispersal, but males are likely to disperse further and more readily than females, as observed in pumas, tigers and lions (Sunquist and Sunquist 2002). Sexual differences in dispersal provide different mechanisms of recruitment for males and females. Field studies of pumas have shown mainly philopatric recruitment of female off-spring, whilst male recruitment in the population is almost entirely via immigration (e.g. Lindzey *et al.* 1992, Sweanor *et al.* 2000). For example in a population of pumas in New Mexico, 68% of female recruits were born in the study area whilst 78% of male recruits were immigrants (Sweanor *et al.* 2000). These contrasting recruitment mechanisms can cause in a shift in the structure of hunted populations, as juvenile males fill the vacated territories and females are not replaced (e.g. Robinson *et* *al.* 2008). This can lead to a less productive and socially unstable population (Stoner *et al.* 2006).

Movement between populations was limited to natal dispersers only; however adult jaguars expand, contract, and shift ranges (e.g. Crawshaw and Quigley 1991, Rabinowitz and Nottingham 1986, Harmsen 2006). Shifts in range boundaries are common in big cat populations following the death of a resident male and may take a year or more to stabilise (Sunquist and Sunquist 2002). Rabinowitz and Nottingham (1986) noted that following the death of two adult males, two other males began to shift into their ranges and the vacancy created by their relocation was filled within 6 weeks by a third male. It is not unreasonable to expect that, following the removal of a male from a neighbouring territory in the unprotected lands, male jaguars predominantly using the protected forest may expand their ranges outwards, in pursuit of increased access to females. For example, within 6 weeks of the death of a male jaguar on Farm #02, another male, previously only recorded in the forest block and predominately within the protected area, was detected on the farm (R. Foster unpubl. data). Thus the ranges of some individuals will span the boundary between protected and unprotected lands (e.g. Chapters 4 and 5) and residents of the protected area will occasionally travel into areas where they may come into conflict with humans. The extent to which this is important will depend on the physiognomy of the protected area in relation to the rest of the landscape. A larger perimeter-area ratio will facilitate greater contact with humans (e.g. Woodroffe and Ginsburg 1998), or conversely, one may argue that the length of the perimeter of the protected area will limit the rate at which immigrants can replenish the hunting zone (e.g. Salas and Kim 2002).

The size and spatial arrangement of protected and hunted areas, as well as the dispersal and ranging behaviour of the target species, will undoubtedly influence population dynamics. The immigration and human-induced mortality modelled in this study had no spatial component, other than being limited to the population inhabiting the unprotected lands. In reality jaguar deaths caused by humans in these lands are likely to be clustered around pastures and villages, and, to a lesser extent, the highways. We may expect very high rates of turnover in these high-risk hotspots, whilst human-induced mortality may be less frequent in areas where monocultures, milpa-farms, forest fragments and savannah dominate. Rather than the entire human-matrix functioning as one large population sink, the mosaic of different habitat types and land-use systems will give rise to a patchy distribution of resource-rich zones where mortality is high, and low-risk zones where mortality, and also production, may be low. The influence on population dynamics of this fine-scale spatial heterogeneity in mortality needs further investigation. The use of spatially explicit models is the obvious next step in investigating the impact of lethal control on jaguars (e.g. Ahearn *et al.* 2001, Ahearn and Smith 2005). Individual-based, spatially explicit, object-oriented models such as those developed by Ahearn *et al.* (2001) to model individual tiger dynamics enhance understanding of interactions between tigers, natural prey and livestock and the likely consequences of different management scenarios, but require long-term field studies of predatory, reproductive, territorial and dispersal behaviour. Such detailed data are not yet available for jaguars; however recent technological advancements in tools such as camera traps and GPS collars have enhanced the study of these otherwise elusive cats and our knowledge of their spatial patterns is improving (e.g. Harmsen 2006, Soisalo and Cavalcanti 2006).

Conclusion

Spatial heterogeneity in hunting and other forms of human-induced mortality across the landscape can cause source-sink population dynamics. This emphasises the need for long-term population monitoring of species that face direct persecution from people. Short-term studies may not detect sink- or trap-like properties of hunted populations. High numbers of transients competing for a territory may inflate the local density, masking an unproductive or declining population, particularly if immigration is male-biased (e.g. Stoner *et al.* 2006, Robinson *et al.* 2008). Habitats with high levels of human-induced mortality that attract individuals can have negative consequences for the source populations, and, depending on the relative rates of dispersal and mortality, for the regional population as a whole. This study has shown that ecological traps, in the form of livestock farms, may pose very real threats to long-term jaguar persistence and indicates that management plans will not only require accurate knowledge of life history parameters, but also a better understanding of habitat selection and dispersal (e.g. Donovan and Thompson 2001). This study also highlights the need to resolve conflicts of interest between farmers and jaguars, replacing lethal control, at least partially, with alternative methods of livestock protection (see Chapter 5 for suggestions).

Chapter 8

Synthesis and way forward

Introduction

The objective of this thesis has been to improve our understanding of the ecology of jaguars (*Panthera onca*) in a human-influenced landscape. During the course of the project, it was deemed necessary also to address various methodological issues associated with studying jaguars effectively in this environment. The aim of this chapter is to draw together the main findings of the thesis, and to consider the future of jaguar conservation in Belize. I will pay particular attention to methods to study jaguars within a human-influenced landscape; the adaptability of jaguars to anthropogenic pressures; and how humans can facilitate coexistence with jaguars in the future.

Studying jaguars

Research on wildlife conservation must involve the interests of local people and other stakeholders. The effectiveness of the work will always be dictated by the level of cooperation that can be sustained with land owners. Diplomacy and patience are essential, as well as an acceptance that it may not always be possible to collect all the information that one desires. During this study, the author was fortunate to receive a high level of interest and support from all private land owners and village chairpersons who were approached for assistance. Even so, planning large-scale surveys for jaguars (*Panthera onca*) across private and communal lands was complicated by the need to seek access permissions and to anticipate risks of damage to the cameras from people and domestic animals. The extent to which these extraneous factors governed camera location meant that camera-traps could not necessarily be deployed in a configuration that maximised the core to edge ratio of the survey area, as is preferable for accurate density estimates (Chapter 2). In addition, it did not allow a random stratification of locations throughout different habitat types for standardised habitat analyses (Chapter 5). Rates of camera failure during surveys were high, due to working in an environment that is harsh for electronic devices and in which cameras may be vandalised or stolen by people or chewed and kicked by cattle (Chapter 3). However manipulation of empirical data showed that camera failure need not mean an unsuccessful survey (Chapter 3). The jack-knife estimator for the closed population model M_h was fairly robust to camera failures of up to ~10% of the trap-occasions. The effect of failure was least marked in surveys with a high capture probability and a high recapture frequency, and pooling trap-occasions reduced the effect further. However it was noted that under some circumstances trap failure can result in an overestimate of abundance. Therefore it is suggested that published estimates based on camera-trap data should always indicate the level of trap-failure, if any, within the study. This is not currently standard practise.

Camera spacing in the surveys for this study adhered to protocols of published jaguar surveys which base the distance between neighbouring stations on the diameter of a circular home range of 10 km^2, which is assumed to be the minimum range of a female jaguar (Wallace *et al*, 2003, Silver *et al*. 2004, Miller and Miller 2005, Miller 2006, Harmsen 2006). Chapter 4 suggested that this spacing could be too wide to detect some female jaguars, resulting in an underestimate of the female component of the population. This effect may be further exacerbated by female avoidance of camera locations that are preferentially placed in areas with high male activity, specifically old logging roads and man-made trails within dense forest. There was some evidence that female activity increases with proximity to streams, and it was speculated that where males dominate forest trails females may preferentially use streams as access routes through the forest. Increasing trap effort in such locations might consequently increase female capture rate and remove the observed sampling bias within forest surveys. Conversely, the male sampling bias was less pronounced in the fragmented landscape. This was attributed to the more heterogeneous environment and open habitat with numerous natural and man-made trails and roads.

This study involved one of the largest camera survey for jaguars conducted at one time, using 46 camera stations with an effective sampling area of ~530 km^2. When these data, and those from the other surveys, were sub-sampled they showed that, in this study at least, survey areas needed to be larger than ~170 km^2 to avoid unreliable density estimates. This was approximately five times the average home range of individuals in the study area. It is similar to the proposal of Maffei and Noss (2008) that reliable density estimates require a camera survey area at least four times the average home range area of the target species.

Collecting long-term data on lethal control of jaguars (Chapter 7) requires discretion, sensitivity and patience in order to build trust with livestock owners and their staff. It became apparent early in the study that the people were wary of a formal approach to data collection via structured interviews or datasheets. The author found that information about farm management, livestock predation and lethal control of jaguars was best collected surreptitiously through informal visits and casual chats with stakeholders that did not necessarily focus on jaguars directly. Most stakeholders were open with the author, however there will always be a certain stigma attached to foreign scientists studying local affairs. It was suggested that long-term work on human-jaguar conflict in the country would benefit greatly from the employment of nationals who are both sympathetic to the conservation goals and also able to converse fluently in Mayan, Spanish, English and Creole (Foster 2007). Indeed, a bi-lingual forestry officer (Creole/English speaker) has recently been employed within the Belize Forest Department to work specifically on issues related to human-jaguar conflict (B. Harmsen, Panthera Belize, pers. comm.). Officers who can also converse in Spanish and Mayan and span cultural barriers would be a great asset as well.

The use of camera traps is often commended as a non-invasive alternative to live-trapping and telemetry (e.g. Harmsen 2006). Telemetry still has an important role in studying carnivore ecology, particularly with the recent technological advancements in GPS collars which provide detailed movement data. However camera-trap data can be used for more than just abundance estimates; for example recently camera data have been used to analyse the spatial and temporal interactions of jaguars and pumas (*Puma concolor*) (Harmsen *et al.* in press). In this study camera traps were effective not only to estimate density (Chapter 4) but also to investigate habitat use (Chapter 5). However camera traps had limited applications for studying problem jaguars that were killing livestock. Although it was possible to monitor which cats frequented pastures it was rarely possible to link an individual to specific depredation events. The use of telemetry would greatly enhance research on livestock predation. A large-scale study is being planned to combine GPS telemetry of jaguars captured around cattle farms with experimental implementation of electric fencing and other measures to protect livestock from attack (subject to funding: B. Harmsen, pers. comm.). Not only will this reveal any specific characteristics defining habitual cattle killers, it will also allow empirical tests of the effectiveness of alternative methods of deterring attacks.

Scat collection and analysis is an important means of investigating the feeding ecology of otherwise elusive species, and is widely used to infer conclusions about the diet of carnivores. Chapter 6 demonstrated that diet studies in areas that support a wide range of potential prey species may underestimate the true richness of the diet and overestimate the importance of the more commonly taken prey taxa, if the sample size is not large enough. It was suggested that studies of big cats from biodiverse regions such as tropical rainforests should aim for samples of at least 100 scats to adequately describe diet. In this study, many of the scats from the protected forest were collected on trails known to be dominated by males (Chapters 5 and 6). A male bias was therefore likely in scat samples from that area. The use of scat-detector dogs to find female scats off-trail may help to correct this bias in future studies.

Living with people

Jaguars were widespread throughout the fragmented landscape. However density was higher within the contiguous forest. Chapter 4 demonstrated that where more than four-fifths of the forested landscape was fragmented, not all of the available land was utilised by jaguars on average, and it was suggested that this may reflect a combination of habitat preferences within the mosaic landscape and vacant territories arising from direct conflict with people.

Often male carnivores are more risk-prone than females and so are more likely to come into conflict with humans (Linnell *et al.* 1999). In this study there was no evidence that female jaguars were less tolerant of lands with human activity than males. In fact, outside the forest block female activity increased closer to areas of human development, and both sexes were equally active on disturbed lands such as pastures and fragmented forests (Chapter 5). Consequently both sexes were equally susceptible to human-induced mortality. This is concerning, as the removal of adult females has a greater impact on the population than the removal of males (Chapter 7).

Studies across the jaguar’s geographical range indicate a flexible diet (see Chapter 1). The rather narrow diet of jaguars observed in this study in the protected forests of the CBWS probably reflects opportunistic exploitation of the superabundance of armadillos in this area (Chapter 6). The differences in diet observed between the CBWS, the unprotected forest buffer, and the fragmented lands (Chapter 6) support the premise that jaguars are indeed opportunistic carnivores with highly flexible feeding habits. White-lipped peccaries featured in jaguar diet in the CBWS but were absent from the diet outside the protected forest. In the fragmented landscape domestic animals replaced large wild ungulates as prey. Although this flexibility in prey choice enables the jaguar to exploit natural habitats and human-influenced landscapes alike, it also provokes conflict with people and direct persecution, and therefore could ultimately cause the jaguar’s demise. Data are urgently required on wild prey abundance to determine whether prey depletion is exacerbating livestock predation (discussed later).

At the time of writing, this study has no data with which to investigate sex differences in prey selection. Genetic techniques to assign sex to jaguar and puma scats are currently being refined and will eventually permit us to categorise the scats used in this study by the sex of the cat that produced them (B. Harmsen, pers. comm.). Models of jaguar energetics suggested that the availability of large prey could limit reproduction because a diet of only medium/small prey would require unrealistically high hunting rates for a mother to feed herself and dependents (Chapter 6). Studying sex differences in diet will help to evaluate this proposition, for example by testing for a higher frequency of large prey in female diet than in male diet.

Chapter 7 suggested that the long-term persistence of jaguars in Belize could be at risk if rates of lethal control are not lowered. However this conclusion was based on models that made numerous as yet un-testable assumptions about demographic rates (birth rate, sex ratio, survival etc), dispersal and the dependency of these parameters on density. Indeed many of the input parameters were derived from other big cat species due to a lack of specific data about jaguars. Models of population persistence will benefit from field data on demographic rates and dispersal of jaguars. Long-term population monitoring in the CBWS (currently 7 years) will soon be sufficient to estimate jaguar survival and recruitment. Previous estimates by Harmsen (2006) of survival, recruitment, immigration and emigration, based on survey data from CBWS, were susceptible to biases from the small size of the survey area, and a blurred distinction between mortality and emigration due to the relatively short study period of 5 years. The survey area has since been enlarged and annual surveys monitoring the population have continued into 2008, though funding for future surveys is uncertain. It is important that these annual surveys do continue as they will ultimately provide the first reliable field-based estimates of jaguar vital rates. The CBWS jaguar monitoring program needs long-term financial commitment to ensure that this significant goal is achieved.

Chapter 7 demonstrated that dispersal rate and its characteristics could influence source-sink dynamics arising from lethal control in a jaguar population, and potentially lead to population decline. The properties of jaguar dispersal are virtually unknown from any part of its geographical range, and they require elucidation. Density estimates from camera-trap studies combined with movement data obtained from radio-collared members of the population could contribute to a better understanding of jaguar dispersal. Valid assessments of the probability of long-term jaguar persistence require more information about dispersal, and ranging behaviour in general, not only in Belize, but in other range countries. Basic data on the natural history of the target species are sometimes undervalued in conservation programs which, understandably, want to solve practical problems with a high degree of urgency. Whilst the natural histories of other endangered big cats such as lions (*Panthera leo*) and tigers (*P. tigris*) are well known (e.g. Sunquist and Sunquist 2002) we are only just beginning to accumulate such data on the jaguar (e.g. Silver *et al. in press*). Funding for conservation research needs to be carefully distributed between practical projects to lower human-jaguar conflict and scientific studies to better understand jaguar ecology.

Compared to jaguars, pumas were relatively scarce in the human-influenced landscape (Chapter 5). However, Chapter 5 demonstrated the capacity for jaguars and pumas to coexist within the contiguous forest. It remains unclear how they partition limiting resources, partly because we cannot know ratios of abundance due to the difficulty of identifying individual pumas from camera-trap photographs. Pumas in the CBWS could not be individually identified to a level which allowed reliable density estimation, although short term recognition of pumas on certain trails indicated that they were less numerous than jaguars (Harmsen 2006). A recent study by Kelly *et al.* (2008) in the Chiquibul Forest Reserve in western Belize has attempted to estimate puma density, despite acknowledging a 32% disagreement between investigators in assigning IDs. There, jaguar density was estimated to be approximately twice the puma density (7.5 jaguars and 3.4 pumas per 100 km^2, Silver *et al.* 2004, Kelly *et al.* 2008). Although the puma density in the current study was unknown, there was no evidence that pumas were displaced to marginal habitats by jaguars as may be expected of a subordinate species in carnivore guilds (Woodroffe 2001). In fact pumas were rarely detected in the fragmented lands and were more common where jaguar density was highest in the contiguous forest block (Chapters 4 and 5). However jaguar and puma food habits differed significantly (Chapter 6) which could facilitate coexistence within the homogenous forest environment.

Pumas were less tolerant of human disturbance than jaguars (Chapter 5). This may be a consequence of selective pressures favouring elusive behaviour in pumas where they coexist with a more dominant species. Where jaguars and pumas coexist, jaguars tend to be larger (Iriarte *et al.* 1990), and intra-guild competition may make the smaller, subordinate puma naturally more wary than the dominant jaguar. Inter-specific segregation has been detected between jaguars and pumas in the CBWS however it is unknown whether this avoidance is mutual or one species is dominant over the other (Harmsen *et al.* in press).

The scarcity of pumas in the fragmented landscape compared to jaguars (Chapter 5) was surprising given the greater range of habitats usually associated with pumas than with jaguars (Sunquist and Sunquist 2002). It is proposed that puma abundance may be depressed in the human-matrix by direct competition with man for their main prey species, pacas and brocket deer, both prime game species among hunters in Belize (Chapter 6). It remains unclear whether this is further exacerbated by competition with jaguars. The apparently better prospects for jaguars than pumas in the fragmented landscape may be influenced by jaguar diet including armadillos and cattle. Although armadillos are killed by hunters when encountered, they do not tend to be a focal game species in Belize (R. Foster pers. obs.). Data from the protected forest suggested that pumas rarely took armadillos (Chapter 6). We may therefore suppose that pumas are disadvantaged outside the protected forest, where favoured games species such as paca and large wild ungulates are potentially scarce. Such propositions need proper qualification by studying wild prey abundance in Belize. Although pumas appear more sensitive to human activity than jaguars, we should not necessarily be more concerned about the puma population. The very fact that jaguars appear capable of exploiting the human-matrix puts them at greater risk of persecution (Chapter 7).

Living with jaguars

Jaguars are a high profile species in Belize. They are economically beneficial as a flagship for tourism which in turn accounts for 17% of gross domestic product (Belize Tourism Board 2008). In contrast predation on domestic animals leads to retaliatory killings by the expanding livestock industry. Unlike other big cats (tigers, leopards, *P. pardus*; lions and pumas), and many other large carnivores (bears, *Ursus sp.*; gray wolves, *Canis lupus*; and spotted hyaenas, *Crocuta crocuta*), there are no reported unprovoked attacks by jaguars on people, and provoked attacks are extremely rare (Quigley and Herrero 2005). Indeed on the few occasions that the author encountered a jaguar, it left rapidly. Although their elusive behaviour minimises contact with people, their refuge habitats are fragmenting and the human population is growing in Belize at 2.2% per year (World Resources Institute 2007). In the study area, retaliation for livestock predation seemed the most common precursor to the killing of jaguars, although illegal capture for live trade or trade in body parts was probably underestimated. Chapter 7 suggested that current levels of human-induced mortality are unsustainable for the jaguar population of Belize, given reasonable assumptions about the extent to which young jaguars disperse from protected to unprotected lands. A reduction in human-jaguar conflict in Belize is desirable for livestock owners, conservationists, and beneficiaries of ecotourism alike, preferably using non-lethal solutions.

A number of methods have been tried for minimising human-predator conflict whilst maintaining carnivore populations: 1) targeted lethal control of the perpetrator, 2) translocation of livestock predators, 3) anti-predator livestock management, 4) wild prey recovery, and 5) economic incentives to protect the predator. Breitenmoser *et al*. (2005) point out that the most appropriate balance between such measures will depend to some extent on the availability of domestic versus wild prey, and the impact of retaliatory killing. For example, lethal control may be acceptable in areas with high availability of wild prey and infrequent depredation on livestock. If wild and domestic prey are equally available, but domestic prey are preferentially killed, preventative measures will be required to encourage the predator to switch to alternative prey. In contrast, if wild prey are depleted and domestic prey are abundant, the best course of action may be compensation schemes and wild prey recovery programmes. Certainly any attempt to mitigate conflict must be site specific and take into account local constraints such as culture, attitudes and economy, as well as the spatial scale of properties involved and the physiognomy of the landscape. Here I discuss methods of conflict mitigation aimed at reducing livestock predation and promoting jaguar conservation within Belize.

Targeted lethal control

Currently Belizean law on lethal control of jaguars is difficult to enforce and does little to prevent indiscriminate killing of non-livestock killers. The correct individual may not be targeted, and pro-active lethal control is common in some areas of the country (Chapter 7). Livestock attacks and retaliatory lethal control are rarely reported to the Government (Brechin and Buff 2005), which limits the ability of the Belize Forest Department (BFD) to monitor or regulate persecution of jaguars. There needs to be an increase in public awareness of what action to take when a problem arises, and simultaneously the BFD require training and resources to help livestock owners correctly target the individual predators that are killing their animals.

Methods such as baiting traps may fail to capture the correct individual (Chapter 7). For example, on one of the study farms a female jaguar was caught in a baited trap and shot, but livestock losses continued. Within 24 hours of her capture camera data showed two female jaguars passing the same spot; and within a couple of weeks a male was also photographed there. One method to target known habitual livestock killers is to wait at the kill site for the perpetrator to return; however there is no assurance that a second individual will not investigate the kill (Chapter 7). Alternatively dogs can be used to track the predator's scent from the kill site. Although this method has a greater probability of targeting the correct individual, its success, like that of the first, depends on finding the carcass within 24 hours or so of the attack. A more elaborate technique is to fit 'toxic collars' around the necks of livestock which contain a capsule of poison below the throat (Nowell and Jackson 1996). In theory this method will target the correct predator, but it depends on the predator using a throat bite whereas jaguars tend to kill by crushing the back of the neck at the base of the skull (Hoogesteijn 2000). The collars are only suitable for adult livestock moreover, and in this study calf predation was more common than attacks on adult cattle (Chapter 5). Such collars are probably not affordable for most livestock owners in Belize, costing around US$20 each, and are currently only used in developed countries (e.g. protecting sheep against coyotes in the USA, Nowell and Jackson 1996, Mitchell *et al.* 2004).

No farm is far from the contiguous forest, for example in this study all pastures lay within 5 km for the forest block (Chapter 5). Since rates of livestock predation in Belize are relatively high (Chapter 5), even tightly regulated targeted lethal control may not be a sustainable option for jaguars or people.

Translocation

Instead of killing known livestock predators, an alternative is to capture them and move them to a location where they will not come into conflict with people. Despite its high public appeal among lovers of big cats, this rarely succeeds as a strategy to manage livestock predators (Jackson and Nowell 1996, Linnell *et al.* 1997). In a review of translocations of problem carnivores, Linnell *et al.* (1997) show that for a good chance of success, the predator must be moved at least 100 km from the capture site to prevent homing, and the release site must include hundreds or thousands of square kilometres of land without conflict potential. In addition vacant yet habitable territories must exist within the new area. For example Seidensticker *et al.* (1976) describe a translocation of a female tiger into the Sundarbans, who was killed by another tiger within 20 m of the release cage. Elsewhere in India, attempts to return Asiatic lions to the Gir Forest after they had dispersed into neighbouring agricultural lands have failed probably because the Gir population is at carrying capacity (Saberwal *et al.* 1994). Although several of the livestock owners and their staff in this study asked about the potential of translocation as an alternative to killing jaguars, the small size of Belize means that there is little potential to translocate a jaguar > 100 km, and there are no sufficiently large areas without potential conflict that are also likely to have vacant territories. People do not want potential livestock killers moved into their district, and such action can harm public relations with conservationists. For example, in 1983-4, two cattle-killing jaguars were translocated ~160 km^2 from northern Belize to the study area of this project (Rabinowitz 1986a). The female began killing cattle again within a month and was shot. The male moved north out of the study area within a week and was never detected again. Over 20 years later, livestock owners in the area still like to blame depredation on ‘those jaguars that were brought here by scientists’ (R. Foster pers. ob.).

In addition to its low success rate, translocation is expensive; requiring experienced trained staff and specialised equipment (Linnell *et al.* 1997), as well as detailed planning. This is exemplified by an event in 2007 when a drugged female jaguar was brought to the CBWS with no advance warning (Figure 8.1). The cat, which had been killing sheep, had been shot with a tranquilizer gun by a local resident in southern Belize. Despite his good intentions the man had failed to alert the BFD or the managers of the CBWS in advance of his plans, and wrongly assumed that it was acceptable to release a livestock killer within the CBWS just 10 km from a local community. The BFD were called in and local jaguar researchers advised that release within CBWS was inappropriate given its already dense jaguar population and the close proximity of villages and cattle farms. Eventually the cat was released in the neighbouring Bladen Nature Reserve further from human habitation and where the density of jaguars is considered to be lower. As the translocation was unplanned there were no resources to available to monitor her post-release behaviour or survival. However a nearby sawmill lost several dogs after her release and reported hearing a jaguar calling every night for a week.

Figure 8.1 Female jaguar captured for translocation in Belize

Anti-predator livestock management

Given the high jaguar density and high rates of livestock predation in Belize, the most appropriate measure to lower human-jaguar conflict may be improvements to livestock management. Chapter 5 discussed in detail a number of husbandry and farm management practises that could help to lower livestock predation and thus reduce lethal control, all of which warrant further research. Candidate options include 1) improved fencing; 2) electric fencing; 3) night corrals; 4) night watchman; 5) reduced reliance on natural water bodies; 6) maintain a cleared buffer between the pasture edge and adjacent forest; 7) bringing herds with vulnerable calves closer to human dwellings; 8) protected calving pastures; 9) incorporation of guard animals into the herd, such as water buffalo, donkeys, dogs; 10) use of repellents and deterrents. In particular, the clearance of buffer strips between pastures and natural vegetation, and good quality fences (Figure 8.2) were associated with lower rates of attack; however sample sizes were small and it is likely that multiple factors interact to influence depredation rates. Plans are in progress, subject to funding, to empirically test the effectiveness of different non-lethal methods to reduce livestock predation (B. Harmsen, pers. comm.).

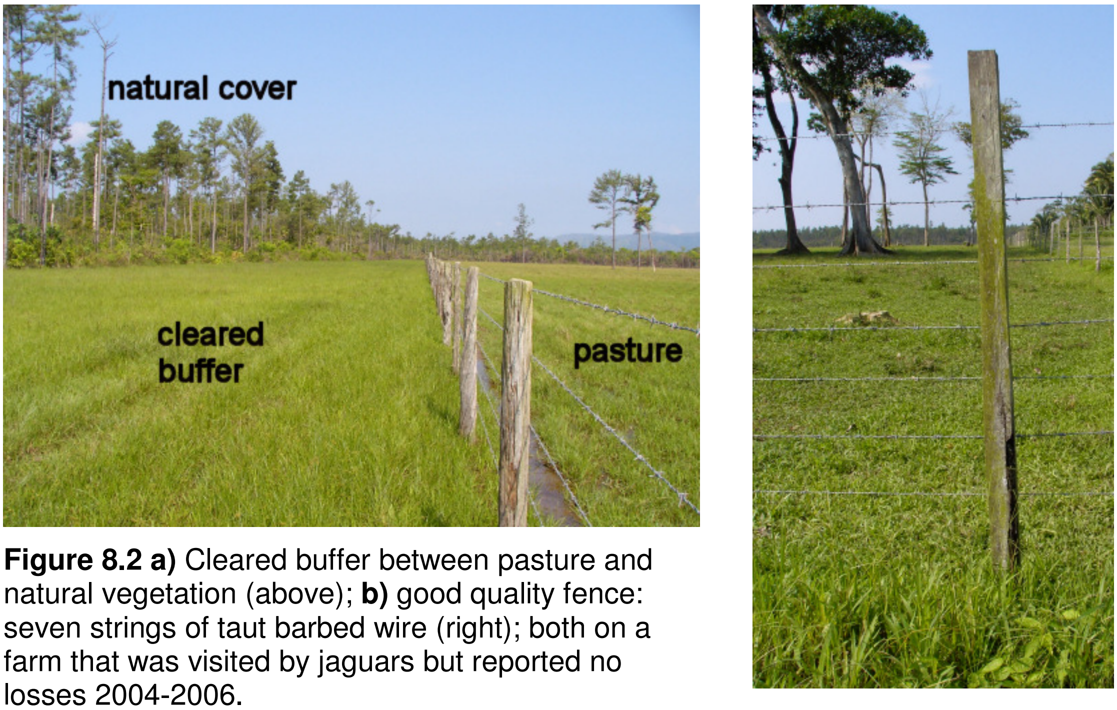


Figure 8.2 a) Cleared buffer between pasture and natural vegetation (above); **b)** good quality fence: seven strings of taut barbed wire (right); both on a farm that was visited by jaguars but reported no losses 2004-2006.

As in other developing countries, lack of money is the greatest impediment to livestock owners in Belize implementing any such preventative measures (Chapter 5). In the short-term, gun shot will always seem cheaper than constructing a fence or purchasing guardian animals. Economic incentives and subsidies from the international community may be necessary to encourage predator-friendly farming.

Economic incentives

Around the world, NGOs and Governments offer economic incentives for people to protect biodiversity (Ferraro and Kiss 2002). Incentives may be positive (payment for protection) or negative (taxes for non-protection); however positive incentives are more likely to get local support. Ideally such programs need to internalise the costs and eventually become self-sustaining. Below I discuss the potential of four types of positive economic incentives to lower lethal control and promote jaguar conservation in Belize: compensation for livestock losses, ecotourism, trophy hunting, and direct payments to protect jaguars and their habitat.

Compensation

Compensating livestock owners for losses aims to increase tolerance towards predators and so reduce lethal control; however it has had mixed success around the world (Nyhus *et al*. 2005). Compensation schemes in developing countries are often ineffective for a variety of reasons. These include bureaucratic inadequacies in verifying damages and making prompt payments, corruption, fraudulent claims, the inability of illiterate famers to make claims, the loss of impetus to properly protect livestock from attacks, and the need for assured funding for payments which may become unsustainable if conflict increases as the target species recovers (Nyhus *et al*. 2005, Bulte and Rondeau 2005, Rondeau and Bulte 2007). Compensation for losses has been likened to an agricultural subsidy which may increase marginal revenues so encouraging farmers to continue rearing livestock, potentially attracting more to the industry and stimulating agricultural expansion and intensification, with negative repercussions for the target species (Bulte and Rondeau 2005, Bulte and Rondeau 2007, Rondeau and Bulte 2007). In addition there is no assurance that lethal control will cease. For example, Naughton-Treves *et al*. (2003) found that livestock owners who were compensated for losses to wolves were no more tolerant of wolves than those who suffered uncompensated losses. Certainly all of these pitfalls could occur in any compensation scheme introduced in Belize to promote jaguar conservation. It is clear that payouts for losses would have to be conditional on first meeting certain approved levels of livestock protection to prevent attacks and an agreement not to kill jaguars on the property. If predation escalates, the farm could be issued with a permit to euthanize the problem cat. Difficulties would arise in verifying that livestock have actually been killed, since jaguars often drag entire calves into the forest leaving behind no remains as evidence. Also, it is likely that owners will not be satisfied with financial compensation, but demand replacement animals of a similar age as those lost. This would require the scheme to have available a source of domestic animals. Such a programme would be expensive to set up and maintain.

Carefully designed conditional compensation schemes which only reward good husbandry and compliance with efforts to protect the target species and its wild prey can work, if geared to the local ecological, social and economic conditions. For example successful compensation schemes have been developed in India and Mongolia to protect snow leopards (Mishra *et al*. 2003) and in Kenya to protect lions (Bruner 2007). Ecotourism based on these target species is being used as a means to partially internalise funding for the pay outs, and so reduce the need for external sources of money.

Ecotourism

The function of ecotourism is to provide economic revenues from tourism that offset the costs of local people cohabiting with and protecting wildlife (Walpole and Thoules 2005). Its success as a method to conserve wildlife depends on net economic benefits accruing to all those who accept the costs associated with wildlife protection, and on an appreciation of the link between those financial gains and conservation (Walpole and Thoules 2005).

Charismatic species such as big cats are big business for the ecotourism industry worldwide. A single internet search for ‘ecotourism’ and ‘jaguar’ brings up ~40,000 hits, 43% of which include ‘Belize’. Tourism is important for the Belizean economy. For example in 1999 tourism revenue made up 69% of the country’s exports (Gossling 1999). Furthermore, the Government levies an environmental departure tax of US$18.75 on every foreign visitor to support the Protected Areas Conservation Trust (PACT) which finances conservation management and sustainable development in and around the protected areas of Belize (Belize Government 2008, PACT 2008).

It is sometimes argued that rainforests are not suited to large-scale tourism because they are difficult to access, the wildlife is elusive and the climate is uncomfortable (e.g. Kiss 2004). However Belize also has attractive beaches and the largest coral reef in the western hemisphere. Tourists who are attracted primarily for a beach holiday frequently take the opportunity to make excursions inland to the national parks. The country’s small size means that most sites are easily accessible, and although highways are still unpaved in places, there is a good infrastructure and the country is politically stable. Moreover the country is English speaking, attracting generally affluent North American tourists.

Belize receives increasing tourist numbers every year; in 2007 arrivals were equivalent in size to the Belizean population (over 250,000 tourists, Belize Tourism Board 2008). However it is debatable whether the link between the tourist economy and wildlife protection is widely appreciated, or whether it can promote jaguar conservation in the long-term, largely due to an imbalance in the distribution of revenue from ecotourism operations within the country. This is common in developing countries, where often only 20-40% of the retail tourist price remains within the destination country’s economy (Gossling 1999), and small-scale community-based ecotourism cannot compete with large-scale commercial operations (Walpole and Thoules 2005).

For example, Belize is a popular destination for cruise ships, but the nature of a cruise is such that excursions on land are limited to short daytrips only and so the ‘cruise-ship dollar’ often fails to reach local business people (R. Foster, pers. obs.). For those tourists who spend more time inland, activities are likely to be centred on national parks and archaeological sites. Communities lying outside the sphere of influence of such protected areas may receive little or no economic benefit from jaguar conservation. The phenomenon was clearly observed during this study in the communities at the periphery of the CBWS unprotected forest buffer. Tourist access to the CBWS is via a single village, Maya Centre. Here park visitors can purchase entrance tickets, hire tour guides, buy handicrafts and food, utilise overnight accommodation and even visit a traditional healer. Five more villages lie along the buffer perimeter but their tourist activity and income is negligible (R. Foster, pers. obs.). With no economic incentive to protect either the jaguar or its wild prey, villagers from these communities often hunt game in the buffer forest and further into the protected area (R. Foster, pers. obs.). Chapter 6 showed that large game species were lacking in jaguar diet outside the protected forest and this may in turn exacerbate livestock predation in the villages and on privately owned farms. Illegal hunting needs to be brought under control and communities need to receive some tangible economic benefits from the CBWS in order to respect its boundaries. However poacher patrols and employment opportunities within CBWS are limited because park funding in inadequate. The CBWS park entrance fees are currently just US$1.25 for nationals and US$5.00 for foreigners. For most Westerners this is less than they would readily spend on a trip to the movies or for a cappuccino in a coffee bar (R. Foster pers. obs.). This is common in developing countries, where entrance fees are often ~0.01-1% of total travel costs (Gossling 1999). When Costa Rica raised park fees for foreigners from US$1.50 to US$15; visitors fell by 44% the following year but total revenue increased (Gossling 1999). Furthermore the reduction in number of tourists probably lowered the negative impacts associated with long-haul flights and high traffic of people within the rainforest. Increasing park fees in Belize would allow the protected areas to hire more wardens for patrols. This would increase local employment opportunities whilst simultaneously improving protection of the forest wildlife. In 2004, a resident from a buffer community other than Maya Centre was hired as Park Director of CBWS. His employment has done much to improve the relationship between his village and CBWS (R. Foster, pers. obs.); however it is doubtful that ecotourism in CBWS could ever provide sufficient economic revenues to all members of its buffer communities to ensure the protection of game species and livestock predators.

Throughout Africa, and in some Latin American countries, large-scale cattle ranches are converting to private wildlife reserves for ecotourism. Such a strategy is less appropriate for Belize where farms are generally small (Chapter 5), the wildlife are difficult to see and the opportunity to visit the country's pristine protected areas is probably more attractive to tourists than visiting a former cattle ranch. Moreover it is unlikely that many could afford the necessary start-up costs. However the wealthy owners of the two largest cattle farms in the study area have begun dabbling in the ecotourism market, offering horse rides or canoe trips on their properties. Unfortunately, this appears to have done little to increase their tolerance of jaguars when livestock are taken, other than some unsuccessful attempts at aversive conditioning by one farm owner (R. Foster, pers. obs.).

Trophy hunting

Unlike ecotourism, in which the link between protecting predators and revenue derived from tourists (for example, staying in guest houses or eating in local restaurants) is not always obvious, trophy hunting clearly presents the predator as a commodity. Indeed, in sub-Saharan Africa trophy hunting is a multi-million dollar business (Whitman *et al*. 2004, Frost and Bond 2008). As with ecotourism and compensation programmes, there are difficulties associated with distributing revenue to fairly off-set the costs of living with a predator and ensuring that people comply with the conservation objectives of the programme.

Sport hunting of jaguars is permitted in Bolivia and can cost up to US$10,000 per trip but does little to deal with the causes of depredation, which is induced mainly by poor livestock management and wild prey depletion (Núňez *et al*. 2000b). It has been suggested that controlled sport hunting of habitual livestock killers could contribute to jaguar conservation by financing better livestock management and compensation programmes in some Latin American countries (Swank and Teer 1988, unpubl. report cited in Nowell and Jackson 1996). Trophy hunting of jaguars in Belize has been proposed by several of the country's influential businessmen who also own cattle ranches. However it is unlikely that this could ever be viable method of conserving the jaguar, even if revenues were reinvested in improved livestock protection. From a practical point of view, it would be no different from targeted lethal control, so the difficulties of killing the correct cat remain. In Africa the open savannahs facilitate identification of specific individuals for removal. In Belize the vegetation is dense and jaguars are elusive, making it almost impossible to predict when or where the target animal will be. Also, in Belize cattle farms are small; with several properties often falling within the home range of a single cat (Chapter 5), complicating the fair distribution of eventual revenue. Furthermore the legal killing of some jaguars would not necessarily prevent the illegal killing of others. Chapter 7 suggests the necessity for a reduction in human-induced mortality of jaguars; as conservationists we want to find ways to decrease lethal control rather than promote it. Finally, Belize is party to CITES which prohibits commercial trade in Appendix I species, including jaguars, between member countries. Therefore, under current law, foreign hunters would be unable to take their trophy home, and this would likely lower the attraction of paying for a hunt. Certain countries have been granted export quotas for some Appendix I cat species (e.g. leopards) on the recognition that it is not endangered in those countries and that some killings are sanctioned to protect life/property. However the restrictions remain tight: trophies must not be sold in the import country and are limited to 2 animals per year per person. As we know so little about jaguar abundance or its resilience to lethal control across its geographical range, easing the law to facilitate trophy hunting is unacceptable.

In northern Mexico a different form of trophy hunting is being used to conserve jaguars. A programme has been established to assist ranches with wildlife management and organise commercial sustainable deer hunts. The ranchers receive the revenues from the hunts in return for conserving jaguars and jaguar habitat on their land (Nistler 2007).

Direct payments

It has been suggested that direct payments such as land purchases or leases, tax breaks and performance payments for supporting conservation are more cost-effective and practical than indirect incentives such as compensation programmes and ecotourism (Ferraro and Kiss 2002, Ferraro and Kiss 2003). Indirect incentives are common in developing countries, but, in attempting to combine conservation and development goals, they often fail (Ferraro and Kiss 2002). Instead direct payments could be made for the protection of predators, their wild prey and natural habitat. For example in Russia owners of livestock and deer farms are paid for the presence of Amur leopards and Siberian tigers on their property (Hötte and Bereznuk 2001). Thus payments for promoting wildlife are received regardless of livestock predation, although a compensation scheme is also run to pay farmers for their losses. Payments conditional on wildlife abundance requires some means to monitor the population, and a fair distribution of rewards may be difficult to achieve (Nyus *et al.* 2005) particularly for wide-ranging species such as jaguars. In northern Mexico an innovative approach is being used in which ranchers are given camera traps and are paid up to US$300 for photos of jaguars on their land (Nistler 2007). Despite its attractive simplicity, any programme of direct payment for jaguar conservation in Belize would require a sustainable source of funding.

Wild prey recovery

In the absence of data on wild prey abundance or the rate of game hunting, it is impossible to know whether Belizean prey populations are depleted and whether this could be exacerbating livestock predation. Research must therefore focus on estimating wild prey populations. A large-scale project, subject to funding, is planned to evaluate wild prey abundance in the fragmented lands separating the Rio Bravo and Maya Mountain protected forest blocks (B. Harmsen, pers. comm.). However attempts must also be made to monitor levels of off-take by hunters, ultimately to better regulate the practise. This is easier said than done, and despite comprehensive wildlife hunting laws the BFD has limited resources for the time and expense required for enforcement.

If wild prey are scarce in the fragmented landscape then livestock predation is inevitable, and recovery of wild prey populations may be the best solution. This may be achieved by restricting game hunting and/or through population augmentation. Larger cattle farms could ban staff and locals from hunting on their property. The second largest farm in this study has recently taken such an approach. Even at this small scale, however, enforcement is difficult: with the owner rarely on-site and four communities within 1.5 km of the property, hunting pressure in forests neighbouring the ranch is likely to be high. Wild prey augmentation remains an untested strategy in Belize. Chapter 6 suggested that large wild ungulates, such as white-lipped and collared peccary, are limited in the diet of jaguars inhabiting the fragmented landscape, and that this absence may encourage predation on cattle. The introduction of peccary from breeding stocks at the Belize Zoo is not inconceivable (S. Matola, Belize Zoo, pers. comm.). Augmentation of collared peccary in particular could be viable in the fragmented landscape as they are relatively adaptable to disturbed habitats (e.g. Peres 1996, Reyna-Hurtado and Tanner 2007). However such a project would need careful investigation prior to any introductions to ensure that the habitat can support an increased peccary population and to guarantee that locals would not over-exploit it.

Public awareness

Whatever methods are employed to reduce jaguar-human conflict, public awareness of the programmes will play an important role. Because Belize is a small country, news travels fast whether positive, as with the praise for the first Belizean to embark on a PhD study of jaguars, or negative as with jaguar attacks on domestic animals. Unfortunately its small size can also facilitate the rapid spread of myths, including misconceptions about wildlife which can be detrimental if not corrected. For example, on several occasions in different parts of the country the author was told of two types of jaguar, one with large rosettes and the other with 'bean-like' pelt pattern, the former supposedly being much more dangerous. One livestock owner even sorted through a stack of ~50 jaguar camera-trap photographs, separating them into two 'different' cats, one group of which he believed it was legal to shoot.

The Belize Zoo has done much to improve public understanding of jaguars and has also established a 'Problem Jaguar Rehabilitation Program' which takes cats that were trapped for preying on livestock into captivity as an alternative to lethal control. Whilst the zoo acknowledges that this does not confront the causes of the problem (poorly managed livestock, depleted wild prey populations and fragmentation of the forest habitat) they see positive outcomes arising from not killing the cat. It is a step towards encouraging livestock owners not to shoot jaguars without first considering the alternatives and it provides the support that may not always be available from the Forestry Department. Once in captivity, the 'problem' jaguars are slowly habituated to humans. This may take over a year to achieve. Eventually they are moved to spacious public exhibits providing education for Belizeans and foreign tourists alike. In particular ~10,000 school children visit the zoo every year, participating in its environmental education programme. These progressive education programmes have undoubtedly contributed to raising public awareness of the jaguar in Belize (Matola 2002, R. Foster pers. obs.). The problem jaguar is eventually transferred to an AZA accredited zoo where it becomes part of the captive breeding programme, contributing to the genetic base of the North American captive jaguar population. In return the zoos are required to exhibit the cat with educational material explaining human-jaguar conflict in Mesoamerica and the associated conservation issues, and they are obliged to contribute funds to the country of origin to support *in situ* conservation. Despite these benefits, the programme cannot continue accepting problem cats indefinitely due to the limits of space and funding, and those it does take represent only a small fraction of those estimated to be killed every year. Furthermore the system must be rigorously controlled to avoid abuse, for example in situations where cats are trapped without evidence of livestock predation or payment is demanded before handing over a trapped cat.

The role of the Government

The BFD must play a greater role in mitigating human-jaguar conflict in Belize. Until recently they have been limited by the lack of resources, particularly vehicles and fuel, to respond to reports of livestock predation and other wildlife related issues. Because of their inability to help effectively in the past, many Belizeans take matters into their own hands when it comes to livestock predation. Once the BFD begins actively responding to calls for assistance with problems with jaguars, it is likely that willingness to report will increase. This year (2008) the Panthera Foundation, a US based NGO, began employing a Belizean Forestry Officer specifically to deal with human-jaguar conflict. This is an important step. Even if an alternative to lethal control cannot always be offered, by working with livestock owners around the country the officer is able to keep records of jaguar deaths which would otherwise go unreported, and to build a database of farms and villages that may be particularly susceptible to attack. These data can then be used to improve methods of recognising the factors associated with depredation, which in turn can be used to identify site-specific alternatives to lethal control.

Epilogue

On my last day in Belize, a cowboy who I had known for almost three years told me that he would not kill anymore jaguars. If only the solution really was that simple! I took his statement lightly, having witnessed the frustration that repeated depredation can bring to livestock owners. But if this project was at least partly responsible for his apparent change in mindset and his refreshing resolution on lethal control then it will have served a purpose. Changing people’s attitudes is surely the starting point of successful jaguar conservation in areas where they co-exist with humans. As a first step we need to understand the basics, such as how many jaguars are there, why they eat livestock and what is the impact of lethal control. When I return to Belize in 2009, I plan to disseminate the findings of this research among livestock owners and local communities with the intention of dissolving myths about jaguars living in the area. Once locals and conservationists have a better understanding of jaguar ecology in the area they can work together to identify some sensible non-lethal alternatives to reduce both livestock predation and lethal control of jaguars.

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Appendix A: Data tables

Chapter 4

Sex Ratio

Table A4.1 Sex ratio (males/ females) of jaguars captured exclusively inside and exclusively outside the forest block based on eight possible ratios: individuals of unknown sex are **a)** excluded (two ratios), **b)** assumed to be males (MJ, two ratios) and **c)** assumed to be females (FJ, four ratios). Sex ratios differ between inside and outside: paired t-test $n = 8$, $t = 6.85$, $p < 0.001$. Ratios are based on 64 to 74 individual capture histories of 36 to 37 males, 14 females and 14 to 23 of unknown sex over the period Jan 2004 to Dec 2006.

		male/ female	
Ratio		IN	OUT
a)	M_{min} : F	3.1	1.2
	M_{max} : F	3.3	1.3
b)	MJ_{min} : F	3.6	1.3
	MJ_{max} : F	5.0	3.0
c)	M_{min} : FJ_{max}	1.2	0.4
	M_{min} : FJ_{min}	2.2	1.0
	M_{max} : FJ_{min}	2.3	1.1
	M_{max} : FJ_{max}	1.2	0.5

Table A4.2 Sex ratio (males/ females) of jaguars captured exclusively inside and exclusively outside the reserve based on eight possible ratios: individuals of unknown sex are a) excluded (two ratios), b) assumed to be males (MJ, two ratios) and c) assumed to be females (FJ, four ratios). Sex ratios differ between inside and outside: paired t-test $n = 8$, $t = 6.76$, $p < 0.001$. Ratios are based on 64 to 74 individual capture histories of 36 to 37 males, 14 females and 14 to 23 of unknown sex over the period Jan 2004 to Dec 2006.

		male/ female	
Ratio		IN	OUT
a)	M_{min} : F	4.7	1.3
	M_{max} : F	5.0	1.4
b)	MJ_{min} : F	5.0	2.4
	MJ_{max} : F	7.3	3.4
c)	M_{min} : FJ_{max}	1.4	0.4
	M_{min} : FJ_{min}	3.5	0.8
	M_{max} : FJ_{min}	3.8	0.8
	M_{max} : FJ_{max}	1.5	0.5

Chapter 5

Contingency tables: habitat use by jaguars and pumas

Table A5.1 Number of locations **a)** inside forest block and **b)** outside forest block, with and without jaguars and pumas.

a) inside forest block

	Presence	Absence	
Jaguar	61	45	106
Puma	64	42	106
	125	87	212

$\chi_1^2 = 0.175$, $p > 0.05$

b) outside forest block

	Presence	Absence	
Jaguar	47	20	67
Puma	7	60	67
	54	80	134

$\chi_1^2 = 49.6$, $p < 0.0001$

Table A5.2 Number of locations **a)** inside protected forest and **b)** outside protected forest, with and without jaguars and pumas.

a) inside protect forest

	Presence	Absence	
Jaguar	46	41	87
Puma	52	35	87
	98	76	174

$\chi_1^2 = 0.841$, $p > 0.05$

b) outside protected forest

	Presence	Absence	
Jaguar	59	24	83
Puma	16	67	83
	75	91	166

$\chi_1^2 = 45.0$, $p < 0.0001$

Table A5.3 Number of locations **a)** inside forest and **b)** outside forest, with and without jaguars and pumas.

a) inside forest

	Presence	Absence	
Jaguar	80	56	136
Puma	68	68	136
	148	124	272

$\chi_1^2 = 2.134$, $p > 0.05$

b) outside forest

	Presence	Absence	
Jaguar	28	9	37
Puma	3	34	37
	31	43	134

$\chi_1^2 = 34.7$, $p < 0.0001$

Table A5.4 Number of jaguar and puma scats found inside and outside the forest block Jan 2004 to Dec 2006.

	Inside	Outside	
Jaguar	224	51	275
Puma	66	3	69
	290	54	344

$\chi_1^2 = 8.4$, $p = 0.004$

Table A5.5 Number of locations **a)** inside forest block and **b)** outside forest block, with and without male and female jaguars.

a) inside forest block

	Presence	Absence	
Male	58	46	104
Female	18	86	104
	76	132	208

$\chi^2_1 = 33.2$, $p < 0.0001$

b) outside forest block

Presence	Absence	
37	26	63
18	45	63
55	71	126

$\chi^2_1 = 11.6$, $p < 0.0001$

Table A5.6 Number of locations **a)** inside protected forest and **b)** outside protected forest, with and without male and female jaguars.

a) inside protected forest

	Presence	Absence	
Male	45	40	85
Female	9	76	85
	54	116	170

$\chi^2_1 = 35.2$, $p < 0.0001$

b) outside protected forest

Presence	Absence	
47	32	79
25	54	79
72	86	158

$\chi^2_1 = 12.4$, $p < 0.0001$

Table A5.7 Number of locations **a)** inside forest and **b)** outside forest, with and without male and female jaguars.

a) inside forest

	Presence	Absence	
Male	70	62	132
Female	30	102	132
	100	164	264

$\chi^2_1 = 25.8$, $p < 0.0001$

b) outside forest

Presence	Absence	
25	10	35
6	29	35
31	39	70

$\chi^2_1 = 20.9$, $p < 0.0001$

Table A5.8 Number of locations **a)** inside forest block and **b)** outside forest block, with and without male and female jaguars. Jaguars of unknown sex are included as females.

a) inside forest block

	Presence	Absence	
Male	58	46	104
Female	24	80	104
	82	126	208

$\chi^2_1 = 4.3$, $p < 0.05$

b) outside forest block

Presence	Absence	
37	30	67
25	42	67
62	72	134

$\chi^2_1 = 23.3$, $p < 0.0001$

Table A5.9 Number of locations **a)** inside protected forest and **b)** outside protected forest, with and without male and female jaguars. Jaguars of unknown sex are included as females.

a) inside protected forest

	Presence	Absence	
Male	45	40	85
Female	14	71	85
	59	111	170

$\chi^2_1 = 24.9$, $p < 0.0001$

b) outside protected forest

Presence	Absence	
47	36	83
33	50	83
80	86	166

$\chi^2_1 = 4.7$, $p < 0.05$

Table A5.10 Number of locations **a)** inside forest and **b)** outside forest, with and without male and female jaguars. Jaguars of unknown sex are included as females.

a) inside protected forest

	Presence	**Absence**	
Male	70	64	134
Female	40	94	134
	110	158	268

$\chi^2_1 = 13.9$, $p < 0.0001$

b) outside protected forest

	Presence	**Absence**	
Male	25	12	37
Female	9	28	37
	34	40	74

$\chi^2_1 = 13.9$, $p < 0.0001$

Table A5.11 Number of locations with and without male jaguars inside and outside pasture. (Note that *n* is four more than in Table 5.2 in Chapter 5 because it excluded the three locations which lie on the boundary of the protected area, and the single location which was in a citrus plantation. These four data points have been included in here).

	Not Pasture	**Pasture**	
Presence	75	17	92
Absence	69	4	73
	144	21	165

$\chi^2_1 = 6.2$, $p < 0.015$

Table 5.12 Number of locations with and without female jaguars inside and outside protected forest. (Note that *n* is one more than in Table 5.3 in Chapter 5 because it excluded the single location which was in a citrus plantation. This data point is included in here).

	Not Protected	**Protected**	
Presence	25	9	34
Absence	46	74	120
	71	83	154

$\chi^2_1 = 13.2$, $p < 0.0001$

Table A5.13 Number of locations associated with forest and >50m from forest with and without male jaguars

	< 50m from forest	**> 50m from forest**	
Presence	82	13	95
Absence	68	4	73
	151	17	168

$\chi^2_1 = 3.06$, $p > 0.05$

Table A5.14 Number of locations associated with forest and >50m from forest with and without male + unknown sex jaguars

	< 50m from forest	**> 50m from forest**	
Presence	88	13	101
Absence	65	5	70
	153	16	171

$\chi^2_1 = 1.44$, $p > 0.2$

Table A5.15 Number of locations associated with forest and >50m from forest with and without female jaguars

	< 50m from forest	> 50m from forest	
Presence	34	2	36
Absence	111	10	121
	145	12	157
	χ^2_1 = 0.29, *p* > 0.5		

Table A5.16 Number of locations associated with forest and >50m from forest with and without female + unknown sex jaguars

	< 50m from forest	> 50m from forest	
Presence	47	2	49
Absence	101	10	111
	148	12	160
	χ^2_1 = 1.19, *p* > 0.2).		

General Linear Models: habitat use by jaguars

Table A5.17 GLM of jaguar activity with sex and habitat. Jaguars of unknown sex included as males
† Error variation for interaction is the highest order term in the model: sex*station'(habitat)

Source	**d.f.**	**Adj. MS**	***F***	***p***
Sex	1	11.34	63.66	< 0.0001
Habitat	4	0.33	1.48	> 0.2
Sex*Habitat	4	1.46	8.19	< 0.0001
Station'(Habitat)	86	0.22	1.25	> 0.1
Error†	86	0.18		
Total	**181**			

Table A5.18 GLM of jaguar activity with sex and habitat. Jaguars of unknown sex included as females.
† Error variation for interaction is the highest order term in the model: sex*station'(habitat)

Source	**d.f.**	**Adj. MS**	***F***	***p***
Sex	1	7.85	45.51	< 0.0001
Habitat	4	0.39	1.63	> 0.1
Sex*Habitat	4	1.80	10.43	< 0.0001
Station'(Habitat)	86	0.24	1.40	> 0.05
Error†	86	0.17		
Total	**181**			

Compared to GLM 5.1 of jaguar activity (Table 5.4, Figure 5.4 in Chapter 5), similar trends are observed if unknown jaguars are included as males or included as females.

Table A5.19 GLM of jaguar individual rate with sex and habitat. Jaguars of unknown sex included as females.
† Error variation for interaction is the highest order term in the model: sex*station'(habitat)

Source	**d.f.**	**Adj. MS**	***F***	***p***
Sex	1	4.84	33.98	< 0.0001
Habitat	4	0.07	0.61	> 0.6
Sex*Habitat	4	0.67	4.72	< 0.005
Station'(Habitat)	46	0.11	0.79	> 0.7
Error†	46	0.14		
Total	**101**			

Table A5.20 GLM of jaguar individual rate with sex and habitat. Jaguars of unknown sex included as females.
† Error variation for interaction is the highest order term in the model: sex*station'(habitat)

Source	**d.f.**	**Adj. MS**	***F***	***p***
Sex	1	3.29	23.54	< 0.0001
Habitat	4	0.07	00.61	> 0.6
Sex*Habitat	4	0.94	06.74	< 0.0001
Station'(Habitat)	46	0.11	00.80	> 0.7
Error†	46	0.14		
Total	**101**			

Compared to GLM 5.1 of number of individuals present per 28 nights (Table 5.5, Figure 5.5 in Chapter 5) , similar trends are observed if unknown jaguars are included as males or included as females with the following exceptions: if unknowns are included as males the number of individuals utilising fragmented forest locations increases such that it is no longer less than the number utilising protected forest sites; if unknowns are included as females the number of individuals utilising contiguous unprotected forest sites increases such that it is more than the number of females utilising savannah sites.

Contingency table: jaguar and puma tolerance to human activity

Table A5.21 Number of months during which jaguars and pumas were present at the reserve boundary Jan04 to May07; $n = 31$ months.

	Present	**Absent**	
Jaguar	30	1	31
Puma	16	15	31
	46	16	62

$\chi_1^2 = 16.5$, $p < 0.0001$

Contingency tables: cat activity on cattle farms

Table A5.22 Number of locations on farms (≤ 20 m from pasture) with and without jaguars and pumas Apr 2004 to Oct 2006.

	Present	Absent	
Jaguar	21	3	24
Puma	3	21	24
	24	24	48

χ_1^2 = 27.0, $p < 0.0001$

Table A5.23 Number of locations on farms (≤ 20 m from pasture) with and without male and female jaguars Apr 2004 to Oct 2006.

	Present	Absent	
Male	18	6	24
Female	7	17	24
	25	23	48

χ_1^2 = 10.1, $p < 0.002$

Table A5.24 Number of locations on farms (≤ 20 m from pasture) with and without male and female + unknown sex jaguars Apr 2004 to Oct 2006.

	Present	Absent	
Male	18	6	24
Female	9	15	24
	27	21	48

χ_1^2 = 6.86, $p < 0.01$

Chapter 6

Contingency tables: jaguar/puma food habits in protected forest

Table A6.1 Number of prey items identified as armadillos in jaguar and puma scats collected in the protected forest.

	Armadillo	Not armadillo	
Jaguar	122	118	240
Puma	8	114	122
	130	232	362

χ_1^2 = 68.9, $p < 0.0001$

Table A6.2 Number of prey items identified as coatis in jaguar and puma scats collected in the protected forest.

	Coati	**Not coati**	
Jaguar	23	217	240
Puma	0	122	122
	23	339	362

$\chi^2_1 = 12.5$, $p < 0.0001$

Table A6.3 Number of prey items identified as pacas in jaguar and puma scats collected in the protected forest.

	Paca	**Not paca**	
Jaguar	11	229	240
Puma	71	51	122
	82	280	362

$\chi^2_1 = 132.7$, $p < 0.0001$

Table A6.4 Number of prey items identified as red brocket deer in jaguar and puma scats collected in the protected forest.

	Deer	**Not deer**	
Jaguar	8	232	240
Puma	11	111	122
	19	343	362

$\chi^2_1 = 5.3$, $p < 0.05$

Table A6.5 Number of prey items identified as white-lipped peccary in jaguar and puma scats collected in the protected forest.

	WL peccary	**Not WL peccary**	
Jaguar	36	204	240
Puma	11	111	122
	47	315	362

$\chi^2_1 = 2.6$, $p > 0.1$

Table A6.6 Number of prey items identified as kinkajou in jaguar and puma scats collected in the protected forest.

	Kinkajou	**Not kinkajou**	
Jaguar	10	230	240
Puma	7	115	122
	17	345	362

$\chi^2_1 = 0.5$, $p > 0.5$

Contingency tables: jaguar/puma food habits in contiguous forest block

Table A6.7 Number of prey items identified as armadillos in jaguar and puma scats collected in the contiguous forest block.

	Armadillo	**Not armadillo**	
Jaguar	161	152	313
Puma	10	125	135
	171	277	448

$\chi_1^2 = 77.5$, $p < 0.0001$

Table A6.8 Number of prey items identified as coatis in jaguar and puma scats collected in the contiguous forest block.

	Coati	**Not coati**	
Jaguar	35	278	313
Puma	0	135	135
	35	413	448

$\chi_1^2 = 16.4$, $p < 0.0001$

Table A6.9 Number of prey items identified as pacas in jaguar and puma scats collected in the contiguous forest block.

	Paca	**Not paca**	
Jaguar	13	300	313
Puma	80	55	135
	93	355	448

$\chi_1^2 = 174.1$, $p < 0.0001$

Table A6.10 Number of prey items identified as red brocket deer in jaguar and puma scats collected in the contiguous forest block.

	Deer	**Not deer**	
Jaguar	10	303	313
Puma	12	123	135
	22	426	448

$\chi_1^2 = 6.5$, $p < 0.02$

Table A6.11 Number of prey items identified as white-lipped peccary in jaguar and puma scats collected in the contiguous forest block.

	WL peccary	**Not WL peccary**	
Jaguar	37	276	313
Puma	11	124	135
	48	400	448

$\chi_1^2 = 1.3$, $p > 0.2$

Table A6.12 Number of prey items identified as kinkajou in jaguar and puma scats collected in the contiguous forest block.

	Kinkajou	Not kinkajou	
Jaguar	10	303	313
Puma	7	128	135
	17	431	448

$\chi^2_1 = 1.0$, $p > 0.3$

Contingency tables: jaguar food habits inside/outside protected forest

Table A6.13 Number of prey items identified as white-lipped peccary in jaguar scats collected inside and outside the protected forest.

	WL peccary	Not WL peccary	
In	36	204	240
Out	0	108	108
	36	312	348

$\chi^2_1 = 18.1$, $p < 0.0001$

Table A6.14 Number of prey items identified as cattle in jaguar scats collected inside and outside the protected forest.

	Cattle	Not cattle	
In	0	240	240
Out	11	97	108
	11	337	348

Odds ratio = 0.02, $p < 0.0001$

Table A6.15 Number of prey items identified as sheep in jaguar scats collected inside and outside the protected forest.

	Sheep	Not sheep	
In	0	240	240
Out	17	91	108
	17	331	348

$\chi^2_1 = 39.7$, $p < 0.0001$

Contingency tables: jaguar food habits in protected forest and unprotected forest buffer

Table A6.16 Number of prey items identified as armadillo in jaguar scats collected inside the protected forest and inside the unprotected forest buffer.

	Armadillo	Not armadillo	
Protect	122	118	240
Buffer	21	22	43
	143	140	283

$\chi^2_1 = 0.1$, $p > 0.8$

Table A6.17 Number of prey items identified as coatis in jaguar scats collected inside the protected forest and inside the unprotected forest buffer.

	Coati	**Not coati**	
Protect	23	217	240
Buffer	10	33	43
	33	250	283

$\chi_1^2 = 6.6$, $p < 0.02$

Table A6.18 Number of prey items identified as collared peccaries in jaguar scats collected inside the protected forest and inside the unprotected forest buffer.

	Col peccary	**Not col peccary**	
In	10	230	240
Out	6	037	43
	16	267	283

Odds ratio = 0.27, $p < 0.05$

Contingency tables: jaguar food habits in unprotected forest buffer and fragmented landscape

Table A6.19 Number of prey items identified as armadillo in jaguar scats collected inside the unprotected forest buffer and in the fragmented landscape.

	Armadillo	**Not armadillo**	
Buffer	21	22	43
Frag	15	50	65
	36	72	108

$\chi_1^2 = 7.7$, $p < 0.01$

Table A6.20 Number of prey items identified as coatis in jaguar scats collected inside the unprotected forest buffer and in the fragmented landscape.

	Coati	**Not coati**	
Buffer	10	33	43
Frag	6	59	65
	16	92	108

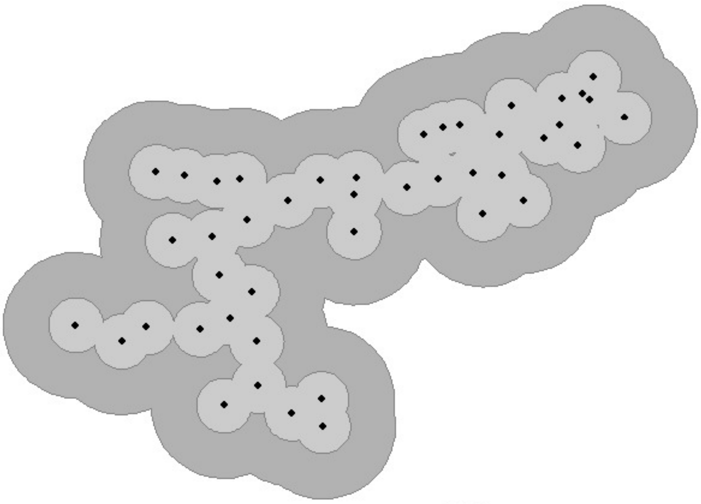
$\chi_1^2 = 4.0$, $p < 0.05$

Table A6.21 Number of prey items identified as collared peccaries in jaguar scats collected inside the unprotected forest buffer and in the fragmented landscape.

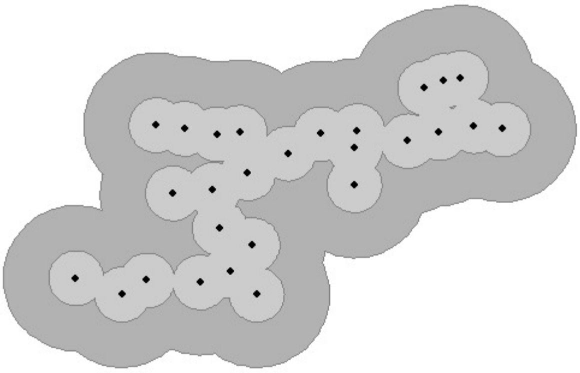
	Col peccary	**Not col peccary**	
Buffer	6	37	43
Frag	1	64	65
	7	101	108

Odds ratio = 10.4, $p < 0.02$

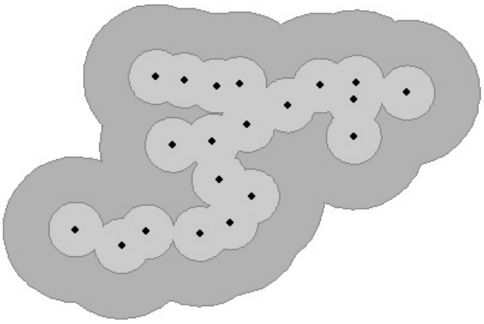
Appendix B: Effective trapping areas for male and female jaguars



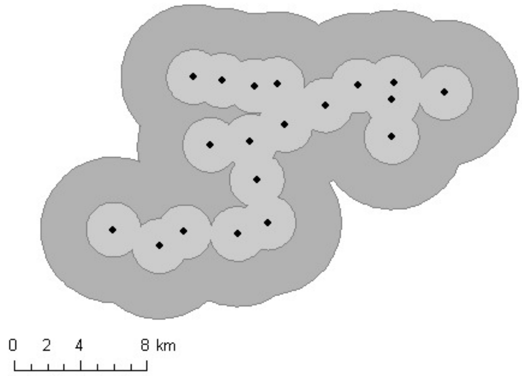
Ext06
protected forest +
unprotected lands
(forest + non forest)



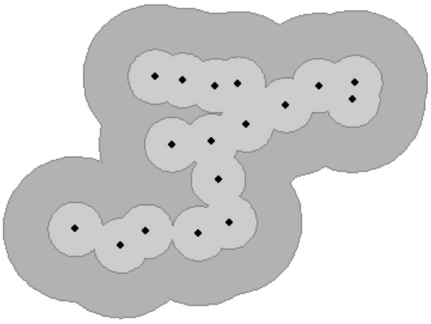
Ext06
protected forest +
unprotected forest



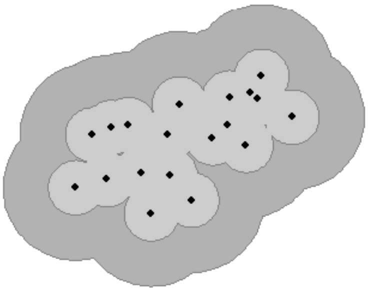
Ext06
protected forest +
boundary forest



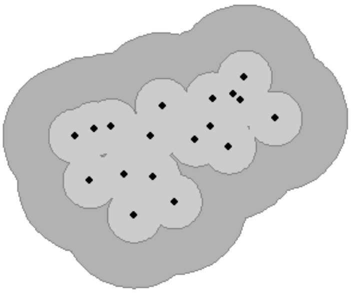
Ext06
protected forest +
boundary forest
(CBWS04, 05, 06)



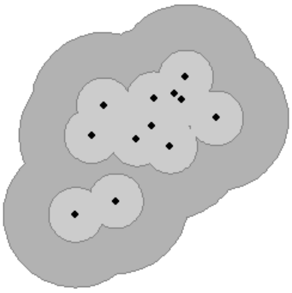
Ext06
protected forest



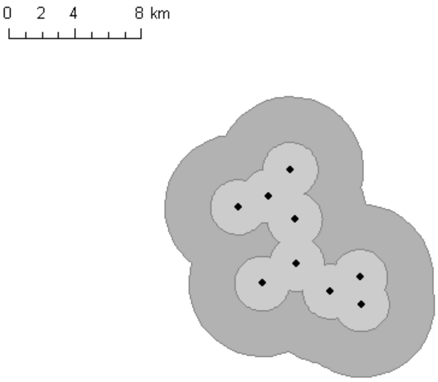
Sit06
boundary +
unprotected lands
(forest + non forest)



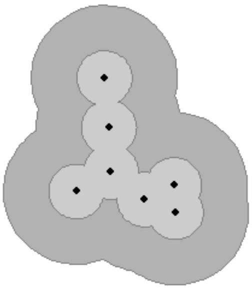
Sit06
unprotected lands
(forest + non forest)



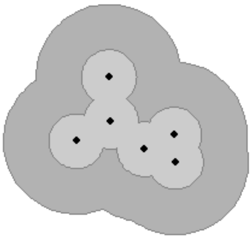
Sit06
unprotected lands
(non forest)



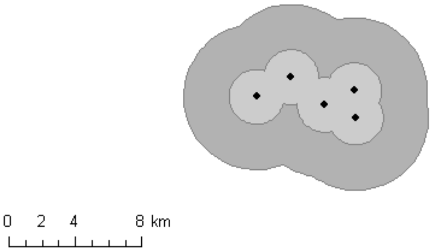
Zab06
protected forest +
unprotected lands
(forest + non forest)



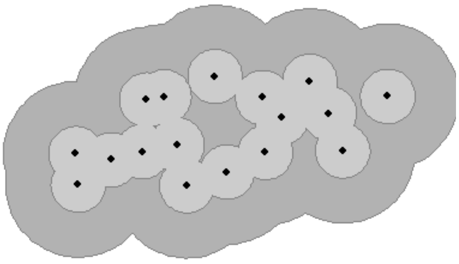
Zab06
boundary +
unprotected lands
(forest + non forest)



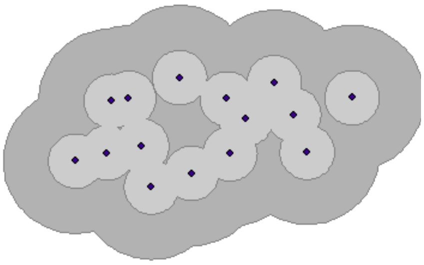
Zab06
unprotected lands
(forest + non forest)



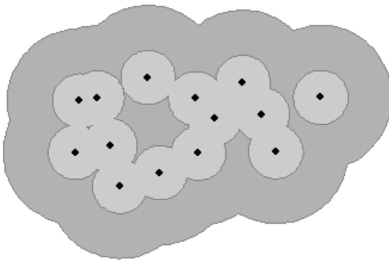
Zab06
unprotected lands
(non forest)



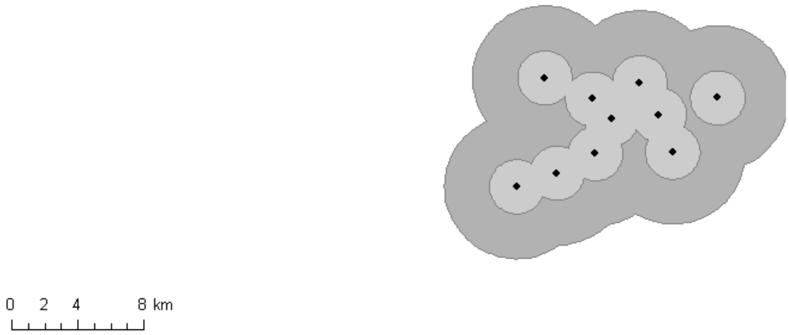
Sit05
protected forest +
unprotected lands
(forest + non forest)



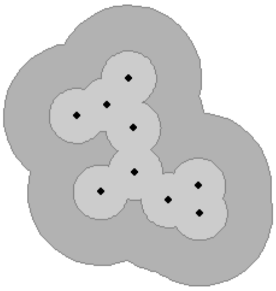
Sit05
boundary +
unprotected lands
(forest + non forest)



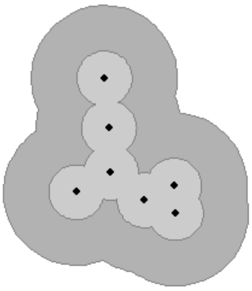
Sit05
unprotected lands
(forest + non forest)



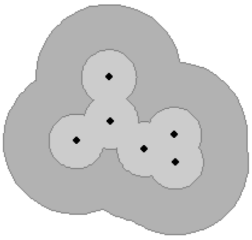
Sit05
unprotected lands
(non forest)



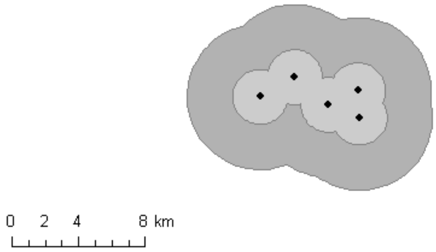
Zab05
protected forest +
unprotected lands
(forest + non forest)



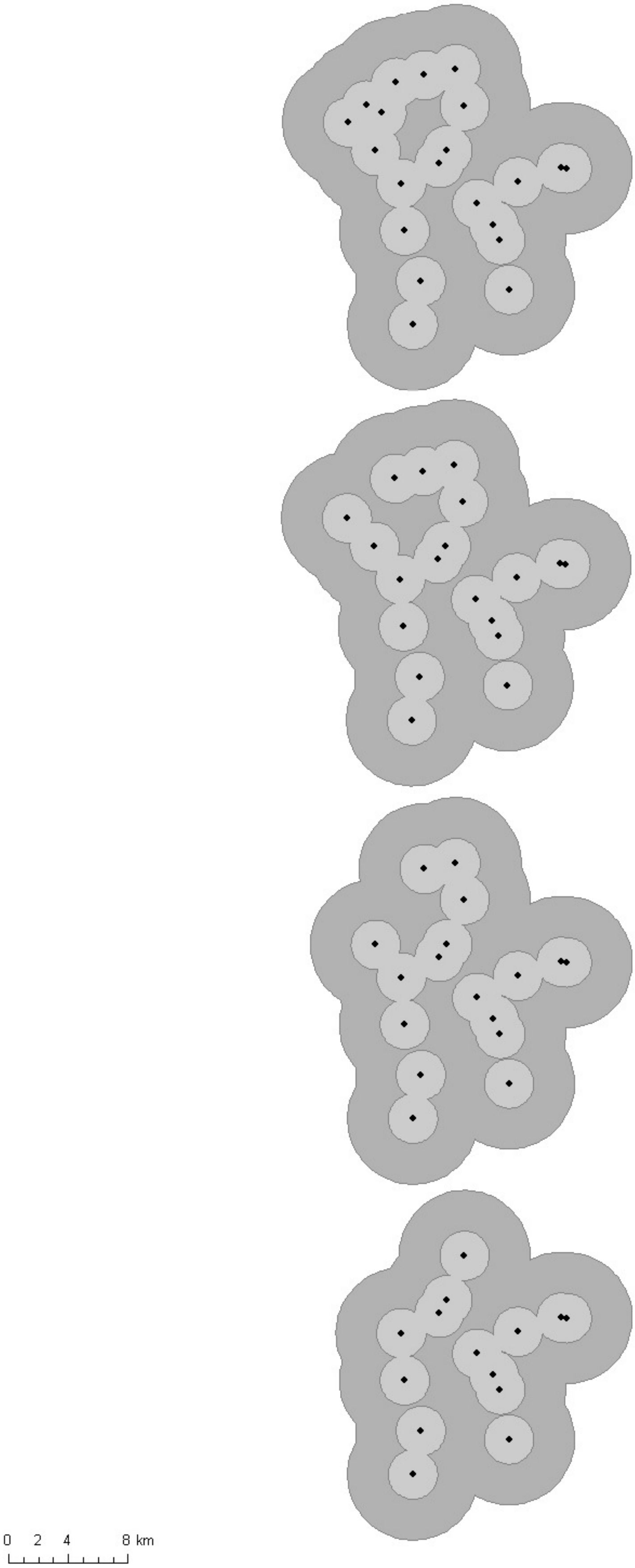
Zab05
boundary +
unprotected lands
(forest + non forest)



Zab05
unprotected lands
(forest + non forest)



Zab05
unprotected lands
(non forest)



Arn06
protected forest +
unprotected lands
(forest + non forest)

Arn06
boundary +
unprotected lands
(forest + non forest)

Arn06
unprotected lands
(forest + non forest)

Arno06
unprotected lands
(non forest)

Figure B.1 Effective trapping areas (ETAs) for male jaguars and female jaguars based on mean maximum distance moved (MMDM) by each sex during the Ext06 survey. Male ETAs shown in dark grey, based on MMDM = 8776m. Female ETAs shown in light grey, based on MMDM = 3312m. Camera locations shown as black dots. Male MMDM is large enough that no gaps or discontinuities exist within the ETAs. Female MMDM is less than THE spacing between neighbouring cameras in some surveys, resulting in gaps and discontinuities in some ETAs.

Appendix C: Examples of habitats in the study area

Figure C.1 Closed forest (lowland broadleaf forest)

Figure C.2 Shrublands (broadleaf lowland shrubland)

Figure C.3 Shrublands (fire-induced fern thicket)

Figure C.4 Terrestrial herbs (lowland savannah ± pine)

Figure C.5 Agriculture (shifting agriculture ‘milpa’)

Figure C.6 Agriculture (pasture)

Figure C.7 Agriculture (semi-woody perennial crops: banana)

Figure C.8 Agriculture (woody perennial crops: citrus)

Figure C.9 Agriculture (aquaculture)

Figure C.10 Residential (settlements)

Appendix D: Detection frequency of common prey species in the protected forest

Distance sampling using line transects can be used to estimate mammal and bird density. A number of lines are randomly positioned through the study area. The observer travels along a line and records the distance from the line to each animal observed. In the simplest situation density is calculated as:

$$\hat{D} = \frac{n}{2Lw}$$

where *n* is the number of animals observed, *L* is the transect length and *w* is the maximum distance at which an animal was observed. A sample size of at least 60 for each species of interest is required for reliable estimation of density (Buckland *et al.* 2004). This may be difficult to achieve in certain habitat types or for certain species due to variable visibility, low visibility, nocturnal habits and the size of the species. A pilot study to assess whether transects would be an effective tool in the secondary forest habitat found throughout the study area was conducted using the tourist trails of CBWS. 42 km of secondary forest trails were walked at an average speed of 2 km/ hour between 5am and 8am over a period of 14 days. Sightings along with acoustic and physical signs of prey species were recorded. The study revealed that visibility and prey species encounter rates were very low (Table 1) and it was decided that establishing and running line transects throughout the study area would not be time or cost effective during this study.

Table 1 Detected frequency of common prey species over 42 km of trails in the protected forest when walking 2 km /hour between 5am and 8am over 14 days.

Species		Sightings	Sounds	Tracks/Signs
Tapir	*Tapirus bairdii*	0	0	6
White-lipped peccary	*Dicotyles pecari*	0	1	0
Collared peccary	*Tayassu tajacu*	2	0	8
Red brocket deer	*Mazama americana*	1	0	6
Paca	*Agouti paca*	0	0	5
Agouti	*Dasyprocta punctata*	0	0	0
Nine-banded armadillo	*Dasypus novemcinctus*	1	0	0
Currasow	*Crax rubra*	5	1	0
Crested guan	*Penelope purpurascens*	0	1	0

Appendix E: Derivation of model input parameters

Demographic rates

1. Age of first reproduction

Age of first reproduction was assumed to be 4 years for males and 3 years for females based on estimate of 36-48 months for male jaguars (*Panthera onca*) and 24-30 months for females (Sunquist and Sunquist 2002).

2. Maximum breeding age

Maximum breeding age was assumed to be 10 years, based on the longevity and age of last reproduction of several cat species, in captivity and the wild (Table A7.1).

Table A7.1 Longevity and age of last reproduction of several cat species (Nowell and Jackson 1996)

Species	Longevity	Age of last reproduction
Jaguar	c >20 y, w ~11 y	-
Lion (*Panthera leo*)	wm 12-16 y wf 15-16 y	wf decline at 11 y, cease at 15 y
Tiger (*Panthera tigris*)	wf up to 16 y	c 14 y
Leopard (*Panthera pardus*)	w 10-15 y	c up to 19 y
Snow leopard (*Uncia uncial*)	c 21y	c 15 y
Puma (*Puma concolor*)	w 8-10, up to 13	-
Clouded leopard (*Neofelis nebulosa*)	c up to 17 y	c 12-15 y
Canadian lynx (*Lynx Canadensis*)	w 15 y	-
Iberian lynx (*Lynx pardinus*)	w up to 13 y	w 10 y

c = captivity, w = wild, m = male, f = female

3. Sex ratio at birth

In the absence of relevant data, the sex ratio at birth was assumed to be 1 male per female.

4. Percent of males in breeding pool

Polygyny is the most common mating system in mammals (Greenwood 1980) and was assumed for jaguars. The social organisation of cats is often described as one in which a dominant male overlaps and breeds exclusively with several females (e.g. tigers, Sunquist 1981). This can lead to high variance in lifetime reproductive success of males (e.g. tigers, Smith and McDougal 1991) as transient males must wait for the resident male to die or be displaced before they have an opportunity to breed. The % of males in the breeding pool will depend on the level of territoriality and intra-specific competition within the population. Harmsen *et al.* (in press) found that male jaguars in the protected forest of Belize showed high levels of overlap in ranges, low levels of avoidance between individuals, and a high flux of individuals contributing to low consistency in home range ownership. As such one may suspect that a high proportion of the male adults may get the opportunity to breed, and this was set at 75%.

5. Percent of females breeding each year

In captivity, the inter-oestrous period of female jaguars lasts 22-65 days, they may remain in oestrus for 6-17 days and pregnancy lasts 91-101 days (Kitchener 1991, Sunquist and Sunquist 2002). Cubs are fully dependent on their mother's milk for the first 10-11 weeks, and will continue to suckle until 5-6 months old (Sunquist and Sunquist 2002). In theory cycling could resume 2-3 weeks following lactational anestrus (Soares *et al.* 2006). The offspring will stay with their mother for up to 24 months (Kitchener 1991, Sunquist and Sunquist 2002) but by the age of 15-18 months young jaguars may travel and hunt independently within their mother's range (Sunquist and Sunquist 2002). Based on these data it was assumed that a female jaguar will produce cubs approximately every 2 years, therefore the % of females breeding each year was set to 50%. In addition it was assumed that as the population approaches the carrying capacity competition for space and prey may limit the breeding potential of a female. Following van Pelt *et al.* (2006), it was assumed that the proportion of females breeding will begin to decline when the population (N) is at 80% of the carrying capacity (K), falling to 30% when $N = K$ (Figure A7.1).

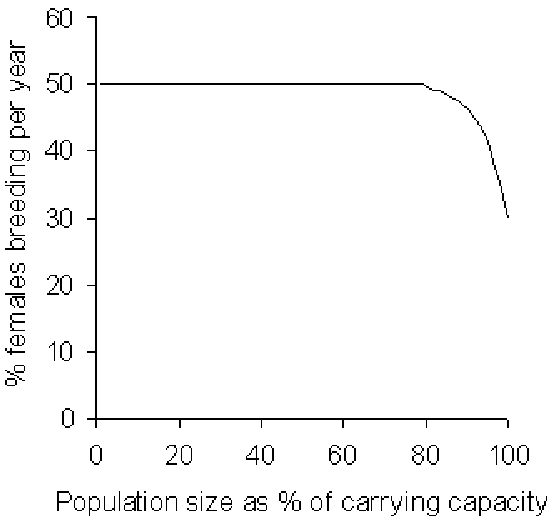


Figure A7.1 Density dependence in % of females breeding each year (after van Pelt *et al.* 2006)

6. Maximum litter size

Estimates of both litter size and cub mortality from field observations are complicated because researchers may not detect cubs until they leave the den (e.g. Lindzey *et al.* 1994)**,** so it is difficult to distinguish between small litter sizes versus high neonatal mortality. Thus estimates of litter size may already incorporate some degree of cub mortality. In captivity jaguar litter sizes range from 1-4 with a mean of ~2 (Mondolfi and Hoogesteijn 1982, Seymour 1989). For the input parameters this was best approximated as a distribution of litter sizes in which 20% of litters were 1 cub, 45% were 2 cubs, 20% were 3 cubs and 15% were 4 cubs, giving a mean litter size of 2.2 cubs. This compares reasonably well with 23 field sightings of jaguars with cubs by Rabinowitz (1986b) who noted that 35% had 1 cub, 52% had 2 cubs and 13% had three cubs. In pumas, Lindzey *et al.* (1994) observed a mean litter size of 2.4 (15% had 1 cub, 35% had 2 cubs, 46% had 3 cubs and 4% had 4 cubs. In tigers litter size varies from 1-4, typically 2 or 3 (Mazák 1981).

7. Cub natural mortality (age 0-1 y)

Big cat cub mortality tends to be relatively high compared to the other age groups. Cubs may be killed by other predators whilst their mother is away from the den (e.g. leopards, Sunquist and Sunquist 2002), or they may be killed by conspecific males seeking to mate with the mother (e.g. tigers, Smith and McDougal 1991). Cubs may also be the first to succumb to nutritional stress and starvation. This may be particularly common in group-living lions, where multiple cubs may compete with adults for an opportunity to feed (Sunquist and Sunquist 2002). No survival data are available for wild jaguar cubs so a mortality of 30% per year (± SD = 10) was selected based on other big cat species (Table A7.2) and the assumption that jaguar cubs are less likely to suffer inter-specific predation and starvation than leopards and lions.

Table A7.2 Cub natural mortality (% per year) of several cat species

Species	Mortality	Comments	Reference
Lion	14-73	- mainly due to food-scarcity; also infanticide	1
	33		2
Tiger	41-47	- 57% of deaths were human-induced	3
	40	- captivity	3
	34	- infanticide most common cause	4
Leopard	41-50		4
Puma	59	- hunted population	5
	3-33	- hunted and un-hunted populations	4
Iberian lynx	50-60	- incl. human-induced mortality	6

1 - van Orsdol *et al.* 1985, **2** - Packer *et al.* 1988, **3** - Kerley *et al.* 2003, **4** - Nowell and Jackson 1996, **5** - Robinson *et al.* 2008, **6** - Gaona *et al.* 1998.

8. Juvenile natural mortality (age 1-2 y)

Juvenile mortality was assumed to be less than cub mortality, as observed in other cat species (Table A7.3), and set at 10% per year (± SD = 3.3).

Table A7.3 Juvenile mortality (% per year) of several cat species

Species	Mortality	Comments	Reference
Tiger	17	- infanticide most common cause	1
Puma	37-49	- hunted population	2
	12	- natural mortality only	3
Eurasian lynx	50	- incl. high human-induced mortality	1

1 - Nowell and Jackson 1996, **2** - Robinson *et al.* 2008, **3** - Logan *et al.* 1986

9. Subadult natural mortality (males 2-4 y, females 2-3 y)

Subadult mortality was assumed to be higher than juvenile mortality because of the risks associated with dispersal and establishing a new territory. Although there are few data on dispersal in jaguars, in other cats males are more likely to disperse and move further than females (e.g. pumas, tigers and lions, Sunquist and Sunquist 2002). Thus the risks associated with dispersal and establishing a territory are probably higher for males than for females. There are few data available on the natural mortality of sub-adult cats. Subadult mortality of leopards is ~ 32% and considered to be relatively high due to poor hunting success resulting in starvation (Table A7.4). In this study none of the photo records detected jaguars in poor body condition, suggesting that rates of starvation are probably low. Therefore, female subadult mortality was set at 15% per year (± SD = 5), and male subadult mortality was set at 25% per year (± SD = 8.3).

Table A7.4 Sub-adult mortality (% per year) of two cat species

Species	Mortality	Comments	Reference
Leopard	32	- higher than adult mortality due to poor hunting success	1
Iberian lynx	30-50	- non dispersing; incl. high human-induced mortality	2
	50	- dispersing female; incl. high human-induced mortality	2
	60	- dispersing male; incl. high human-induced mortality	2

1 - Nowell and Jackson 1996, **2** - Gaona *et al.* 1998

10. Adult natural mortality (males 4+ y, females 3+ y)

Male jaguars, like other cats, have larger ranges than females (e.g. Chapter 1, Chapter 4) and so are more likely to be involved in territorial disputes than are females. For this reason male mortality was assumed to be higher than female mortality, which was set at 15% and 10% per year respectively based on the adult mortality rates of other cat species (Table A7.5). Mortality was assumed to increase with age if a cat survived to 8 years old, due to the accumulation of injuries, damage to teeth and arthritis. This was modelled as a linear increase in mortality up to 80% at age 15 years, following van Pelt *et al.* (2006) (Figure A7.2).

Table A7.5 Adult mortality (%) of several cat species

Species	Mortality	Comments	Reference
Tiger	23	- mortality and permanent emigration	1
Leopard	30	- old male	2
	17	- prime male	2
	17	- old female	2
	10	- prime female	2
Puma	< 5	- un-hunted	2
	22-44	- male, hunted population	3
	9-16	- female, hunted population	3
	24	- 54% of deaths were human-induced	4
	16	- natural mortality only	5
	28	- incl. human-induced mortality	6
Iberian lynx	10-30	- with territory	7
	30-40	- without territory	7

1 - Karanth *et al.* 2006, **2** - Nowell and Jackson 1996, **3** - Robinson *et al.* 2008, **4** - Stoner *et al.* 2006, **5** - Logan *et al.* 1986, **6** - Lindzey *et al.* 1988, **7** - Gaona *et al.* 1998.

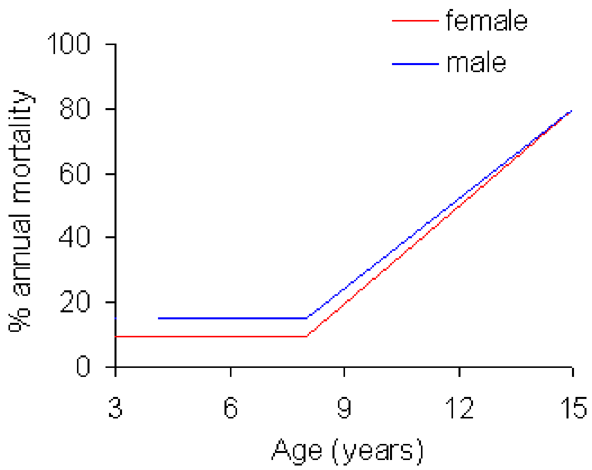


Figure A7.2 Liner increase in adult mortality with age (after van Pelt *et al.* 2006).

Initial population sizes and carrying capacities

1. Maya Mountain protected forest block (MM)

The MM is made up of 13 contiguous protected areas of forest, 12 of which are broadleaf and one which is pine forest (Table A7.6). The mean jaguar density within the Cockscomb Basin Wildlife Sanctuary, calculated over 5 annual surveys, is 10.6 jaguars per 100 km^2 (Harmsen 2006). This is assumed to be the highest density in the MM. The mean density from the Chiquibul Forest Reserve, calculated over 3 annual surveys, is half this value, just 5.2 jaguars per 100 km^2 (M. Kelly unpubl. data). This is assumed to be low within the MM due its close proximity to the Guatemala border where prey are depleted by poachers crossing the national border into Belize. Jaguar density is lower still in the pine forest, averaging at 3.2 jaguars per 100 km^2 over 2 annual surveys (M. Kelly unpubl. data). Assuming a density of 10.6 jaguars per 100 km^2 in the CBWS, 5.2 jaguars per 100 km^2 in the remaining broadleaf forest, and 3.2 jaguars per 100 km^2 in the pine forest, gives a 'low' population estimate for the MM of 277 (Table A7.6). Assuming a density of 10.6 jaguars per 100 km^2 throughout the entire MM gives a 'high' population estimate of 496 (Table A7.6). A conservative estimate of initial population size, and carrying capacity, was 350 individuals.

Table A7.6 Jaguar population estimates for the Maya Mountain protected forest block. Areas derived from Meerman and Sabido (2001).

Protected area	**Area km^2**	**Jaguar Population**	
		Low	**High**
1) Broadleaf			
Vaca Forest Reserve	212	11.0	22.5
Sittee River Forest Reserve	381	19.8	40.4
Chiquibul National Park	1073	55.8	113.7
Silk Grass Forest Reserve	9	0.5	0.9
Chiquibul Forest Reserve	598	31.1	31.1
Caracol Archaeological Reserve	103	5.4	11.0
Victoria Peak National Monument	20	2.1	2.1
Maya Mountain Forest Reserve	169	8.8	17.9
Cockscomb Basin Wildlife Sanctuary	495	52.4	52.4
Bladen Nature Reserve	404	21.0	42.8
Columbia River Forest Reserve	600	31.2	63.6
Sibun Forest Reserve	431	22.4	45.7
2) Pine			
Mountain Pine Ridge Forest Reserve	493	16	52
Total	**4987**	**277**	**496**

2. Rio Bravo protected forest block (RB)

The RB is made up of three contiguous protected areas of broadleaf forest (Table A7.7). The mean jaguar density within the Gallon Jug Private Reserve, calculated over 2 annual surveys, is 10.1 jaguars per 100 km^2 (Miller 2006). Assuming this density throughout the RB protected forest block gives a jaguar population of 172 individuals (Table A7.7). A conservative estimate of initial population size, and carrying capacity, was 170 individuals.

Table A7.7 Jaguar population estimates for the Rio Bravo protected forest block. Areas derived from Meerman and Sabido (2001).

Protected area	**Area km^2**	**Jaguar Population**
Gallon Jug Private Reserve	623	62.9
Aguas Turbias National Park	36	3.6
Rio Bravo Private Reserve	1049	105.9
Total	**1707**	**172**

3. Unprotected lands (UP)

The lands outside the two protected forest blocks totalled 15,608 km^2. The population of UP was based on the author's own density estimates from the unprotected lands neighbouring the MM in southern Belize (Chapter 4). Jaguar density on these lands declines with distance from the forest block, tending to be higher in the west (closer to the forest block) and lower to the east (near the coast). A conservative density estimate of 1.6 jaguars per 100 km^2 was used giving a population of 240 individuals living outside the two protected forest blocks across the entire country. The carrying capacity of UP was set at 440 jaguars based on field estimates of human-induced mortality in the unprotected lands (Chapter 7) and the assumption that natural and human-induced mortality was additive. This is a reasonable assumption, given that density-independent natural mortality of big cats is expected due to intra-specific killings and injuries sustained when attacking prey (e.g. as observed in a hunted puma population, Lindzey *et al.* 1988, 1992). Note that the higher carrying capacity in the UP than the protected forest blocks reflects the larger area of UP rather than a higher jaguar density (UP is almost three times as large as MM and UP combined).

References

Ackerman, B. B., Lindzey, F. G. and Hemker, T. P. (1984) Cougar food habits in Southern Utah. *Journal of Wildlife Management*, 48 (1):147-155.

Ahearn, S., Smith, J. L. D., Joshi, A. R. and Ding, J. (2001) TIGMOD: an individual-based spatially explicit model for simulating tiger/human interaction in multiple use forests. *Ecological Modelling*, 140: 81-97.

Ahearn, S. and Smith, J. L. D. (2005) Modelling the interaction between humans and animals in multiple-use forests: as case study of *Panthera tigris*. Chapter 18 in D. J. Maguire, M. Batty and M. Goodchild, eds. *GIS Spatial Analysis and Modelling*, ESRI Publications.

Amstrup, S. C., McDonald, T. L. and Manly. B. F. (2005) *Handbook of Capture-Recapture Analysis*. Princeton University Press, Oxford.

Anon (2007) Great cats and rare canids fact sheet. *Defenders of Wildlife*, http://www.defenders.org/resources/publications/policy_and_legislation/great_cats_and_rare_canids_species_fact_sheet.pdf Downloaded November 2007.

Aranda, M. and Sánchez-Cordero, V. (1996) Prey spectra of jaguar (*Panthera onca*) and puma (*Puma concolor*) in tropical forests of Mexico. *Studies of Neotropical Fauna and Environment*, 31: 65-67.

Arc GIS 9 (2004) ESRI Inc.

Arrendal, J., Vila, C., and Bjorklund, M. (2007) Reliability of non-invasive genetic census of otters compared to field censuses. *Conservation Genetics*, 8 (5): 1097-1107.

Azevedo, F. C. C. and Murray, D. L. (2007) Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological Conservation*, 137: 391-402.

Azevedo, F. C. C. (2008) Food habits and livestock depredation of sympatric jaguars (*Panthera onca*) and pumas in the Iguaçu National Park area, South Brazil. *Biotropica,* 40(4): 494-500.

Azlan, M. J. and Engkamat, L. (2006) Camera trapping and conservation in Lambir Hills National Park, Sarawak. *The Raffles Bulletin of Zoology*, 54 (2): 469-475.

Azlan, M. J. and Sharma, D. S. K. (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. *Oryx*, 40 (1): 1–6.

Baillie, J. E. M, Hilton-Taylor, C. and Stuart, S. N. (2004) *2004 IUCN Red List of Threatened Species: A Global Species Assessment.* Gland, Switzerland.

Balme, G., Hunter, L., Goodman, P., Ferguson, H., Craigie, J., Hughes, S. de Jager, S. and Slotow, R. (2007) A model for sustainable trophy hunting of leopards in South Africa. Paper given at *Felid Biology and Conservation Conference*, Oxford.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, 18 (6): 1482-1491.

Beaumont, M. and Barratt, E. M., Gottelli, D., Kitchener, A. C., Daniels, M. J., Pritchard, J. K. and Bruford, M. W. (2001) Genetic diversity and introgression in the Scottish wildcat. *Molecular Ecology*, 10 (2): 319–336.

Beck-King, H. M., von Helversen, O. and Beck-King, R. (1999) Home range, population density, and food resources of *Agouti paca* (Rodentia: Agoutidae) in Costa Rica: a study using alternative methods. *Biotropica*, 31 (4): 675-685.

Beckmann, J. P. and Berger, J. (2003a) Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *Journal of Zoology, London*, 261: 207-212, Part 2.

Beckmann, J. P. and Berger, J. (2003b) Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*, 84 (2): 594-606.

Beier, P. (1993) Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology*, 7 (1): 94-108.

Beissinger, S. R. and Westphal, M. I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, 62 (3): 821-841.

Belize Government (2006) http://www.agriculture.gov.bz/ Downloaded September 2006.

Belize Government (2007) http://www.agriculture.gov.bz/bfr/_mafc.htm Downloaded June 2007.

Belize Government (2008) http://www.governmentofbelize.gov.bz/weather_travel.html Downloaded November 2008.

Belize Tourism Board (2008) *Tourism Revenues*. http://www.belizetourism.org/belize-tourism/tourism-revenues.html Downloaded November 2008.

Belize Wildlife Protection Act (2000) *Chapter 220*. Government Printer, Belmopan.

Belize Wildlife Protection Act (2003) *Chapter 220, revised edition 2003 showing subsidiary laws*. Government Printer, Belmopan.

Bertram, B. C. R. (1982) Leopard ecology as studied by radio tracking. *Symposia of the Zoological Society of London*, 49: 341-352.

di Bitetti, M. S., Paviolo, A. and De Angelo, C. (2006) Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology*, *London*, 270: 153-163.

Bonesi, L. and Macdonald, D. W. (2004) Differential habitat use promotes sustainable coexistence between the specialist otter and the generalist mink. *Oikos*, 106: 509-519.

Bothma, J. D. P., Nel, J. A. J. and Macdonald, A. (1984) Food niche separation between four sympatric Namib desert carnivores. *Journal of Zoology*, *London*, 202: 327-340.

Branch, L. C., Pessino, M. and Villarreal, D. (1996) Response of pumas to a population decline of the plains vizcacha. *Journal of Mammalogy*, 77 (4): 1132-1140.

Brechin, S. R. and Buff, J. (2005) *Exploring human-jaguar conflicts in Belize, Central America, part II: a nation-wide study*. Twelve-month final progress report to Wildlife Conservation Society June 2005.

Breitenmoser, U., Angst, C., Landry, J. M., Breitenmoser-Würsten, C., Linnell, J. D. C. and Weber, J. M. (2005) Non-lethal techniques for reducing depredation. Pp 49-85 in R. Woodroffe, S. Thirgod and A. Rabinowitz, eds. *People and Wildlife: Conflict of coexistence,* Cambridge University Press.

Bruner, A. (2007) *Ol Donyo Wuas Trust: Community protection for predators*. Conservation International Fact Sheet. http://www.conservtion.org Downloaded November 2008.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L. (2004) *Introduction to distance sampling*. Oxford University Press, UK.

Bulte, E. H. and Rondeau, D. (2005) Why compensating wildlife damages may be bad for conservation. *Journal of Wildlife Management*, 69 (1): 14-19.

Bulte, E. and Rondeau, D. (2007) Compensation for wildlife damages: Habitat conversion, species preservation and local welfare. *Journal of Environmental Economics and Management*, 54: 311-322.

Burnham, K. P., and Overton, W. S. (1978) Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika*, 65: 625-633.

Butler, J. R. A., du Toit, J. T. and Bingham, J. (2004) Free-ranging domestic dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: threats of competition and disease to large wild carnivores. *Biological Conservation*, 115 (3): 369-378.

Cam Trak Inc., 1050 Industrial Drive, Watkinsville, Georgia 30677 US.

Cat Specialist Group (2002) *Panthera leo*; *Panthera onca*; *Panthera tigris*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species*. http://www.iucnredlist.org Downloaded November 2007.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J. R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D. W., Martyr, D., McDougal, C., Nath, L., O'Brien, T., Seidensticker, J., Smith, D. J. L., Sunquist, M., Tilson, R., Shahruddin, W. N. W. (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4: 75-79.

Carbone, C. and Gittleman, J. L. (2002) A common rule for the scaling of carnivore density. *Science*, 295: 2273-2276.

Cardillo, M., Purvis, A. Sechrest, W. Gittleman, J. L., Bielby, J. and Mace, G. M. (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biology*, 2 (7): 0909-0914.

Carrillo, E., Saenz, J. C. and Fuller, T. K. (2002) Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. *Biological Conservation*, 108: 317-324.

Ceballos, G. and Ehrlich, P. R. (2002) Mammal population losses and the extinction crisis. *Science*, 296 (3): 904-907.

Ceballos, G., Chávez, C., Rivera, A., Manterola, C. and Wall, B. (2002) Tamáno poblacional y conservación del jaguar en la reserve de la bioserfa Calakmul, Campeche, México. Pp 403-417 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Chao, A., Lee, S. M. and Jeng, S. L. (1992). Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics*, 48: 201-216.

Chao, A. and Huggins, R. M. (2005a) Classical closed-population capture-recapture models. Pp 22-35 in Amstrup, S. C., McDonald, T. L. and Manly, B. F. J., eds. *Handbook of Capture-Recapture Analysis*, Princeton University Press.

Chao, A. and Huggins, R. M. (2005b) Modern closed-population capture-recapture models. Pp 58-87 in Amstrup, S. C., McDonald, T. L. and Manly, B. F. J., eds. *Handbook of Capture-Recapture Analysis*, Princeton University Press.

Chinchilla, F. A., (1997) La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*) y el manigordo (*Felis pardalis*) (Carnivoraa: Felidae) en el Parque acional Corcovado, Costa Rica. *Revista de Biologica Tropical*, 45 (3): 1223-1229.

Chundawat. R. S., Sharma, K., Malik, P. K. and Gogate, N. (2007) Resource selection function model to identify habitat suitability of tigers in a dry tropical forest of India. Paper given at *Felid Biology and Conservation Conference*, Oxford.

Cleaveland, S., Mlengeya, T., Kaare, M., Haydon, D., Lembo, T., Laurenson, M. K. and Packer, C. (2007) The conservation relevance of epidemiological research into carnivore viral diseases in the Serengeti. *Conservation Biology*, 21 (3): 612-622.

Colwell, R. R. and Futuyma, D. J. (1971) On the measurement of niche breadth and overlap. *Ecolog*y, 52: 567–572.

Conforti, V. A. and Azevedo, F. C. C. (2003) Local perceptions of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Iguacu National Park area, south Brazil. *Biological Conservation*, 111: 215-221.

Conn, P. B., Arthur, A. D., Bailey. L. L. and Singleton, G. R. (2006) Estimating the abundance of mouse populations of known size: promises and pitfalls of new methods. *Ecological Applications*, 16 (2): 829–837.

Costa, D. S., Paula, T. A. R. and da Matta, S. L. P. (2006) Cat, cougar, and jaguar spermatogenesis: a comparative analysis. *Brazilian Archives of Biology and Technology*, 49 (5): 725-731.

Coulson, T., Mace, M. G., Hudson, E. and Possingham, H. (2001) The use and abuse of population viability analysis. *Trends in Ecology and Evolution*, 16 (5): 219-221.

Crawshaw, P. G. Jr. and Quigley, H. B. (1991) Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. *Journal of Zoology, London*. 223: 357-370.

Crawshaw, P. G. Jr. (2002) Mortalidad inducia por humanos y conservación de jaguares: el Panatanl y el parque nacional Iguaçu en Brasil. Pp 451-463 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Crawshaw, P. G. Jr and Quigley, H. B. (2002) Hábitos alimentarios del jaguar y el puma en el Pantanal, Brazil, con implicaciones para su manejo y conservación. Pp 223-235 in in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Crawshaw, P. G. Jr, .Mähler, J. K., Indrusiak, C., Cavalcanti, S. M. C., Leite-Pitman, M., R. P. and Silvius. K. M. (2004) Ecology and Conservation of the Jaguar (*Panthera onca*) in Iguaçu National Park, Brazil. Pp 271-285 in K. M. Silvius, R. E. Bodmer and J. M. V. Fragoso, eds. *People in Nature: Wildlife Conservation in South and Central America*, Columbia University Press, NY.

Creel, S. (2001) Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15 (1): 271-274.

Creel, S., Spong, G. and Creel, N. (2001) Interspecific competition and the population biology of extinction-prone carnivores. Pp 35-60 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne eds. *Carnivore Conservation*, Cambridge University Press.

Crooks, K. R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16 (2): 488-502.

Cuellar, E., Maffei, L., Arispe, R. and Noss, A. (2006) Geoffroy's cats at the northern limit of their range: Activity patterns and density estimates from camera trapping in Bolivian dry forests. *Studies on Neotropical Fauna and Environment*, 41 (3): 169-177.

Cullen, L. Jr, Abreu, K. C., Sana, D. Nava. A. F. D. (2005) Jaguars as landscape detectives for the upper Paraná River corridor, Brazil. *Natureza and Conservação*, 3 (1): 43-58.

Cypher, B. L. and Frost, N. (1999) Condition of San Joaquin kit foxes in urban and exurban habitats *Journal of Wildlife Management*, 63 (3): 930-938.

Dahle, B. and Swenson, J. E. (2003) Seasonal range size in relation to reproductive strategies in brown bears (*Ursus arctos*). *Journal of Animal Ecology*, 72(4): 660-667.

Dalponte, J. C. (2002) Diet del jaguar y depredación of ganado en el Norte del Pantanal, Brazil. Pp 209-221 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Dawydiak, O. and Sims, D. E. (2004) *Livestock Protection Dogs - Selection, Care and Training, 2nd Edition*, Alpine Publications.

Deem, S. L. and Emmons, L. H. (2005) Exposure of free-ranging maned wolves (*Chrysocyon brachyurus*) to infectious and parasitic disease agents in the Noel Kempff Mercado National Park, Bolivia. *Journal of Zoo and Wildlife Medicine*, 36 (2): 192-197.

Delibes, M., Gaona, P. and Ferreras, P. (2001) Effects of an attractive sink leading to maladaptive habitat selection. *The American Naturalist*, 158 (3): 277-285.

Dice, L. R. (1938) Some census methods for mammals. *Journal of Wildlife Management*, 2: 119-130.

Dickson, B. G., Jenness, J. S. and Beier, P. (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management*, 69 (1): 264-276.

Dillon, A. (2005) Ocelot density and home range in Belize, Central America: Camera-trapping and radio-telemetry. MSc dissertation. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Dillon, A. and Kelly, M. J. (2007) Ocelot activity, trap success, and density in Belize: the impact of trap spacing and distance moved on density estimates. *Oryx*, 41: 469-477.

Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., Forrest, J., Bryja, G., Heydlauff, A., Klenzendorf, S., Leimgruber, P., Mills, J., O'Brien, T. G., Shrestha, M., Simons, R. and Songer, M. (2007) The fate of wild tigers. *Bioscience*, 57 (6): 508-514.

Doncaster, C. P. and Davey, A. J. H. (2007) *Analysis of variance and covariance: how to choose and construct models for the life sciences*. Cambridge University Press, UK.

Donovan, T. M. and Thompson III, F. R. (2001) Modelling the ecological trap hypothesis: a habitat and demographic analysis for migrant song birds. *Ecological Applications*, 11 (3): 871-882.

Dubost, G., Herny, O. and Comizzoli, P. (2005) Seasonality of reproduction in the three largest terrestrial rodents of French Guiana Forest. *Mammalian Biology*, 70 (2): 93-109.

Dunstone, N. (1993) *The Mink*. Poyser Natural History.

Durant, S. (1998) Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology*, 67: 370-386.

van Dyke, F. G., Brocke, R. H., Shaw, H. G., Ackerman, B. B., Hemker, T. P. and Lindzey, F. G. (1986) Reactions of mountain lions to logging and human activity. *Journal of Wildlife Management*, 50: 95-102.

Efford, M. (2004) Density estimation in live-trapping studies. *Oikos*, 106: 598-610.

Efford, M. G., Dawson, D. K. and 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. Warburton, B., Coleman, M. C. and Barker, R. J. (2005) A field test of two methods for density estimation. *Wildlife Society Bulletin*, 33 (2): 731-738.

Eizirik, E., Kim, J. H., Menotti-Raymond, M., Crawshaw, P. G. Jr., O'Brien, S. J. and Johnson, W. E. (2001) Phylogeogprahy, population history, and conservation genetics of jaguars (*Panthera onca*, Mammalis, Felidae). *Molecular Ecology*, 10: 65-79.

Eizirik, E., Indrusiak, C.B. and Johnson, W. E. (2002) Análisis de la viabilidad de las poblaciones de jaguar: evaluación de parámetros y estudios de caso en tres poblaciones remanentes del sur de sudamérica. Pp 501-518 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Emmons, L. H. (1987) Comparative feeding ecology of felids in a neotropical rainforest. *Behavioural Ecology and Sociobiology*, 20: 271-283.

Emmons, L. and Feer, F. (1990) *Neotropical Rainforest Mammals: A Field Guide*. University of Chicago Press, London.

Facure, K. G. and Giaretta, A. A. (1996) Food habits of carnivores in a coastal Atlantic Forest of southeastern Brazil. *Mammalia*, 60 (3): 499-502.

Farrell, L. E., Roman, J. and Sunquist, M. E. (2000) Dietary separation of sympatric carnivores identified by molecular analysis of scats. *Molecular Ecology*, 9: 1583-1590.

Fedriana, J. M., Palomares, F. Delibes, M. (1999) Niche relations among three sympatric Mediterranean carnivores. *Oceologia*, 121: 138-148.

Fedriani, J. M., Fuller, T. K. and Sauvajot, R. M. (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, 24 (3): 325-331.

Ferguson, S.H., Higdon J. W. and Lariviere, S. (2006) Does seasonality explain the evolution and maintenance of delaye dimpantationin the family Mustelidae (Mammalia : Carnivora)? *Oikos*, 114 (2): 249-256.

Ferraro, P. J. and Kiss, A. (2002) Direct payments to conserve biodiversity. *Science*, 292: 1718-1719.

Ferraro, P. J. and Kiss, A. (2003) Response to Swart: 'Will direct payments help biodiversity?' *Science*, 299: 1981-1982.

Ferreras, P., Aldama, J. J., Beltran, J. F. and Delibers, M. (1992) Rates and causes of mortality in a fragmented population of Iberian Lynx *Felis pardina* Temminck, 1824. *Biological Conservation*, 61 (3): 197-202.

Fiorello, C. V., Deem, S. L., Gompper, M. E. and Dubovi, E. J. (2004) Seroprevalence of pathogens in domestic carnivores on the border of Madidi National Park, Bolivia *Animal Conservation*, 7: 45-54.

Fiorello, C. V., Noss, A. J., and Deem, S. L. (2006) Demography, hunting ecology, and pathogen exposure of domestic dogs in the Isoso of Bolivia. *Conservation Biology*, 20 (3): 762-771.

Fiorello, C. V., Noss, A. J., Deem, S. L., Maffei, L. and Dubovi, E. J. (2007) Serosurvey of small carnivores in the Bolivian Chaco. *Journal of Wildlife Diseases*, 43 (3): 551-557.

Foster, R. J. (2007) *Jaguars on the edge: addressing jaguar-human conflict in Belize*. Final report to the Panthera Foundation March 2007.

Fournier-Chambrillon, C., Berny, P.J., Coiffier, O., Barbedienne, P., Dasse, B., Delas, G., Galineau, H., Mazet, A., Pouzenc, P., Rosoux, R. and Fournier, P. (2004) Evidence of secondary poisoning of free-ranging riparian mustelids by anticoagulant rodenticides in France: Implications for conservation of European mink (*Mustela lutreola*). *Journal of Wildlife Diseases*, 40 (4): 688-695.

Fowler, C. W. (1981) Density dependence as related to life history strategy. *Ecology*, 62 (3) 602-610.

Fragoso, J. M. V. (1998) Home range and movement patters of white-lipped peccary (*Tayassu pecari*) herds in the Northern Brazilian Amazon. *Biotropica*, 30 (3): 458-469.

Frank, L. G. and Woodroffe, R. (2001) Behaviour of carnivores in exploited and controlled populations. Pp 419-442 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne, eds. *Carnivore Conservation*, Cambridge University Press.

Frankham, R. (2005) Genetics and extinction. *Biological Conservation*, 126: 131-140.

Frost, P. G. H. and Bond, I. (2008) The CAMPFIRE programme in Zimbabwe: payments for wildlife services. *Ecological Economics*, 65: 776-787.

Fuller, T. K. and Sievert, P. R. (2001) Carnivore demography and the consequences of changes in prey availability. Pp 163-177 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne, eds. *Carnivore Conservation*, Cambridge University Press.

Garla, R. C., Setz, E. Z. F. and Gobbi, N. (2001) Jaguar (*Panthera onca*) food habits in Atlantic Rain Forest of Southeastern Brazil. *Biotropica*, 33 (4): 691-696.

Gaydos J. K., Conrad P. A., Gilardi K. V. K., Blundell, G. M. and Ben-David, M. (2007) Does human proximity affect antibody prevalence in marine-foraging river otters (*Lutra canadensis*)? *Journal of Wildlife Diseases*, 43 (1): 116-123.

George, S. L. and Crooks, K. R. (2006) Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, 133 (1): 107-117.

Gittleman, J. L., Funk, S. M., Macdonald, D. W. and Wayne, R. K. (2001) Why 'carnivore conservation'? Pp. 1-7 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne, eds. *Carnivore Conservation*, Cambridge University Press

Goana, P., Ferreras, P. and Delibes, M. (1998) Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs*, 68(3): 349-370.

González, C. A. L. and Miller, B. J. (2002) Do jaguars (*Panthera onca*) depend on large prey? *Western North American Naturalist*, 62: (2) 218-222.

González-Fernández, A. (1995) Lievstock predation in the Venezuelan Llanos. *Cat News*, 22: 14-15.

Gössling, S. (1999) Ecotourism: a means to safeguard biodiversity and ecosystem functions? *Ecological Economics*, 29: 303-320.

Gotelli, N. J. and Entsminger, G. L. (2008) EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim/index.htm. Downloaded August 2008

Gottdenker, N., and Bodmer, R. E. (1998) Reproduction and productivity of white-lipped and collared peccary in the Peruvian Amazon. *Journal of Zoology*, *London*, 245: 423-430.

Greenwood, P. J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28: 1140-1162.

Griffiths, D. (1975) Prey availability and the food of predators. *Ecology*, 56: 1209-1214.

Griffiths, M. and van Schaik, C. P. (1993) The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Conservation Biology*, 7 (3): 623-626.

Haines. A. M., Tewes, M. E. and Laack, L. L. (2005) Survival and sources of mortality in ocelots. *Journal of Wildlife Management*, 69 (1): 255-263.

Haines, A. M., Janecka, J. E., Tewes, M. E., Grassman Jr, L. I. and Morton, P. (2006) The importance of private lands for ocelot *Leopardus pardalis* conservation in the United States. *Oryx*, 40 (1): 1-5.

Harcourt, A. H., Parks, S. A. and Woodroffe, R. (2001) Human density as an influence on species/area relationships: double jeopardy for small African reserves? *Biodiversity and Conservation*, 10: 1011–1026.

Harmsen, B. (2006) *The use of camera traps for estimating abundance and studying the ecology of jaguars* (*Panthera onca*). PhD thesis. University of Southampton, England.

Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T. and Doncaster, C.P. (In press) Spatial and temporal interactions of two sympatric cats in a neotropical forest: the jaguar (*Panthera onca*) and the puma (*Puma concolor*). *Journal of Mammalogy*.

Harris, S. and Saunders, G. (1993) The control of canid populations. *Symposia of the Zoological Society of London*, 65: 441-464.

Harrison, R. L. (2006) A comparison of survey methods for detecting bobcats. *Wildlife Society Bulletin*, 34 (2): 548-552.

Hass, C. C., and Valenzuela, D. (2002) Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). *Behavioural Ecology and Sociobiology*, 51: 570-578.

Heilbrun, R. D., Silvy, L. J., Peterson, M. J. and Tewes, M. E. (2006) Estimating bobcat abundance using automatically triggered cameras. *Wildlife Society Bulletin*, 34 (1): 69-73.

Hendrick, P. W. (1995) Gene flow and genetic restoration: the Florida Panther as a case study. *Conservation Biology*, 9 (5): 996-1007.

Hoelzel, A. R. and Green. A. (1992) Analysis of population-level variation by sequencing PCR-amplified DNA. Pp 159-186 in A. Hoezel, ed. *Molecular genetic analysis of populations: A practical approach*. Oxford University Press, New York.

Holekamp, K. E. and Smale, L.(1995) Rapid change in offspring sex-ratios after clan fission in the spotted hyena. *American Naturalist*, 145 (2): 261-278.

Hoogesteijn, R. and Mondolfi, E. (1996) Body mass and skull measurements in four jaguar populations and observations on their prey base. *Bulletin of the Florida Museum of Natural History*, 39 (6): 195-219.

Hoogesteijn, R. (2000) Manual on the problem of depredation caused by jaguars and pumas on cattle ranches http://www.savethejaguar.com/media/general Downloaded January 2005.

Hoogesteijn, R. and Hoogesteijn, A. (2008) Conflicts between cattle ranching and large predators in Venezuela: could use of water buffalo facilitate felid conservation? *Oryx*, 42 (1): 132-138.

Hötte, M. and Bereznuk, S. (2001) Compensation for livestock kills by tigers and leopards in Russia. *Carnivore Damage Prevention News*, 3: 6-7.

Howe, R. W., Davis, G. J. and Mosca (1991) The demographic significance of 'sink' populations. *Biological Conservation*, 57: 239-255.

Huggins, R. M. (1989) On the statistical analysis of capture experiments. *Biometrika*, 76: 133-140.

Huggins, R. M. (1991) Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics*, 47: 725-732.

Hurtado-Gonzales, J. L. and Bodmer, R. E. (2006) Reproductive biology of female Amazonian brocket deer in northeastern Peru. *European Journal of Wildlife Research*, 52 (3): 171-177.

Iriate, J.A., Franklin, W. L., Johnson, W. E., Redford, K. H. (1990) Biographic variation of food habits and body size of the American puma. *Oecologia*, 85: 185-190.

IUCN 2007. *2007 IUCN Red List of Threatened Species*. http://www.iucnredlist.org. Downloaded September 2007.

Jackson R. M., Roe, J. D., Wangchuk, R. and Hunter, D. O. (2006) Estimating snow leopard population abundance using photography and capture–recapture techniques. *Wildlife Society Bulletin*, 34 (3): 772-81.

Jaksić, F. M. and Braker, H. E. (1983) Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. *Canadian Journal of Zoology*, *London*, 61: 2230-2241.

Janis, M. W. and Clark, J. D. (2002) Response of Florida panthers to recreational deer and hog hunting. *Journal of Wildlife Management*, 66 (3): 839-848.

Jarrige, R. and Auriol, P. (1992) An outline of beef production. Pp 3-30 in R. Jarrige and C. Béranger, eds. *World Animal Science 5,* Elsevier Health Sciences.

Jedrzejewska, B., Jedrzejewski, W., Bunevich, A. N., Milkowski, L. and Okarma, H. (1996) Population dynamics of wolves *Canis lupus* in Bialowieza primeval forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. *Mammal Review*, 26 (2-3): 103-126

Jett, D. A. and Nichols J. D. (1987) A field comparison of nested grid and trapping web density estimates. *Journal of Mammalogy*, 68 (4): 888-892.

Jhala, Y. V. (1993) Predation on blackbuck by wolves in Velavadar National-Park, Gujarat, India. *Conservation Biology*, 7 (4): 874-881.

Johnson, W. E., Eizirik, E. and Lento, G. M. (2001) The control, exploitation and conservation of carnivores. Pp 196-219 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne, eds. *Carnivore Conservation*, Cambridge University Press.

Karanth, K. U. (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture recapture models. *Biological Conservation*, 71: 333-338.

Karanth, U. K. and Nichols, J. D. (1998) Estimation of tiger densities in India using Photographic captures and recaptures. *Ecology*, 79 (8): 2852-2862.

Karanth, K. U. and Stith, B. M. (1999) Prey depletion as a critical determinant of tiger population viability. Pp 100-113 in J Seidensticker, S. Christie and P. Jackson eds. *Riding the Tiger*, Cambridge University Press.

Karanth, K. U. and 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, London*, 250: 255-265.

Karanth, K. U., Nichols, J. D., Kumar, N. S., Link, W. A. and Hines, J. E. (2004) Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101 (14): 4854-4858.

Karanth, K. U., Nichols, J. D., Kumar, N. S. and Hines, J. E. (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, 87 (11): 2925-2937.

Kawanishi, K. and Sunquist, M. E. (2004) Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation*, 120: 329–344.

Kays, R. W. and Gittleman, J. L. (2001) The social organisation of the kinkajou *Potos flavus* (Procyonidae). *Journal of Zoology, London*, 253: 491-504.

Kelly, M. J., Noss, A. J., Di Bitetti, M. S., Maffei, L., Arispe, R. L., Paviolo, A., De Angelo, C. D. and Di Blanco, Y. E. (2008) Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, Belize. *Journal of Mammalogy*, 89 (2): 408-418.

Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B. and Hornocker, N. G. (2002) Effects of roads and human disturbance on Amur tigers. *Conservation Biology*, 16 (1): 97-108.

Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley. H. B. and Hornocker, M. G. (2003) Reproductive parameters of wild female Amur (Siberian) tigers (*Panthera tigris altaica*). *Mammalogy*, 84 (1): 288-298.

Kiss, A. (2004) Is community-based ecotourism a good use of biodiversity conservation funds? *Trends in Ecology and Evolution*, 19 (5): 232-237.

Knick, S. T. (1990) Ecology of bobcats relative to exploitation and a prey decline in Southeastern Idaho. *Wildlife Monographs*, 108: 1-42.

Knight, R. R., Blanchard, B. M., and Eberhardt, L. L. (1988) Mortality patterns and population sinks for Yellowstone Grizzly bears, 1973-1985. *Wildlife Society Bulletin*, 16: 121-125.

Kissui, B. M. and Packer, C. (2004) Top-down regulation of a top predator: lions in the Ngorongoro Crater. *Proceedings of the Royal Society London*, 271: 1867-1874.

Kitchen, A. M., Gese, E. M., and Schauster, E. R. (2000) Changes in coyote activity patterns due to reduced exposure to human persecution *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 78 (5): 853-857

Kitchener, A. (1991) *The Natural History of the Wild Cats*. A and C Black, London.

Knowlton, F. (1972) Preliminary interpretations of coyote population mechanics with some management implications. *Journal of Wildlife Management*, 36 (2): 369-383.

Knowlton, F. F., Gese, E. M. and Jaeger, M. M. (1999) Coyote depredation control: an interface between biology and management. *Journal of Range Management*, 52: 398-412.

Krebs, C. J. (1999) *Ecological Methodology*. Addison-Wlset Educational Publishers, Inc.

Krebs, J., Lofroth, E., Copeland, J., Banci, V., Cooley, D., Golden, H., Magoun, A., Mulders, R. and Shults, B. (2004) Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management*, 68 (3): 493-502.

Kristan, W. B. III (2003) The role of habitat selection behaviour in population dynamics: source-sink systems and ecological traps. *Oikos*, 103: 457-468.

Kuriowa, A. and Ascorra, C. (2002) Dieta y densidad de posibles presas de jaguar en las inmediaciones de lad zona de reserve Tambopata-Candamo, Perú. Pp 199-207 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Lacy, R. C., Borbat, M. and Pollak, J. P. (2005) *Vortex: A stochastic simulation of the extinction process: Version 9.92*. Brookfield, IL: Chicago Zoological Society.

Laikre, L., Andrén, R. Larsson, H. O. and Ryman, N. (1996) Inbreeding depression in brown bear *Ursus arctos*. *Biological Conservation*, 76: 69-72.

Laing, S. P. and Lindzey, F. G. (1993) Patterns of replacement of resident cougars in Southern Utah. *Journal of Mammalogy*, 74 (4): 1056-1058.

Laundré, J. W. (2005) Puma energetics: a recalculation. *Journal of Wildlife Management*, 69 (2): 723-732.

Leite, R. M. P. and Galvão, F. (2002) El jaguar, el puma y el hombre en tres áreas protegidas del bosque atlántico costero de Paraná, Brasil. Pp 237-250 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Levins, R. (1968) *Evolution in changing environments*. Princeton University Press, Princeton, NJ.

Lindsey, P. A., Roulet, P. A., and Romanach, S. S. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, 134 (4): 455-469.

Lindzey, F. G., Ackerman, B. B., Barnhurst, D. and Hemker, T. P. (1988) Survival rates of mountain lions in southern Utah. *Journal of Wildlife Management*, 52 (4): 664-667.

Lindzey, F. G., van Sickle, W. D., Laing, S. P. and Mecham, C. S. (1992) Cougar population response to manipulation in southern Utah. *Wildlife Society Bulletin*, 20: 224-227.

Lindzey, F. G., van Sickle, W. D., Ackerman, B. B., Barnhurst, D., Hemker, T. P. and Laing, S. P. (1994) Cougar population dynamics in southern Utah. *Journal of Wildlife Management*, 58 (4): 619-624.

Linke, M., Chapron, G., Martyr, D. J., Holden, J. and Leader-Williams, N. (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology*, 43: 579-589.

Linnell, J. D. C., Aanes, R. and Swenson, J. E. (1997) Translocation of carnivores as a method for managing problem animals: a review. *Biodiversity and Conservation*, 6: 1245-1257.

Linnell, J. D. C., Odden J., Smith, M. E., Aanes, R. and Swenson, J. E. (1999) Large carnivores that kill livestock: do problem carnivores really exist? *Wildlife Society Bulletin*, 27 (3): 698-705.

Linnell, J. D. C., Swenson, J. E. and Andersen, R. (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation*, 4 (4): 345-349.

Logan, K. A., Irwin, L. L. and Skinner, R. (1986) Characteristics of a hunted mountain lion population in Wyoming. *Journal of Wildlife Management*, 50 (4): 648-654.

Long, R. A., Donovan, T. M., Mackay, P., Zielinkski, W. J., Buzas, J. S. (2007) Effectiveness of scat detection dogs for detecting forest carnivores. *The Journal of Wildlife Management*, 71 (6): 2007-2017.

Loughry, W. J. and McDonough, C., M. (2001) Natal recruitment and adult retention in a population of nine-banded armadillos. *Acta Theriologica*, 46 (4): 393-406.

Loveridge, A. J., Searle, A. W., Murindagomo, F., Macdonald, D. W. (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation*, 134 (4): 548-558.

Loveridge, G. G. (1986) Bodyweight changes and energy intake of cats during gestation and lactation. *Animal Technology*, 37 (1): 7-15.

Lozano, J., Virgos, E., Cabezas-Diaz, S. and Mangas, J. G. (2007) Increase of large game species in Mediterranean areas: Is the European wildcat (*Felis silvestris*) facing a new threat? *Biological Conservation*, 138 (3-4): 321-329.

Lukacs, P. (2007) Closed population capture-recapture models. Pp.15.1 to 15.18 in E. Cooch and G. C. White, eds. *MARK: A Gentle Introduction 6th Edition.* http://www.phidot.org/software/mark/docs/book/ Downloaed April 2007.

Lyra-Jorge, M. C., Ciocheti, G. and Pivello. V. R. (2008). Carnivore mammals in a fragmented landscape in northeast of São Paulo State, Brazil. *Biodiversity Conservation*, 17: 1573-1580.

Maffei, L., Cuellar, E. and Noss, A. (2004) One thousand jaguars (*Panthera onca*) in Bolivia's Chaco? Camera trapping in the Kaa-Iya National Park. *Journal of Zoology*, *London*, 262: 295-304.

Maffei, L., Noss, A. J., Cuéllar, E. and Rumiz, D. I. (2005) Ocelot (Felis pardalis) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping. *Journal of Tropical Ecology*, 21: 1–6.

Maffei, L. and Noss, A. J. (2008) How small is too small? Camera trap survey areas and density estimates for ocelots in the Bolivian Chaco. *Biotropica*, 40 (1): 71-75.

Manly, B. F. J., McDonald, T. L. and Amstrup, S. C. (2005) Introduction to the Handbook. Pp1-21 in Amstrup, S. C., McDonald, T. L. and Manly, B. F. J., eds. *Handbook of Capture-Recapture Analysis*. Princeton University Press.

Marceau, J. (2001) *Nasua narica* (on-line). *Animal Diversity Web*. http://animaldiversity.ummz.umich.edu/site/accounts/information/Nasua_narica.html. Accessed September 05, 2008.

Matola, S. (2002) Belice y el Zoológico de Belice: esfuerzos fortalecidos que han incremenetado la conciencia sobre los jaguares de la nación. Pp 493-500 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Mazák, V. (1981) Panthera tigris. *Mammalian Species*, 152: 1-8.

Mazzolli, M., Graipel, M. E. and Dunstone, N. (2002) Mountain lion depredation in southern Brazil. *Biological Conservation*, 105: 43-51.

McDonough, C. M., DeLaney, M. J., Le, P. Q, Blackmore, M. S. and Loughry, W. J. (2000) Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America. *Revista de Biología Tropical*, 48 (1): 109-120.

McMahan, L. R. (1982) The international cat trade. Pp 461-488 in S. D. Miller and D. D. Everett, eds. *Cats of the World: Biology, Conservation and Management*, National Wildlife Federation, Washington DC.

Mech, L. D. and Boitani, L. (2004) *Canis lupus*. In: *IUCN 2007. 2007 IUCN Red List of Threatened Species*. http://www.iucnredlist.org Downloaded October 2007.

Meerman, J. C. and Sabido, W. (2001) *Central American Ecosystems Map: Belize.* Programme for Belize, Belize.

Meerman, J. C. (2004) *Protected Areas Policy and System Plan: Protected Areas System Assessment and Analysis*. http://biological-diversity.info/NPAPSP.htm

Michalski, F. and Peres, C. A. (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, 124: 383-396.

Michalski, F. Boulhosa, R. L. P., Faria, A. and Peres, C. A. (2006) Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Animal Conservation*, 9 (2): 179-188.

Miller, C. (2002) Jaguares, ganado y humanos: un ejemplo de coexistencia pacífica en el noroeste de Belice. Pp 477 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Miller, B. and Rabinowitz, A. (2002) ¿Por qué conservar al jaguar? Pp 303-316 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Miller, C. M. and Miller, B. (2005) *Jaguar Density in the Selva Maya*. Report for the Wildlife Conservation Society, NY.

Miller, C. M. (2006) *Jaguar Density in the Fireburn, Belize*. Report for the Wildlife Conservation Society, NY

Miller, P. S. and Lacy, R. C. (2005) *Vortex: A stochastic simulation of the extinction process: Version 9.50 User's Manual*. Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).

Mills, L. S. and Smouse, P. E. (1994) Demographic consequences of inbreeding in remnant populations. *The American Naturalist*, 144 (3): 412-431.

Mills, L. S., Hayes, S. G., Baldwin, C., Wisdom, M. J., Citta, J., Mattson, D. J., and Murphy, K. (1996) Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology*, 10 (3): 863-873.

Milner-Gulland, E. J., Bennett, E. L., and the SCB 2002 Annual Meeting Wild Meat Group (2003) Wild meat: the bigger picture. *Trends in Ecology and Evolution*, 18 (7): 351-357.

Milner, J. M., Nilsen. E. B., and Andreassen, H. P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, 21 (1): 36-47.

Ministry of Defence (1995) *Belize 1:50,000 UTM OS Maps*. Military Survey, UK.

Mishra, C., Allen, P., McCarthy, T., Madhusudan, M. D., Bayarjargal, A. and Prins, H. H. T. (2003) The role of incentive programs in conserving the snow leopard. *Conservation Biology*, 17 (6): 1512-1520.

Mitchell, B. R., Jaeger, M. M. and Barrett, R. H. (2004) Coyote depredation management: current methods and research needs. *Wildlife Society Bulletin*, 32 (4): 1209-1218.

Mizutani, F., Jewell P. A. (1998) Home-range and movements of leopards (*Panthera pardus*) on a livestock ranch in Kenya. *Journal of Zoology, London.* 244: 269-286.

Mondolfi, E. and Hoogesteijn, R. (1982) Notes on the biology and status of jaguar in Venzuela. Pp 85-123 in S. D. Miller and D. D. Everett, eds. *Cats of the World: Biology, Conservation and Management*, National Wildlife Federation, Washington DC.

Moreno, R. S., Kays, R. W. and Samudio, R. Jr. (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy*, 87 (4): 808-816.

Mowat, G. and Paetkau, D. (2002) Estimating marten *Martes americana* population size using hair capture and genetic tagging. *Wildlife Biology*, 8 (3): 201-209.

Mustelid Specialist Group (1996) *Mustela lutreola*. In: IUCN 2007. *2007 IUCN Red List of Threatened Species.* http://www.iucnredlist.org Downloaded November 2007.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.

Naughton-Treves, L., Grossberg, R. and Treves, A. (2003) Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*, 17 (6): 1500-1511.

Ngoprasert, D., Lynam, A. J. and Gale, G. A. (2007) Human disturbance affects habitat use and behaviour of Asiastic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx*, 41 (3): 343-351.

Nichols, J. D. and Karanth, K. U. (2002) Statistical concepts: Estimating absolute densities of tigers using capture-recapture sampling. Pp121-136 in K. U. Karanth and J. D. Nichols, eds. *Monitoring Tigers and their Prey*, Centre for Wildlife Studies, India.

Nielsen, C. K. and Woolf, A. (2002) Survival of unexploited bobcats in southern Illinois. *Journal of Wildlife Management*, 66 (3): 833-838.

Nistler, C. (2007) The return of the jaguar. *The Property and Environment Research Centre Reports*, 25: (4). http://www.perc.org/articles/article1016.php Downloaded November 2008.

Noss, A. J., Cuéllar, R. L., Barrientos, J., Maffei, L., Cuéllar, E. Arispe, R., Rúmiz, D. And Rivero, K. (2003) A camera trapping and radio telemetry study of lowland tapir (*Tapirus terrestris*) in Bolivian dry forests. *Tapir Conservation*, 12 (1): 24-32.

Noss, A. J. and Rumiz, D. I. (2004) Camera trapping *Priodontes maximus* in the dry forests of Santa Cruz, Bolivia. *Endangered Species Update*, 21: 43-52.

Novack, A. (2003) *Impacts of subsistence hunting on the foraging ecology of jaguar and puma in the Maya Biosphere Reserve, Guatemala*. MSc Thesis, University of Florida.

Novack, A. J. , Main, M. B., Sunquist, M. E. and Labisky, R. F. (2005) Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. *Journal of Zoology, London*, 267: 167-178.

Novaro, A. J., Funes, M. C., and Walker, S. (2005) An empirical test of source-sink dynamics induced by hunting. *Journal of Applied Ecology*, 42 910-920.

Nowell, K. and Jackson, P. (1996) *Wild Cats: Status Survey and Conservation Action Plan*. IUCN/SSC Cat Specialist Group. IUCN, Gland, Switzerland.

Núñez, R., Miller, B. and Lindzey, F. (2000a) Food habits of jaguars and pumas in Jalisco, Mexico. *Journal of Zoology, London*, 252: 373-379.

Núñez, R., López-González, C. and Miller, B. (2000b) Jaguar. Pp. 159-163 in R. P. Reading and B. Miller, eds. *Endangered Animals: as reference guide to conflicting issues*, Greenwood Publishing Group.

Núñez, R., Miller, B. and Lindzey, F. (2002) Ecología del jaguar en la reserva de la bioserfa Chamela-Cuixmala, Jalisco, México. Pp 107-126 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Nyhus, P. J., Osofsky, S. A., Ferraro, P., Maddedn, F. and Fischer. H. (2005) Bearing the costs of human-wildlife conflict: the challenges of compensation schemes. Pp 107-121 in R. Woodroffe, S. Thirgod and A. Rabinowitz, eds. *People and Wildlife: Conflict of coexistence,* Cambridge University Press.

O'Brien, T. G., Kinnaird, M. F. and Wibisono, H. T. (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6: 131-139.

de Oliveira, T. G. (2002) Ecología comparastiva de la alimentación del jaguar y del puma en el neotrópico. Pp 265-288 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Olmos, F. (1993) Notes on the food habits of Brazilian 'caatinga' carnivores. *Mammalia*, 57 (1): 126-130.

O'Regan, H. J., Turner, A. and Wilkinson, D. M. (2002) European Quaternary refugia: a factor in large carnivore extinction? *Journal of Quaternary Science*, 17 (8): 789-795.

Orlowski, G. and Nowak, L. (2006) Factors influencing mammal road kills in the agricultural landscape of South-Western Poland. *Polish Journal of Ecology*, 54 (2): 283-294.

van Orsdol, K.G., Hanby, J. P. and Bygott, J. D. (1985) Ecological correlates of lion social organisation (*Panthera leo*). *Journal of Zoology, London*, 206: 97-112.

Otis, D. L., Burnham, K. P., White, G. C. and Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62: 1-135.

Packer, C., Herbst, L., Pusey, A. E., Bygott, J. D., Hanby, J. P., Cairns, S. J. and Mulder, M. B. (1988) Reproductive success of lions. Pp 363-383 in T. H. Clutton-Brock, ed. *Reproductive success*, The University of Chicago Press, Chicago and London.

PACT Protected Areas Conservation Trust (2008) http://www.pactbelize.org Downloaded November 2008.

Palmeira, F. B. L., Crawshaw, P. G. Jr., Haddad, C. M., Ferraz, K. M. P. M. B., and Verdade, L. M. (2008) Cattle predation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biological Conservation*, 141: 118-125.

Parks, S. A. and Harcourt, A. H. (2002) Reserve size, local human density, and mammalian extinctions in US protected areas. *Conservation Biology*, 16 (3): 800-808.

Patterson, B. D., Kasiki, S. M., Selempo, E. and Kays, R. W. (2004) Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighbouring Tsavo National Parks, Kenya. *Biological Conservation*, 119: 507-516.

Payán, E. and Trujillo, L. A. (2006) The Tigrilladas in Colombia. *CAT News*, 44: 25-28.

van Pelt, B., Chávez, C., Azuara, D., Cruz, E. Cornejo, J., Araiza, M., Díaz, M., López, M., Aguilar, R. and Medellín, R. (2006) Reporte del grupo de trabajo de biología de la población y mdelación poblacional in 2^{o} Simposio el jaguar mexicano en el siglo XXI: Taller de análissi de viabilidad de poblaciones y del hábitat del jaguar (*Panthera onca*) en México. Reporte Final. CBSG México.

Peres, C. A. (1996) Population status of white-lipped (*Tayassu pecari*) and collared peccaries (*T. tajacu*) in hunted and unhunted Amazonian forests. *Biological Conservation*, 77: 115-123.

Pfennig, D. W., Rice, A. M. and Martin, R. A. (2006) Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. *Ecology*, 87 (3): 769-779.

Pianka, E. R. (1969) Sympatry of desert lizards (Ctenotus) in Western Australia. *Ecology*, 50 (6): 1012-1030.

Pianka, E. R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4: 53-74.

Pierpaoli, M., Biro, Z. S., Herrmann, M., Hupe, K., Fernandes, M., Ragni, B., Szemethy, L., and Randi, E. (2003) Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. *Molecular Ecology*, 12 (10): 2585-2598.

Platt, S. G., Rainwater, T. R. and Brewer, S. W. (2004) Aspects of the burrowing ecology of nine-banded armadillos in northern Belize. *Mammalian Biology*, 69 (4): 217-224.

Pledger, S. (2000) Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics*, 6: 434-442.

Pledger, S. (2005) The performance of mixture models in heterogeneous closed population capture–recapture. *Biometrics*, 61: 868–876.

Polisar, J., Maxit, I., Scognmillo, D., Farrell, L., Sunsquist, M. E. and Eisenberg, J. F. (2003) Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation*, 109: 297-310.

Pollock, K. H., and Otto, M. C. (1983) Robust estimation of population size in closed animal population from capture-recapture experiments. *Biometrics*, 39: 1035-1049.

Prange, S., Gehrt, S. D., and Wiggers, E. P. (2003) Demographic factors contributing to high raccoon densities in urban landscapes. *Journal of Wildlife Management*, 67 (2): 324-333.

Pulliam, H. R. (1988) Sources, sinks and population regulation. *American Naturalist*, 132: 652-661.

Pulliam, H. R. (1996) Sources and sinks: Empirical evidence and population consequences. Pp 45-69 in O. E. Jr Rhodes, R. K. Chesser and M. H. Smith, eds. *Population dynamics in ecological space and time*, The University of Chicago Press.

Pyare, S., Cain, S., Moody, D., Schwartz, C. and Berger, J. (2004) Carnivore re-colonisation: reality, possibility and a non-equilibrium century for grizzly bears in the southern Yellowstone ecosystem. *Animal Conservation*, 7: 71-77, Part 1.

Quigley, H. B. and Crawshaw, P. G. Jr. (1992) A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. *Biological Conservation*, 61: 149-157.

Quigley, H. B. and Crawshaw, P. G. Jr. (2002) Reproducción, crecimiento y dispersión del jaguar en la región del Pantanal de Brasil. Pp 289-302 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Quigley, H. and Herrero, S. (2005) Characterization and prevention of attacks on humans. Pp 27-48 in R. Woodroffe, S. Thirgod and A. Rabinowitz, eds. *People and Wildlife: Conflict of coexistence,* Cambridge University Press.

Rabinowitz, A. R. (1986a) Jaguar depredation on domestic livestock in Belize. *Wildlife Society Bulletin*, 14: 170-174.

Rabinowitz, A. (1986b) *Jaguar*. Arbor House, New York.

Rabinowitz, A. R. and Nottingham, B. G. (1986) Ecology and behaviour of the jaguar (*Panthera onca*) in Belize, Central America. *Journal of Zoology*, *London*. 210: 149-159.

Rabinowitz, A. (1989) The density and behaviour of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thaliand. *Natural History Bulletin*, 37 (2) 235-251.

Rabinowitz, A. (2005) Jaguars and livestock: living with the world's third largest cat. Pp 278-285 in R. Woodroffe, S. Thirgood, and A. Rabinowitz, eds *People and Wildlife: Conflict or Coexistence?* Cambridge University Press.

Rabinowitz, A. (2006) Connecting the dots: saving the jaguar throughout its range. *Wildlife Conservation Magazine*, Jan/Feb 2006.

Ralls, K., Ballou, J. D. and Templeton, A. (1988) Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology*, 2(2): 185-193

Randall, D. A., Marino, J., Haydon, D. T., Sillero-Zubiri, C., Knobel, D. L., Tallents, L. A., Macdonald, D. W., Laurenson, M. K. (2006) An integrated disease management strategy for the control of rabies in Ethiopian wolves. *Biological Conservation*, 131 (2): 151-162.

Rau, J. R., Tilleria, M. S., Martinez, D. R. and Muñoz, Andres, H. (1991) Dieta de *Felis concolor* (Carnivores: Felidae) en areas silvestres protegidas del sur de Chile. *Revista Chilena de Historia Natural*, 64: 139-144

Rau, J. R. and Jiménez, J. E. (2002) Diet of puma (*Puma concolor*, Carnivora: Felidae) in costal and Andean ranges of Southern Chile. *Studies on Neotropical Fauna and Environment*, 37 (3): 201-205.

Redford, K. H., (1992) The empty forest. *Bioscience*, 42: 412-422.

Rehder, D. and Olson, L. (2007) *Potos flavus* (on-line). *Animal Diversity Web*. http://animaldiversity.ummz.umich.edu/site/accounts/information/Potos_flavus.html. Accessed September 08, 2008.

Reid, F. A. (1997) *A Field Guide to the Mammals of Central America and Southeast Mexico*. Oxford University Press, Oxford.

Remeš, V. (2000) How can maladaptive habitat choice generate source-sink population dynamics. *Oikos*, 91 (3): 579-582.

Revilla, E., Palomares, F. and Delibes, M. (2001) Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Donana National Park. *Conservation Biology*, 15 (1): 148-158.

Rexstad, E., and Burnham, K. P. (1991) *User's guide for interactive program CAPTURE*. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins.

Reyna-Hurtado, R. and Tanner, G. W. (2007) Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern Mexico). *Biodiversity and Conservation*, 16: 743-756.

Riley, S. P. D., Sauvajot, R. M., Fuller, T. K., York, E. C., Kamradt, D. A., Bromley, C. and Wayne, R. K. (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*, 17 (2): 566-576.

Riley, S. P. D. (2006) Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *Journal of Wildlife Management*, 70 (5): 1425-1435.

Riley, S. P. D., Pollinger, J. P., Sauvajot, R. M., York, E. C., Bromley, C., Fuller, T. K. and Wayne, R. K. (2006) A southern California freeway is a physical and social barrier to gene flow in carnivores *Molecular Ecology*, 15 (7): 1733-1741.

Riley, S. P. D., Bromley, C., Poppenga, R. H., Uzal, F. A., Whited, L. and Sauvajot, R. M. (2007) Anticoagulant exposure and notoderic mange in bobcats and mountain lions in urban southern California. *Journal of Wildlife Management*, 71 (6): 1874-1884.

Robinson, H. S., Wieglus, R. B., Cooley. H. S. and Cooley. S. W. (2008) Sink populations in carnivore management: cougar demography and immigration in a hunted population. *Ecological Applications*, 18(4): 1028-1037.

Robinson, J. G. and Redford, K. H. (1986) Intrinsic rate of natural increase in neotropical forest mammals: relationship to phylogeny and diet. *Oceologia*, 68: 516-520.

Robinson, J. G. and Redford, K. H. (1991) Sustainable harvest of neo-tropical mammals. Pp 415-429 in J. G. Robinson and K. H. Redford eds. *Neotropical Wildlife Use and Conservation* University of Chicago Press.

Robinson, J. G. and Bodmer, R. E. (1999) Towards wildlife management in tropical forests. *Journal of Wildlife Management*, 63: (1) 1-13.

Rodriguez, A. and Delibes, M. (2002) Internal structure and patterns of contraction in the geographic range of the Iberian lynx. *Ecography*, 25 (3): 314-328.

RoelkeParker, M. E., Munson, L. Packer, C. Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S. J., Pospischil, A., HofmannLehmann, R., Lutz, H., Mwamengele, G. L. M., Mgasa, M. N., Machange, G. A., Summers, B. A., Appel, M. J. G. (1996) A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature*, 379 (6564): 441-445.

Roemer, G. W., Coonan, T. J., Garcelon, D. K., Bascompte, J. and Laughrin, L. (2001) Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. *Animal Conservation*, 4: 307-318.

Romo, M. C. (1995) Food habits of the Andean fox (*Pseudalopex culpaeus*) and notes on the mountain cat (*Felis colocolo*) and puma (*Felis concolor*) in the Río Abiseo National Park, Perú. *Mammalia*, 59 (3): 335-343.

Rondeau, D. and Bulte, E. (2007) Wildlife damage and agriculture: a dynamic analysis of compensation schemes. *American Journal of Agricultural Economics*, 89 (2): 490-507.

Ross, P. I. and Jalkotzy, M. G. (1992) Characteristics of a hunted population of cougars in southwestern Alberta. *Journal of Wildlife Management*, 56 (3): 417-426.

Ross, P. I., Jalkotzy, M. G. and Daoust, P. Y. (1995) Fatal trauma sustained by cougars, *Felis concolor*, while attacking prey in southern Alberta. *The Canadian Naturalist*, 109: 261-263.

Saberwal, V. K., Gibbs, J. P., Chellam, R. and Johnsingh, A. J. T. (1994) Lion-human conflict in the Gir Forest, India. *Conservation Biology*, 8 (2): 501-507.

Sáenz, J. C. and Carrillo, E. (2002) Jaguares depredarores de ganado en Costa Rica: ¿un problems sin solución? Pp 127-137 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Salas, L. A. and Kim, J. B. (2002) Spatial factors and stochasticity in the evaluation of sustainable hunting of tapirs. *Conservation Biology*, 16 (1): 86-96.

Salom-Pérez, R., Carrillo, E., Sáenz, J. C. & Mora, J. M. (2007) Critical condition of the jaguar *Panthera onca* population in Cocovado National Park, Costa Rica. *Oryx*, 41 (1): 51-56.

Sandell, M. (1989) The mating tactics and spacing patterns of solitary carnivores. Pp 164-182 in J. L. Gittleman, ed. *Carnivore Behaviour, Ecology and Evolution*, Cornell University Press.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V. and Woolmer, G. (2002a) The human footprint and the last of the wild. *BioScience*, 52 (10): 891-904.

Sanderson, E. W., Redford, K. H., Chetkiewicz, C. B., Medellin R. A., Rabinowitz A. R., Robinson J. G., Taber A. B. (2002b) Planning to save a species: the jaguar as a model. *Conservation Biology*, 16 (1): 58-73.

Sanderson, E. W., Chetkiewicz C. B, Medellin R. A., Rabinowitz A. R., Redford K. H., Robinson, J. G. And Taber, A. B. (2002c) Un análisis geográfico del estado de conservación y distribucion de los jaguarares a través de su área de distribución. Pp 551-600 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Schaller, G. B. and Crawshaw, P. G. Jr. (1980) Movement patterns of jaguar. *Biotropica*, 12 (3): 161-168.

Schiaffino, K., Malmierca, L. and Pervoic, P. G. (2002) Depredación de cerdos domésticos por jaguar en un área rural vecina a un parque nacional en el noreste de Argentina. Pp 251-264 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Schoener, T. W. (1974) Resource partitioning in ecological communities. *Science*, 185 (4145): 27-39.

Schwartz, C. C., Haroldson, M. A., White, G. C., Harris, R. B., Cherry, S., Keating, K. A., Moody, D. and Servheen, C. (2006) Temporal, spatial and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs*, 161: 1-68.

Scognamillo, D. Maxit, I. E., Sunquist, M. and Farrell, L. (2002) Ecología del jaguar y el problems de la depredación de ganado en hu hato de los llanos Venesolanos. Pp 139-150 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Scognamillo D., Maxit I. E., Sunquist M., and Polisar, J. (2003) Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology, London*, 259: 269-279.

Seidensticker, J. C. (1976) On the ecological separation between tigers and leopards. *Biotropica*, 8 (4): 225-234.

Seidensticker, J., Lahiri, J. E., Das, K. C. and Wright, A. (1976) Problem tiger in the Sunderbans. *Oryx*, 11: 267-273.

Seiler, A., Helldin, J. O. and Seiler, C. (2004) Road mortality in Swedish mammals: results of a drivers' questionnaire. *Wildlife Biology*, 10 (3): 225-233.

Seymour, K. L. (1989) Panthera onca. *Mammalian Species*, 240: 1-9.

Shaffer, M. L. (1981) Minimum population sizes for species conservation. *BioScience*, 31: 131-4.

Shivik, J. A., Treves, A., and Callahan, P. (2003). Nonlethal techniques for managing predation: primary and secondary repellents. *Conservation Biology*, 17(6): 1531-1537.

Sillero-Zubiri, C. and Laurenson, M. K. (2001) Interactions between carnivores and local communities: conflict or co-existence? Pp 282-312 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne, eds. *Carnivore Conservation*, Cambridge University Press.

Silveira, L. (2004) *Ecologia comparada e conservação da onça-pintada (Panthera onca) e onça-parda (Puma concolor), no Cerrado e Pantanl*. PhD dissertation, Distrito Federal, Universidade de Brasília, Brasília.

Silver, S. C., Ostro, L. E. T., Marsh, L. K., Maffei, L., Noss, A. J., Kelly, M. J., Wallace, R. B., Gomez, H. and Ayala, G. (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. *Oryx*, 38: (2) 1-7.

Silver, S.C., Harmsen, B.J., Ostro, L.E.T., Foster, R.J. and Doncaster, C.P. (*In press*) The ecology of jaguars in the Cockscomb Basin Wildlife Sanctuary, Belize. In D. W. Macdonald and A. Loveridge, eds. *The Biology and Conservation of Wild Felids*. Oxford University Press.

Slade, N. A., Gomulkiewicz, R, and Alexander, H. H. (1998) Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. *Conservation Biology*, 12 (1): 148-155.

Slough, B. G. and Mowat, G. (1996) Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management*, 60 (4): 946-961.

Smith, H. T. and Engeman, R. M. (2002) An extraordinary raccoon, *Procyon lotor*, density at an urban park. *Canadian Field-Naturalist*, 116 (4): 636-639.

Smith, J., L., D. (1993) The role of dispersal in structuring the Chitwan tiger population. *Behaviour*, 124 (3-4): 165-195.

Smith, J. L. D. and McDougal, C. (1991) The contribution of variance in lifetime reproduction to effective population size in tigers. *Conservation Biology*, 5 (4): 484-490.

Smith, J. L. D., Ahearn, S. C. and McDougal, C. (1998) Landscape analysis of tiger distribution and habitat quality in Nepal. *Conservation Biology*, 12 (6): 1338-1346.

Smith, M. E., Linnell, J. C. D., Odden, J. and Swenson, J. E. (2000a) Review of methods to reduce livestock depredation I. Guardian animals. *Acta Agriculturae Scandinavica*, 50: 279-290.

Smith, M. E., Linnell, J. C. D., Odden J. and Swenson, J. E. (2000b) Review of methods to reduce livestock depredation II. Aversive conditioning, deterrents and repellents. *Acta Agriculturae Scandinavica*, 50: 304-315.

Smith, N. J. H. (1976) Spotted cats and the Amazon skin trade. *Oryx*, 13 (4): 362-371.

Soares, T. N., Telles, M. P. C., Resende, L. V., Silveira, L., Jácomo, A. T. A., Morato, R. G., Diniz-Filho, J. A. F., Eizirik, E. Brondani, R. P. V. and Brondani, C. (2006) Paternity testing and behavioural ecology: A case study of jaguars (*Panthera onca*) in Emas National Park, Central Brazil. *Genteics and Molecular Biology*, 29 (4): 735-740.

Soisalo, M. K. and Cavalcanti, S. M. C. (2006) Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation*, 129 (4): 487-496.

Stanley, T. R. and Burnham, K. P. (1998) Information-theoretic model selection and model averaging for closed-population capture-recapture studies. *Biometrical Journal*, 40 (4): 475-494.

Stoner, D. C., Wolfe, M. L. and Choate, D. M. (2006) Cougar exploitation levels in Utah: implications for demographic structure, population recovery and metapopulation dynamics. *The Journal of Wildlife Management*, 70 (6): 1588-1600.

Sunquist, M. E. (1981) The social organization of tigers in Royal Chitawan National Park, Nepal. *Smithsonian Contributions Zoology*. 336: 1-98.

Sunquist, M. E., Sunquist, F. and Daneke, D. E. (1989) Ecological separation in a Venezuellan llanos carnivore community. Pp. 197-232 in K. H. Redford and J. F. Eisenberg eds. *Advances in Neotropical Mammalogy*, Sandhill Crane Press. Gainesville, Florida.

Sunsquist, M., Karanth, U. K. and Sunsquist, F. (1999) Ecology, behaviour and resilience of the tiger and its conservation. Pp 5-18 in J Seidensticker, S. Christie and P. Jackson, eds. *Riding the Tiger*, Cambridge University Press.

Sunsquist, M. (2002) Historia de la investigación sobre el jaguar en el continente americano. Pp535-550 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Sunquist, M. and Sunquist, F. (2002) *Wild Cats of the World*. The University of Chicago Press, London.

Sweanor, L. L., Logan, K. A. And Hornocker, M, G, (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation *Conservation Biology*, 14 (3): 798-808.

Sweanor, L. L., Logan K. A., Bauer, J. W., Millsap. B., and Boyce. W. M. (2008). Puma and human spatial and temporal use of a popular California State Park. *Journal of Wildlife Management*, 72 (5): 1076-1084.

Swenson, J. E., Sandegren, F., Soderberg, A., Bjarvall, A., Franzen, R. and Wabakken, P. (1997) Infanticide caused by hunting of male bears. *Nature*, 386 (6624): 450-451.

Taber, A. B., Novaro, A. J., Neris, N. and Colman, F. H. (1997) The food habits of sympatric jaguar and puma in the Paraguayan Chaco. *Biotropica*, 29 (2): 204-213.

Taylor, S. K., Buergelt, C. D., Roelke-Parker, M. E., Homer, B. L. and Rotstein, D. S. (2002) Causes of mortality in free-ranging Florida panthers. *Journal of Wildlife Diseases*, 38 (1): 107-114.

Theuerkauf, J., Jedrzejewski, W., Schmidt, K. and Gula, R. (2003) Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland) *Journal of Wildlife Management*, 67 (4): 706-716.

Thirgood, S. Woodrofffe, R. and Rabinowitz, A. (2005) The impact of human-wildlife conflict on human lives and livelihoods. Pp 13-26 in R. Woodroffe, S. Thirgood, and A. Rabinowitz, eds. *People and Wildlife: Conflict or Coexistence?* Cambridge University Press.

Trolle, M. and Kéry (2003) Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera-trapping data. *Journal of Mammalogy*, 84 (2): 607–614.

Trolle M. and Kéry M. (2005) Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. *Mammalia*, 69 (3-4): 405-412.

United Nations Statistics Division (2008) http://unstats.un.org/unsd/default.htm

US Census Bureau (2007) *Population Division.* http://www.census.gov/ipc/www/idb/worldpopinfo.html Downloaded October 2007.

U.S. Naval Observatory (2007) http://aa.usno.navy.mil/data/docs/RS_OneYear.html Downloaded June 2007.

Valdes, B. (2006) *Food habits of large felids in the Cockscomb Basin Wildlife Sanctuary, Belize, and the effects of human subsistence hunting*. BSc Thesis, University of Southampton, England.

Vaughan, C. and Temple, S. (2002) Conservación del jaguar en Centroamérica. Pp 355-366 in R. A. Medellín, C. Equihua, C. L. B. Chetkiewicz, P. G. Crawshaw, A. Rabinowitz, K. H. Redford, J. G. Robinson, E. W. Sanderson, and A. Taber, eds. *El Jaguar en el Nuevo Mileno*, Fondo de Cultura Economica, Universidad Nacional Autonoma de Mexico, Wildlife Conservation Society.

Virgos, E. and Travaini, A. (2005) Relationship between small-game hunting and carnivore diversity in central Spain. *Biodiversity and Conservation*, 14 (14): 3475-3486.

Wade, P. R. (1998) Calculating limits to the allowable human caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, 14: 1-37.

Walker, S. R., Novaro, A. J., Perovic, P., Palacios, R., Donadio, E., Lucherini. M., Pia, M., and Lópes, M. S. (2007) Diets of threes species of Andean carnivores in high-altitude deserts of Argentina. *Journal of Mammalogy*, 88 (2): 519-525.

Wallace, R. B., Gomez, H. Ayala, G. and Espinoza, F. (2003) Camera trapping for jaguar (*Panthera onca*) in the Tuichu Valley, Bolivia. *Journal of Neotropical Mammalogy*, 10 (1): 133-139.

Walpole, M. J. and Thoules, C. R. (2005) Increasing the value of wildlife through non-consumptive use? Deconstructing the myths of ecotourism and community-based tourism in the tropics. Pp 122-139 in R. Woodroffe, S. Thirgod and A. Rabinowitz, eds. *People and Wildlife: Conflict of coexistence,* Cambridge University Press.

Weaver, J. L., Paquet, P. C. and Ruggiero, L. F. (1996) Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology*, 10 (4): 964-976.

Weckel, M., Giuliano, W. and Silver, S. (2006a) Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *Journal of Zoology*, *London*, 270: 25-30.

Weckel, M., Giuliano, W. and Silver, S. (2006b) Cockscomb revisited: jaguar diet in the Cockscomb Basin Wildlife Sanctuary, Belize. *Biotropica*, 38 (5): 687-690.

Wegge, P., Pokheral, C. Pd. and Jnawali, S. R. (2004) Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation*, 7: 251-256.

Wielgus, R. B. and Bunnell, F. L. (2000) Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation*, 93 (2): 145-154.

Wilkinson, D. M. and O'Regan, H. J. (2003) Modelling differential extinctions to understand big cat distribution on Indonesian islands. *Global Ecology and Biogeography*, 21: 519-524.

White, G. C., Anderson, D. R., Burnham, K. P. and Otis, D. L. (1982) *Capture-recapture and removal methods for sampling closed populations*. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.

White, G. C., and Burnham, K. P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46 Supplement: 120-138.

White, G. C. (2005) *Closed population estimation models and their extensions in Program MARK*. Colorado State University, Fort Collins, USA.

Whiteman, C. W., Matushima, E. R., Confalonieric, U. E. C., Palha, M. D. C., da Silva, A. D. L. and Monteiro, V. C. (2007) Human and domestic animal populations as a potential threat to wild carnivore conservation in a fragmented landscape from the Eastern Brazilian Amazon. *Biological Conservation,* 138 (1-2): 290-296.

Whitman, K. L., Starfield, A. M., Quadling, H. and Packer, C. (2007) Modelling the effects of trophy selection and environmental disturbance on a simulated population of African lions. *Conservation Biology*, 21 (3): 591-601.

Whittington, J., St Clair, C. C. and Mercer, G. (2004) Path tortuosity and the permeability of roads and trails to wold movement *Ecology and Society*, 9 (1): article 4.

Wilson, K. R. and Anderson, D. R. (1985) Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy*, 66: (1) 13-21.

Woodroffe, R., Ginsberg, J. R. and Macdonald, D, eds. (1997) *The African wild dog: status survey and conservation action plan.* Gland, Switzerland: IUCN

Woodroffe, R. and Ginsberg, J. R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, 280: 2126-2128.

Woodroffe, R. and Ginsberg, J. R. (1999) Conserving the African wild dog *Lycaon pictus*. I. Diagnosing and treating causes of decline. *Oryx*, 33 (2): 132-142.

Woodroffe, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation*, 3: 165-173.

Woodroffe, R. (2001) Strategies for carnivore conservation: lessons from contemporary extinctions. Pp 62-92 in J. L. Gittleman, S. M. Funk, D. W. Macdonald and R. K. Wayne, eds. *Carnivore Conservation*, Cambridge University Press

Woodroffe, R., Thirgood, S. and Rabinowitz, A. (2005) The impact of human-wildlife conflict on natural systems. Pp 1-12 in R. Woodroffe, S. Thirgood, and A. Rabinowitz, eds. *People and Wildlife: Conflict or Coexistence?* Cambridge University Press.

Woodroffe, R., Lindsey, P. A., Romanach, S. S., and Ranah, S. M. K. O. (2007a) African wild dogs (*Lycaon pictus*) can subsist on small prey: Implications for conservation. *Journal of Mammalogy*, 88 (1): 181-193.

Woodroffe, R., Davies-Mostert, H., Ginsberg, J., Graf, J., Leigh, K., McCreery, K.,Mills, G., Pole, A., Rasmussen, G., Robbins, R., Somers, M., and Szykman, M. (2007b) Rates and causes of mortality in Endangered African wild dogs *Lycaon pictus*: lessons for management and monitoring. *Oryx*, 41 (2): 215-223.

World Bank (2007) Mesoamerican Biological Corridor: Mexico to Panama. http://www.worldbank.org/gef Downloaded October 2007.

World Bank (2008) http://web.worldbank.org/. Downloaded September 2008.

World Resources Institute (2007) Earth Trends database http://earthtrends.wri.org/. Downloaded October 2007

Xu, Y. C., Fang, S. G. and Li, Z. K. (2007) Sustainability of the South China tiger: implications of inbreeding depression and introgression. *Conservation Genetics*, 8: 1199-1207.

Yáñez, J. L., Cárdenas, J. C.Gezelle, P. and Jaksić, F. M. (1986) Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked ranges. *Journal of Mammalogy*, 67 (3): 604-606.

Yau, F. (2007) Determining effective sample area of photographic capture-recapture surveys to estimate jaguar (*Panthera onca*) density in Cockscomb Basin, Belize. MSc Thesis, Columbia University, New York.

Zimmermann, A., Walpole, M. J. and Leader-Williams, N. (2005) Cattle ranchers' attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. *Oryx*, 39 (4): 406-412.