University of Southampton

Faculty of Environmental and Life Sciences

Biological Sciences

Interactions of Large Felids with Their Prey and Humans in the Yucatán Peninsula of Mexico and Belize

by

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Thesis for the degree of Doctor of Philosophy

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Abstract

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Tropical-forest biodiversity is currently undergoing an unprecedented mass extinction caused by human exploitation of natural resources, and fragmentation and loss of forest habitat in conversion to human uses. Felids (wild cats) are particularly vulnerable because of their requirements for contiguous tracts of forest. This thesis addresses the status and value to human wellbeing of natural capital associated with felids that have biotic boundaries extending beyond the boundaries of areas designated for their protection. The principal aim is to evaluate locally viable conservation options for minimising human-wildlife conflict, in relation to populations of jaguars and pumas and their prey that occupy discontinuous areas of protected forest interspersed with farmland. *Chapter 1* introduces the general context and background to this issue. *Chapter 2* uses empirical data from systematic surveys by camera-trapping and scat sampling to estimate the availability of prey to jaguars and pumas in and between two small private nature reserves in the Northern Yucatán Peninsula. The chapter delivers the first sex-specific estimate of jaguar abundance in the area. It evaluates presence and abundance of potential prey for jaguars and pumas, and associations between daily activity patterns of jaguars and pumas with their prey. It quantifies jaguar and puma diets, and assesses prey exploitation and niche overlap. *Chapter 3* uses questionnaire surveys to evaluate human-wildlife interactions between Maya communities and large felids. It includes a first assessment of perceptions about wildlife, hunting and wild meat consumption in the Northern Yucatán Peninsula. The chapter delivers an evaluation of livestock management practices, wild-meat consumption, hunting habits and experiences of human-wildlife conflict. *Chapter 4* addresses the need to monitor cryptic sources of human exploitation of natural forest resources in the Yucatán Peninsula. The chapter describes the development and testing of a probabilistic method for near-optimal placement of acoustic loggers to detect and localise gunshots. Field tests in Mexico and Belize demonstrate for the first time the potential for flooding large areas of forest with small and low-cost acoustic devices to monitor rates of hunting activity.

Chapter 5 delivers a synthesis of general conclusions from the study. Within the Northern Yucatán Peninsula, jaguars and pumas were found to have largely overlapping resource niches and activity patterns, consistent with a lack of options for niche separation in this heavily human modified and disturbed habitat. There was little evidence of declines in their populations with respect to earlier studies, despite ongoing habitat fragmentation. The viability of these large felids depends entirely on their ability to sustain access to prey in unprotected forests between nature reserves, as well as effective protection of prey in the reserves. Maya communities report a generally reducing availability of game – which are also prey to large felids – in the unprotected forests. They also report attacks by large felids on their livestock which, although infrequent, have potential to inflict severe economic injury. Hunters attributed a lack of game to overhunting in unprotected forests, and expressed a desire for support on this issue. The recent development of low-cost and power-efficient acoustic loggers opens up new potential for rural communities to monitor rates of hunting and logging, as a first step to policing their own natural resources.

To my parents Guadalupe and Manuel

To my brother Manelo

To Baloocito

To Demoncio (✝)

Imagination is more important than knowledge

Albert Einstein

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Research Thesis: Declaration of Authorship

Print name:	Evelyn Piña Covarrubias
Title of thesis:	Interactions of Large Felids with their Prey and Humans in the Yucatán Peninsula of Mexico and Belize

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
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Chapter 1 - General introduction

Over the past 500 years, humans have triggered a wave of extinctions, threats and local population declines comparable in both rate and magnitude to the five previous mass extinctions in Earth's history (Dirzo & Raven 2003; Barnosky *et al*. 2011). The expansion of human populations beyond safe operating spaces underlies many of these extinctions and declines (Rockström *et al.* 2009; Dearing *et al.* 2014; Dirzo *et al.* 2014). The global human population is set to rise from its current 7.5 billion to 9 billion by 2042 (United States Census Bureau 2019). Most population increase is occurring in tropical and sub-tropical regions of the world, which have the fastest rates of land conversion to human uses (Hoekstra *et al.* 2005). Deforestation and degradation of tropical forests particularly threatens biodiversity, because tropical forests support two-thirds of Earth's biodiversity despite covering less than 10% of land surface (Giam 2017).

Worldwide human activities have affected forests by dramatically reducing their total area, by the fragmentation of forest cover, and by changing the structure and composition of the remaining forests, which has led to biodiversity loss (Agra *et al.* 2016) and the 'empty forest' syndrome (Redford 1992). Empty forests result from the extirpation of the many vertebrate forest animals, as a consequence of human activities, such as burning, furtive agriculture and hunting. Recent changes in hunting regimes have increased the extent and scale of hunting, and for large-bodied species, this constitutes a severe threat, since they are particularly vulnerable to extirpation by hunting. In addition, extirpation of top predators can trigger prey hyperabundance and increases mesopredator abundance, causing overpredation on smaller species (Terborgh *et al.* 2001; Wright *et al.* 2007; Nasi *et al.* 2011; Wilkie *et al.* 2011; Reider *et al.* 2013; Ripple *et al.* 2015). Throughout the 20th Century, deforestation increased in developing countries, and by the end of the century, the forest area of Latin America had declined to around 50% of its pre-industrial area. These losses have continued into the 21st Century. Between 2000 and 2010, approximately 7 million hectares of forest were lost per year in the tropics (FAO 2016).

In this thesis, I address the impacts of these increasing human pressures on biodiversity in tropical forest of the Mexican Yucatan Peninsula, with a particular focus on large felids and their prey. Mexico has 34% forest cover (2015 estimate, World Bank 2018), ranking the country 112th of 263 countries in percent land area. Its forest area has reduced from 35.9% in 1990, representing a loss of 3.78 million ha. Much of the Mexican forest is concentrated in the Yucatan Peninsula, where contiguous tracts of the tropical Selva Maya extend into Guatemala and Belize to form the best preserved continuous tropical forest north of the Amazon in the Western Hemisphere. In this general introduction, I will set the wider context for studying interactions of large felids with their prey and humans in this region.

Human activities modify habitats, and create new environments that are hostile to many wild species. Large carnivores are likely to be especially sensitive to these changes (Woodroffe 2000). They are usually highly mobile and viable populations require large tracts of suitable habitat to survive (Loveridge *et al.* 2010). Even nominally protected populations may be at risk, since contact with people at reserve borders is a major cause of mortality, and may cause local population extinctions where reserves are too small to enclose the home ranges of the animals that inhabit them (Woodroffe & Ginsberg 1998; Woodroffe 2000). Thus, future conservation efforts depend upon understanding the interactions between predators and people and the mitigation of human impact upon wildlife (Woodroffe & Ginsberg 1998; Woodroffe 2000).

The dramatic declines that many carnivore species have suffered over the past few hundred years arise mainly because of their predatory habits. These trigger a widespread human-wildlife conflict, when carnivores are – or become – predators of domestic livestock, possibly influenced by depletion of their natural prey by human hunters. The result is often persecution of the carnivores. Direct killing by people is considered the greatest threat to the persistence of many large carnivore species (Woodroffe & Ginsberg 1998; Woodroffe 2000; Inskip & Zimmermann 2009; Treves & Karanth 2003). Persecution is only the proximal expression, however, of the far more intractable driver of habitat degradation and loss.

Against a backdrop of global habitat loss for carnivores, the Felidae is one of the most vulnerable Families to immediate anthropogenic threats. Of the 40 extant species, 38 are included in the IUCN Red List, of which 29 have declining populations (IUCN 2018). Increasing fragmentation of habitats particularly affects large felids, by forcing their extensive home ranges to overlap with human-influenced landscapes. The amount and size of natural protected areas often does not suffice to encompass their lifetime movements or even their daily ranging (Woodroffe & Ginsberg 1998; Inskip & Zimmermann 2009; Loveridge *et al.* 2010). The frequency and economic costs of conflicts between humans and carnivores appear to be increasing in many areas, due to the expansion and growth of human populations, farming frontiers and housing (Treves & Karanth 2003), and because conservation and human development goals usually do not align, and tend to separate people from nature (West *et al.* 2006). Solutions are urgently needed to mitigate this human-wildlife conflict, to characterise and quantify the underlying causes that threaten carnivore conservation (Cavalcanti 2008; Chávez & Zarza 2009; Inskip & Zimmermann 2009). Effective mitigation requires quantitative information on the ecology of these species, coupled with a full understanding of the socio-economic conditions of rural communities that share the forest with felids. Of particularly relevance to felids is the evaluation of underlying values, attitudes and norms forest dwellers that may be driving their behaviours. Combined with ecological data on felid movements, prey preferences, and health, an understanding of patterns of human-large felid conflict will facilitate the prediction and prevention of incidents of conflict (Krafte Holland *et al.* 2018).

The jaguar and the puma are the two largest felid species in the Neotropics, coexisting throughout almost their entire regional distributions (Currier 1983; Rabinowitz & Nottingham 1986; Seymour 1989). The IUCN Red List records the jaguar as ‘near threatened’ and the puma as ‘least concern’, and both as ‘decreasing’. Jaguars are also included in the Appendix I CITES (2017). Threats to the persistence of both mainly take the form of habitat loss and fragmentation, poaching of their wild prey base, retaliatory hunting due to livestock predation and due to fear that they pose a threat to human life. Jaguars additionally suffer hunting for their pelts, paws, teeth and other body parts (Caso *et al.* 2008a, b; IUCN 2018).

Jaguars and pumas have a keystone role in the Neotropics as top predators that regulate their prey populations. The loss of these predators may trigger an ‘ecological meltdown’ in predator-free forest fragments, when the elimination of top-down regulations causes trophic cascades that will in turn cause increases on consumer populations and reductions on producer populations, with the endpoint being a biologically impoverished system (Terborgh *et al.* 2001). According to Ripple & Beschta (2006), in Zion National Park, Utah, USA, the cougar population declined because of increased tourist traffic. This resulted in an increase in mule deer densities, higher browsing intensities, and reduced recruitment of cottonwood trees, leading to bank erosion and reductions in terrestrial and aquatic species abundance. Although they adapt well to human-influenced landscapes, even with persecution (Foster 2008), large felids may function as indicator species, evidencing the health of populations of medium-sized mammalian prey.

Jaguars and pumas can serve as umbrella species for conservation, with protection of their habitat supporting the conservation of many other flora and fauna, acting as buffers for the conservation of forest wildlife and tropical forest vegetation in the Neotropics (Redford 1992). For example, a conservation network designed for jaguar conservation from Mexico to Argentina has been found to be an effective umbrella for conserving high-quality habitat of co-occurring mammal species (Thornton *et al.* 2016). Likewise, puma habitat was found to have high potential for the conservation of Western Hemisphere felids generally (Burdett *et al.* 2011).

The jaguar is a charismatic species, which has been used as flagship to establish wildlife reserves in the Neotropics (e.g. Cockscomb Basin Wildlife Sanctuary in Belize) and to focus the allocation of conservation funding destined for the protection of regional ecosystems (Caro 2010), with profound impacts on the success of projects like the Mesoamerican Biological Corridor. The puma, on the other hand, is one of the top five most popular cover animals on conservation and nature magazines (Clucas *et al.* 2008).

Jaguars have a cultural value in many ancient and modern societies throughout the American continent. In the general view of Mesoamerican societies, the jaguar is confined to live in the underworld where it has a strong bond with deities that are associated with the underworld and with the many gateways that lead there, such as caves, as well as the interiors of mountains and forests (Valverde 2005). The earliest jaguar icon appears in the Olmec culture (3250-2400 B. P.) as a creature part human and part jaguar, or a ‘man-jaguar’, which is a supernatural being created by the union of an Olmec ruler with a mythic jaguar being. For the Maya of the Classic period (250-800 B. P.), it was a recurrent icon that symbolised leadership, sacrifice and war. Jaguar skins were used as emblematic clothing of king-warriors and they covered thrones that had the shape of a jaguar. Examples of this can be found in Palenque, Chiapas and Uxmal, and Chichen Itzá in Yucatán. For ancient Aztecs, the jaguar was the bravest creature and the proud ‘lord of the animals’. Those who were born under the *océlotl*, or jaguar, calendar sign shared with the jaguar its aggressive nature and would become audacious warriors. Rulers often wore jaguar pelts at war, and in court, they sat on thrones that were covered with jaguar pelts. Currently, in many rural communities in Mexico there are festivities that include symbolic elements associated with felids, and especially with jaguars. The dances of the ‘tlacololeros’ and ‘tecuanis’ are two better-known examples. In Totoltepec, Guerrero, dancers use jaguar masks and yellow suits with spots and combine Catholic beliefs with

Pre-Hispanic ideas in order to protect their crops and cattle from predators. In Chamula, Chiapas, in SE Mexico, a common belief is that political leaders and healers have a jaguar as a companionship animal (Saunders 1998, 2005). Pumas were the most important of the 'Beast Gods' for Pueblo Indians in New Mexico and Arizona, in South-western United States. They were associated with the horned, or plumed, serpent, and became the supernatural helpers of warriors and hunters. For northern Iroquoians from North America, pumas were considered as one of the entities that controlled the waters, served as personal guardian spirits, animal medicine society patrons and protectors of the people, and were thought to be the alter ego of the meteor/comet man-being, or the fire-dragon man-being (Saunders 1998).

The jaguar and puma are threatened by loss of their habitat due to land-use conversion and the human-wildlife conflict triggered by direct hunting of the species and of their prey base (Chávez & Ceballos 2006; Foster *et al.* 2010a; Quiroga *et al.* 2016). In Mexico, the puma is not listed under any endangerment category, likely due to the lack of information regarding the state of its populations (Núñez *et al.* 2000). The jaguar, on the other hand, is a top priority species for conservation (CONANP 2012), being considered as threatened under Mexican law (NOM-059-SEMARNAT-2010; SEMARNAT 2010).

Three principal actions are needed to manage conflict between humans, and jaguars and pumas (Saracho *et al*. 2006): 1) *protection*, by four principal routes: a) conservation actions to increase the density of the main wild prey species of jaguars and pumas, in order to reduce levels of livestock predation; b) preservation and restoration of natural habitat; c) analysis of population viability to target protection and recovery methods based on scientific criteria, and d) broadcasting media campaigns on the value of jaguars and pumas, as well as the reactivation and diffusion of current government programmes implemented to help preserve these felids; 2) *mitigation*, including compensation to ranchers for livestock losses by large felids; and 3) *adaptation*, including generation of viable economic alternatives to livestock ranching and local changes in livestock grazing patterns. Adaptation could be achieved by preventing livestock from entering forests, concentrating calving seasons with artificial insemination, replacing calves with older animals or donkeys or water buffalos in pastures with chronic predation, locating maternity pastures away from cover types that felids may prefer, moving all animals away from vulnerable areas, keeping records of livestock losses from all causes, and the use of electric fences as a method of non-lethal control of livestock predation (Scognamillo *et al.* 2002; Polisar *et al*. 2003; Foster *et al*. 2010a).

In Mexico, the government has committed to consolidate, boost and implement specific actions and conservation strategies for the jaguar, in order to preserve and recover its populations in Mexico. To this end, the Mexican department of the environment (SEMARNAT) is committed to four conservation actions (SEMARNAT 2009): 1) to promote the generation of biological, ecological and social-perception information on the species, as inputs for decision making aimed at the recovery of the species and its habitat; 2) to promote actions and to add stakeholders to strengthen a culture of environmental protection and biodiversity conservation, with emphasis on vulnerable species including jaguars; 3) to promote social participation as a key strategy aimed at the conservation and protection of populations of jaguar as umbrella species; and 4) to generate an inter-sectorial synergy involving all actors of Mexican society, to participate actively within the scope of their powers to ensure recovery of the species. Specific goals include the promotion of scientific research to develop local and regional strategies for jaguar conservation and population recovery, specifically by the standardisation of research protocols for the monitoring of its populations; protection, management and restoration of jaguar habitat, and of their natural prey; identification of priority natural protected areas for jaguar conservation; inspection and surveillance activities; livestock management; and local community training (local community surveillance networks) and environmental education.

Tropical forests of the Yucatán Peninsula and their biodiversity are severely threatened by illegal logging and hunting (Primack *et al.* 1998; Turner *et al.* 2001; Urquiza-Haas *et al.* 2009, 2011). Hunting is actively and openly practiced in rural communities to supplement diets that may otherwise lack protein and as a traditional practice (Escamilla *et al*. 2000; León & Montiel 2008). These forests contain the largest area of jaguar habitat in Mexico, the largest regional population of jaguars above the equator (Sanderson *et al.* 2002a, b; Ceballos *et al.* 2002, 2006; Chávez & Ceballos 2006; Rodríguez-Soto *et al.* 2011), and constitute one of the key regions for the long-term persistence of jaguar populations in Mexico (Carrillo *et al.* 2007).

Given the broad extent of coexistence between jaguars and pumas, the forests probably also contain the largest area of puma habitat and largest puma population.

However, we lack corroborating data or the means to obtain such data, because pumas (unlike jaguars) cannot be identified to individual from their coat patterns. The forests have suffered substantial land-use conversion resulting from increasingly intense anthropogenic disturbance since ca. 2700 years BP, leading to severe fragmentation of primary forest (Morley & Brainerd 1983). These changes accelerated during the 20th Century, with a regional expansion of agriculture and livestock farming. Particular growth sectors have included cultivation of henequen *Agave fourcroydes* for fibre production (Mizrahi *et al.* 1997; Primack *et al.* 1998; González-Iturbe *et al.* 2002) and cattle ranching (Conde *et al.* 2010). The associated growth in numbers of agricultural and ranch workers has contributed to an increase in hunting of the prey of large felids (Naranjo *et al.* 2004; Reyna-Hurtado & Tanner 2007; Santos-Fita *et al.* 2012), to the extent that it now threatens the subsistence of jaguars and pumas by reducing the availability of wild prey and by triggering human-wildlife conflicts when the felids turn to domestic animals (Chávez & Zarza 2009).

In the Northern Yucatán Peninsula, the local municipalities of Tizimín in Yucatán and Lázaro Cárdenas in Quintana Roo play a vital role in the regional connectivity of populations of jaguars and other felids, and their prey. The region constitutes a wildlife corridor, potentially uniting the reserves of Ría Lagartos and Yum Balam, the former being one of the most important UNESCO biosphere reserves and the latter a refuge for the jaguar and its prey species (CONANP 2018; Ramsar 2018; SEMARNAT 2018c). During 2014, a megaproject for tourism on the offshore island of Holbox, within the protected area of Yum Balam, abruptly tripled the flow of tourists to 60,000 people per year. This influx sparked vigorous protests amongst the local population and civil society, which culminated in a temporary suspension of the megaproject. Amongst the impacts felt by communities was the increasing conversion of forest to tourist development, which was recognised as entailing a significant decline in opportunities for ecotourism activities generated by rural communities, as has happened in the tourist resort of Cancún (C. Chávez pers. comm.).

Within the study region, villagers in rural communities mostly find work only as janitors or maintenance staff in hotels or as informal traders. A few city-based families and investors obtain most of the economic benefit from tourism within rural areas. Local communities maintain a semi-rural way of life, supplemented by tourism-related service jobs in catering and hospitality, taxis and tour guides, masonry and maintenance. Local people take multiple occupations to offset the small income and lack of government support for activities related to sustainable rural development. The communities nevertheless obtain barely sufficient income for quotidian survival, and family emergencies or economic failure are often met by selling off tropical forest lands at greatly reduced prices. There is constant pressure from investors to acquire more land for tourist and commercial complexes, as well as tourist passageways that connect tourism hotspots (Escamilla *et al.* 2000; León & Montiel 2008).

Although biodiversity conservation generally benefits from protection of natural habitat across large contiguous areas (Noss & Cooperrider 1994; Newmark 1995; Meffe & Carrol 1997; Primack 2008), modern landscapes are often fragmented by increasing human activity and dominated by agriculture and/or forestry. In consequence, small protected areas (<50 ha) have relative value in complementing larger tracts of natural habitat, since they may persist as high-quality remnants (Shafer 1995; Turner & Corlett 1996; Schwartz & van Mantgem 1997; Schwartz 1999). Even as vital as they are for conservation, they usually cannot suffice alone to satisfy conservation goals, and are strongly influenced by forces from other habitats in the landscape mosaic. Thus, proper conservation requires management of the mosaic, rather than only the reserves contained within it (Harris 1984; Hobbs *et al.* 1993).

It has been recognised that puma populations in Santa Ana Mountain Range, in Southern California, cannot survive without a movement corridor between currently protected areas, allowing migration between protected areas (Beier 1993). On the other hand, despite the large size of Yellowstone National Park, in Wyoming, it has proven too small to contain the biotic boundaries of the grizzly bears that occupy it, and has triggered conflicts with people who expect bears to only persist inside the limits of the reserve or to be eliminated (Primm & Murray 2005). However, successful example for a small-protected area include the Central Belize Corridor, which gave formal Government-level commitment to the corridor, triggered formal monitoring of mammals, and promoted capacity building and an awareness for the corridor and its function at a national-level (Doncaster *et al.* 2012).

In this thesis, I test the hypothesis that small nature reserves, and their surrounding communal forests, can contribute usefully to the conservation of jaguars (*Panthera onca*) and pumas (*Puma concolor*). El Edén Ecological Reserve (henceforth 'EEER') and El Zapotal Conservation Area (henceforth 'EZCA') are two typical examples of small-scale nature reserves protecting habitat of potential value to many species including some that have biotic boundaries extending beyond their perimeters.

EEER (21°14’14” - 21°09’48” N; 87°12’22” - 87°09’08” W; Reserva Ecológica El Edén 2015) is a private natural protected area of 30.77 km^2, containing jaguar and puma populations. It is situated in the northern Yucatán Peninsula, Mexico, in the municipality of Lázaro Cárdenas, state of Quintana Roo (Fig. 1.1). It was created in 1993 and it is the first private reserve dedicated to biological research and conservation in Mexico (González 2006; Gómez-Pompa *et al.* 2010; Ávila Nájera 2015). EEER is owned/managed by the Non-Government Organisation (NGO) Reserva Ecológica El Edén, A. C., founded by Mexican Researcher Dr Arturo Gómez-Pompa, amongst other. Its principal aim is to develop a research model for the conservation, management and restoration of the biodiversity, ecosystems and ecological processes of tropical forests in Mesoamerica. It also supports experimental research, environmental education, and ecotourism.

EZCA (21°26’10” - 87°41’12” W; 21°19’41” - 87°32’51” W; Pronatura 2015) was created in 2002 by the NGO Pronatura Península de Yucatán, A. C., and purchased from private and communal owners with the support of The Nature Conservancy and the Mexican programme of The North American Wetlands Conservation Act. It has an area of 23.58 km^2 and it is situated in the municipality of Tizimín, state of Yucatán, in the Yucatán Peninsula (Fig. 1.1). EZCA is a private conservation area that aims to protect habitat for avifauna and wild cats, and to mitigate the pressure generated by the expanding farming and livestock frontier, poaching and forest fires on coastal wetlands and tropical forests in Ría Lagartos Biosphere Reserve (Faller-Menéndez 2007; Pronatura 2015; CONANP 2016), in order to increase local biodiversity and regional habitat connectivity. It contributes to the conservation of priority ecosystems outside natural protected areas, under a scheme of collaboration with local rural communities (ejidos).

Small, rural Maya communities inhabit the intermediate area (henceforth ‘IA’) between EEER and EZCA. The main productive activities include agriculture, cattle ranching and bee keeping. The most prevalent land tenure system in IA are communal ‘ejidos’. Subsistence hunting is practiced throughout this area (Pronatura 2015; pers. obs.).

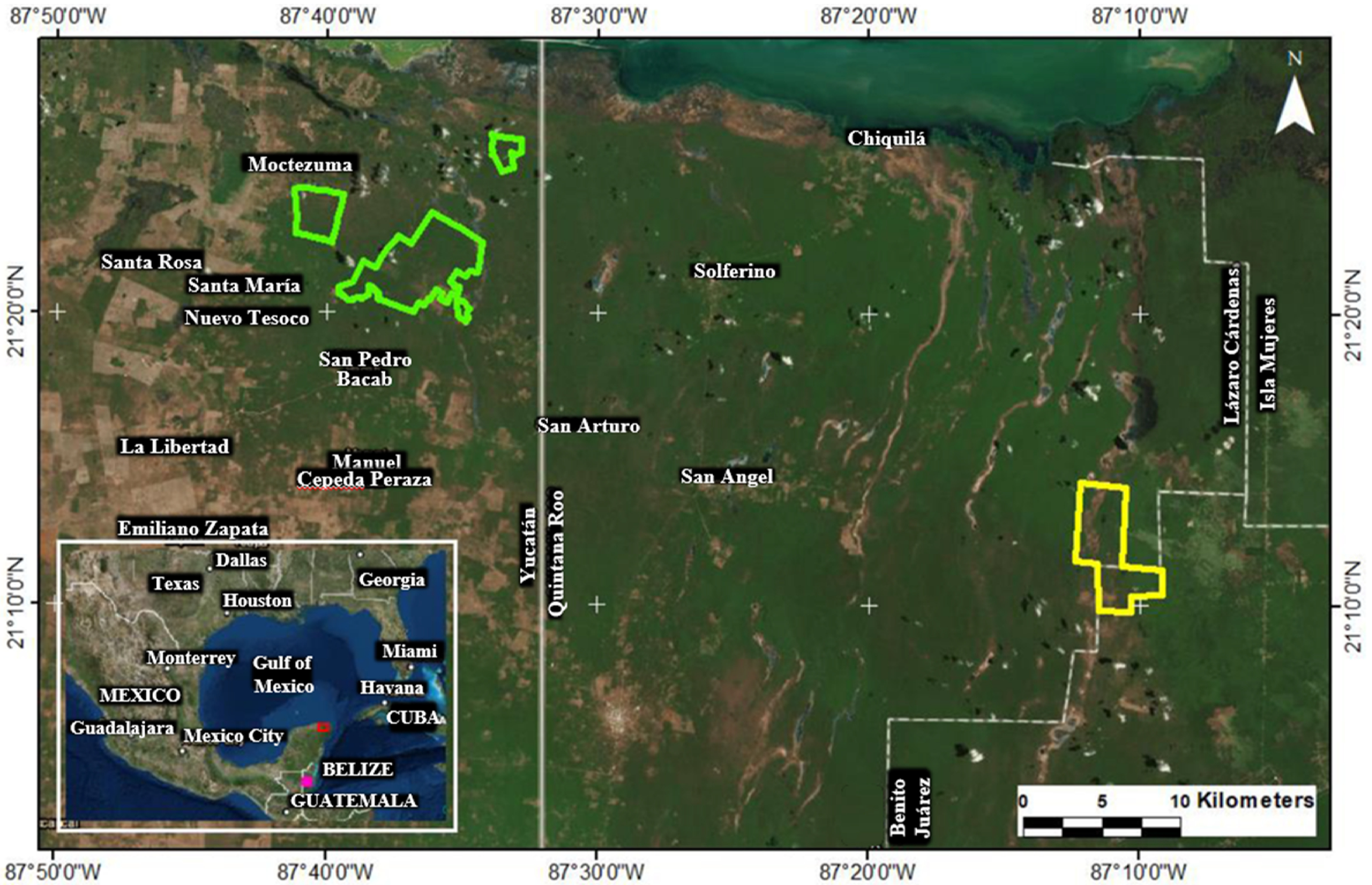


Figure 1.1. The principal study area in the Yucatán Peninsula, showing its location in Mexico (red in inset map), nearby settlements, reserve boundaries of EEER (yellow) and EZCA (green), and the second study area in Belize (pink dot in inset map). Forests show in green and agricultural land in brown.

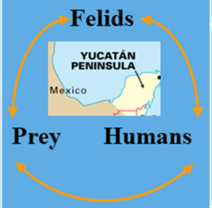
Effective conservation efforts need an integrated view of the links between biodiversity, ecosystems, and societies. An appreciation of the relationships between the natural world and humankind is thus essential for understanding the crucial role of human institutions as sources of both environmental problems and solutions, and for valuing the contribution of nature to quality of life (Cardinale *et al.* 2012; Díaz *et al.* 2015). This thesis aims to evaluate conservation options for minimising human-wildlife conflicts for species that have biotic boundaries larger than the areas designated for their protection. The three thesis objectives include an analysis of aspects of the ecology of large felids and their prey relevant to an assessment of the health of the large-felid community. These ecological insights are complemented by a survey and analysis of current human-large felid interactions in the Northern Yucatán Peninsula. The socio-ecological information is then applied to an exploration of new potential for acoustic monitoring of cryptic human agents of disturbance in protected forest areas. The overall vision for the thesis is that the three evidence-based approaches: understanding ecology, collating knowledge of social factors, and development of solutions, might contribute to facilitating a more harmonious coexistence between people and nature. The logical framework in Table 1.1 summarises these aims and objectives, and outlines the methods underpinning each objective. Here I summarise the specific objectives for the three data chapters of the thesis.

Chapter 2 evaluates the density of jaguars, and the availability and selection of prey for jaguars and pumas in the Northern Yucatán Peninsula (EEER and EZCA, in combination with IA), and on the local scale of EEER and EZCA. Prey limitation may be one of the main triggers for human-wildlife conflicts involving large felids, if starvation threat forces them to supplement their diets with domestic livestock (Fuller & Sievert 2001; Khorozyan *et al.* 2015). Densities of jaguars were estimated robustly with spatially-explicit capture-recapture models. The availability of natural prey was assessed from their presence in camera-trap photos and in felid scats, and associations between daily activity patterns of jaguars and pumas and their prey. Camera trapping provided information on prey distribution and abundance. Scat analysis provided information on dietary breadth and overlap between species.

Chapter 3 evaluates the interactions between local Maya communities and large felids in the Northern Yucatán Peninsula, by recording livestock management practices, wild meat consumption, hunting habits and human-wildlife conflict experiences. This was assessed with questionnaire surveys of villagers.

Chapter 4 explores a potential solution to some aspects of the conservation issues raised in chapters 2 and 3. The major threats to intact forest ecosystems throughout Mesoamerica are in the form of land conversion to agriculture, and exploitation of forest resources such as fuelwood and wild meat (Dirzo *et al*. 2014; Foster *et al.* 2014). In particular, illegal logging and hunting often remain undetected because of their cryptic nature (Peres *et al.* 2006). Developing countries often lack sufficient funds to engage enough well-equipped, properly trained and motivated park personnel who are willing to carry out park policy, which leaves remote protected areas unprotected, especially from threats such as hunting (Bruner *et al.* 2001, 2004; Primack 2008). Chapter 4 reports on the development of a novel acoustic approach to monitoring human agents of disturbance in protected and unprotected forests of the Yucatán Peninsula, by giving local communities support in maintaining their communal forests, and providing them with low-cost, but high-tech acoustic loggers to allow them to monitor exploitation activity in the forest. Cost-effective and small-size AudioMoth acoustic loggers developed by Hill *et al*. (2017) open up new opportunities for acoustic monitoring of hunting and logging activities. The results obtained in this chapter suggest some possible ways forward for sustaining the value of small reserves such as EEER and EZCA in providing natural prey for jaguar and puma, and for helping local communities to live in sustainable harmony with their natural resources.

Table 1.1. Logical framework of the thesis, summarising the main issue and aim, the objectives (data chapters), their contributing outputs (results) and the activities (methods) that will deliver them. [Photo credits: Bart Harmsen and Rebecca Foster]

Issue	Aim	Objectives	Results	Methods
 Human-induced declines in large-felid populations 	Evaluate conservation options for minimising human-wildlife conflict: 	Measure availability of prey to jaguars and pumas in two nature reserves in the Northern Yucatán Peninsula, in Mexico	Jaguar and puma, and prey abundance and occurrence	Fieldwork monitoring of wildlife populations (camera-trap sampling)
			Association between daily activity patterns	
			Jaguar and puma diets	Field evaluation of jaguar and puma prey consumption and niche overlap
		Evaluate human-wildlife conflict in the Northern Yucatán Peninsula, in Mexico	Evaluation of livestock management practices, bush meat consumption, hunting habits and human-wildlife conflict experiences	Questionnaire surveys in local communities: to villagers, cattle owners, and people who hunt
		Assess human exploitation of protected forests in the Yucatán Peninsula, in Belize	Monitoring acoustic signs of cryptic human agents of disturbance in protected areas	Compilation of a soundscape library of human activity
				Test of optimal locations for cost-effective, small-size acoustic loggers

Chapter 2 - Ecology of jaguars (*Panthera onca*), pumas (*Puma concolor*) and their prey in the Northern Yucatán Peninsula, Mexico

Contributions

This chapter was conceived and led by me, in collaboration with UoS co-supervisor Professor C Patrick Doncaster and UAM supervisor Dr Cuauhtémoc Chávez. I organised and managed camera-trap sampling in El Edén Ecological Reserve and in the neighbouring unprotected area. Camera-trap samplings in El Zapotal Conservation Area was managed by personnel from NGO Pronatura Península de Yucatán, A. C., led by Mr Abraham Puc, who I assisted during fieldwork. I organised and managed felid scat sampling in the three areas. In 2015, Cuauhtémoc Chávez and three Mexican undergraduate students assisted with the first deployment of camera-traps in El Edén Ecological Reserve and in the unprotected area, and Cuauhtémoc Chávez trained me in scat sampling during the first scat collection in El Zapotal Conservation Area. I analysed all felid scat samples. Preparation of samples for analysis (washing) was conducted at the Laboratorio de Biología de la Conservación at Universidad Autónoma Metropolitana, campus Lerma, in Mexico. Cuauhtémoc Chávez managed access to the facilities and provided space and equipment. I identified prey bones in felid scat samples at the Laboratorio de Arqueozoología, Instituto Nacional de

Antropología e Historia, in Mexico, with technical assistance from Ms Montserrat Morales and Dr Joaquín Arroyo-Cabrales, who granted access to specimens in their vertebrate bone collection. Cuauhtémoc Chávez provided first contact with Joaquín Arroyo-Cabrales. I prepared prey hair from felid scats at the Departamento de Zoología in the Escuela Nacional de Ciencias Biológicas from the Instituto Politécnico Nacional, in Mexico, with technical assistance from Dr Cynthia Elizalde-Arellano. I conducted identifications of prey hair at the University of Southampton, and molecular identification of felid scats with technical assistance from Dr Mark A. Chapman. Fieldwork and laboratory analysis were conducted with grants that I obtained from CONACyT (studentship 202650), two SEP Beca Complemento (studentships 2014: BC-3606; 2015: BC-4118), and a Rufford Small Grant (17047-1), and with resources loaned by Cuauhtémoc Chávez. Dr Chávez also managed arrangements to obtain access to the three study sites in Mexico, providing links with personnel from NGO Pronatura Península de Yucatán, A. C., the management team of El Edén Ecological Reserve, and with neighbouring communities of IA, and provided loan of vehicular transport to access sites for camera-trap and scat sampling. I designed and conducted all analyses of results, except for the randomisation tests of spatial segregation, which were led by C. Patrick Doncaster. I wrote the chapter, and C. Patrick Doncaster and Cuauhtémoc Chávez provided comments on draft versions.

Abstract

Jaguars and pumas are the largest felids in the Neotropics, and coexist throughout almost their entire regional distributions. As top predators, they have a keystone role in the Neotropics, and they constitute flagship and umbrella species for conservation. They remain threatened, however, by the destruction of their habitat, illegal poaching and by the human-wildlife conflict that arises when they attack livestock. Their loss risks triggering an extinction cascade, with elimination of top-down regulations that eventually ends with a biologically impoverished system. Successful long-term conservation of these two felids needs evidence-based knowledge of their biological and ecological requirements. We studied the distributions of jaguars and pumas, and the availability of their prey, in two areas of the Northern Yucatán Peninsula (NYP), in Mexico. El Edén Ecological Reserve (EEER, 30.8 km^2) and El Zapotal Conservation Area (EZCA, 23.6 km^2) constitute two elements of the largest jaguar refuge in the Northern Hemisphere, yet both remain highly threatened by human development and the expansion of the cattle frontier. During a 2-year camera-trapping study in 2015 and 2016, we detected 21 jaguars in NYP, from which we estimated jaguar densities of respectively 3.07 ± 1.91 (mean ± SE) and 3.54 ± 1.85 individuals/100 km^2 in EEER, 3.09 ± 1.16 and 3.08 ± 1.62 individuals/100 km^2 in EZCA, and 2.24 ± 1.32 and 2.37 ± 0.79 individuals/100 km^2 in NYP. Jaguars and pumas were widespread and common in the study area, as were collared peccary, Yucatán brown brocket deer, ocellated turkeys and ocelots. Jaguars and pumas in NYP had largely similar activity patterns, with pumas slightly more active during the day. Both felids had activity patterns that were more nocturnal than those of their most preferred prey. Both felids preferred to eat collared peccary, deer and white-nosed coati, and both selected against ocellated turkey; pumas ate a higher proportion of deer compared to jaguars, while jaguars also ate nine-banded armadillo and Northern tamandua. Overall, dietary niche breadth was more species rich for pumas, but more evenly distributed for jaguars; dietary niche overlap exceeded random expectation. Given the broadly similar activity patterns and prey preferences for jaguars and pumas in NYP, differential use of their habitat in space might be a mechanism that drives coexistence for these two felids in the area. Neither species, however, showed strong evidence of excluding the other from any areas of the trapping grid. Jaguars and pumas both select the same prey species as those hunted by local communities, which will likely intensify human-wildlife conflicts in the area when prey become scarce for both felid and human predators. Private reserves of EEER and EZCA

will not support local populations of these felids by themselves, and surrounding communal forests play a vital role for felid conservation in this area.

Introduction

Legal boundaries of national parks are those established by the highest legislative authority of a country. The biotic boundary of a species, on the other hand, is the hypothetical boundary necessary to maintain a minimum viable population, or the number of individuals necessary for the long-term survival for this species (Schaffer 1981; Newmark 1985). The enormous potential size of biotic boundaries makes it very unlikely that legal and biotic boundaries will be congruent in many national parks, which might lead them to become true habitat islands, unless an active effort is made to manage cooperatively the public and private lands that adjoin the parks (Newmark 1985). Large carnivores are particularly affected by these issues. They require vast amounts of suitable habitat, making them very prone to landscape fragmentation (Schaffer 1981; Castilho *et al.* 2015), and consequently the loss of entire populations due a reduced potential for dispersing individuals to rescue habitat fragments from local extinction (Newmark 1995). This chapter describes a case study in the utility of forest reserves designated for the conservation of large felids whose biotic boundaries greatly exceed reserve boundaries.

An essential priority in conservation studies is to determine accurately what constitutes the limiting resource or the suitable habitat, particularly for field research on rare species (Doncaster *et al*. 1996). A predator might make little impact on prey density if the prey has effective defences against predation (they are present in numbers, but difficult to catch). Highly disturbed environments are likely to be inhabited by species that use the majority of suitable habitat, whereas historically undisturbed environments will also support species that are less efficient in this respect. Knowledge of the unused fraction of habitat or unconsumed fraction of prey density thus provides a way of indexing environmental disturbance. Most of the species-specific details that are commonly sought in conservation studies, such as migration rates between patches and foraging efficiency for limiting prey, are superfluous to this estimate of minimum habitat requirements (Nee 1994). Deficiency of wild prey biomass has been addressed as a driver of conflict between large felids and humans, by triggering livestock predation (Khorozyan *et al.* 2015). Evidence based conservation management of wild felids clearly needs information on prey densities and habitat use as well as felid densities.

Jaguars and pumas are the largest felids in the Neotropics. They coexist across almost the entire regional distribution of the jaguar (Rabinowitz & Nottingham 1986; Scognamillo *et al.* 2003; Sunquist & Sunquist 2014). The jaguar is generally slightly larger in size and thought to dominate the puma competitively (Schaller & Crawshaw 1980). They are keystone species to the extent that they exert top-down influence on the abundance and distribution of their prey species, and thereby also impact pollinators (Terborgh 1988; Terborgh *et al.* 1999) and small predators, and the structure and diversity of plant communities. For example, jaguars have a known dietary preference for peccaries, which are important dispersers of guava and other seeds (Bodmer 1991; Mandujano *et al.* 1994; Foster *et al.* 2010c; Kuprewicz 2012). Jaguar and puma populations need large contiguous areas of habitat, making them umbrella species in the sense that their conservation will guarantee the protection of many other animal and plant species (Terborgh 1992; Miller & Rabinowitz 2002). They make excellent model species for exploring mechanisms of coexistence between larger sympatric carnivores, given their similar sizes and habitat preferences (Harmsen *et al.* 2009).

Successful long-term conservation of jaguars and pumas requires knowledge of their ecological requirements, population-limiting factors and threats to persistence, as a foundation for the design and implementation of appropriate management strategies (Amín *et al.* 2006). Knowledge of the biology and ecology of their prey is essential to understanding the causal factors that lead to changes in densities of jaguar and puma populations. This in turn requires analysis of dietary partitioning by felids and their hunting behaviour, and prey availability and anti-predator strategies, to understand the ecological constraints that may mediate jaguar and puma persistence, as well as their coexistence. Consistent and reliable data about predation on native prey and livestock could be employed to improve conservation management decisions, which consequentially will help minimize livestock predation by these felids (Crawshaw & Quigley 1991; Azevedo & Murray 2007; Cavalcanti & Gese 2010).

Socially sensitive conservation may be most relevant in areas where both felids are threatened by human-induced reductions in their preferred prey and by persecution for depredation on livestock (Scognamillo *et al.* 2003). For example, favouring game species breeding in unprotected areas raises their densities in surrounding forest patches, offsetting livestock depredations (Smith 2005). Overhunting of the natural prey of large carnivores will impact on carnivore hunting habits, which might lead to a rise in human-wildlife conflicts in rural areas with livestock ranching (Loveridge *et al.* 2010). In the Nam Et-Phou Louey National Protected Area, Laos, low abundance of large wild ungulates forced tigers to depend on smaller prey and livestock, and caused declines in tiger (*Panthera tigris*) densities due to retaliatory hunting (Johnson *et al*. 2006). In Belize, hunting pressures by jaguars and people on wild prey commonly consumed by both have been assessed, and findings showed that humans have a much higher impact on prey populations, with jaguars taking less than one-quarter of the total amount of wild mammals extracted by both humans and jaguars. This pressure, coupled with the current expansion of cattle ranching in Belize, is likely to lead to rising livestock depredation by jaguars, which ultimately will intensify conflicts between felids and humans (Foster *et al.* 2014). In a protected area of Los Llanos, Venezuela, with abundant natural prey for jaguars and pumas, biomass of natural prey sufficed to support jaguars and pumas without any livestock subsidy (Polisar *et al.* 2003).

Coexistence of jaguars and pumas seems to be facilitated by low dietary overlap, reflecting small differences in their physiognomies. In central Belize, Foster (2008) obtained a Pianka index of dietary niche overlap of 0.246, substantially lower than random expectation of 0.479 ± 0.013 (mean ± SE). Here, the more powerfully-built jaguar favours armadillos and peccaries (white-lipped and collared), while the longer-legged puma favours pacas and deer (Foster *et al.* 2010a). Such dietary studies have yet to determine whether the dietary differences are intrinsic to their fundamental niches, or whether competition partitions an otherwise near-identical fundamental niche into more separate realised niches. Their different methods of killing large prey – the jaguar breaks the back of the neck, while the puma suffocates the throat – suggests an element of intrinsic difference. Further dietary studies in regions with different prey composition will help to clarify differences between realised and fundamental niches. The presence of large ungulates may determine the long-term reproductive success of both jaguar and puma populations, and the availability and vulnerability of large natural prey may be correlated to frequency of jaguar and puma livestock attacks (Aranda 2002; Polisar *et al.* 2003; Cavalcanti & Gese 2010). Female jaguars may need to supplement their diet with larger prey in order to fulfil their own needs plus those of their offspring during the first two years of dependency. Hence, reproduction may depend on a minimum availability of larger prey, below which the long-term persistence of jaguars may be threatened (Foster *et al.* 2010a). Without an adequate native large prey base inside reserves, jaguars tend to move outside and increase their predation on livestock (Azevedo 2008). It is therefore essential to generate site-specific information about prey partitioning between jaguars and pumas (Foster *et al.* 2010a).

A full understanding of hunting by predators, and predator avoidance behaviour by prey, requires quantification of associations in the local daily activity patterns of jaguars and pumas and their prey (Gliwicz & Dabrowski 2008). Daily activity patterns of jaguar and puma vary considerably within and amongst study sites, between mainly nocturnal (Harmsen *et al.* 2011; Scognamillo *et al.* 2003, Núñez *et al.* 2002), crepuscular (Maffei *et al.* 2004), diurnal (Crawshaw & Quigley 1991; Dobbins *et al.* 2018) or remaining active all day and night (Schaller & Crawshaw 1980). Evidence has been found of different degrees of overlap (Harmsen *et al.* 2011) and segregation (Monroy-Vilchis *et al.* 2009) between the activity schedules of jaguars and pumas (Núñez *et al.* 2002, Scognamillo *et al.* 2003) and between these felids and their main prey species (Emmons 1987; Harmsen *et al.* 2011). However, prey may alter their daily activity patterns specifically to reduce predation threat (Gliwicz & Dabrowski 2008). The resulting inefficiency in resource exploitation can contribute to raising the vulnerability of predators to habitat loss (Doncaster *et al*. 1996).

The jaguar is considered as endangered in Mexico (NOM-059-ECOL-2010; SEMARNAT 2010), and the IUCN Red List records the jaguar as 'near threatened' and the puma as 'least concern' (IUCN 2018). However, until recently, there had not been a sufficiently thorough and updated assessment on the status of jaguar populations to be able to design appropriate strategies for its conservation, and the status of the jaguar and its population size had never been determined simultaneously across an entire country (Ceballos *et al*. 2006; Chávez *et al*. 2011; Chávez *et al.* 2013). In 2006, about 50 jaguar experts from universities, social organisations, the Mexican government, and the private sector, gathered for the 2nd Symposium 'The Mexican Jaguar in the 21st Century: Current Status and Management', where they acknowledged the need to implement specific actions on a national scale to reduce the extinction risk of the jaguar, and to plan the basis of a strategy for the long-term conservation of the species with objectives, targets and specific actions, including the preparation of a national survey in Mexico (Ramírez & Oropeza 2011). This symposium resulted in the development of the 'National Census of the Jaguar and its prey' (henceforth referred to as 'CENJAGUAR'; Chávez *et al.* 2007b). The main aim of CENJAGUAR is to assess the distribution and population status of the species in areas where its presence, population stability, habitat suitability and prey base are uncertain, and in priority areas (Ceballos *et al.* 2006; Chávez & Ceballos 2006; Zarza *et al.* 2011). The long-term goal of CENJAGUAR is to assess the habitat and population viability for jaguars on a regular basis, which needs the use of a relatively easy and reliable method of standardising demographic data. The implementation of CENJAGUAR, alongside actions to address conflicts with livestock, will lead to a better understanding of human-wildlife conflict (SEMARNAT 2009; Chávez *et al*. 2011).

Tropical forests in the Yucatán Peninsula contain the largest area of jaguar habitat in Mexico (Sanderson *et al.* 2002a, b; Rodríguez-Soto *et al.* 2011), but they remain threatened by human development and the expansion of the cattle frontier (Primack *et al.* 1998; González-Iturbe *et al.* 2002; Conde *et al.* 2010). El Edén Ecological Reserve (henceforth EEER, 30.77 km^2) and El Zapotal Conservation Area (EZCA, 23.58 km^2) are situated within these forests. They provide suitable study sites for long-term censuses of large felids, because of their potential for acting as stepping stones for species with large biotic boundaries, and because of the wide range of potential prey species for large carnivores found in them. In EEER and EZCA, potential jaguar and puma prey species include white-tailed deer (*Odocoileus virginianus*), brocket deer (*Mazama pandora* and *M. temama*), collared peccary (*Pecari tajacu*), nine-banded armadillo (*Dasypus novemcinctus*), spotted paca (*Cuniculus paca*), Central American agouti (*Dasyprocta punctata*), Northern raccoon (*Procyon lotor*), grey fox (*Urocyon cinereoargenteus*), kinkajou (*Potos flavus*), black spider monkey (*Alouatta pigra*) and Northern tamandua (*Tamandua Mexicana*; Faller-Menéndez *et al*. 2005; González-Marín *et al*. 2008; Ávila-Nájera *et al*. 2018). The long-term survival of felids in the Yucatán Peninsula will depend on the persistence of their natural prey, which are all also hunted for food by people living in rural communities in the region (Aranda 1994, 2002; Oliveira 2002; González-Marín *et al.* 2008; Foster *et al.* 2010a).

There is a lack of studies regarding the ecology of jaguars, pumas and their prey in the Yucatán Peninsula. One study has examined the density and distribution of ungulates in EEER (white-tailed deer, brocket deer and collared peccary; González-Marín *et al.* 2008). Another study in EEER (Ávila-Nájera *et al.* 2018) has assessed resource selection and coexistence between jaguars, pumas and their prey, albeit from a limited sample size of 49 felid scats. She found spatial and temporal associations with jaguar and puma for nine-banded armadillo, opossum, white-nosed coati, grey fox, ocelot, collared peccary, brocket and white-tailed deer, ocellated turkey and great curassow. The reported results date from

2012, since when populations of jaguars and pumas, and their prey, are likely to have suffered significant impacts associated with increases in human population density (e.g., by 14% from 2010 to 2015 in Quintana Roo: INEGI 2018). These protected areas are virtually unpatrolled by forest rangers, due to a lack of funds to support them, and they consequently suffer an ever-increasing hunting pressure on game species from nearby communities (pers. obs.). Ávila-Nájera *et al.* (2018) found that the main prey for jaguars were red brocket deer, collared peccary, nine-banded armadillo and kinkajou, while pumas preferred red brocket and white-tailed deer, collared peccary and spider monkeys. In EZCA, Faller-Menéndez *et al.* (2005) assessed the presence of medium-sized land mammals, finding jaguar and puma prey species (brocket and white-tailed deer, collared peccary, and medium-sized mammals). In the nearby area of Calakmul Biosphere Reserve, in the Southern Yucatán Peninsula, Chávez (2010) found that the preferred prey of jaguars were collared peccary and nine-banded armadillo, whereas puma fed mainly on lowland paca. In well-preserved forests from Cockscomb, Belize, however, nine-banded armadillo was found to be the main prey taken by jaguars (Foster *et al.* 2010a).

The low-density populations and elusive and wide-ranging nature of most carnivores render them difficult to study with observational or traditional capture-based methods. This makes non-invasive survey methods, such as camera-trapping and the remote collection of natural sign surveys, such as scat samples from free-ranging animals, essential for studying site occupancy, estimating population distribution and abundance, and dietary analysis (MacKay *et al.* 2008). In particular, the use of camera-traps has become a common capture-recapture sampling method to estimate abundance of elusive terrestrial mammal species, particularly in the tropics. Many of the species studied are wide-ranging and occur in low densities, as is the case of jaguars and pumas. The use of spatially explicit capture-recapture models has provided to be the best method of obtaining demographic information on these rare and elusive species, information that is required for effective conservation (Royle *et al.* 2014). Natural sign surveys, on the other hand, can be a powerful and efficient means for collecting information about many species of carnivores. In particular, scat analysis can enable the reliable identification of species and individuals, through DNA analysis, and determination of diet. They have been conducted mainly for the study of carnivore diets, and the advent of more accurate techniques, such as DNA analysis, has significantly increased its utility (Heinemeyer *et al.* 2008).

The aim of this chapter is to estimate distributions of jaguars and pumas, and the availability of their prey, in and between two small forest reserves of the Northern Yucatán Peninsula (NYP), in Mexico. Our main goal is to evaluate the sustainability of large felid populations in NYP and the utility of smaller reserves in sustaining the wildlife necessary to support top predators. The study had three objectives for addressing this goal: (1) Systematically monitor large felids and their prey in NYP with camera-trap surveys spread over 2 years; use jaguar detections to estimate jaguar population densities with the first application in NYP of a maximum-likelihood approach to spatially explicit and sex-dependent capture recapture models; use detections of jaguars, pumas and other animals to assess the population health of large felids and their prey in and between the forest reserves of El Edén Ecological Reserve (EEER) and El Zapotal Conservation Area (EZCA). (2) Quantify daily activity patterns of large felids and their prey in NYP, EEER and EZCA, to test for overlap or segregation amongst potential competitors (jaguars and pumas) and between predators and prey. (3) Collect large felid scats and identify prey within them, to test for overlap or segregation in the trophic niches of jaguars and pumas.

Methods

Camera-trap sampling design

We conducted camera-trap surveys during 2015 and 2016 in EEER (21°14’14” - 21°09’48” N; 87°12’22” - 87°09’08” W; Reserva Ecológica El Edén 2015) and in EZCA (21°26’10” - 21°19’41” N; 87°41’12” - 87°32’51” W; Pronatura 2015), during 2-5 month periods each year. In order to connect our sampling sites of EEER and EZCA, and to increase total sampling area of the Northern Yucatán Peninsula (NYP), supplementary camera-traps were deployed in an intermediate area (henceforth IA; 21°25’11” N - 87°28’12” W; Fig. 2.1).

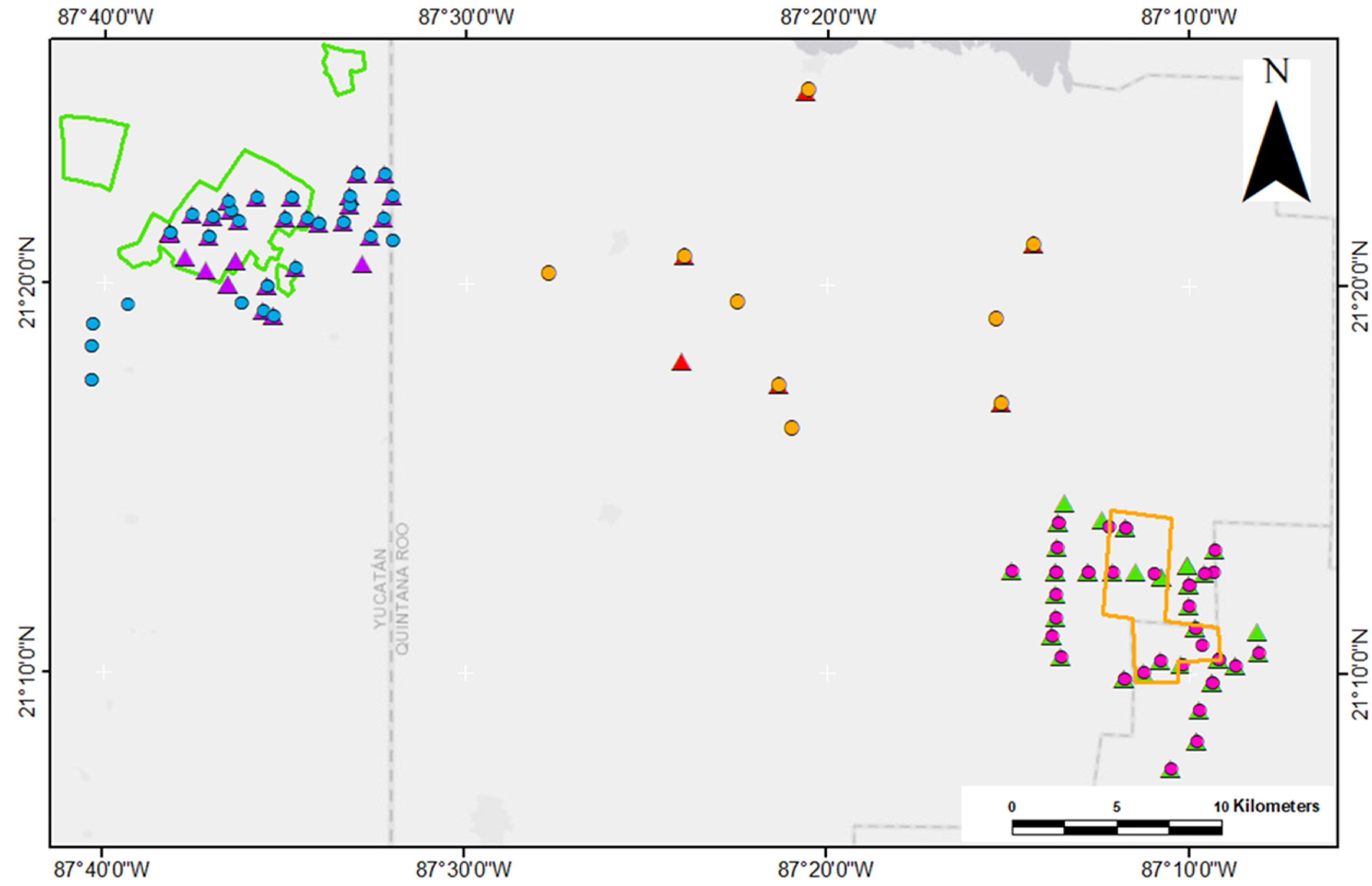


Figure 2.1. Camera-traps deployed in NYP: EEER (2015: pink dots; 2016: green triangles), EZCA (2015: blue dots; 2016: purple triangles) and IA (2015: orange dots; 2016: red triangles), showing limits of EEER (orange) and EZCA (green).

The most predominant vegetation types in the study sites constituted: medium-statured, semi-deciduous forest and secondary-growth semi-deciduous forest in EEER (Schultz 2003); semi-deciduous forest and secondary-growth semi-deciduous forest in EZCA (Faller-Menéndez *et al.* 2005); and medium-statured semi-deciduous forest, secondary-growth semi-deciduous forest in IA (pers. obs.).

For EEER and EZCA, the sampling design followed the CENJAGUAR design for jaguars and prey > 6.8 kg, with camera-traps deployed with minimum separation of 1 km (Chávez *et al.* 2007b). Camera-trap stations adhered to pre-established locations used for previous studies, which were demonstrably successful at capturing jaguars (Chávez *et al.* 2013; C. Chávez, pers. comm.). We mapped the station locations in Fig. 2.1 and in the Results section (Fig. 2.4), in relation to an analysis of space use by jaguars and pumas. We used a combination of Cuddeback and Bushnell passive infrared digital cameras, activated by a heat-motion sensor. The different makes were interspersed across the survey area to avoid biases from minor differences in sensibility (Quiroga *et al.* 2016). Each camera-trap station was set to function 24 hours/day. Cameras were checked every three to four weeks. A total survey effort of 11,824 trap days was achieved in the NYP (covering EEER, EZCA and IA) in 2015 and 2016 (Table 2.1).

Table 2.1. Camera-trap survey information.

Survey	Date	Length (days)	Stations	Functional trap days
EEER (2015)	04 August - 13 October	71	31	2712
EEER (2016)	24 March - 27 May	65	33	2707
EZCA (2015)	27 April - 12 September	139	30	2747
EZCA (2016)	03 April - 13 August	133	30	2524
IA (2015)	08 August - 13 October	67	9	796
IA (2016)	06 April - 05 June	61	6	338

Photographic images were managed with the software package Timelapse2 (Greenberg 2018), and jaguars were identified with the software package HotSpotter (Crall *et al.* 2013). For jaguar identification, a second researcher conducted blind jaguar identifications in order to compare results and check for disagreements (Kelly *et al.* 2008; Foster & Harmsen 2012). Pumas could not be identified to individual, due to the low quality of a large proportion of photographs (especially in EZCA and IA), rendering identifying marks difficult to see for these non-spotted cats. Jaguar photographs that could not be reliably identified were also excluded from analysis (Foster & Harmsen 2012).

Density of jaguars

In order to estimate jaguar population densities in NYP (pooled data from EEER, EZCA and IA), and in EEER and EZCA, we followed the camera-trap sampling design for CENJAGUAR. The design assumes that every individual in the study area has the same probability of capture (i.e. of being photographed) in at least one camera-trap station during the study. It is therefore important to avoid gaps inside sampling areas sufficient to contain an entire home range. In addition, capture probability should be maximised by placing camera-trapping stations strategically inside each sampling cell (e.g. close to tracks, scats, water bodies, hunting trials, scrape marks, etc.). The sampling session should preferably take place during the dry season. It should last for a minimum of 30 days, to maximise the chance of catching all individuals, and a maximum of 90, to minimise the chance of violating the assumption of closed population (Karanth & Nichols 1998). The study area must cover a minimum of 81 km^2, divided into sampling cells of 9 km^2, which in turn need subdividing into 1-km^2 sub-cells. For practical reasons, it is recommended to sample only three sub-cells per cell, with stations separated by 1 to 3 km. The position of each camera-trap station is selected on the quality of habitat found within the cell, choosing the location with the best suitable conditions. A minimum of 27 camera-trap stations need to be positioned in an area of 81 km^2 (3 stations per 9-km^2 cell), assuming that this area is the minimum activity area of a female jaguar during a 20- to 60-day period (Soisalo & Cavalcanti 2006). For every three camera-trap stations, there should be a double station (with two camera-traps), to guarantee captures and identification of spotted felids, which gives a total of 36 camera-traps. The design is the same for prey > 6.8 kg.

For non-spatial models, camera-traps should be spaced close enough in order to capture individuals in more than one location. Sites should be separated by less than an average home-range radius, and ideally considerably less (0.3 – 0.8 × a home range radius: Sollmann *et al.* 2012; Sun *et al.* 2014; Wearn & Glover-Kapfer 2017). According to Chávez (2010), mean annual home ranges of jaguars (calculated with a minimum convex polygon method) in Calakmul, in Southern Yucatán Peninsula, are 328 ± 84 km^2 (males) and 204 ± 203 km^2 (females). If we assume circular home ranges, a home-range radius would be 10.22 km (males) and 8.06 km (females), and 0.3 and 0.8 × a radius would be respectively 3.07 and 8.18 km (males) and 2.42 and 6.45 km (females). Camera-trap stations should therefore be spaced by no more than these distances. According to these criteria, stations located in IA between EEER and EZCA were likely placed too far apart

(Fig. 2.1). Their spacing was a necessary consequence of logistic constraints on safe access to secure sites. These holes, however, are of no concern for spatially explicit capture-recapture (SECR) models (Royle *et al.* 2014).

The use of camera-traps has become a common capture-recapture sampling method to estimate abundance of elusive terrestrial mammal species, particularly in the tropics, and many of the species studied are wide-ranging and occur in low densities. Traditionally, camera-trap studies estimated abundance using conventional capture-recapture models (Foster & Harmsen 2012). However, SECR models (Borchers & Efford 2008; Royle *et al.* 2009) have gained increasing recognition for their advantages over conventional models. In particular, with conventional models, there are strong restrictions on the study design, derived from the assumption that each individual needs to have a non-zero probability of detection (Karanth & Nichols 1998). In addition, density estimation with conventional models requires estimating the effective sampling area, which depends on the spacing of the camera-traps. The overall area sampled by camera traps should also be large enough to capture the full extent of individual movements, and > 20 individuals should be captured to avoid overestimations of density. This presents a logistical and financial challenge for a great number of studies (Zimmermann & Foresti 2016). Geographical closure is an important assumption of conventional models, which should be maximised by regular arrays organised in circular designs. However, in practice it does not guarantee population closure (Foster & Harmsen 2012; Zimmermann & Foresti 2016).

To overcome these limitations, SECR models have provided a much more profound framework that makes explicit various ecological processes, such as spatial organisation, movement and space usage by individuals, in addition to density (Royle *et al.* 2014). They make use of location-specific individual encounter histories, which allows them to relax a number of important assumptions. They explicitly model the movement and distribution of individuals in space, relative to the trap array, thus avoiding the need for an effective sampling area. Instead, the trap array is embedded in a large area called the state space. In SECR models, because gaps are not a concern, some individuals in the sample might have a capture probability close to zero. The population size is explicitly tied to the state space, which eliminates the problem of heterogeneous capture probabilities associated with locations of animal ranges relative to trap locations (Royle *et al.* 2014; Zimmermann & Foresti 2016). Thus, it is possible to make predictions outside the range of the data by making inferences from the sample to individuals that live in these holes, based on the explicit declaration that SECR models applies to any area within the state space, even to unsampled areas (Royle *et al.* 2014).

In order to estimate jaguar population densities in EEER and EZCA and the overall density in NYP, we selected two alternative spatially explicit capture-recapture (SECR) models (Borchers & Efford 2008; Royle *et al.* 2009). We used a maximum likelihood method (R package secr, Efford *et al.* 2009) and a Bayesian approach with Markov and Monte Carlo simulations (R package SPACECAP, Gopalaswamy *et al.* 2012). Both approaches require the capture-recapture history of all identified individuals at each camera-trap station, in combination with the spatial distribution of the captures and recaptures (Noss *et al.* 2012). They assume: 1) closed model capture-recapture sampling (conventional SECR analysis); 2) independent activity centres for captured individuals; 3) fixed locations for activity centres during the sampling period; 4) a declining probability of detecting an individual at a camera station with increasing distance of the trap from the individual's activity centre; and 5) independent capture events (Otis *et al* 1978; Efford *et al.* 2009; Foster & Harmsen 2012; Gopalaswamy *et al.* 2012, 2014).

The maximum likelihood method provides larger choice of possible models, and is able to calculate an estimate for the entire population accounting for no sex differences, or alternatively to incorporate sex-specific detection probabilities into the model, and to calculate an estimate excluding all potential activity centres falling outside suitable habitat (Zimmermann & Foresti 2016). The Bayesian approach, on the other hand, deals well with issues presented by individual heterogeneity in capture probabilities. It also provides non-asymptotic inferences, which are more appropriate for the small samples of capture data that are typical of photo-capture studies (Royle *et al.* 2009; Gopalaswamy *et al.* 2012, 2014).

For the maximum likelihood approach, we started by generating a series of alternative areas of influence (masks) around the camera-trap arrays (Zimmermann & Foresti 2016), using increasing buffer widths of 1, 3, 5, 7, 9, 11, 13, 15, 17, 20, 25 and 30 km. We then ran a series of null non-spatial models (each one associated with each buffer), assuming constant values for the baseline encounter probability ($g_{0;}$ i.e. encounter probability when the distance between the activity centre of an individual and the camera-trap is zero) and the spatial scale parameter (σ). Following Royle *et al.* (2014), we then selected the best model by choosing a buffer with a width of 2-3σ, which guarantees that individuals outside the area of influence have zero detection probability by the camera-trap array during the sampling period. Using the mask associated with the best model, we ran a mixture of alternative SECR equivalents to conventional capture-recapture models, in order to explore their effect on g_0, while keeping σ constant (Zimmermann & Foresti 2016). Selected models followed Zimmermann & Foresti (2016). Models included a series of sources of variation (and various combinations of them):1) *M0:* is the most basic capture-recapture model, where encounter probability is strictly constant for all individuals and occasions; 2) *Mt*, *MT*: all individuals have equal capture probabilities for a particular trapping occasion, but probabilities can differ amongst occasions (*Mt*); or there is a linear trend in baseline encounter probability over occasions (*MT*); 3) *MB*, *Mb*; individuals become either 'trap happy' or 'trap shy', following either a learned response to the first capture (*Mb*) or a transient response to a preceding capture (*MB*); 4) *Mk*, *MK*: capture probabilities are specific to a particular site (local response: *Mk*), or to all sites (global response: *MK*); and 5) *Mh2*, a 'finite mixture model', in which individuals have heterogeneous capture probabilities across two undefined latent classes, and the likelihood uses a weighted sum over the classes. Our data set was too sparse to fit models *Mt* and *Mbt*, which were not included in any subsequent analysis. Models used either the Newton-Raphson algorithm (default) or the Nelder-Mead algorithm (less prone to settling in local minima: Otis *et al.* 1978; Royle *et al.* 2014; Zimmermann & Foresti 2016; Efford 2018a, b). Model selection for estimating jaguar densities used Akaike's Information Criterion (AIC: Burnham & Anderson 2002; Royle *et al.* 2014). The best model had the lowest AIC value, and alternative models with ΔAIC < 2 also had strong support, where ΔAIC is the difference in AIC of the alternative from the best model (Zimmermann & Foresti 2016). Jaguar density was estimated from the best model, hereafter referred to as model 'no_sex'.

Camera-trapping studies with large felids tend to show differences in captures depending on sex, usually finding substantially more males than females due to males preferring to use trails and females to avoid them, and camera-trap surveys tending to place cameras on trails (to maximise overall trapping success: Foster *et al.* 2010c; Foster & Harmsen 2012). We therefore accounted for possible sex-specific capture probabilities with a hybrid-mixture model that accounted for missing information on sex for some individuals (Zimmermann & Foresti 2016; Efford 2018a), hereafter referred to as model 'sex'. We then analysed its effect on g_0 and σ by comparison to the null and the best spatial model found in the previous analysis with model 'no_sex' (following Zimmermann &

Foresti 2016). We compared the models with the AIC method described above, and averaged all best-fitting models with a ΔAIC value <2 to calculate jaguar densities (Burnham & Anderson 2002).

The above models had no restriction on the locations of jaguar activity centres. We compared these models to alternative sets that restricted potential jaguar activity centres to lie inside EEER and EZCA boundary limits. The extreme assumption in this case was that only areas inside the reserve polygons were suitable jaguar habitat, and that everything outside was not (hereafter model 'habitat'). We created a habitat mask to eliminate all potential activity centres falling in non-jaguar habitat, using a mesh cell size of 1 km^2 (Fig. 2.2), and applied it to the models used for model 'sex'. We estimated jaguar density by model selection using the AIC and ΔAIC method described above. All analyses used the R package 'secr' (Efford 2018a), with some analyses adapting R scripts in Zimmermann & Foresti (2016) to conduct our analysis. Each model took between 9 hours and 20 days to run on a PC with 12 Gb RAM and 3.20 GHz processor.

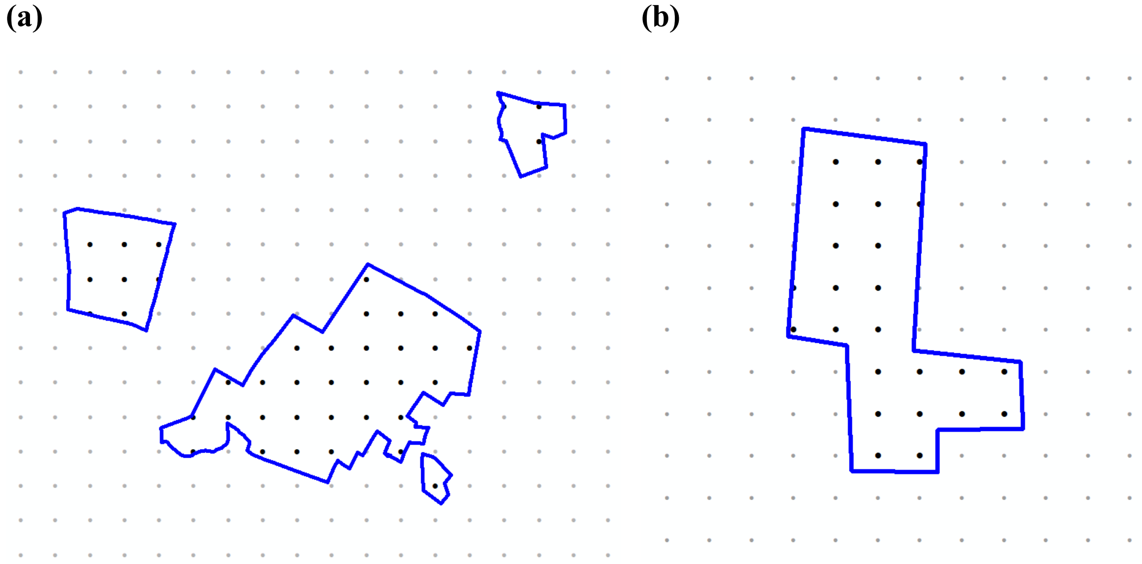


Figure 2.2. Habitat mask grid used to estimate jaguar density in (a) EZCA, and (b) EEER. Boundary limits for both reserves are shown in blue. Distance between points = 1 km. Black dots inside reserve boundaries represent potential jaguar habitat and pale grey dots outside reserves represent non-jaguar habitat.

The second method for estimating jaguar densities involved a Bayesian approach, using the R package SPACECAP (Gopalaswamy *et al.* 2014). For parameter definition in our models, we followed recommendations by Noss *et al.* (2012), studying jaguars and pumas in Kaa-lya National Park, Bolivia. We used the following parameter definitions: 1) ‘trap response absent’, which is the conventional, global behavioural response, with the same response to all traps everywhere after first capture; 2) ‘spatial capture-recapture’ model; 3) ‘half-normal’ detection function, which generally has a good fit to the data; and 4) ‘Bernoulli process’ binary encounter model (the only encounter model available in SPACECAP), in which the probability of success is derived as the probability of a positive response under a Poisson encounter rate model (Gopalaswamy *et al.* 2014). For the same habitat grid that we generated with model ‘habitat’, we set Markov and Monte Carlo simulation parameters at: 1) ‘iterations’ (total number of Markov-Chain Monte Carlo iterations) = 100,000; 2) ‘burn-in’ (number of initial values to be discarded during the analysis) = 10,000; 3) ‘thinning’ (proportion of iterations included in the output) = 1 (all iterations stored); 4) ‘data augmentation’ (maximum number of uncaught animals in the whole state space) in EEER and EZCA = 100, and NYP = 200; and 5) ‘habitat mesh cell size’ = 1 km^2. Each model took ca. 9 hours – 4.5 days to run on a PC with 12 Gb RAM and 3.20 GHz processor.

For both methods used to estimate jaguar density during 2015 and 2016 in EEER and EZCA, and in NYP (pooling EEER, EZCA and IA), we restricted our camera-trap records to periods of ≤ 90 camera days. We did this in order to minimise the risk of violating the assumption of demographic closure (no births or deaths), on which conventional SECR models depend for accurate density estimations (Otis *et al.* 1978; Karanth & Nichols 1998; Royle *et al.* 2014). In order to obtain an insight into the closure state of our populations, we ran the population closure test developed by Otis *et al.* (1978; Table 2.2) for non-spatial capture-recapture models. We used this test with the caveat that although it can handle heterogeneity in detection probability, it does not perform well in the presence of time or behavioural variation in probability of captures (Royle *et al.* 2014). No population closure test is yet available specifically for SECR models, because a lack of population closure cannot easily be distinguished from violation of other assumptions. Thus, if other effects are present, such as individual behavioural responses and time trends in capture probabilities, tests may indicate non-closure even when a population is closed (Otis *et al.* 1978; White *et al.* 1982). Nonetheless, according to Royle *et al.* (2014), when population closure is violated, estimates will show positive bias. In practice, however, without a means of guaranteeing a closed population, we have to weigh the risk of violation against the need to collect sufficient data, which for elusive species often needs longer sampling periods (White *et al.* 1982).

Our population closure tests for whole-survey periods (Table 2.2) show that EEER in 2016 (33 days), and NYP in 2015 (180 days) and 2016 (71 and 144 days) display signs of lack of population closure. However, data from our 2016 camera-trap sampling season in EEER exhibited evidence of behavioural effects in probability of captures (detailed in the Results section), which might have resulted in an apparent lack of closure, when in fact there is none. These effects might also apply to population closure estimates for NYP in 2016 for the 71-day survey. Estimates from NYP in 2015 (180 days) and 2016 (144-day period in EEER) nevertheless are consistent with the postulate that long sampling periods violate the assumption of population closure.

Table 2.2. Results for population closure test (Otis *et al.* 1978) run on camera-trapping surveys. Estimate (z) and p-value are given. Significant *p*-values (rejection of closure) are shown in bold. Input data used in analysis is also shown: total trap days for the survey, number of trap stations (each with 1 or 2 cameras), start and end dates of sampling for the survey, individuals captured and total number of captures.

Site (year)	z	*p*	Trap days	Stations	Date	Individuals captured	Captures
EEER (2015)	1.10	0.87	71	31	04 August – 13 October	6	54
EEER (2016)	-2.84	**0.02**	65	33	24 March – 27 May	9	57
EZCA (2015)	0.24	0.59	90	25	29 April – 27 July	3	7
EZCA (2016)	-0.93	0.18	90	27	03 April – 13 august	6	26
NYP (2015)	-0.78	0.22	75	70	25 July – 07 October	8	49
NYP (2016)	-2.41	**<0.01**	71	65	31 March – 09 June	16	84
NYP (2015)	-4.24	**<0.001**	180	71	27 April – 23 October	11	64
NYP (2016)	-5.34	**<0.001**	144	69	24 March – 14 August	17	93

Given these results, we estimated jaguar densities from periods not exceeding 90 days. In EEER, we used records from August to October (*n* = 71) in 2015 and from March to May (*n* = 65) in 2016, and in EZCA we used records from June to September (*n* = 90) in 2015, and from April to July (*n* = 90) in 2016. For NYP, we used records from July - October (*n* = 75 days) in 2015, and March - June (*n* = 71) in 2016. Each of these ≤ 90-day periods was selected to maximize the number of detected jaguars.

In order to calibrate the above closed-population estimates of jaguar densities in NYP against estimates that are more likely to violate the closure assumption, we conducted a second density estimation in NYP using all our camera-trap sampling records, taken from April to October in 2015 (*n* = 179 days) and from March to August (*n* = 144) in 2016. The magnitude of difference in density estimates from long- and short-period sessions should be informative about the influence of closure on density estimation.

Spatial distribution of jaguars and pumas in NYP

We tested for evidence of spatial attraction or segregation between jaguars and pumas in the observed fractions of camera-trap stations that detected them both, or either one alone. For each of 2015 and 2016, we generated 10,000 replicate random and independent redistributions of jaguar and puma detections amongst the actual set of stations (plotted in Results Fig. 2.4). These replicates quantified the probabilities of non-interacting jaguars and pumas producing at least as many as the observed number of:

H_1: stations with co-occurring jaguars and pumas;
H_2: nearest-neighbour pairs detecting only jaguars at both stations;
H_3: nearest-neighbour pairs detecting only pumas at both stations.

Rejection of H_1 ($p < 0.05$) indicates evidence of non-random attraction between jaguars and pumas to the same stations. Rejection of H_2 ($p < 0.05$) indicates that jaguars create an enclave free of pumas. Rejection of H_3 ($p < 0.05$) indicates that pumas create an enclave free of jaguars.

These tests assume that each species finds all stations equally attractive in the absence of the other species. This means it assumes that none of the actually empty stations are inaccessible, and the only possible non-random influence on either species using a station is the presence there of the other species.

Relative abundances of jaguars and pumas, and their potential prey species

In order to assess the completeness of the faunal inventory recorded by our camera-trapping sampling method, a species accumulation curve was created for surveys in EEER, EZCA, and across NYP, to account for species richness as camera-trap days increase, and its standard deviation, using a species accumulation method with partial match. Species detection order was randomised 1000 times to obtain 95% confidence intervals of the mean (Rovero *et al.* 2014; Rovero & Spitale 2016).

Since pumas and their potential prey species could not be reliably identified to individuals by photographs, ruling out a mark-recapture-based estimate that incorporates capture probability (Karanth & Nichols 1998; Jennelle *et al.* 2002; Johnson *et al.* 2006), we calculated a naïve occupancy estimate from the proportion of camera trap stations where species were captured, relative to the total number of sampled camera stations, using independent hourly records taken by our camera-trap sampling effort. This served as a basic descriptor at least of species presence across the sampled areas of EEER, EZCA, and NYP (Rovero & Spitale 2016).

In addition, we calculated a relative abundance index (RAI) to obtain a descriptive metric about population abundance for large felids, and their potential prey species, in NYP, and in EEER and EZCA, using camera-trapping record rates. RAI was calculated for each species by dividing its independent hourly records by the survey effort (camera-trap days), and multiplying the result by 100 (Rovero & Spitale 2016). This estimate depends on trapping rates, which are influenced by the activity levels of individuals, as well as population abundance. For example, animals that are active for longer, or cover more ground, will trigger cameras more frequently. RAI is also influenced by animal size, with detection more likely for larger than smaller animals (Sollmann *et al.* 2013; Wearn & Glover-Kapfer 2017). Despite these sources of bias, RAI is widely used for meaningful insights into wildlife populations, and has provided positive and linear correlations when compared to robust density estimates (Johnson 2008; Wearn & Glover-Kapfer 2017).

Availability of prey and anti-predator strategies

The 24-h activity patterns of jaguars and pumas, and their potential prey species, were estimated for EEER, EZCA and NYP. We used camera-trap records taken from August to October in 2015 and March to May in 2016 (2-month periods) in EEER, from April to September in 2015 and April to August in 2016 (4-month periods) in EZCA, and from August to November 2015 (3.5-month period) and April to June 2016 (2-month period) in IA. Activity records were pooled across sampling years for all species in order to raise hourly sample sizes, on the assumption that species detection and activity would vary little between years (Azevedo *et al.* 2018).

Activity patterns were classified only for species with >10 independent hourly records (Monroy-Vilchis *et al.* 2011). Classification of activity patterns was based on Schaik & Griffiths (1996), using the proportion of hourly records during the night (sunset – sunrise) and day (sunrise – sunset). Sunrise (7:00) and sunset (19:00) were defined following Monroy-Vilchis *et al.* (2011), who reported from a similar latitude in Central Mexico, where dawn was set to last from 6:00 – 8:00 and dusk from 18:00 – 20:00.

Species were classified as diurnal if < 10% records were recorded at night, nocturnal if ≥ 90% records were recorded at night, mostly diurnal if 10 – 29% records were recorded at night, mostly nocturnal if 70 – 89% records were recorded at night, or cathemeral if 30 – 69% records were recorded at night (Gómez *et al.* 2005). The category crepuscular, defined as records that were recorded in dawn and dusk, was not separately defined due to low numbers of records. Radial plots of activity were calculated for all species with >10 hourly records (Rovero & Spitale 2016).

Levels of association between species in their activity patterns were estimated by the method of Ridout & Linkie (2009) and Linkie & Ridout (2011). Species-specific patterns of activity were first predicted using non-parametric kernel density estimations. Multiple records of the same species at the same camera station were considered as independent if they were taken > 30 minutes apart (Linkie & Ridout 2011). Records of several individuals of social species were considered a single record (Azevedo *et al.* 2018). A coefficient of activity overlap (Δ; Weitzman 1970) between two species was calculated from the minimum of the density functions for the set of two samples compared at each time point. The area under both density curves was taken as the overlap between the activity patterns (0 = no overlap, 1 = complete overlap). Following Linkie & Ridout (2011) we used the estimator $\hat{\Delta}_1$ if the smaller sample in the pair of species had < 75 records, and $\hat{\Delta}_4$ if it had more than > 75 (see Ridout & Linkie 2009 for a technical discussion of these alternative ways of estimating Δ). We calculated confidence intervals for the coefficients of overlap with a smoothed bootstrap non-parametric technique, using 10,000 bootstraps (Meredith & Ridout 2018a). Pairwise bootstrapped overall activity patterns were compared using the Wald statistic (W) with a χ^2 distribution over 1 d. f., to test for differences between the overall activity levels of jaguars and pumas, and between large felids and their prey (Zimmermann *et al.* 2016). Consecutive detections of a given species at the same site occurring within less than 30 minutes were not included in the analysis (Linkie & Ridout 2011). Likewise, species were not included if they had a small number of records (Azevedo *et al.* 2018), which we set at < 10, in order to compare our results with findings those of Ávila-Nájera *et al.* (2016) who studied activity patterns in EEER. We used R packages ‘overlap’ (Meredith & Ridout 2018b) and ‘activity’ (Rowclife 2016) to conduct analysis of activity. Radial plots of activity were calculated using the R package ‘plotrix’ (Lemon 2006).

Prey consumption by large felids

Dietary preferences by jaguars and pumas were analysed from felid scat (faecal) samples. Scats were sought systematically, and collected opportunistically, along trails in EEER (*n* = 109 scats) and EZCA (*n* = 38 scats) from May to July in 2015 and from March to June in 2016 (Fig. 2.3).

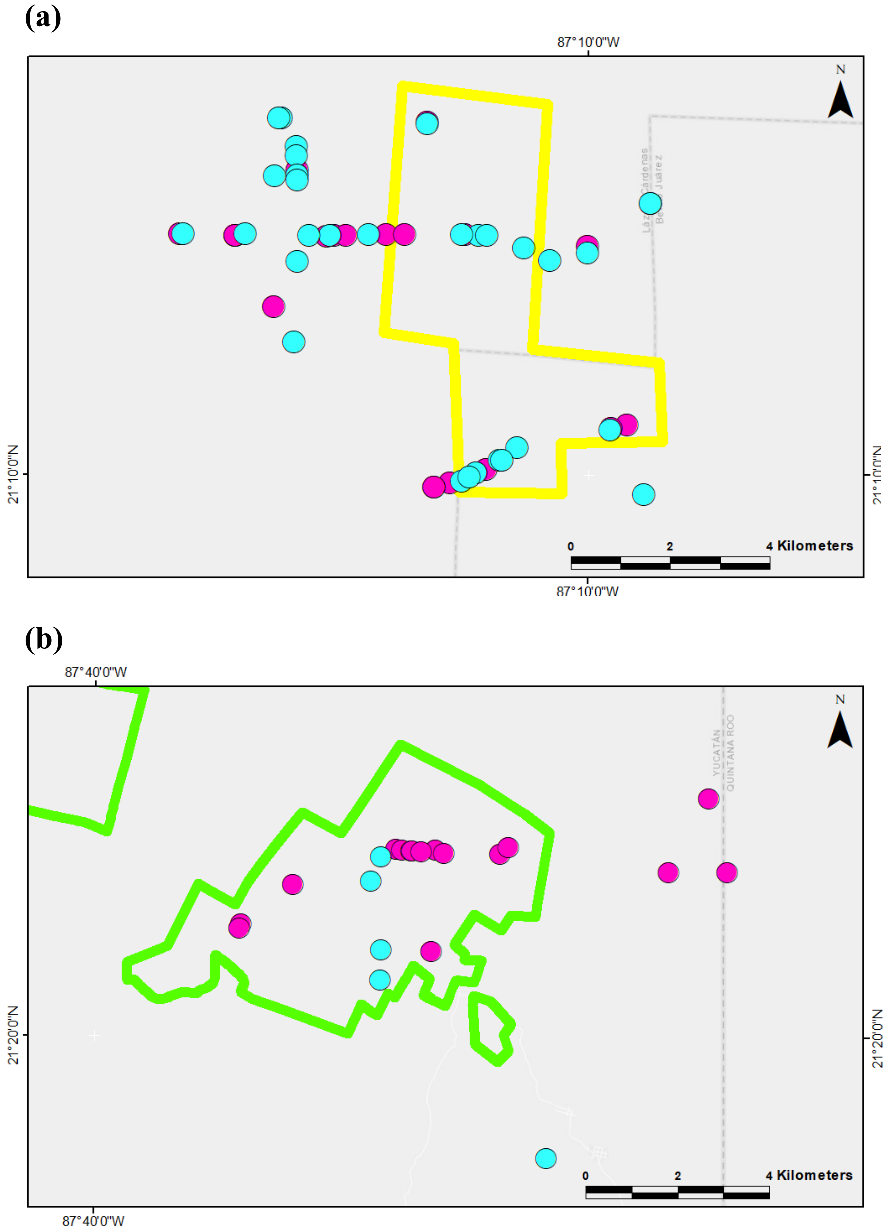


Figure 2.3. Locations of all 147 jaguar (pink circles) and puma (blue circles) scats. (a) EEER (reserve boundary limit shown in yellow); (b) EZCA (reserve boundary limit shown in green); during 2015 and 2016.

Scat samples were collected and stored in new and clean plastic bags. Each sample was divided into two parts, one destined for diet analysis and one for molecular identification of predator species. Fresh or moist samples were immersed in a 95% ethanol solution during 24 hours and subsequently dried in the sun prior to storage. All samples were stored with silica gel beads at room temperature (Wasser *et al.* 1997) for 2-3 years before laboratory analyses of diet and molecular identification.

For the analysis of felid diets, scat samples were washed at Universidad Autónoma Metropolitana-Lerma, using a solution of water and a small amount of detergent. They were then sifted to isolate hair, bone, hooves, teeth and undigested remnants of consumed prey. Bone, hooves, teeth and other remnants were identified at the Laboratorio de Arqueozoología, affiliated to the Instituto Nacional de Antropología e Historia in Mexico, using a magnifying glass, a vertebrate bone collection and reference guides by Schmid (1972) and Olsen (1973, 1982). Hair mounting was conducted at the Laboratorio de Arqueozoología, and at the Departamento de Zoología in the Escuela Nacional de Ciencias Biológicas affiliated to the Instituto Politécnico Nacional in Mexico. A modified protocol by Moore *et al.* (1974) was followed to prepare slides of prey hair. Five to 10 hairs were fixed onto slides using the synthetic resin Entellan®, designed for rapid mounting in microscopy. Microscopic identification of prey hair was conducted at the University of Southampton. A colour light photomicroscope Nikon Eclipse E400 was used to examine medullar structure patterns. A magnification of 20× was used to capture microphotographs. Species identifications were made by comparison to the reference hair collections of Harmsen (2006) and Valdes (2006) from mammals of Belize, and reference guides by Monroy-Vilchis & Rubio-Rodríguez (2003), Baca Ibarra & Sánchez-Cordero (2004), Debelica & Thies (2009), Palacio (2009), Pech-Canché *et al.* (2009) and Cornally & Lawton (2016).

Due to the very similar morphologies of jaguar and puma faeces (Roques *et al.* 2011; Aranda Sánchez 2012), scat samples were identified to species of donor using molecular genetic techniques. DNA extraction was conducted at the University of Southampton, following the CTAB protocol of Doyle & Doyle (1990), designed to extract DNA from plant leaves and adapted for faeces (M. A. Chapman; unpublished).

Primers were designed from published ND5 sequences from jaguars and pumas (Genbank accessions KF483864, KM236783, KP202264 [jaguar]; KX808222, KP202261, KX808229, and KX808231 [puma]). Sequences were aligned in GeneDoc (Nicholas and Nicholas 1997). Three primer pairs were designed to amplify ca. 150-200bp regions, from which was selected the one that provided the most reliable and clean PCR amplification product. PCR was carried out in 15 µl reaction volumes containing 1.5 µl 10X buffer (peqGold Taq buffer S), 0.2 mM dNTPs, 0.1 mM of each primer (ND5_1625F [TAACTATAAGCCAAA AATCCGCA] and ND5_1771R [GCTAAGGGYTAAGGTGA TTATGAA]), and 0.5U Taq polymerase (peqGOLD Taq). Amplification success was determined on 1% agarose gels. PCR amplicons were prepared for sequencing by incubating with 4 units Exonuclease I and 0.8 units Shrimp Alkaline Phosphatase (Fisher Scientific, UK) at 37 °C for 45 min, followed by enzyme denaturation at 80 °C for 15 min. PCR sequencing was carried out using BigDye v3.1 (at 1/8th the recommended volume) and the BigDye protocol (Applied Biosystems, UK). Reactions were precipitated with ethanol and sent to the Department of Zoology at the University of Oxford for resolution on an ABI 3730xl (Applied Biosystems). Sequencing electropherograms were visualised using Chromas (Technelysium Pty Ltd 1998-2001) and diagnostic SNPs were used to identify whether the scat was from a puma or jaguar.

Prey exploitation and niche overlap

Biomass consumed

Relative occurrence (%) of each prey species in jaguar and puma diets was calculated as the number of prey items belonging to species x divided by the total number of prey items, and multiplying the result by 100. Number of prey items was defined as the number of scats containing each species (Foster *et al.* 2010a).

Relative occurrence tends to overestimate smaller prey species when compared with larger ones; thus relative biomass per species was also calculated, using mean body weights extracted from published data (Ceballos 2014 and Reid 2009 for mammals; del Hoyo *et al.* 2018 for birds). For prey species with mean body weights ≥ 2 kg, the correction factor of Ackerman *et al.* (1984) was applied to mean live weight to account for their incomplete presence in an individual scat:

$$\text{Biomass of species } x = 1.98 + 0.035 * \text{mean live weight of species } x \qquad \text{(Eq. 2.1)}$$

Smaller species were assumed to have been eaten whole and therefore to have biomass given directly by their mean live weight (Foster *et al.* 2010a).

The relative biomass consumed of each species *x* was calculated with:

$$\frac{(\text{Relative occurrence of species } x)(\text{Biomass of species } x)}{\sum_{i=1}^{n}(\text{Relative occurrence of species } i)\ (\text{Biomass of species } i)} \qquad \text{(Eq. 2.2)}$$

Food niche breadth

The observed food niche breadth index (B_{obs}) was calculated for jaguars and pumas in terms of their dietary diversity, following Levins (1968):

$$B_{obs} = \frac{1}{\sum_{i=1}^{n} p_i^2} \qquad \text{(Eq. 2.3)}$$

where p_i is the relative occurrence of a prey species in the diet of the felid. B_{obs} values range from 1 (minimum niche breadth, maximum specialization) to n, where n is the total number of prey taxa consumed (Krebs 1999). In order to allow for comparisons of diet breadth between jaguars and pumas, the index was standardised for each species following Colwell & Futuyma (1971):

$$B_{sta} = \frac{(B_{obs} - B_{min})}{(B_{max} - B_{min})} \qquad \text{(Eq. 2.4)}$$

B_{sta} = standardised niche breadth (values range from 0 to 1);

B_{obs} = observed niche breadth;

B_{min} = minimum niche breadth (1);

B_{max} = maximum niche breadth (n).

Dietary niche overlap

Dietary niche overlap between jaguars and pumas was calculated with the Pianka (1973) measure, using the R package ‘EcoSimR’ (Gotelli *et al.* 2015):

$$O_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}} \qquad \text{(Eq. 2.5)}$$

O_{jk} = Pianka's measure of dietary niche overlap between species j and species k (values range from 0 [no overlap] to 1 [complete overlap]);

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

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

n = total number of resource states (species consumed).

In order to determine whether the observed dietary niche overlap (O_{jk}) was higher or lower than expected from random overlap, a null model was generated to simulate possible overlaps between jaguars and pumas, generating 1000 Monte Carlo randomisations of proportions of different food items in the diets of jaguars and pumas. The algorithm retained the observed zero states (prey species not consumed in our dataset were also not consumed in simulations) and randomised the dietary niche breadth (prey species with relative occurrence > 0 were replaced with random prey proportions in simulations). All species were assumed to have equal availability to both felid species (Foster *et al.* 2010a; Gotelli *et al.* 2015).

Results

Density of jaguars

We identified 21 jaguar individuals in NYP (n = 361 captures), of which 10 were identified only in EEER (6 males, 2 females, 3 undetermined), 8 only in EZCA (4 males, 3 females, 1 undetermined), and 3 only in IA (1 male, 1 female, 1 undetermined). No individuals were detected in more than one of these three areas. Reference photographs are given in Appendix 1. We could not identify individuals in 100 photographs of jaguars due to poor image quality. These records were therefore excluded from further analysis.

Models that best explained our data from the maximum likelihood approach were *MB* (behavioural, transient response to the first capture) for EEER in 2015, *Mh2* (heterogeneity of capture probabilities among individuals from two undefined, latent classes) for NYP in 2015 (75 and 179 days) and *Mk* (local response to a particular site) for EEER, EZCA and NYP (71 and 144 days) in 2016. Given the male bias in detection across all sites (11:6 male:female), we focus our interpretation of results from the maximum likelihood approach on density estimates that accounted for sex differences in capture probabilities (model ‘sex’ in Table 2.3). Jaguar density estimates for NYP were 2.24 ± 1.32 individuals/100 km^2 (75 days) for 2015 and 2.37 ± 0.79 individuals/100 km^2 (71 days) for 2016. Little difference was found in estimates for NYP calculated over longer periods, at 2.76 ± 1.56 individuals/100 km^2 (179 days) for 2015, and 2.49 ± 0.77 individuals/100 km^2 (144 days) for 2016. Jaguar density estimates were higher for the reserves within NYP. Estimates for EEER were 3.07 ± 1.91 individuals/100 km^2 for 2015 and 3.54 ± 1.85 individuals/100 km^2 for 2016, and for EZCA were 3.08 ± 1.62 individuals/100 km^2 for 2016. We could not estimate jaguar density for EZCA in 2015, due to the small sample size of camera-trap records. When we excluded potential jaguar activity centres outside reserve boundaries in EEER and EZCA, we obtained density estimates that were higher by up to an order of magnitude (Table 2.3 ‘habitat’ model). These extremely unrealistic sizes expose the vital contribution of the surrounding communal forested areas to the maintenance of jaguar populations in NYP.

The Bayesian approach to density estimation gave lower estimates than those from the maximum likelihood approach that accounts for sex differences, but similar estimates to those that do not account for sex differences, and again with little influence of length of trapping period. Jaguar density estimates in NYP for 2015 were 0.76 ± 0.32 (75 days) and 0.76 ± 0.26 individuals/100 km^2 (179 days), and for 2016 were 1.48 ± 0.41 (71 days) and 1.50 ± 0.41 (144 days). Jaguar density estimates for EEER were 1.18 ± 0.53 for 2015 and 1.26 ± 0.52 individuals/100 km^2 for 2016, and for EZCA were 3.09 ± 1.16 for 2015 and 2.96 ± 1.21 individuals/100 km^2 for 2016.

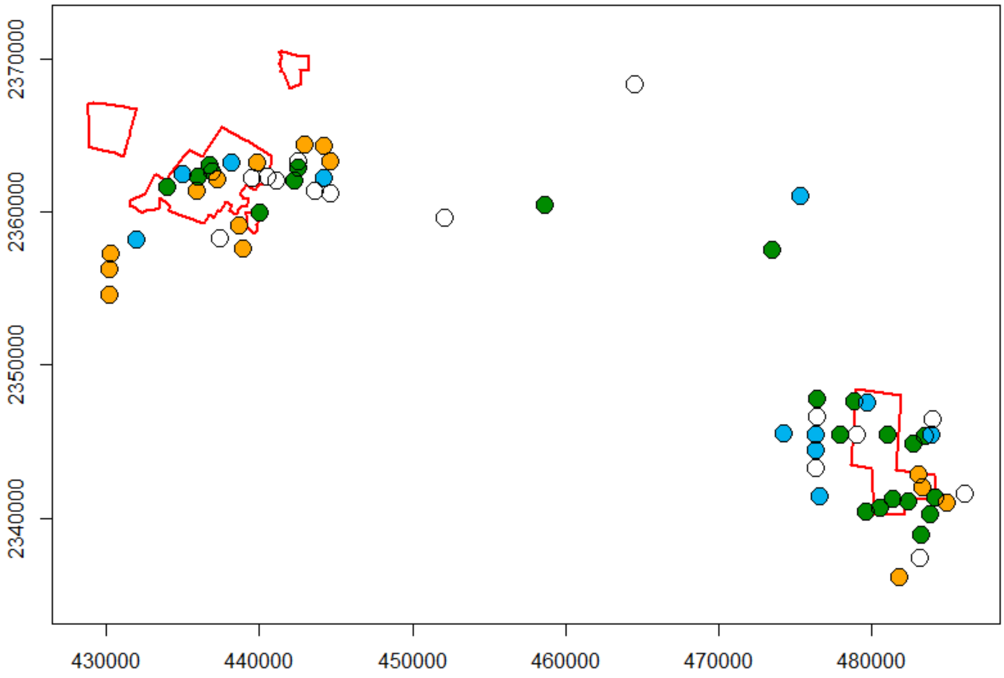
Table 2.3. Density estimates for jaguars in EEER and EZCA and NYP (combining EEER and EZCA) using a Bayesian approach, and a maximum likelihood spatially explicit capture-recapture model without and with differences depending on sex ('no_sex' and 'sex'), and excluding activity centres outside reserve boundaries ('habitat'). The right-hand column gives the diffuse area: the smallest area just encompassing all detectable individuals (detailed in Methods).

Site (year)	SECR model	Model	Density ± SE (Ind./100 km^2)	Sampling area (km^2)
EEER (2015)	Bayesian	-	1.18 ± 0.53	-
	Maximum likelihood	no_sex	1.12 ± 0.59	1444
	Maximum likelihood	sex	3.07 ± 1.91	1444
	Maximum likelihood	habitat	25.82 ± 11.16	25
EEER (2016)	Bayesian	-	1.26 ± 0.52	-
	Maximum likelihood	no_sex	2.14 ± 0.99	1482
	Maximum likelihood	sex	3.54 ± 1.85	1482
	Maximum likelihood	habitat	44.06 ± 16.93	25
EZCA (2015)	Bayesian	-	3.09 ± 1.16	-
	Maximum likelihood	no_sex	NA	NA
	Maximum likelihood	sex	NA	NA
	Maximum likelihood	habitat	NA	NA
EZCA (2016)	Bayesian	-	2.96 ± 1.21	-
	Maximum likelihood	no_sex	2.77 ± 1.26	357
	Maximum likelihood	sex	3.08 ± 1.62	357
	Maximum likelihood	habitat	14.71 ± 7.00	43
NYP (2015)	Bayesian (75 days)	-	0.76 ± 0.32	-
	Bayesian (179 days)	-	0.76 ± 0.26	-
	Maximum likelihood (75 days)	no_sex	1.39 ± 0.62	4756
	Maximum likelihood (179 days)	no_sex	1.57 ± 0.61	4212
	Maximum likelihood (75 days)	sex	2.24 ± 1.32	4756
	Maximum likelihood (179 days)	sex	2.76 ± 1.56	4212
NYP (2016)	Bayesian (71 days)	-	1.48 ± 0.41	-
	Bayesian (144 days)	-	1.50 ± 0.41	-
	Maximum likelihood (71 days)	no_sex	2.38 ± 0.77	3996
	Maximum likelihood (144 days)	no_sex	2.54 ± 0.78	4524
	Maximum likelihood (71 days)	sex	2.37 ± 0.79	3996
	Maximum likelihood (144 days)	sex	2.49 ± 0.77	4524

Spatial distribution of jaguars and pumas in NYP

Of the 65 camera-trap stations in 2015 across NYP, 23 (35%) detected both jaguars and pumas, 15 (23%) detected only jaguars, 11 (17%) detected only pumas, and 16 (25%) detected neither felid (Fig. 2.4). Random and independent redistributions of the 38 jaguar and 24 puma detections in 2015 had probability $p = 0.09$ of obtaining at least this many co-occurrences. Far from avoiding co-occurrence, the two felids tended towards mutual attraction in 2015. This suggestion of non-random attraction disappeared in 2016, however, amongst the 69 stations across NYP. Then, 24 of 69 stations (35%) detected both felids, 19 (28%) detected only jaguars, 14 (20%) detected only pumas, and 12 (17%) detected neither felid. Random and independent redistributions of the 43 jaguar and 38 puma detections in 2016 had $p = 0.54$ of obtaining at least this many co-occurrences. The difference in probability between years was due in part to the larger number of pumas detected in 2016, and fewer empty stations.

(a)



(b)

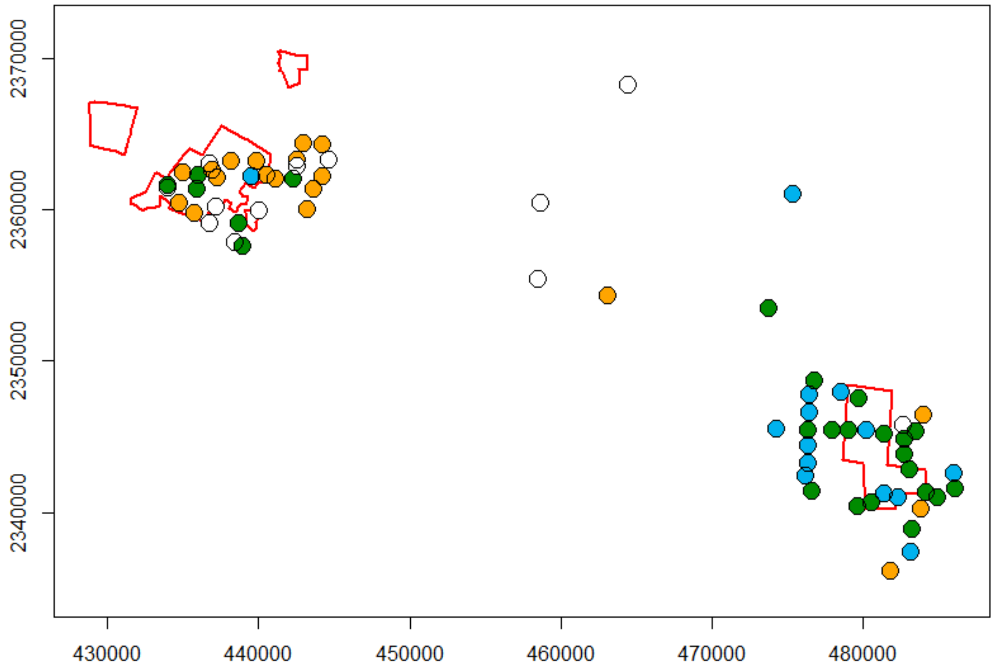


Figure 2.4. Distribution of camera-trap stations in NYP during (a) 2015 and (b) 2016, on UTM coordinates in metres. Each plot shows stations detecting both jaguars and pumas (green dots), jaguars only (orange dots), pumas only (blue dots) and neither felid (white dots). Red lines demark the boundaries of EZCA (upper left polygons) and EEER (lower right polygon).

Of the total of 46 pairs of nearest neighbouring stations in 2015 across NYP, 4 pairs detected only jaguars, and 2 pairs detected only pumas. Random and independent redistributions of the 38 jaguar and 24 puma detections in 2015 had $p = 0.47$ of at least this many jaguar-only pairs, and $p = 0.64$ of at least this many puma-only pairs. There was thus no evidence of either species holding enclaves from the other during 2015. The evidence for enclaving increased in 2016, however, amongst the 48 pairs of nearest neighbouring stations across NYP. Then, 7 pairs detected only jaguars, and 3 pairs detected only pumas. Random and independent redistributions of the 43 jaguar and 38 puma detections in 2016 had $p = 0.05$ of at least this many jaguar-only pairs, and $p = 0.32$ of at least this many puma-only pairs. Jaguars tended to have exclusive use of areas in and around EZCA in 2016, whilst pumas occupied more of EEER and its surrounds although mostly sharing the space with jaguars (Fig. 2.4b).

Relative abundances of jaguars and pumas, and their potential prey species

Species accumulation curves show that our sampling effort of 13115 camera-trap days was adequate to detect a high proportion of species of large mammals and birds present in the Northern Yucatán Peninsula. Across both sampling years, we captured a total of 25 species, with 24 species in 2015 and 23 in 2016. In the study sites of EEER and EZCA, we captured respectively 22 and 23 species across both sampling years (Fig. 2.5). Appendix 2 gives accumulation curves for the individual study sites of EEER and EZCA.

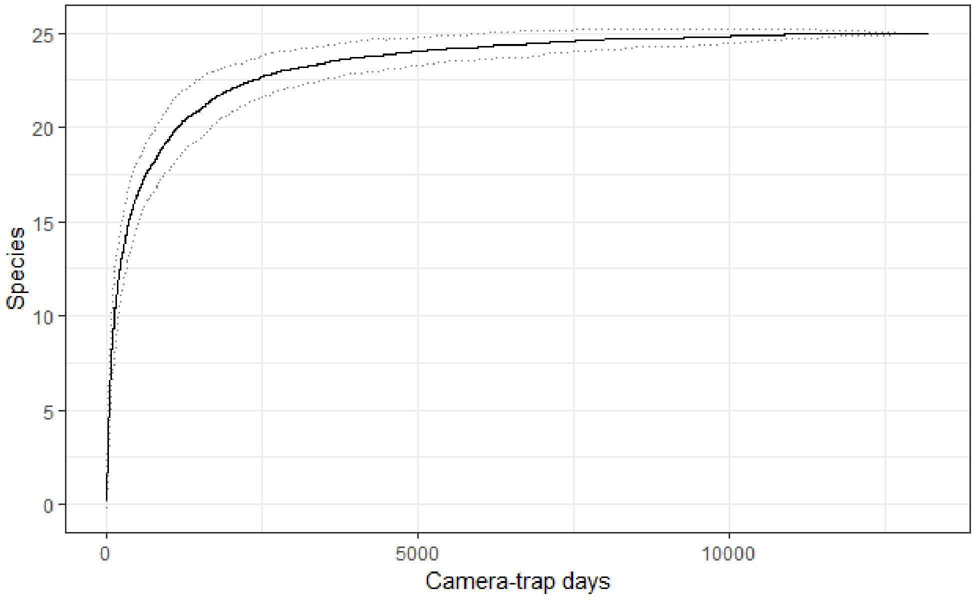


Figure 2.5. Randomised species accumulation curve (solid line) for camera-trap sampling effort, and confidence intervals (dashed lines), in NYP. Data pooled across years (2015 and 2016).

Results of naïve occupancy (NO) and the relative abundance index (RAI) for NYP (Table 2.4) revealed signs of association between these two estimates. We correlated the NO and RAI estimates for each camera-trap sampling year, to find a strong positive correlation in both sampling years (2015: $r = 0.84$, 95% C. I. = 0.66 – 0.93, $t_{22} = 7.2$, $p < 0.005$; 2016: $r = 0.93$, 95% C. I. = 0.84 – 0.97, $t_{22} = 11.6$; $p < 0.005$). According to our estimates, jaguars, pumas, collared peccary, Yucatán brown brocket deer, ocellated turkeys, and ocelots, were widespread (being registered in a high proportion of camera-trap stations), and were common (multiple recaptures) in a high proportion of camera-trap stations.

Our use of a camera-trap sampling design tailored for sampling large felids and large prey (see CENJAGUAR) means that values of NO and RAI are very likely underestimated at least for smaller species (e.g. both species of opossum, eastern cottontail, striped hog-nosed skunk), arboreal species (e.g. margay, chachalaca) and burrowing species (e.g. nine-banded armadillo). This is due to low capturability related to their size or habits. Appendix 2 contains the results of naïve occupancy and relative abundance indices for the individual study sites of EEER and EZCA.

Table 2.4. Naïve occupancy (NO) and Relative Abundance Index (RAI, events per hour/100 days) of large felids and their potential prey species captured in NYP, from camera-trap data in this study. Body weights are given as median (source[1]: Ceballos 2014 and source[2]: del Hoyo *et al.* 2018) or mean (source[3]: Reid 2009). Largest values of NO and RAI are shown in bold. Taxonomy ordered according to IUCN (2018).

Order	Family	Latin name	Common name	Median body weight (kg)	NO (2015)	NO (2016)	RAI (2015)	RAI (2016)
CLASS MAMMALIA								
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	Common opossum[1]	1.1	0.06	0.02	0.28	0.03
		Didelphis virginiana	Virginia opossum[1]	2.0	0.10	0.05	0.35	0.12
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo[3]	5.0	0.09	0.02	0.13	0.05
Pilosa	Myrmecophagida	*Tamandua mexicana*	Northern tamandua[1]	5.1	0.02	-	0.03	-
Rodentia	Cuniculidae	*Cuniculus paca*	Lowland paca[1]	9.0	0.17	0.03	1.06	0.75
	Dasyproctidae	*Dasyprocta punctata*	Central American agouti[1]	2.7	0.09	0.08	0.61	0.35
Lagomorpha	Leporidae	*Sylvilagus floridanus*	Eastern cottontail[1]	1.4	0.02	0.01	0.06	0.05
Carnivora	Canidae	*Canis latrans*	Coyote[1]	12.0	0.08	0.04	0.10	0.07
		Urocyon cinereoargenteus	Grey fox[1]	4.0	0.21	0.17	0.65	0.71
	Procyonidae	*Nasua narica*	White-nosed coati[1]	5.0	0.28	0.25	0.56	0.55
		Procyon lotor	Northern raccoon[1]	6.0	-	0.01	-	0.20
	Mephitidae	*Conepatus semistriatus*	Striped hog-nosed skunk[1]	2.5	0.10	0.14	0.16	0.43
	Mustelidae	*Eira barbara*	Tayra[1]	4.9	0.03	0.05	0.04	0.08
	Felidae	*Herpailurus yagouaroundi*	Jaguarundi[1]	6.3	0.02	-	0.03	-
		Leopardus pardalis	Ocelot[1]	12.0	0.45	0.47	1.26	1.71
		Leopardus wiedii	Margay[1]	4.0	0.07	0.06	0.08	0.12
		Panthera onca	Jaguar[3]	65.0	0.52	0.58	1.48	2.49
		Puma concolor	Puma[3]	44.5	0.45	0.56	1.30	2.89
Cetartiodactyla	Cervidae	*Mazama pandora*	Yucatan brown brocket deer[1]	21.0	0.47	0.59	1.92	3.27
		Mazama temama	Central American red brocket deer[3]	22.0	0.05	0.10	0.06	0.20
		Odocoileus virginianus	White-tailed deer[3]	34.0	0.02	0.09	0.06	0.20
	Tayassuidae	*Pecari tajacu*	Collared peccary[1]	23.5	0.26	0.41	0.64	1.63
CLASS AVES								
Galliformes	Cracidae	*Crax rubra*	Great curassow[2]	3.9	0.28	0.33	0.78	1.23
		Ortalis vetula	Chachalaca[2]	0.6	0.14	0.18	0.24	0.88
	Phasianidae	*Meleagris ocellata*	Ocellated turkey[2]	5.5	**0.70**	**0.63**	**5.98**	**4.93**

Availability of prey and anti-predator strategies

Jaguars and pumas in NYP had largely similar activity patterns, with pumas slightly more active during the day (Table 2.5, and Figs. 2.6 and 2.7). In contrast, activity patterns of large mammal species, such as ungulates, were mostly diurnal. Smaller species, however, were mostly nocturnal.

We avoided the category ‘crepuscular’ for activity pattern classification due to a low number of records (as detailed in the Methods). According to Gómez *et al.* (2005), this category includes records taken from one hour before and after sunrise and sunset (6:00 – 8:00 and 18:00 -20:00). From all the species captured with our camera-trap sampling method in NYP, the only one that might have a crepuscular activity pattern is the Central American agouti (*Dasyprocta punctata*; Fig. 2.7). Appendix 2 classifies activities, activity records, and plots of activities for large felids and their potential prey species separately in EEER and EZCA.

Table 2.5. Classification of activity of large felids and their potential prey species captured from our camera-trap sampling data in NYP (see Methods for classification criteria).

Order	Family	Latin name	Common name	Classification
CLASS MAMMALIA				
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	Common opossum	Mostly diurnal
		Didelphis virginiana	Virginia opossum	Mostly nocturnal
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	Nocturnal
Rodentia	Cuniculidae	*Cuniculus paca*	Lowland paca	Nocturnal
	Dasyproctidae	*Dasyprocta punctata*	Central American agouti	Cathemeral
Carnivora	Canidae	*Canis latrans*	Coyote	Mostly nocturnal
		Urocyon cinereoargenteus	Grey fox	Cathemeral
	Procyonidae	*Nasua narica*	White-nosed coati	Mostly diurnal
		Procyon lotor	Northern raccoon	Nocturnal
	Mephitidae	*Conepatus semistriatus*	Striped hog-nosed skunk	Nocturnal
	Felidae	*Leopardus pardalis*	Ocelot	Nocturnal
		Leopardus wiedii	Margay	Mostly nocturnal
		Panthera onca	Jaguar	Mostly nocturnal
		Puma concolor	Puma	Cathemeral
Cetartiodactyla	Cervidae	*Mazama pandora*	Yucatan brown brocket deer	Mostly diurnal
		Mazama temama	Central American red brocket deer	Mostly diurnal
		Odocoileus virginianus	White-tailed deer	Mostly diurnal
	Tayassuidae	*Pecari tajacu*	Collared peccary	Mostly diurnal
CLASS AVES				
Galliformes	Cracidae	*Crax rubra*	Great curassow	Mostly diurnal
		Ortalis vetula	Chachalaca	Diurnal
	Phasianidae	*Meleagris ocellata*	Ocellated turkey	Mostly diurnal

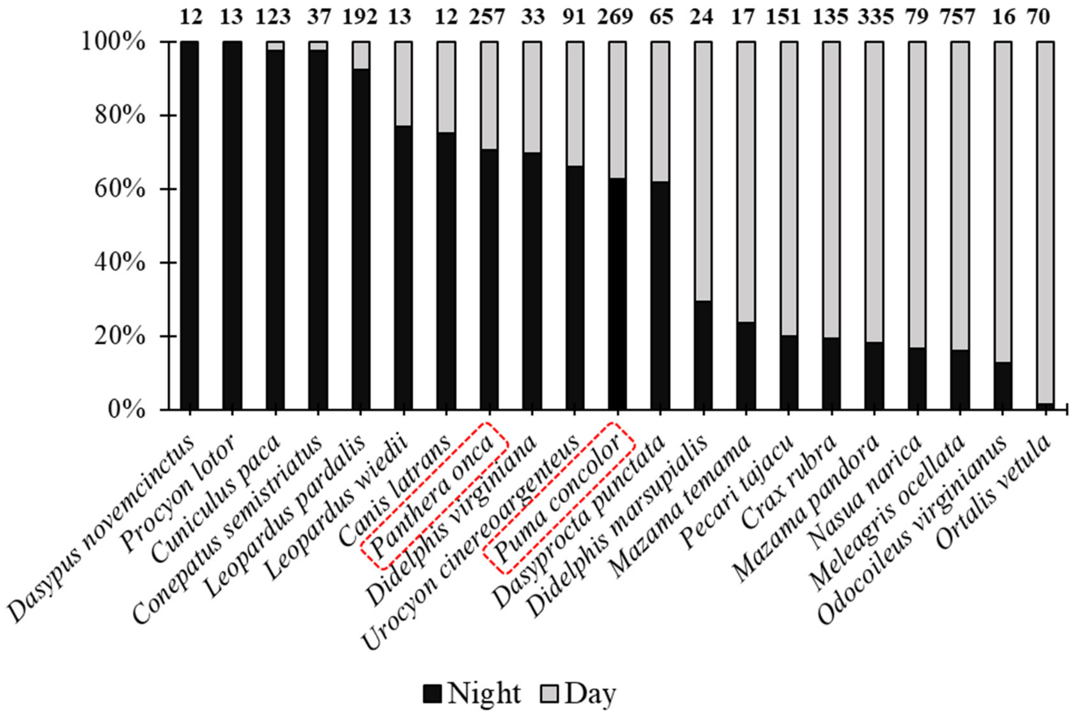
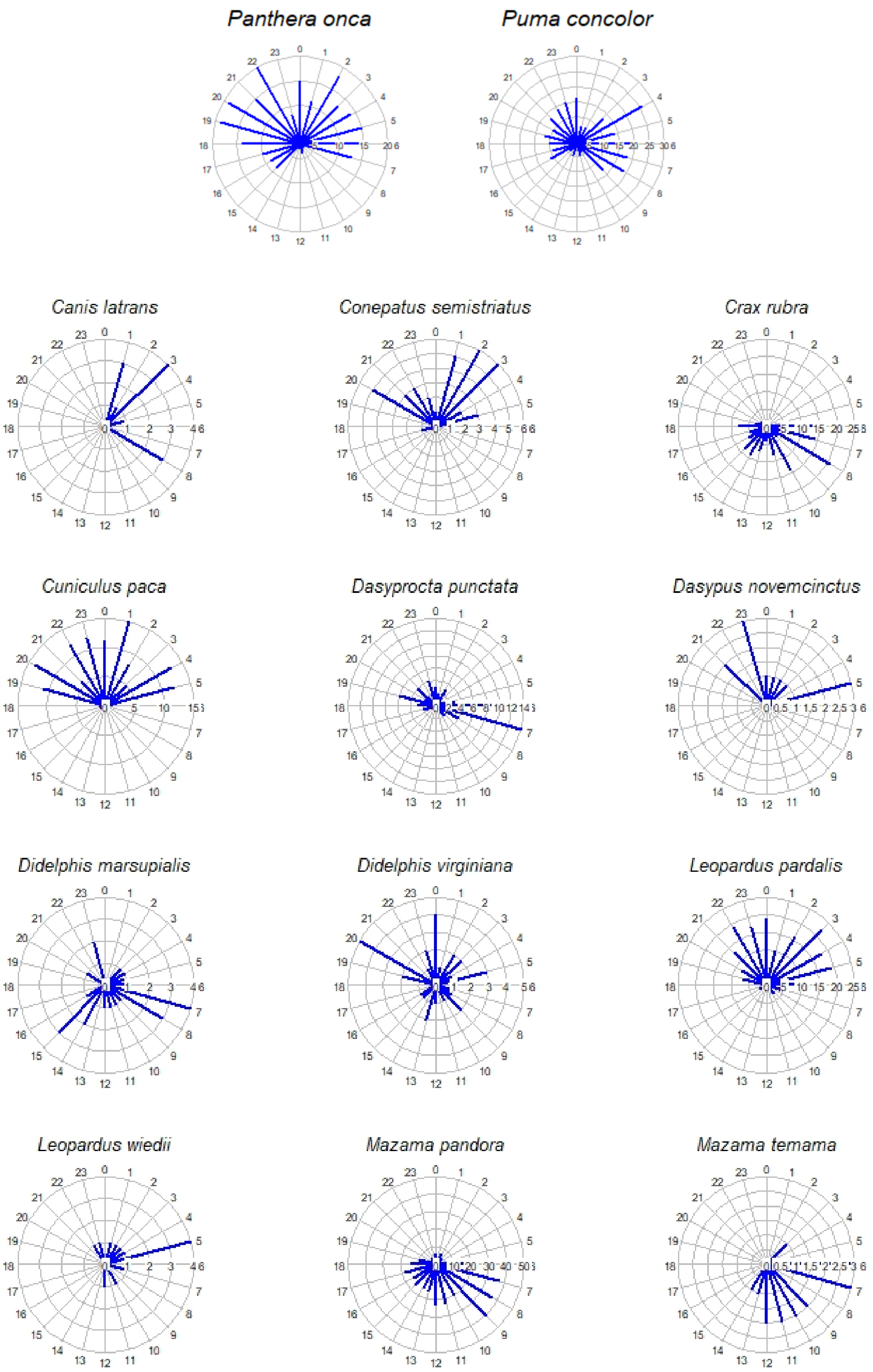


Figure 2.6. Activity records of large felids and their potential prey species (> 10 records) found in NYP. Species are ordered by proportion of night-time, with total number of observations above each bar.



Panthera onca

Puma concolor

Canis latrans

Conepatus semistriatus

Crax rubra

Cuniculus paca

Dasyprocta punctata

Dasypus novemcinctus

Didelphis marsupialis

Didelphis virginiana

Leopardus pardalis

Leopardus wiedii

Mazama pandora

Mazama temama

Figure 2.7. Radial plots of activity patterns for jaguar and puma, and their potential prey species, in NYP. The length of each line signifies number of hourly events. Jaguar and puma are shown at the top of the figure. Below, their potential prey species are ordered by Latin name.

Figure 2.7 (cont.).

A total of 2717 independent activity records were collected during 2015 and 2016 in study sites of EEER (n = 1369), EZCA (n = 1093) and in IA (n = 255). Of these records, 257 were from jaguars (EEER: n = 125, EZCA: n = 120, IA: n = 12) and 267 from pumas (EEER: n = 192, EZCA: n = 56, IA: n = 19).

Daily activity patterns of jaguars and pumas in NYP showed signs of overlap (W = 0.02, p = 0.89, Table 2.6). Both species were largely nocturnal, and had minimal activity around noon (Fig. 2.8). Pumas tended to stay active later into the morning than jaguars, and jaguars were more active than pumas around dusk.

Activity patterns of both felids differed from those of most of their prey. Wald tests showed evidence of temporal segregation from 15 of their potential prey species, and evidence of overlap only with Virginia opossum (*Didelphis virginiana*), grey fox (*Urocyon cinereoargenteus*), Common opossum (*Didelphis marsupialis*) and white-nosed coati (*Nasua narica,* Table 2.6). Activity patterns of large mammal species such as ungulates, were more diurnal than those of felids; smaller species, however, tended to be more strictly nocturnal than the felids (Fig. 2.9). Appendix 2 gives results in each of EEER and EZCA for overlap in activity patterns, activity curves and overlap between jaguars and pumas, and their potential prey species.

Table 2.6. Overlap in activity patterns between jaguars and pumas, and between large felids and their potential prey species, in NYP. Wald statistic (*W*), p < 0.05 (bold) signifies less than 5% chance of the two samples coming from the same activity pattern. Jaguar and puma are shown at the top of the table. Below, their potential prey species are ordered by overlap (*W*) with jaguars.

Species	***n***	**Coefficient of overlapping (± C. I.) *Panthera onca***	***W***	***p***	**Coefficient of overlapping (± C. I.) *Puma concolor***	***W***	***p***
Panthera onca	257	-	-	-	0.84 (0.77 - 0.90)	0.02	0.89
Puma concolor	267	0.84 (0.77 - 0.90)	0.02	0.89	-	-	-
Didelphis virginiana	33	0.86 (0.74 - 0.96)	0.08	0.78	0.82 (0.69 - 0.92)	0.13	0.71
Urocyon cinereoargenteus	91	0.77 (0.68 - 0.85)	0.15	0.70	0.77 (0.67 - 0.85)	0.06	0.80
Didelphis marsupialis	24	0.59 (0.41 - 0.73)	3.34	0.07	0.70 (0.53 - 0.83)	2.92	0.09
Nasua narica	77	0.46 (0.37 - 0.55)	3.37	0.07	0.53 (0.44 - 0.62)	2.68	0.10
Mazama temama	14	0.38 (0.23 - 0.51)	5.52	**0.02**	0.51 (0.33 - 0.64)	4.67	**0.03**
Leopardus wiedii	13	0.64 (0.44 - 0.78)	7.00	**0.01**	0.70 (0.50 - 0.85)	6.30	**0.01**
Pecari tajacu	143	0.54 (0.46 - 0.62)	7.94	**<0.005**	0.61 (0.53 - 0.69)	6.68	**0.01**
Cuniculus paca	119	0.74 (0.67 - 0.81)	9.00	**<0.005**	0.64 (0.56 - 0.71)	7.18	**0.01**
Leopardus pardalis	192	0.73 (0.66 - 0.80)	9.86	**<0.005**	0.70 (0.63 - 0.77)	7.90	**<0.005**
Procyon lotor	13	0.65 (0.48 - 0.81)	10.34	**<0.005**	0.61 (0.42 - 0.76)	8.86	**<0.005**
Mazama pandora	336	0.48 (0.42 - 0.54)	12.42	**<0.005**	0.58 (0.51 - 0.64)	10.14	**<0.005**
Odocoileus virginianus	14	0.38 (0.20 - 0.55)	12.76	**<0.005**	0.48 (0.30 - 0.65)	11.46	**<0.005**
Dasypus novemcinctus	13	0.62 (0.44 - 0.75)	13.99	**<0.005**	0.59 (0.40 - 0.73)	12.29	**<0.005**
Crax rubra	129	0.46 (0.38 - 0.53)	15.54	**<0.005**	0.55 (0.47 - 0.62)	13.36	**<0.005**
Conepatus semistriatus	35	0.67 (0.55 - 0.79)	16.27	**<0.005**	0.60 (0.48 - 0.70)	14.03	**<0.005**
Dasyprocta punctata	65	0.69 (0.56 - 0.80)	20.52	**<0.005**	0.74 (0.62 - 0.83)	17.80	**<0.005**
Canis latrans	12	0.48 (0.30 - 0.58)	21.44	**<0.005**	0.54 (0.33 - 0.67)	8.88	**<0.005**
Ortalis vetula	71	0.28 (0.19 - 0.34)	21.54	**<0.005**	0.38 (0.29 - 0.46)	17.99	**<0.005**
Meleagris ocellata	745	0.43 (0.37 - 0.49)	24.34	**<0.005**	0.51 (0.46 - 0.57)	19.88	**<0.005**

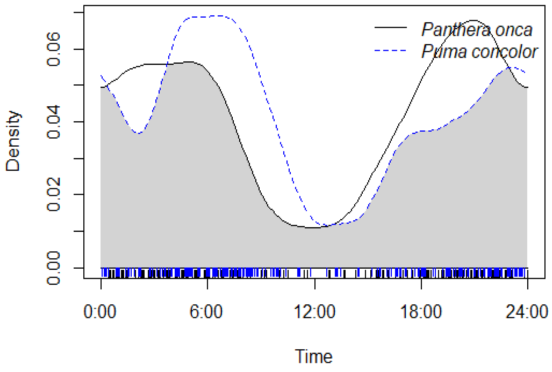
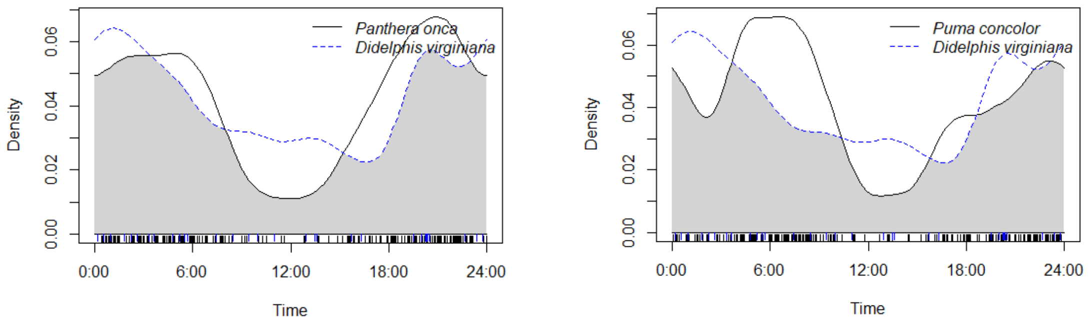
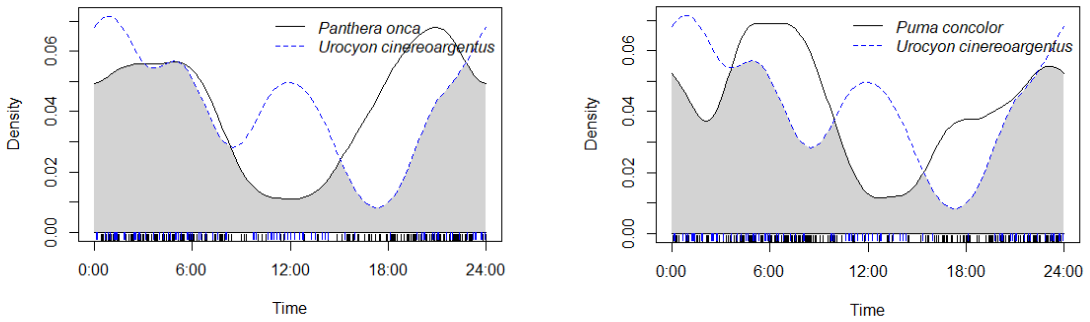


Figure 2.8. Activity curves and overlap between jaguars (black, continuous line) and pumas (blue, dotted line) in NYP. The coefficient of overlap equals the area in grey below both curves. The original records for jaguar (black) and puma (blue) are shown in the 'rug' at the foot of the chart.

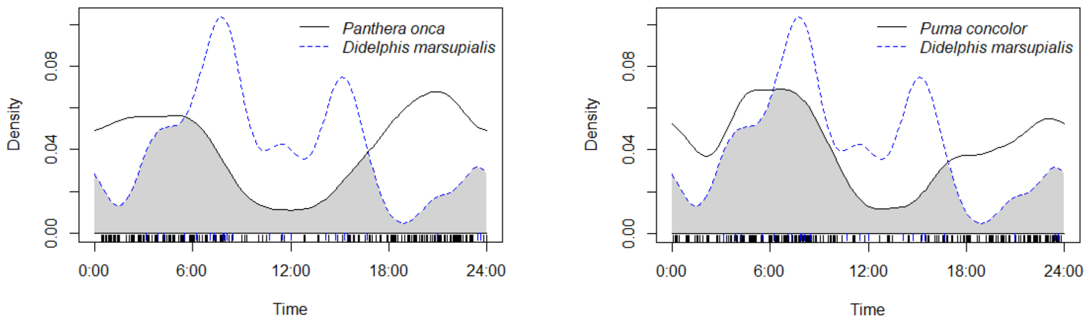
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



Virginia opossum
(Didelphis virginiana)



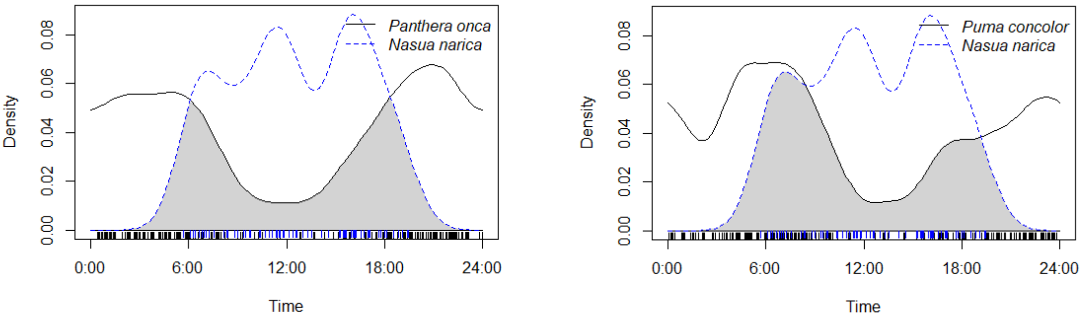
Grey fox
(Urocyon cinereoargenteus)



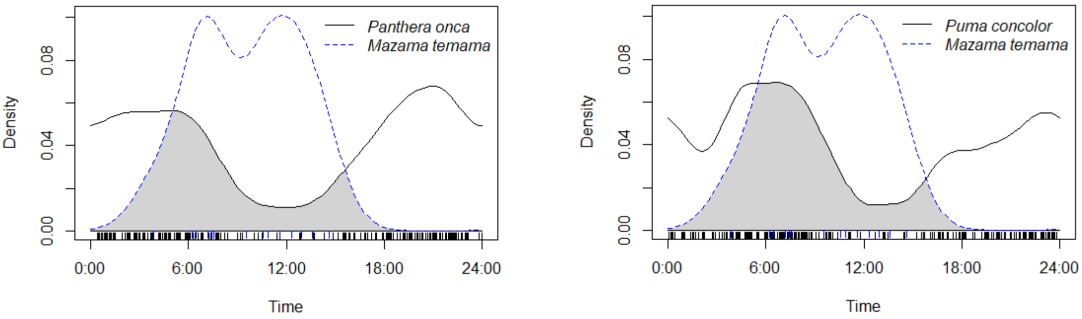
Common opossum
(Didelphis marsupialis)

Figure 2.9. Activity curves and overlap between jaguars (black, continuous line on the left-hand side) and pumas (black, continuous line on the right-hand side), and their potential prey species (blue, dotted line) in NYP. The coefficient of overlapping equals the area in grey below both curves. The original records for jaguar (black) and puma (blue) are shown at the foot of the chart as a 'rug'. Ordered from the highest to the lowest Coefficient of overlapping between jaguars and prey.

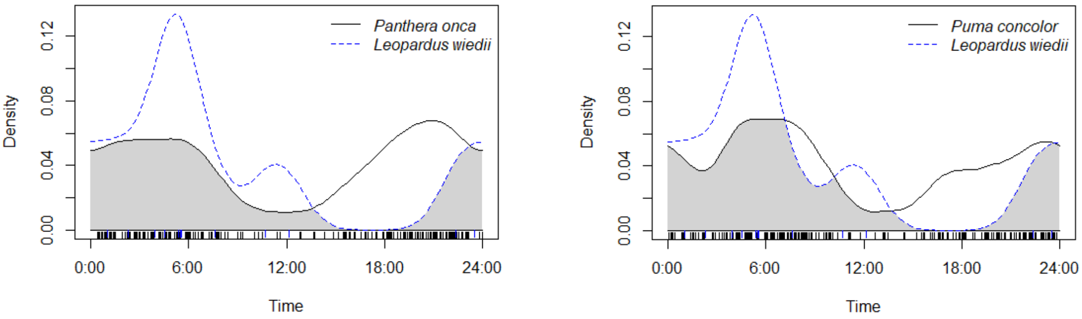
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



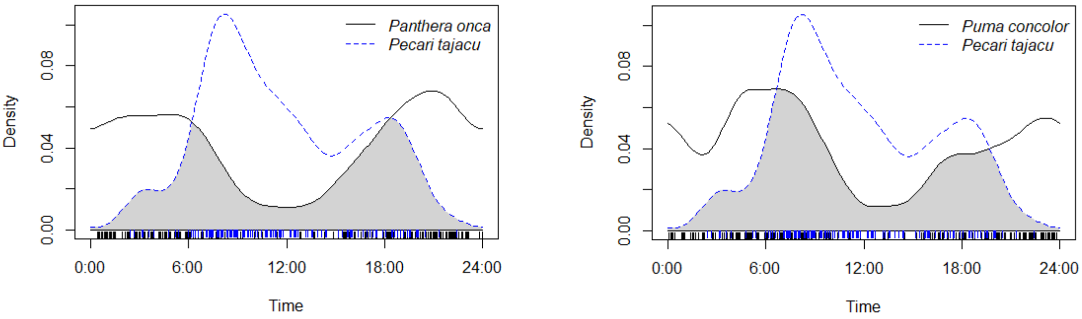
White-nosed coati
(Nasua narica)



Central American red brocket deer
(Mazama temama)



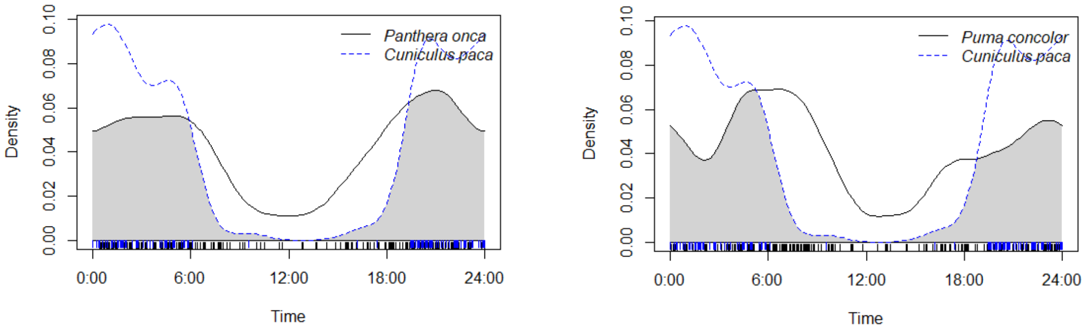
Margay
(Leopardus wiedii)



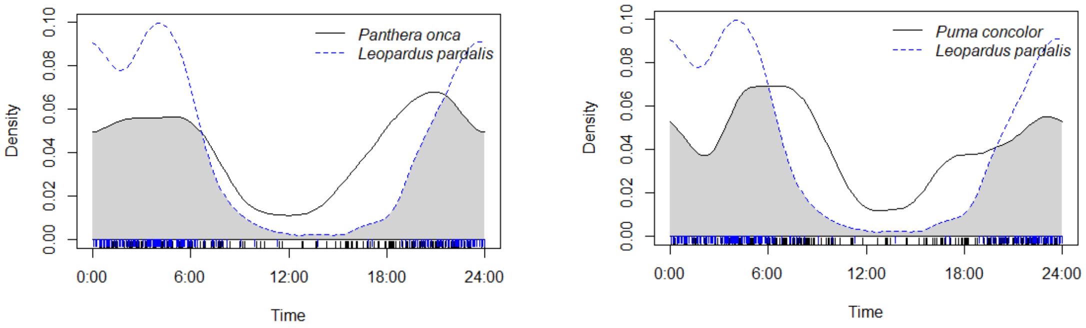
Collared peccary
(Pecari tajacu)

Figure 2.9 (cont.).

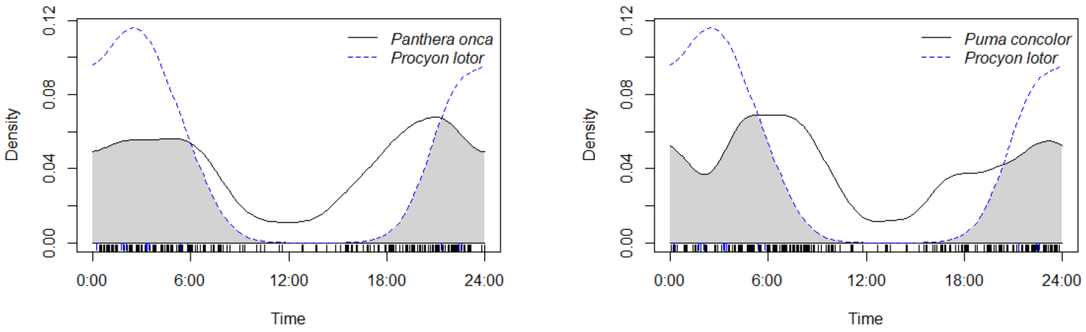
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



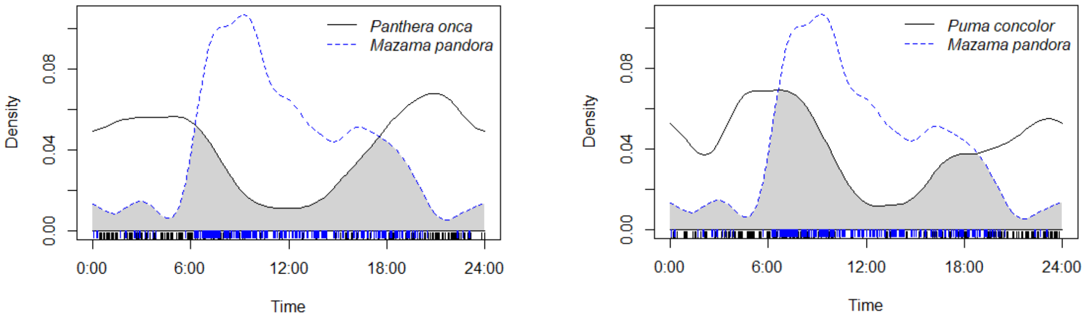
Lowland paca
(*Cuniculus paca)*



Ocelot
(Leopardus pardalis)



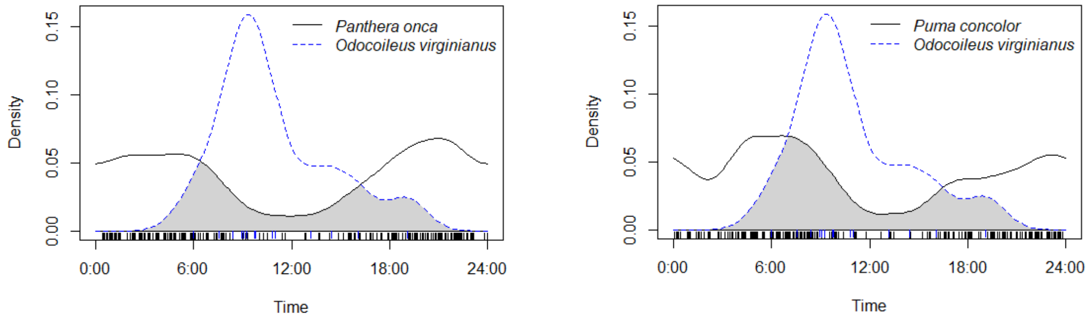
Northern raccoon
(Procyon lotor)



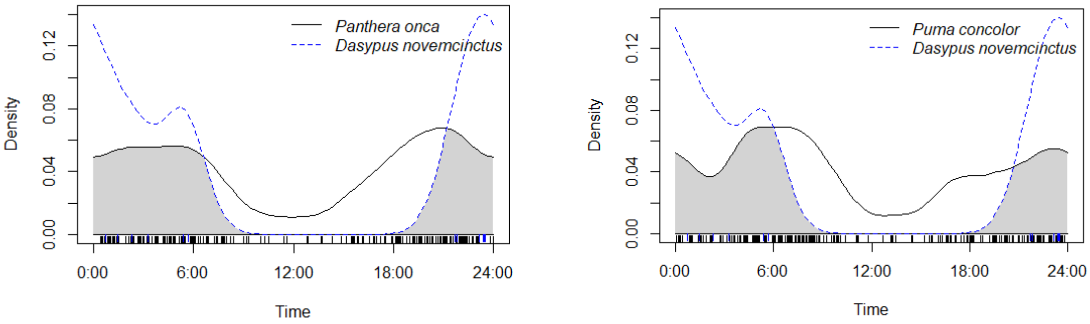
Yucatan brown brocket deer
(Mazama pandora)

Figure 2.9 (cont.).

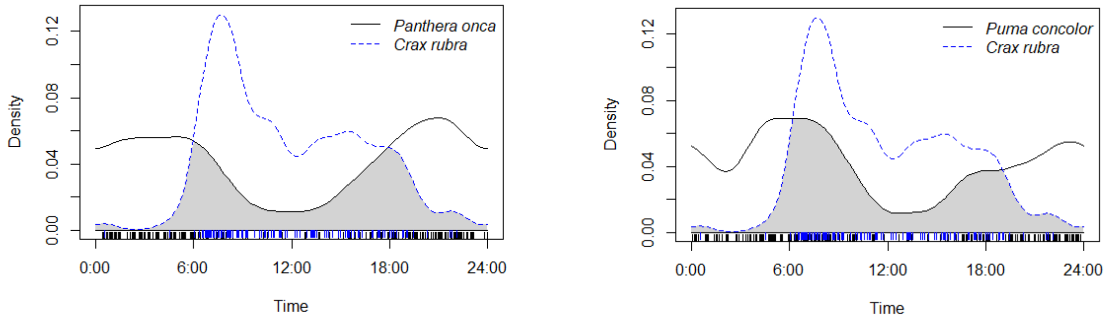
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



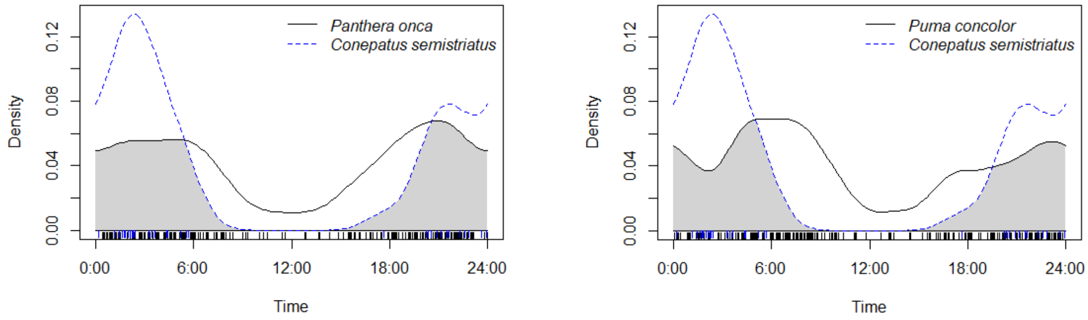
White-tailed deer
(Odocoileus virginianus)



Nine-banded armadillo
(Dasypus novemcinctus)



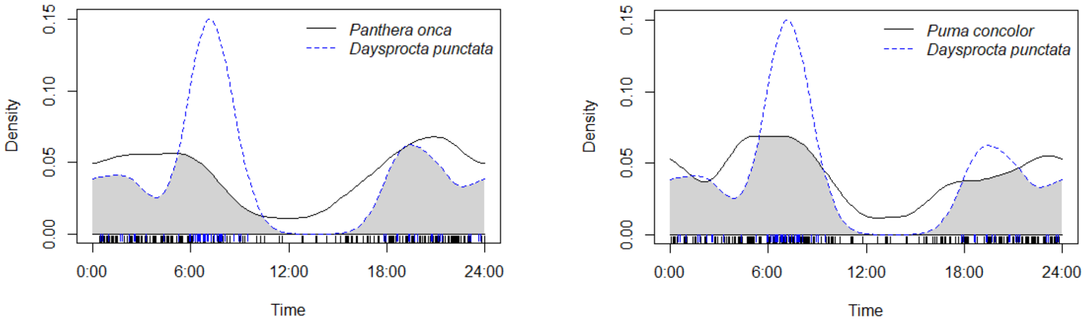
Great curassow
(*Crax rubra*)



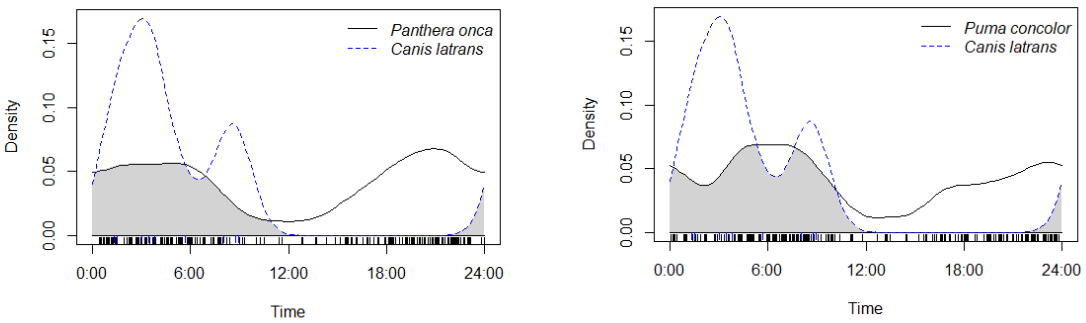
Striped hog-nosed skunk
(*Coneptaus semistriatus*)

Figure 2.9 (cont.).

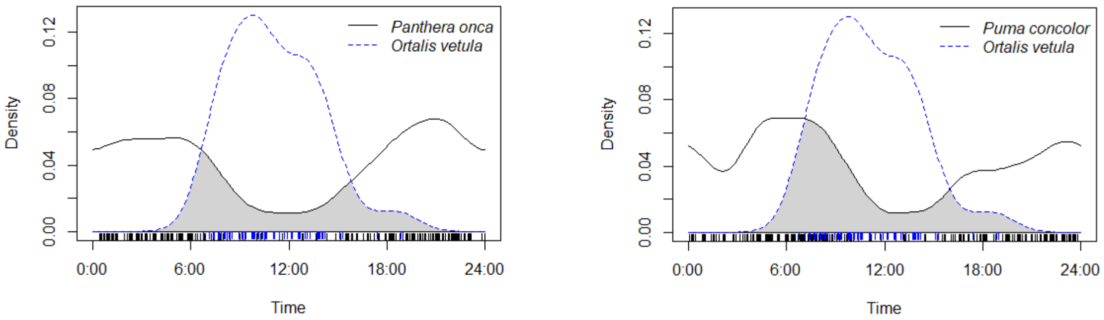
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



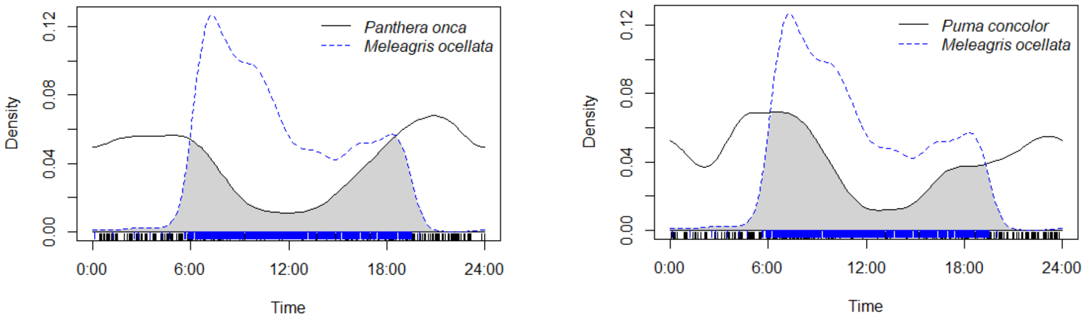
Central American agouti
(*Dasyprocta punctata)*



Coyote
(*Canis latrans*)



Plain chachalaca
(*Ortalis vetula)*



Ocellated turkey
(*Meleagris ocellata)*

Figure 2.9 (cont.).

Prey consumption, prey exploitation and niche overlap by large felids

Jaguar and puma diets

A high proportion of remnants of cervids (*Odocoileus virginianus, Mazama pandora* and *M. temama*) contained in jaguar and puma scats could not be identified to the species level. Thus, we grouped remnants that could belong to any of these species into the category 'Cervids'. For analysis using body mass, we calculated an average of the median weights for these three species in the Yucatán Peninsula. In addition, species that could not be identified were not included in subsequent analysis.

Across NYP, jaguar diet contained at least 15 species: 13 mammals, 1 bird and 1 reptile (*n* = 36 scats, Table 2.7). Jaguar and puma scats contained an average of 1.39 (maximum = 3) and 1.17 (maximum = 2) identifiable prey items per scat, respectively. We registered consumption of grass by one jaguar. We did not register consumption of domestic prey species by either felid, although the 2 instances of canid could have included domestic dog, if not coyote (*Canis latrans*). Puma diet contained at least 19 species (*n* = 36 scats): 16 mammals, 2 birds and 1 fish. Jaguars ate most frequently (> 5% relative occurrence and biomass) two large-prey taxa (>10 kg): collared peccary (*Pecari tajacu*) and Cervids (large prey >10 kg); these were followed in frequency by medium-sized prey (2 – 10 kg): white-nosed coati (*Nasua narica*), nine-banded armadillo (*Dasypus novemcinctus*) and Northern tamandua (*Tamandua mexicana*). Together the large and medium-sized prey constituted 68% of prey items consumed and 86% of total biomass eaten (Fig. 2.10). Pumas also ate most frequently the same two large-prey taxa: collared peccary (*Pecari tajacu*) and Cervids, followed by medium-sized species: particularly white-nosed coati (*Nasua narica*). Together, they constituted 53% of prey items consumed and 77% of total biomass eaten. Niche breadths were B_{sta} = 0.33 and 0.27 for jaguars and pumas respectively. Although the diet of jaguars was less species-rich than the diet of puma, it was more diverse, consuming prey species more evenly.

Table 2.7. Body weights, relative occurrences and consumed biomasses (absolute and relative) of prey species in jaguar and puma scats collected in EEER and EZCA. Ordered by body weight class.

Prey species	**Body weight (kg)**	**Relative occurrence (%)**		**Biomass consumed (kg)**		**Relative biomass (%)**	
		Jaguar	**Puma**	**Jaguar**	**Puma**	**Jaguar**	**Puma**
> 10 kg							
Odocoileus virginianus	34.0	-	9.4	-	29.9	-	0.16
Unknown Cervidae	25.7	13.3	9.4	38.4	27.2	0.19	0.14
Pecari tajacu	23.5	28.3	26.4	79.4	74.0	0.39	0.39
Canis sp.	12.0	-	3.8	-	9.1	-	0.05
5 - 10 kg							
Cuniculus paca	9.0	1.7	-	3.8	-	0.02	-
Ateles geoffroyi	6.2	1.7	-	3.7	-	0.02	-
Procyon lotor	6.0	3.3	1.9	7.3	4.1	0.04	0.02
Tamandua mexicana	5.1	5.0	1.9	10.8	4.1	0.05	0.02
2 - 5 kg							
Dasypus novemcinctus	5.0	10.0	-	21.6	-	0.11	-
Nasua narica	5.0	11.7	7.5	25.1	16.3	0.12	0.08
Eira barbara	4.9	1.7	1.9	3.6	4.1	0.02	0.02
Leopardus wiedii	4.0	-	3.8	-	8.0	-	0.04
Urocyon cinereoargenteus	4.0	-	1.9	-	4.0	-	0.02
Crax rubra	3.9	-	1.9	-	4.0	-	0.02
Potos flavus	3.0	1.7	-	3.5	-	0.02	-
Conepatus semistriatus	2.5	3.3	-	6.9	-	0.03	-
Didelphis virginiana	2.0	-	1.9	-	3.9	-	0.02
< 2 kg							
Bassariscus sumichrasti	1.1	-	1.9	-	2.1	-	0.01
Spilogale angustifrons	0.5	-	1.9	-	1.0	-	0.01
Philander opossum	0.4	1.7	-	0.7	-	0.00	-
Ototylomys phyllotis	0.1	-	1.9	-	0.2	-	0.00
Unknown size							
Unknown mouse	-	-	3.8	-	-	-	-
Unknown bird	-	1.7	5.7	-	-	-	-
Unknown fish	-	-	1.9	-	-	-	-
Unknown mammal	-	13.3	11.3	-	-	-	-
Unknown Colubridae	-	1.7	-	-	-	-	-

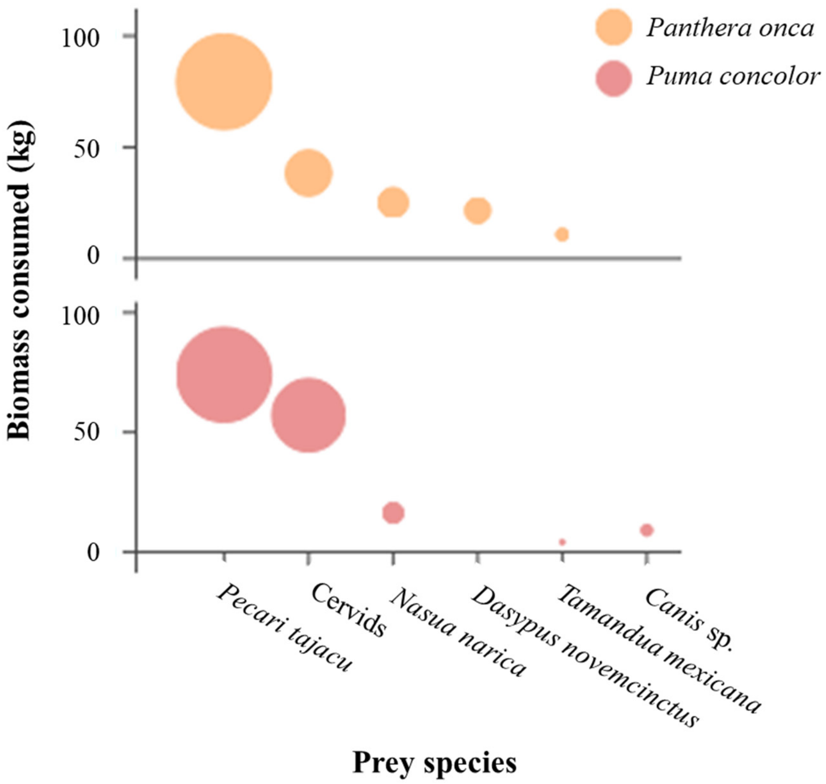


Figure 2.10. Estimate of consumed biomass, derived for main prey (relative biomass > 5%) from the mass per species summed across all scats of jaguars (orange circles) and pumas (pink circles) in NYP. Size of the bubble is proportional to relative biomass.

Prey exploitation and niche overlap

Jaguars and pumas from NYP showed a high diet overlap (Pianka index = 0.89). This value was larger than expected by chance. The simulated mean overlap index (expected overlap) obtained from 1,000 randomisations was 0.23 ± 0.06 (mean ± SE), and was significantly lower than the observed overlap ($p = 0.003$).

In order to compare the consumption of prey by jaguars and pumas in NYP to prey availability, we constructed plots of relative biomass consumed (%) against RAI for prey species in 2015 and 2016 (Fig. 2.11). Preferred prey show high ratios of consumption to abundance (Fig. 2.11a), and avoided prey show low ratios (Fig. 2.11d), with the strong caveat that RAI is not a robust estimate of abundance. Jaguars and pumas both appeared to prefer collared peccary (*Pecari tajacu*) and Cervids over other species, with a suggestion of a higher preference for Cervids by pumas than jaguars. Jaguars showed a strong preference for nine-banded armadillo (*Dasypus novemcinctus*) despite its low detection (although it was very likely under-detected by camera traps). Both felids appear to select white-nosed coati (*Nasua narica*), and both avoided ocellated turkey (*Meleagris ocellata*) despite their great abundance in the area (this was the species with the largest number of camera-trap records).

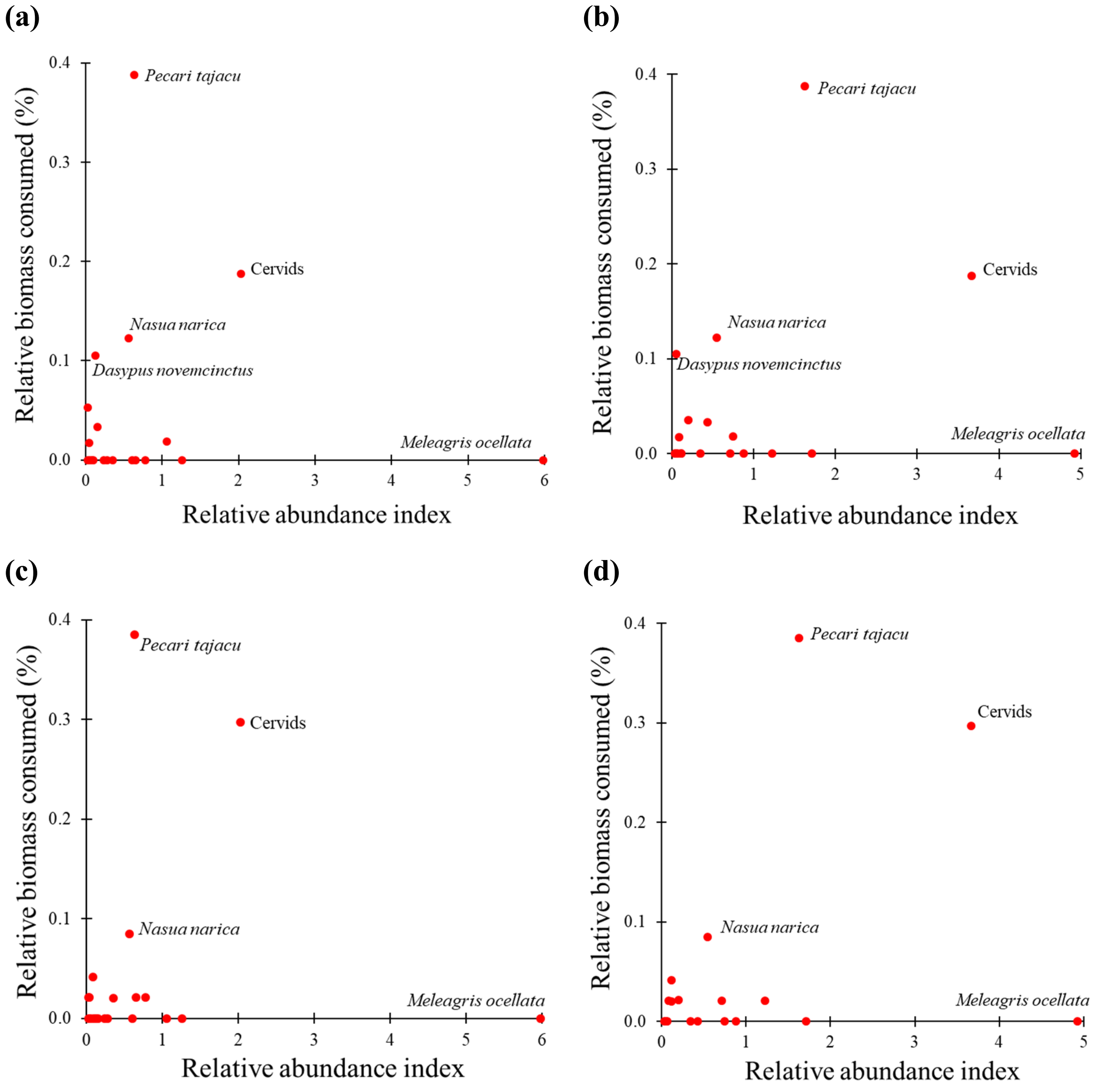


Figure 2.11. Relative biomass consumed (%) vs relative abundance index of jaguars (2015: a, 2016: b) and pumas (2015: c, 2016: d) in NYP. Only outliers are labelled.

Discussion

Holistic understanding of the health of large felid populations requires knowledge of the abundances and behaviours of prey species as well as the predators, and the methods available for acquiring this knowledge all provide empirical data of low information content per observation. This chapter has aimed to compensate for information-poor observations by collating observational evidence from diverse sources on the population ecologies of jaguars and pumas in NYP. Our study reports the first usage to our knowledge of a maximum likelihood spatially explicit capture-recapture method for estimating jaguar densities in the Northern Yucatán Peninsula. Best estimates suggested densities of 2 to 3 individuals per 100 km^2. Jaguars and pumas in NYP showed some indication of spatial aggregation together, although jaguars appeared to dominate some unshared areas. Jaguar and puma daily activity patterns differed more from those of their potential prey species than from each other. The two felids also showed a high dietary overlap with each other, preferring to eat the same prey species: mainly collared peccary and deer, which were abundant and widespread in NYP. Here we discuss how the two species can coexist, given the large overlap in their ecologies within NYP.

Although our study was only two years long, our results provided estimations for jaguar population densities in NYP that varied little between years, or spatially between EEER and EZCA. By contrast, findings by Ávila-Nájera *et al.* (2015) in EEER, using a Bayesian approach to estimate jaguar densities in EEER (without accounting for sex differences in detection), showed considerable variations in a 4-year study (0.7 ± 0.05 to 3.65 ± 1.39 individuals/100 km^2). Faller *et al.* (2007) also found highly variable estimations in an area from the Northern Yucatán Peninsula (including EZCA), using a non-spatial approach in a three-year study (1.82 ± 0.17 – 6.18 ± 0.33 individuals/100 km^2). The temporal consistency in our study could reflect consistent environmental conditions throughout the 2 years, with no natural catastrophes impacting on abundance (Michalski & Peres 2007). In contrast, both the studies of Ávila-Nájera *et al.* (2015) and Faller *et al.* (2007) encompassed natural catastrophes. During the study of Faller *et al.* (2007), two hurricanes, Emily and Wilma (category 5), and forest fires during 2006, severely affected the region. During the study of Ávila-Nájera *et al.* (2015), a forest fire affected EEER in May 2011.

Male-biased capture probabilities have been found in a number of studies of jaguar density (e.g. Silver *et al.* 2004; Harmsen 2006; Foster 2008, Tobler & Powel 2013; Ávila-Nájera *et al.* 2015). Extreme heterogeneity in capture probability of a subset of the population will lead to lower reliability in abundance estimates (Harmsen *et al.* 2010). The inclusion of sex as a covariate has been shown to improve estimates (Sollmann *et al.* 2011). We therefore place most confidence in our maximum likelihood model 'sex' as providing the most reliable assessments of jaguar density in NYP, and EEER and EZCA. Estimates using alternative models that did not account for sex differences in capture probabilities (i.e. Bayesian approach and maximum likelihood model 'no_sex') generally provided lower values, consistent with underestimating an undetected female component of density. Where the best-fitting 'no_sex' model included heterogeneous capture, however, its estimates tended to be more similar to those of the 'sex' model. The capture heterogeneity was likely responding to the sex difference that is built into the 'sex' model.

Jaguar densities estimated with the maximum likelihood and Bayesian methods showed higher values in EZCA than in EEER, and NYP (pooled data of EEER, EZCA and IA). The sampling area in EZCA was very small (see Table 2.3), and it has been recognised that small sampling areas are likely to produce inflated density estimates (Foster & Harmsen 2012; Royle *et al.* 2014), which could have led to overestimations in jaguar densities in EZCA.

It has been recognised that a choice of camera-trap locations based on optimisation of capture probabilities could result in biased sampling if the camera locations are only optimal for a subset of the sampled population (Foster & Harmsen 2012; Wearn & Glover-Kapfner 2017). Extrapolations of density estimates across areas encompassing lower-quality habitat should be done with caution (Foster & Harmsen 2012), and correction for this heterogeneity can ultimately influence density estimates in SECR models (Sollmann *et al.* 2011). Our study sites of EEER and EZCA, as private reserves, are likely to maintain good quality habitat inside their limits; however, surrounding areas are owned by communal 'ejidal' lands, which are likely to have lower quality agricultural land. At EEER and EZCA, our camera-trap stations were placed both inside and outside reserve limits (which was a consequence of the area requirements needed for the CENJAGUAR design). Likewise, some stations in IA were located in communal 'ejidal' lands. Thus, our sampling design allowed us to cover a wide range of habitat types, and ultimately to minimise this source of bias.

The camera-trap stations between EEER and EZCA, and in IA, which we used to estimate jaguar densities in NYP (the pooled data), were spaced with larger distances than those recommended for studies of large felids (Wegge *et al.* 2004; Tobler & Powell 2013). Cameras spaced too widely may fail to detect individuals if they occupy home ranges that fall between trap locations, breaking the assumption of non-zero probabilities of capture for each individual, which is necessary for conventional capture-recapture models (Foster & Harmsen 2012). On the other hand, it has been recognised that predictions are possible outside the range of the data by making inferences from the sample to individuals that live in these holes, based on the explicit declaration that SECR models apply to any area within the state space, even to unsampled areas (Royle *et al.* 2014). We therefore treat our density estimates for NYP with more caution than those for EEER and EZCA, but consider nonetheless that they provide a useful first insight into jaguar density in this area.

The jaguar densities estimated for EEER and EZCA with the maximum likelihood model assuming suitable habitat only inside reserve limits (the 'habitat' model) show evidence of the important hold that these surrounding communal 'ejidal' lands have on the survival of jaguar populations in NYP. If these communal areas were lost, jaguar populations would not persist within the remaining protected fragments of EEER and EZCA. With areas of respectively 30.8 km^2 and 23.6 km^2, each would barely suffice to support a single individual at the densities of 2-3 per 100 km^2 estimated from our study. Jaguar home ranges are typically an order of magnitude larger than the areas of these reserves (Chávez 2010). Although the movements of individual jaguars can overlap considerably within and between sexes (Harmsen *et al.* 2009), the densities of 14 to 44 per 100 km^2 that would result from constraining the current population to only EEER and EZCA (Table 2.3, 'habitat' model) would be an order of magnitude higher than those found in any free-ranging populations.

Due to the difficulty of identifying individual pumas from camera trap photographs, it was not possible to estimate puma densities in our study. Values for naïve occupancy (NO) and relative abundance index (RAI) where similar for pumas and jaguars in NYP (Table 2.4), although generally higher for pumas than jaguars in EEER (Appendix 2, Table A2.1) and lower for pumas than jaguars in EZCA (Appendix 2, Table A2.2). Harmsen *et al.* (2010) found that pumas in Belize tended to use forest trails more than jaguars, with jaguars more likely to use the forest matrix. If this holds true also for our study sites, then pumas will have had higher capture probabilities than jaguars in our sampling sites, due to our deployment of camera-trap stations mainly along trails. In this event, we have reasonable grounds for concluding that pumas may be present at somewhat lower densities than jaguars in EZCA, and at commensurate densities in EEER. Likewise, Ávila Nájera (2015) found that the most abundant species in EEER, estimated by RAI, were jaguar, ocellated turkey, grey fox and puma.

Values of RAI for all species showed a strong correlation with values of NO, which suggests that these estimates provide some evidence of species abundance in our study sites. We, nevertheless, advise using our RAI estimates with caution. We note that in our own data, where we were able to make comparisons for jaguars, values of RAI show no correspondence to the robust SECR estimates (Table 2.3 and Appendix 2, Tables A2.1 and A2.2). RAI and NO for species captured in our study area could reflect actual abundance and occupancy, but are likely also to reflect heterogeneity in capture probabilities (Harmsen *et al.* 2010; Sollmann *et al.* 2013). The design of CENJAGUAR that we adopted was tailored to work best for large species (> 6.8 kg). There is an extension of CENJAGUAR that targets smaller species (1.3 – 6.8 kg) with home range areas < 1 km^2. Four camera-trap stations should be placed in 0.25-km^2 (0.5 x 0.5 km) sub-cells, with stations separated by 150 m. At least two 0.25 km^2 sub-cells should be placed inside each main vegetation type of the sampling area, and they should remain active for 10 days (Chávez *et al.* 2013). In order to deploy this design, we would have needed three times more camera-traps, which was not logistically feasible. We therefore consider that our estimates for smaller species are probably underestimates.

In NYP, jaguars and pumas showed high overlap in their activity patterns. However, jaguars were slightly more nocturnal, showing a peak of activity at dusk, whereas pumas were slightly more diurnal and showed a peak of activity at dawn. Similar results were found in a previous study in EEER (Ávila Nájera 2015), where activity patterns of jaguars and pumas overlapped. Both species showed cathemeral activity patterns, remaining active all day and night, although jaguars were active predominantly at night.

Activity patterns vary across the geographic distributions of jaguars and pumas. For example, in Calakmul Biosphere Reserve in the Southern Yucatán Peninsula of Mexico, jaguars and pumas are mainly crepuscular, but pumas show a greater tendency towards nocturnal behaviour (Middleton *et al.* in submission). In Central Mexico, jaguars are nocturnal, while pumas are mostly crepuscular (Monroy-Vilchis *et al.* 2009). In Hato Piñero, Venezuela, jaguars and pumas are both more active at night (Scognamillo *et al.* 2003). Likewise, in Cockscomb, Belize, jaguars and pumas are nocturnal, exhibiting high overlap in their activity patterns (Weckel *et al.* 2006; Harmsen *et al.* 2009). However, in Southern Belize, jaguars are mostly active in the daytime, and pumas are nocturnal (Dobbins *et al.* 2018). In Gran Chaco, Bolivia, jaguars remain active all day, but show peaks at dawn and dusk, and reduce their activity at night (Maffei *et al.* 2004).

Activity patterns of jaguars and pumas in NYP showed signs of segregation from the patterns of their main prey. Similar results were found previously in EEER by Ávila Nájera (2015). In contrast, in Cockscomb, Belize, jaguars have shown high temporal overlap with their main prey species (Weckel *et al.* 2006). In El Pantanal, Brazil, jaguars and pumas have also shown activity overlap between each other, and with their main prey (Foster *et al.* 2013). Likewise, in a human-modified landscape in South-Eastern Brazil, pumas have shown a high overlap of activity with their preferred prey (Azevedo *et al.* 2018). Of these different regions, the NYP area is the most disturbed by human activities, which may provide more opportunities for favoured prey to avoid being active at the same times as their most frequent predators.

Our analysis of prey remains in jaguar and puma scats revealed broad diets for both species and substantial overlap between them, consistent with considerable opportunism in their carnivorous diet (Foster *et al.* 2010c). Ungulates were the preferred prey of jaguars and pumas in NYP. Collared peccary was the most preferred species for both felids, followed by deer, and the activity patterns of jaguars and pumas differed with the patterns of collared peccary and deer. Jaguars showed a broader dietary niche than pumas, but jaguars consumed a smaller number of species. Pumas, on the other hand, showed stronger preferences for a few prey species. Wider evidence for omni-carnivory in these felids is found in the notable geographic variations in diet according to prey availability. In a previous smaller study in EEER (Ávila Nájera 2015), deer was found to be the main prey species consumed by jaguar, followed by collared peccary and nine-banded armadillo; pumas preferred collared peccary, followed by deer and spider monkey. In Calakmul, in the Southern Yucatán Peninsula, jaguars and pumas have shown a high dietary overlap, and consumed a large number of species, but preferred a few medium and large species, with jaguar particularly selecting for larger species (Chávez 2010). In contrast, jaguars and pumas in Cockscomb, Belize have shown low dietary breadths and low dietary overlap, in an area with abundant armadillos (*Dasypus novemcinctus*) that were greatly favoured by jaguars, and abundant pacas (*Cuniculus paca*) that were favoured by pumas (Foster *et al.* 2010a). Both species also consumed large prey, such as peccaries (*Pecari tajacu* and *Tayassu pecari*) and red brocket deer (*Mazama americana*), although adult peccaries were favoured by jaguars and juveniles by pumas (Foster *et al.* 2010a). Weckel *et al.* (2006) also found that jaguars in Cockscomb selected larger prey types, especially collared peccaries. A low dietary overlap has also been found in the Maya Biosphere Reserve, in Guatemala, where jaguars preferred medium-sized prey species while pumas selected both large and medium-sized prey (Novack *et al.* 2005). In other sites, large-sized prey species, and especially peccaries, have been found as the preferred prey for jaguars (Oliveira 2002; Polisar *et al.* 2003; Scognamillo *et al.* 2003), while pumas select medium-sized prey, including juvenile collared peccary (Scognamillo *et al.* 2003). If we consider jaguars and pumas to be opportunistic carnivores, then their limiting resource is less likely to be any specific prey than the availability of sufficient habitat to support prey of any kind. These felids are efficient users of limiting resource in this respect, tolerant of disturbance to the extent that little suitable habitat is left unused by their populations and by the populations of their prey (Doncaster 1996).

Stable coexistence of carnivore species requires some level of segregation along trophic, temporal and/or spatial niche dimensions, or else segregation in trade-offs between competitive dominance and vital rates (Schoener 1974; Karanth & Sunquist 2000; Doncaster 2009). Jaguars and pumas are thought to coexist by differential use of their habitats (Schaller & Crawshaw 1980; Emmons 1987; Scognamillo *et al.* 2003; Harmsen *et al.* 2009; Chávez 2010; Sollmann *et al.* 2012; Polisar *et al.* 2003). Spatiotemporal differences in habitat use are likely to facilitate coexistence when these species share the same prey with different activity patterns, or select different prey with similar activity patterns (Harmsen *et al.* 2011, Foster *et al.* 2013). The felids might have limited scope for temporal segregation, however, in areas with high ambient temperatures such as NYP, since heat generally supresses predator activity (Scognamillo *et al.* 2003; Estrada 2008; Sunquist 1981; Hayward & Slotow 2009). In our study both jaguars and pumas showed minimal activity around noon, when ambient temperatures typically exceeded 30 °C and frequently exceeded 40 °C. Moreover, the felids have few options for spatial segregation in NYP, with its highly disturbed landscape presenting only a largely homogeneous secondary forest on flat karst limestone (Wilson 1980), containing all of their prey and frequently used by hunters, or inhospitable land converted to human uses of agriculture or settlement (Primack *et al.* 1998; González-Iturbe *et al.* 2002). In our study, jaguars and pumas showed possible evidence of mutual attraction (in 2015), which in the light of their high temporal and dietary overlap is consistent with a forcing together of the two species. Jaguars moreover made exclusive use of some habitat in EZCA (in 2016) which is consistent with an outcome of competitive dominance in otherwise shared areas.

Indirect evidence accumulated over many studies suggests that jaguars achieve competitive dominance over pumas, probably due to their larger size (Harmsen *et al.* 2009; Sollmann *et al.* 2012; Elbroch & Kusler 2018). For example, in heterogeneous landscapes where jaguars and pumas are sympatric, pumas tend to use more open habitats than jaguars, including disturbed areas such as croplands and pasture, and jaguars favour forests over exposed areas (Scognamillo *et al.* 2003). Pumas are able to occupy a subdominant generalist niche, adjusting their behaviour to maximise overlap with prey species while avoiding peaks in jaguar activity. They showed a greater variety of prey selection than jaguars, which might allow them to coexist using altered activity schedules or hunting smaller prey (Iriarte *et al.* 1990; Taber *et al.* 1997; Núñez *et al.* 2000; Scognamillo *et al.* 2003; Azevedo 2008; Harmsen *et al.* 2009).

We suggest that patterns of jaguars and pumas in NYP are likely to be determined by the high daytime temperatures prevalent during a large portion of the year, and that jaguars dominate over pumas. The more diurnal activities of pumas might be a consequence of the dominance exerted by jaguars, forcing them to hunt when temperatures are higher. In addition, nocturnal activity patterns might advantage jaguars in hunting, since attacking inactive, non-vigilant, animals, can increase capture success (Foster *et al.* 2013; Romero-Muñoz *et al.* 2010) and can reduce risks of injury (Azevedo & Murray 2007). Since pumas are more active in daytime, they are likely to have access to a higher number of prey, reflecting their greater species richness in our data. However, evidence suggests that temporal partitioning is a less important mechanism in driving coexistence between competitors, and it is more likely that animals segregate by food or habitat use (Schoener 1974). Our results are consistent with dietary and spatial partitioning in habitat use playing an important role for coexistence of felids in NYP, in combination with competitive dominance. Although both felids prey on similar species, pumas seemed to select deer more than jaguars. In this study, we identified a possible component of spatial segregation that may fluctuate between years. We recommend that this spatial niche dimension be further assessed in future studies using GPS or satellite collars on individuals, in order to determine its role in facilitating coexistence of these two species in NYP. Sex-dependent temporal differences in habitat use have also been identified as a mechanism that can drive coexistence between these felids. Given the strong male bias in camera-trap records, the activity records that we report are predominantly those of males. Our study had insufficient data to partition activity by sex, and we recommend that future studies assess intraspecific variation in activity patterns between jaguars and pumas in NYP (Azevedo *et al.* 2018).

It has been suggested that a sample size of 70-100 scats is required to estimate jaguar and puma dietary richness accurately, but less than half is enough to detect the most common prey species (≥ 5% occurrence), while likely overestimating their presence in proportion to the underestimation of rare prey (Foster *et al.* 2010b). The sample size of jaguar and puma scats available to estimate jaguar and puma diets in NYP was smaller than the recommendation to make accurate estimations of diet, but sufficient to detect the most common prey species in the diet of these felids. We suggest that future studies aiming to determine dietary niche partitioning of jaguars and pumas in NYP should seek a larger sample size to accurately estimate diets, since it has been recognised that these felids can coexist on small differences in prey spectra (Aranda & Sánchez-Cordero 1996).

The Northern Yucatán Peninsula still maintains vast areas of jaguar habitat with healthy conservation status, and it constitutes one of the areas in Mexico where jaguar conservation has good chances of success in the long-term (Sanderson *et al.* 2002a; Carrillo *et al.* 2007). There is nevertheless a lack of knowledge about jaguar populations (Navarro *et al.* 2007). Our study has contributed to fill this gap. Long-term monitoring of jaguar populations should continue in order to monitor changes in population trends of jaguars and pumas, and in their prey. The main prey in the diets of large felids are also important sources of wild meat for local people in NYP (see Chapter 3). The effects of subsistence hunting by local people on these felids are of particular concern, and require a full assessment, since felids and people both compete for the same large prey. Long-term game hunting may force a higher foraging effort on large felids, which will eventually lead to an increased likelihood of encounters with humans and their livestock, resulting in lower felid carrying capacities and threats to their long-term persistence (Novack *et al.* 2005).

Conclusion

Jaguars and pumas are relatively abundant and widely distributed in NYP, and able to exploit a wide diversity of forest prey. Their largely similar diets, patterns of daily activity and use of space may reflect a reduced access to niche dimensions by which they might otherwise avoid competing with each other, caused by human pressures on land and natural resources. The extent of niche sharing by these felids, noted in many studies, suggests also an ability to make efficient use of whatever space remains available to them. The private reserves of EEER and EZCA are nevertheless far too small to maintain viable populations of jaguars and pumas without the continuing presence of surrounding communal forests. Here and in the largely unpatrolled reserves, both felids compete for the same prey with human hunters. Long-term anthropogenic pressures on land and trophic resources will inevitably diminish the prey base for everyone, which will likely promote felid attacks on livestock, and raise human-wildlife conflicts in the area. The reserves continue to provide vital forest refuges for felids and their prey, and felid conservation depends on effective management of the reserves to regulate extraction of wildlife resources. Successful conservation management of the felids will additionally require maintaining the surrounding communal forests, and the welfare of people in the rural communities who are the main caretakers of forests outside reserve borders.

Chapter 3 - Evaluation of livelihoods in Maya forest communities of Northern Yucatán, and potential for coexistence with large felids

Contributions

I initiated the idea for the study and developed the aims, objectives, and methods. I designed the questionnaire, managed the evaluation of ethics in accordance with UoS policy, performed the surveys, analysed the results, and wrote the chapter. Personnel from NGO Pronatura Península de Yucatán, A. C. provided links to key informants and interviewees. Specifically, Abraham Puc acted as a gatekeeper. Gabriela Oxté (Pronatura) assisted me with some of the interviews. UoS co-supervisor Professor C. Patrick Doncaster provided comments on drafts of the questionnaire and the chapter. UAM supervisor Dr Cuauhtémoc Chávez provided loan of vehicular transport to access sites, and provided early contacts with personnel from Pronatura. Fieldwork was conducted with resources obtained with a CONACyT studentship (202650), two SEP Beca Complemento studentships (2014: BC-3606; 2015: BC-4118), a Rufford Small Grant (17047-1), and with resources granted from Cuauhtémoc Chávez.

Abstract

Human-wildlife conflict presents a widespread threat for large carnivore persistence. Its mitigation is urgently needed to protect these species, all of which are threatened with extinction, and to alleviate impacts on rural livelihoods. In the Yucatán Peninsula, human-wildlife conflict is one of the main threats for large felids. It has been triggered largely by predation on livestock, following expansion of the cattle-ranch frontier since the 1950**s**, and lax management of livestock. The increasing number of complaints about livestock attacks by large felids and subsequent retaliatory jaguar killings, make the need to seek alternatives to mitigate this conflict an urgent matter in the conservation for the species. This chapter explores interactions between humans and large felids in three small, rural Maya communities from the northern Yucatán Peninsula in Mexico. A questionnaire survey of 30 villagers was conducted to evaluate their livestock husbandry practices, wild meat consumption, hunting habits and experiences of human-wildlife conflict. Interviewees represented a sample of typical rural forest dwellers in this region, in owning small, fenced plots of land where they predominantly kept domestic animals for consumption. They had wide knowledge of the wildlife present in their local area. They showed perception biases with respect to estimating higher abundances of game species over others, and preferring to live amongst wild herbivores than carnivores. Interviewees had concerns about perceived decreases in the abundances of local wildlife over recent years, and attributed these reductions mainly to regular subsistence hunting by their communities. Only a small proportion of interviewees reported large-felid attacks on their livestock, and those that did had subsequently changed their livestock management practices to prevent further attacks. Interviewees believed that current law facilitates a reduction in wildlife conflicts, and that the Livestock Insurance Fund is the best mitigation tool. The principal game species in the area, as identified by the survey, were also the main prey for jaguars and pumas in the two nearby natural protected areas of El Edén Ecological Reserve and El Zapotal Conservation Area. Survey results suggested a valuable contribution in technical assistance by local NGO Pronatura, aimed at reducing conflicts with large felids in these communities. The presence of this NGO provides an important bridge between local communities and government policy.

Introduction

Large terrestrial carnivores play important roles in the regulation of ecosystems. However, they are threatened with extinction on all continents where they occur (Ripple *et al.* 2014). The decline of their populations is thus a global issue. In Asia, Africa and the Americas, large felids, canids, and ursids suffer from multiple extinction pressures (Weber & Rabinowitz 1996). These pressures are mostly attributable to lethal control in response to interactions between them and people (van Eeden *et al*. 2017). Human-wildlife interactions arise whenever the needs and activities of free-ranging animals impact negatively on human endeavours, or when human activities negatively impact wildlife needs (Madden 2004). The jaguar (*Panthera onca*) and puma (*Puma concolor*) in Latin America provide exemplars of human-wildlife conflicts. These large felids often share their habitats with livestock ranches. Competition for limited resources leads to multiple negative impacts on people, including livestock depredation and reduced economic welfare, and negative impacts on the felids including mortality in retaliation killings and reduced food availability (Amit & Jacobson 2017).

Jaguars and pumas play important roles in the culture and religion of many Native Latin American peoples from Mexico, Central and South America. They have had a profound effect on human sensibilities since the beginning of recorded time, and they continue to be revered and respected in rural communities (Saunders 1998; 2005). As large-felid habitats have become increasingly fragmented, however, they have become labelled as dangerous livestock killers and have been persecuted for that reason (Weber & Rabinowitz 1996; Polisar *et al.* 2003; Saracho *et al.* 2006; Moreno & Olmos 2008; Chávez & Zarza 2009; Garrote 2012). In a cattle ranch in Costa Rica, jaguars were responsible for 176 livestock attacks from 1991 to 1998, which resulted in the elimination of 21 jaguars (Sáenz & Carrillo 2002). In Los Llanos, Venezuela, jaguars and pumas were responsible for cattle losses in 73% of 37 assessed cattle ranches (González-Fernández 1995). In one cattle ranch in the same area, jaguars and pumas were responsible for 13% of cattle losses from 1991 to 1997 (total loss of $36,000 American dollars; Scognamillo *et al.* 2002). In El Pantanal, Brazil, jaguars and pumas were responsible for 43 livestock kills from 1980 to 1983 (Crawshaw & Quigley 2002). Jaguars and pumas have also been reported to attack domestic livestock in Paraná state in SE Brazil (Leite & Galvão 2002). In a cattle ranch near Iguaçu National Park, Argentina, jaguars have been reported to attack domestic pigs (Schiaffino *et al.* 2002). Around Calakmul Biosphere Reserve, in Southern Yucatán

Peninsula, in Mexico, at least 100 cattle ranches have reported livestock predation by large-felids, with only 3% of the animals killed by these predators, and ca. 30 jaguars killed by retaliation every year (Zarco-González *et al.* 2018). Only one study has assessed human-large felid interactions in rural communities from the Northern Yucatán Peninsula (Hernández 2009). In their results, now dating from more than a decade ago, 33% of interviewees reported attacks by large felids and coyotes in a period of 5 years, and perceived large carnivore predation as the main cause of loss. Here we provide recent evidence from a questionnaire survey assessing human-large felid conflict in rural communities from the Northern Yucatán Peninsula.

Conflicts with jaguars and pumas have been aggravated by the disappearance of their natural prey species, the reduction of forest cover, the expansion of the cattle frontier, and traditional subsistence hunting by local people (Polisar 2002; Polisar *et al.* 2003; Chávez 2010). Nonetheless, it has been shown that many livestock losses are caused by disease, flooding, theft, due to poor husbandry management practices, where animals are left alone and are allowed to roam freely throughout the forest, or when jaguars become sick or injured as a result of shooting by ranchers and cannot feed on wild prey (Weber & Rabinowitz 1996; Scognamillo *et al.* 2002; Saracho *et al.* 2006; Moreno & Olmos 2008). In this study, we will evaluate local game hunting practices in relation to the natural prey of jaguars and pumas in the region (as detailed in Chapter 2).

Although the impact of jaguar and puma killings on livestock economy is often exaggerated, the loss of a cow worth in the order of US$1400 (estimated for southern Mexico; SNIIM 2018) can be unsustainable to a small farmer (Azevedo & Murray 2007; Amit *et al.* 2013). In addition, ranchers can feel especially powerless to protect their enterprises (Naughton-Treves *et al.* 2003) when restrictions are imposed on lethal control (Bergstrom *et al.* 2009). Lethal control is a dominant component of this conflict and often occurs illegally in retaliation for a livestock predation event (Creel & Rotella 2010).

A high mortality of jaguars and pumas, as well as the growing number of protests about their livestock kills, suggests the need for options to help livestock owners and conservation biologists to manage this conflict. This could only be possible with prior understanding of the particular determinants of the conflict at each location. Although general principles can be applied to human-wildlife interaction management strategies, differences in the determinants of interactions at each location indicate that strategies must be situation-specific. Each situation is unique, due mainly to evident variations in the spatial, temporal and socio-economic determinants for human-large felid interactions. A detailed assessment of the conflict factors at each location is therefore essential, and must generate a management strategy tailored to each situation to achieve maximum impact (Cavalcanti 2008; Inskip & Zimmermann 2009; Peña 2011; Amit *et al.* 2013; van Eeden *et al.* 2017).

In this regard, Mexican NGO Pronatura, through its Feline Conservation Program (Pronatura 2017), works with local communities and ejidos in the Yucatán Peninsula to promote jaguar conservation, and to minimise human-wildlife conflicts between livestock farmers and large felids. Their actions include monitoring of felid populations and their prey using camera-traps, by giving advice and applying actions for better livestock management, to minimise attacks. They also build capacity to access the Livestock Insurance Fund, developed by the Ministry of Agriculture, Livestock, Rural Development, Fisheries and Food ('SAGARPA', now 'SADER') and managed by the National Confederation of Livestock Organisations. This programme covers losses of cows, sheep, pigs, horses and goats to medium and large predators (black bears, coyotes, Mexican wolves, feral dogs, ocelots, bobcat, jaguars and pumas (CNOG 2016; Pronatura 2017). They also collaborate with Mexican government officials to relocate problem felids, along with the 'Grupo de Expertos en la Conservación y Manejo Sustentable del Jaguar y otros Felinos Silvestres' and the 'National Alliance for Jaguar Conservation' (C. Chávez, pers. comm.; Alianza Nacional para la Conservación del Jaguar 2018). Here, we evaluate local perceptions on human-large felid conflict and we provide new insights about effectiveness of local NGO Pronatura in helping mitigate human-large felid conflict in the Northern Yucatán Peninsula.

The northern Yucatán Peninsula between the states of Yucatán and Quintana Roo constitutes a wildlife corridor potentially uniting the reserves of Ría Lagartos and Yum Balam, the former being one of the most important UNESCO biosphere reserves (Ramsar 2018), and the latter a refuge for the jaguar and puma, and their prey species, some considered as endangered by Mexican law (e.g. brocket deer, white-lipped peccary, Mexican tamandua, ocellated turkey and great curassow; CONANP 2018; SEMARNAT 2018c). The largest poles of economic development in the area are the cities of Cancún and Mérida, at distances of 90 and 170 km respectively, with tourism being the main economic driver of the region. Additionally, Holbox has become an important tourism centre in the area for the past three decades, leading to higher pressures for the area, due to building construction to accommodate larger numbers of tourists, and consequently, to the community due to significant rise in land value, making land ownership by local inhabitants increasingly difficult (Tran *et al.* 2002).

Villagers in rural communities mostly find work only as janitors or maintenance staff in hotels or as informal traders. A small number of city-based families and investors obtain most of the economic benefit from tourism within rural areas. Local communities maintain a semi-rural way of life, supplemented by tourism-related service jobs in catering and hospitality, taxis and tour guides, masonry and maintenance. Local people take multiple occupations to offset the small income and lack of government support to the activities of sustainable rural development. However, the communities get only meagre income for quotidian survival, and family emergencies or economic failure are often met by selling off tropical forest lands at greatly reduced prices. There is constant pressure from investors to acquire more land for tourist and commercial complexes, as well as tourist passageways that connect tourism hotspots of Cancún, Mérida and Holbox (Escamilla *et al*. 2000; León & Montiel 2008). A clear example is the nearby community of Chiquilá, which constitutes the main connection between the mainland Yucatán Peninsula and Holbox Island, and where the provision of tourism services is its main economic activity (SEMARNAT 2018c). Likewise, the nearby rural community of Solferino (ca. 13 km away from Chiquilá) has experienced similar pressures during the past decade (pers. obs.).

The highly fragmented forests on the Yucatán Peninsula (states of Yucatán, Quintana Roo and Campeche) face severe anthropogenic threats, such as the development of agriculture and livestock husbandry (Sanderson *et al.* 2002b; Faller *et al.* 2007). Livestock husbandry constitutes a key economic activity in the region, which has gradually increased the frequency of human-wildlife conflicts over the last few years. Jaguar and puma predation events on livestock are now reported regularly, and conflict has become one of the main threats to the conservation of these felid species in the area (Faller *et al.* 2007; Navarro *et al*. 2007; Chávez & Zarza 2009; Rodríguez-Soto *et al.* 2011; C. Chávez, pers. comm.). In particular, the state of Yucatán maintains the smallest surface (7,814 km^2) of potential habitat for jaguars in the Yucatán Peninsula, compared to the states of Quintana Roo (24,410 km^2) and Campeche (22,764 km^2). This surface is also highly fragmented, also maintaining the highest surface for potential attacks by jaguars to livestock (7,459 km^2), compared to Quintana Roo (5,417 km^2) and Campeche (6,035 km^2; Chávez & Zarza 2009).

Subsistence hunting of jaguar and puma prey species is actively and openly practiced in rural communities. It involves deep traditional knowledge, represents a vital subsistence strategy of many rural populations, and acts as a supplementary activity to agriculture, cattle ranching, bee-keeping, gardening, fishing and forest extraction (Escamilla *et al*. 2000; Terán & Rasmussen 1994; Barrera-Bassols & Toledo 2005; León & Montiel 2008). Historically, many wild animal species were part of the resource complex managed by traditional Maya practices, and were important elements in their 'cosmovision' of the natural world (Anderson & Medina 2005; Barrera-Bassols & Toledo 2005). Currently over 60 terrestrial vertebrate species are extracted for subsistence purposes in rural communities from the Yucatán Peninsula (Jorgenson 1995; Quijano-Hernández & Calmé 2002; Rodríguez *et al.* 2012; Ramírez & Naranjo 2005; Santos-Fita *et al.* 2012).

Under Mexican law, the jaguar is considered as threatened, and a top priority species for conservation. In consequence, its hunting is prohibited (NOM-059-SEMARNAT-2010: SEMARNAT 2010; CONANP 2012). However, subsistence hunting of its non-endangered prey is allowed outside protected areas in Mexico, which in many cases are overexploited due to lack of effective monitoring by the Mexican government (Chávez *et al.* 2016). If effective conservation measures are not put into place in the next few decades, jaguars and pumas will face a high risk of extinction in the Yucatán Peninsula and, consequently, in the Maya region (Ceballos *et al.* 2002).

The aim of this chapter is to make a new assessment of human-wildlife conflict, combined with a first assessment on perceptions about local wildlife, hunting and wild meat consumption habits, for local people from rural communities in the northern Yucatán Peninsula, living in coexistence with jaguars and pumas and their prey. The purpose of the assessment is proximally to explore options for reducing livestock predation by jaguars and pumas, and crop losses to local wildlife, and ultimately to contribute to the welfare of local communities and the conservation of felids. Through the communication of the results of this study to researchers and NGOs working on sustainable rural biodiversity, and Pronatura in particular working with Maya communities in Yucatán forests, we are taking steps to give a voice to the people most reliant on rural biodiversity, and to hear their needs for sustainable wellbeing.

Methods

Focal populations

Three small, adjacent communities to the tropical forests of the private protected area of El Zapotal Conservation Area (ca. 2-5 km; Pronatura 2015) were sampled. Local residents from the rural Maya communities of Nuevo Tesoco, Santa María and San Pedro Bacab, were interviewed. They belong to Tizimín municipality (ca. 73,100 inhabitants) in Yucatán, which holds the largest number of cattle in the Yucatán Peninsula (Hernández *et al*. 2004). These communities maintain ca. 180, 420 and 200 inhabitants, respectively (INEGI 2010).

The nearest poles of economic development for the municipality of Tizimín are the cities of Cancún and Mérida, at distances of 90 and 170 km respectively. Amongst the inhabitants of Tizimín, 43% have only primary-school education (INEGI 2016). Value of the Human Development Index (HDI, a composite index of life expectancy, education, and per capita income indicators) of 0.651 in the municipality of Tizimín is well below the average of 0.739 for the State of Yucatán (OIDH 2014; PNUD 2015). By comparison, HDI is 0.774 in Mexico, and exceeds 0.9 throughout the USA, Canada, Europe, Australia, New Zealand and Japan (UNDP 2018).

Both men and women ≥18 years old were interviewed with the structured questionnaire 'Questionnaire to evaluate livestock management practices, perceptions of wildlife, wild meat consumption and human-wildlife conflict in the Yucatán Peninsula, Mexico' (ERGO ID number: 13836). Only one individual per household was interviewed, in order to obtain representative samples of the surveyed communities (Fink 2009) and to avoid duplication of answers (e.g. individuals from the same household likely share livestock ranches, have the same past experiences of human-wildlife conflict, etc.). The original intention to interview ~30 people from each of three communities, in roughly equal sex ratio, had to be scaled down, due to dependence on Pronatura for providing the link with potential interviewees, time constraints on access to transport to these remote communities and limited numbers of suitable interviewees, who migrate temporarily to nearby cities (mainly Mérida and Cancún) to seek jobs to support their families. We also planned to interview an equal number of men and women, but we encountered issues at having access to women due to their roles in the household (e.g. they were usually unavailable due to childcare, household work, etc.)

Questionnaire design

The questionnaire (Appendix 3) was developed based in questionnaires and findings from Miller (2002), Quijano-Hernández & Calmé (2002), Conforti & Azevedo (2003), Polisar *et al.* (2003), Ramírez & Naranjo (2005), Johnson *et al*. (2006), Saracho *et al*. (2006), González-Maya (2007), Foster *et al*. (2014), Peña (2011), Santos-Fita *et al.* (2012) and Boulhosa & Azevedo (2014). The questionnaire was designed as a face-to-face interview lasting ca. 50 minutes in total. It contained 37 questions distributed in five sections: (1) Livestock management, (2) Perceptions towards wildlife, (3) Hunting habits and wild meat consumption, (4) Human-carnivore conflict, and (5) Socio-demographic characteristics of interviewee. The order of questions, and the order of species in Section 2, were determined by recommendations in Fink (2009) and Bryman (2012) on design and organisation of surveys. Sensitive questions, here relating to hunting habits (Section 3) and human-wildlife conflict (Section 4), were placed towards the end of the interview. Questions about species of felids and their main prey (Section 2) were placed in the middle of the interview, and towards the end of the perceptions section. In order to minimise the possibility of confusion about species names, interviewees were shown colour plates with photographs of each species in Section 2.

In June 2015, a pilot test of a first version of the questionnaire survey was run on 2 local villagers from the northern Yucatán Peninsula. The aim was to explore potential sources of error in the design of the questionnaire, such as the relevance and clarity of one or a set of questions and the real duration of the questionnaire (Fink 2009). The pilot run led to clarifications of several questions (e.g. language used, order of questions, inclusion of additional wildlife species in the questionnaire), and removal of some questions on livestock management that proved unsuitable or non-applicable to this area (e.g. occupation of interviewee, which could lead to a break in anonymity, selling livestock nationally or internationally, which does not happen here) to keep the questionnaire to a manageable length.

Interview technique

Potential participants were identified by key informants identified by Pronatura, and were approached during weekday working hours (Mondays to Fridays 8:00 am – 6:00 pm, in their workplaces or households. They were contacted with the collaboration of personnel from Pronatura. Personnel from Pronatura acted as gatekeepers, facilitating access to interviewees and encouraging their trust in the interviewer (Singh & Wassenaar 2016).

For each potential participant, the researcher introduced herself, gave her affiliation, and briefly outlined the character and purpose of the study. She then asked the person if they would be willing to take part in the survey. In case of acceptance, they were asked if it was convenient to perform the interview immediately, or if they would wish the researcher to come back later or to conduct the interview in another location. All potential interviewees agreed to undertake the interview, and all agreed that the questionnaire could be conducted immediately. This method of direct approach was selected on the basis that most potential participants had no access to a home telephone, had poor literacy skills, and were untrained in operating a computer or using the Internet.

Before starting the questionnaire, a Participant Information sheet (Appendix 4) was read to the potential participant. This took about 5 minutes, to explain the purpose of the study, the kinds of questions they would answer, the benefits of collecting this information, how the findings were going to be used (only for research), an assurance of anonymity, their right to refuse to answer any question, and their right to withdraw from the interview at any point in case of discomfort. It was specified that, if during the interview a participant expressed their discomfort or refusal to answer one or several questions, the questions would be excluded and the interview would then continue. If at any point the participants chose to withdraw from the interview, it would stop immediately and the paper sheets associated with it would be destroyed in front of the participants and handed to them. This never happened.

At the beginning of the study, it was assumed that a considerable proportion of the potential participants lacked basic reading and writing skills, and that some questions might be perceived as sensitive issues, such as their involvement in illegal activities (e.g. wildlife poaching and consumption of meat from endangered species). This made the guarantee of identity protection a prerequisite. For this reason, the potential participants were not asked to sign an Informed Consent form. They were only asked to provide an express verbal agreement to participate in the study, after the Participant Information sheet was read out to them and before the start of the questionnaire. Only in the event of their agreement to become a participant in the study could the questionnaire begin. The questionnaire was performed in private, with the participants verbally answering questions, and the researcher filling out a paper-based questionnaire. After the questionnaire was conducted, interviewees were asked if they wished to suggest additional potential participants. This 'snowball' technique amplifies a study sample through referrals made among people who share, or know of others who possess, some characteristics that are of research interest. It is particularly applicable when the focus of study is on a sensitive issue, and thus requires the knowledge of insiders to locate people for study (Biernacki & Waldorf 1981). In this case, it led to 10 additional interviewees, which helped reach the final $n = 30$.

Analysis of questionnaires

To protect personal data and study results, the questionnaire sheets were stored in a locked cupboard in the operations base at the research stations of El Edén Ecological Reserve (EEER) and El Zapotal Conservation Area (EZCA), during the period of data collection. During subsequent analysis of the data, they were stored in a secure location at the University of Southampton. After transcription of the data to anonymised electronic format, all questionnaire sheets were destroyed.

A code book was constructed to organise and code the data extracted from the survey questionnaires in a database suitable for analysis. For open-ended questions, a content analysis was performed prior to the construction of the code book in order to identify common ideas and to classify them into categories (Fink 2009; Bryman 2012).

Descriptive statistics were used to illustrate proportions and overall patterns in the raw data. Univariate analyses were used to describe frequency distributions of individual questions. Log-linear models on contingency tables were used to test for frequency dependence between categories in question pairs: (a) ownership of domestic animals or livestock losses by large felids vs perception of intentional attacks by large felids to humans; (b) opinions (positive, neutral and negative), and perceptions of local abundance, on carnivores and herbivores; and (c) perceptions of local abundance on species that are eaten by people vs species that are not eaten. Tables with low frequency counts were analysed with Fisher's exact test (Sokal & Rohlf 1991; Fink 2009; Bryman 2012).

Results

Individuals ($n = 30$; males = 23; females = 7) ≥18 years old living in different households from the communities of Nuevo Tesoco (males = 8; females = 2), Santa María (males = 8; females = 2) and San Pedro Bacab (males = 7; females = 3), were interviewed during 2015 and 2016. Most interviewees were middle-aged and had a low educational level (Fig. 3.1).

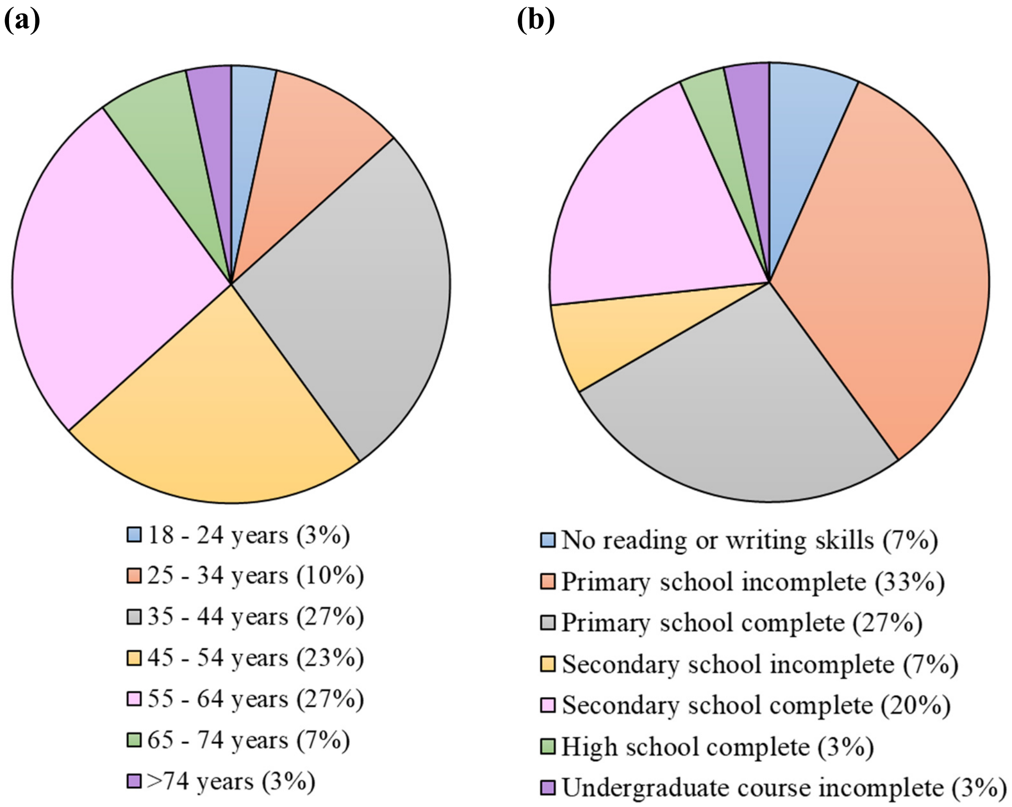


Figure 3.1. Demographic characteristics of interviewees: (a) age and (b) school level. The annotated lists show segments clockwise from the top.

Perceptions towards wildlife

Of the 37 wildlife species included in the questionnaire, all of which occur in the northern Yucatán Peninsula, 36 were recognised as present by at least two interviewees ($\bar{x} = 23 \pm 9$ recognitions per species; Fig. 3.2; Question 8 in Appendix 3). Baird's tapir (*Tapirus bairdii*) was the only species that was not recognised as occurring in the area; however, some interviewees recognised its name or image, and pointed out that it had been present in the past.

When we pooled wildlife species into groups of herbivores and carnivores, and tested for differences in abundance as a group, we found no differences between carnivores and herbivores in allocations by interviewees to high, medium and low abundances (χ^2 = 0.15; d.f. = 2; p = 0.93; Question 9 in Appendix 3). Nevertheless, individual species belonging to either group were perceived as having high, medium or low abundance (Fig. 3.2). However, they considered that game species (eaten by humans) were more abundant than other species (χ^2 = 28.72; d.f. = 2; $p < 0.001$; Questions 9 and 13 in Appendix 3).

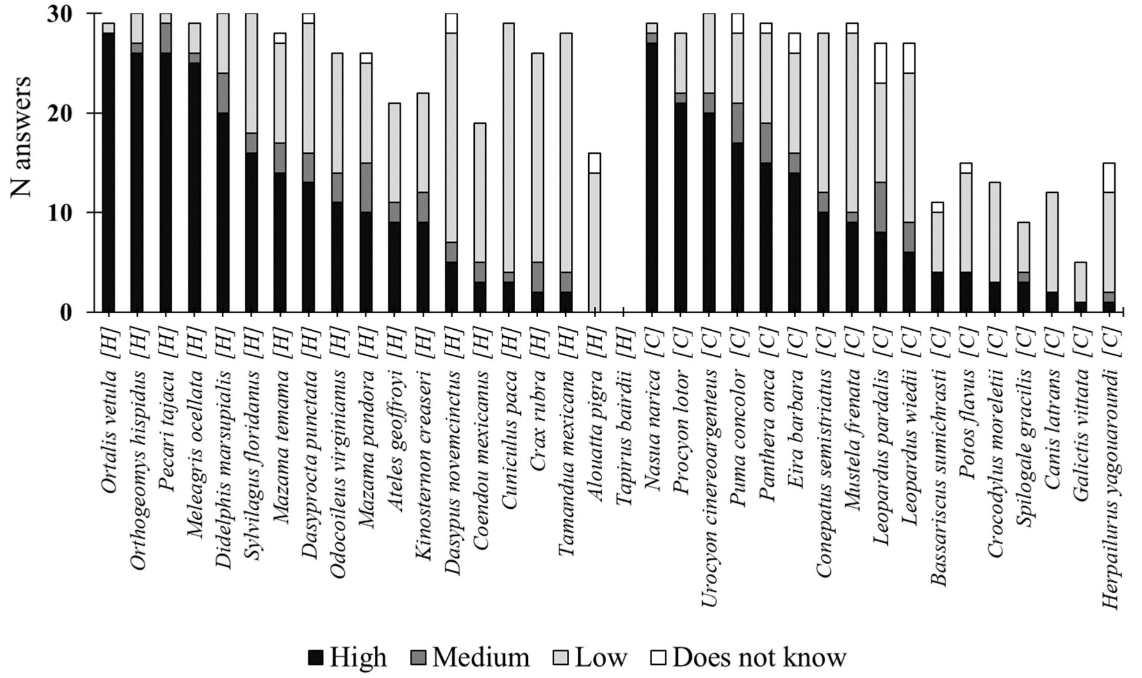


Figure 3.2. Opinion on local abundance (high, medium, low, does not know) of wildlife species. Species are classified by type: herbivore ([H], left) and carnivore ([C], right), and ordered left-to-right within each category by frequency of answers giving high abundance. See Table 3.1 for English names of species.

People were more likely to have a positive opinion about the presence of herbivore species in their communities (they liked having them) and a negative opinion about carnivores (χ^2 = 97.4; d.f. = 2; $p < 0.001$; Fig. 3.3; Question 12 in Appendix 3). These preferences did not depend on their perceptions about local abundances (high, medium or low; χ^2 = 0.27; d.f. = 4; p = 0.99, pooling across species for response frequencies in the three presence and three opinion categories; Questions 9 and 12 in Appendix 3).

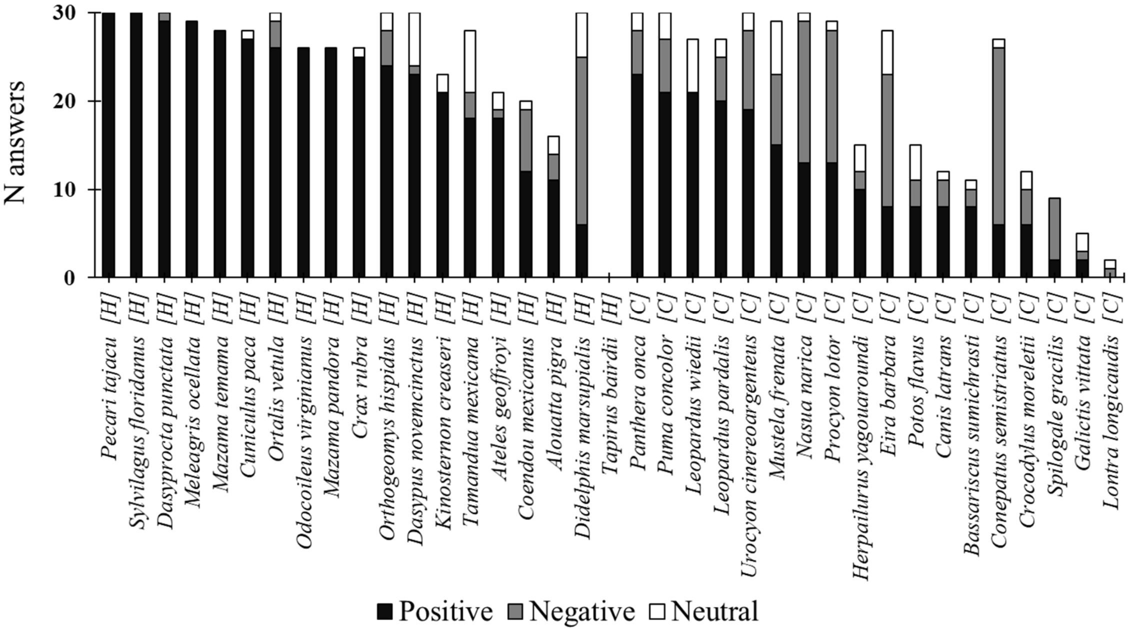


Figure 3.3. Opinion on presence (positive, negative or neutral) of wildlife species. Species are classified by type: herbivore ([H], left) and carnivore ([C], right), and ordered left-to-right within each category by frequency of positive opinion. See Table 3.1 for English names of species.

The principal role of wildlife species in nature (their ‘purpose’; Question 13 in Appendix 3) was most frequently perceived to be ‘aesthetic’, followed by roles as ‘source of food’ to people, and as ‘predators of animals/crops’. Together, these roles comprised 76% of the total answers. Table 3.1 contains a list of the 36 wildlife species included in the questionnaire that were recognised as present in the community, with the most frequent, and second most frequent, answers regarding perceptions about their roles in nature.

Table 3.1. List of wildlife species with the 1st and 2nd most frequent answers on their roles in nature (taxonomies following IUCN 2018).

Order	Family	Latin name	English name	Most frequent answer	*n*	2nd most frequent answer	*n*
CLASS MAMMALIA							
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	Common opossum	Predator (animals/crops)	19	Beautiful (aesthetic value)	3
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	Beneficial/not harmful	11	Beautiful (aesthetic value)	7
				Source of food for people	11	-	
Pilosa	Myrmecophagidae	*Tamandua mexicana*	Northern tamandua	Beautiful (aesthetic value)	12	Beneficial/not harmful	11
Primates	Atelidae	*Alouatta pigra*	Black howler monkey	Beautiful (aesthetic value)	6	Unpleasant/harmful	4
		Ateles geoffroyi	Geoffroy's spider monkey	Beautiful (aesthetic value)	15	Beneficial/not harmful	4
Rodentia	Erethizontidae	*Coendou mexicanus*	Mexican porcupine	Beautiful (aesthetic value)	5	Beneficial/not harmful	4
				Predator (animals/crops)	5	Unpleasant/harmful	4
	Cuniculidae	*Cuniculus paca*	Spotted paca	Source of food for people	22	Beautiful (aesthetic value)	5
	Dasyproctidae	*Dasyprocta punctata*	Central American agouti	Source of food for people	19	Beautiful (aesthetic value)	7
	Geomyidae	*Orthogeomys hispidus*	Hispid pocket gopher	Source of food for people	22	Predator (animals/crops)	7
Lagomorpha	Leporidae	*Sylvilagus floridanus*	Eastern cottontail	Source of food for people	16	Beautiful (aesthetic value)	12
Carnivora	Canidae	*Canis latrans*	Coyote	Predator (animals/crops)	8	Beautiful (aesthetic value)	4
		Urocyon cinereoargenteus	Grey fox	Predator (animals/crops)	10	Beautiful (aesthetic value)	9
				-		Beneficial/not harmful	9
	Procyonidae	*Bassariscus sumichrasti*	Cacomistle	Beneficial/not harmful	4	Beautiful (aesthetic value)	3
		Nasua narica	White-nosed coati	Predator (animals/crops)	19	Beautiful (aesthetic value)	6
		Potos flavus	Kinkajou	Beneficial/not harmful	6	Beautiful (aesthetic value)	5
		Procyon lotor	Northern raccoon	Predator (animals/crops)	18	Beautiful (aesthetic value)	6
	Mephitidae	*Conepatus semistriatus*	Striped hog-nosed skunk	Unpleasant/harmful	18	Predator (animals/crops)	5
		Spilogale angustifrons	Spotted skunk	Unpleasant/harmful	5	Predator (animals/crops)	3
	Mustelidae	*Eira barbara*	Tayra	Predator (animals/crops)	17	Beautiful (aesthetic value)	7
		Galictis vittata	Greater grison	Beautiful (aesthetic value)	2	-	
				Predator (animals/crops)	2	-	
		Lontra longicaudis	Neotropical river otter	Unpleasant/harmful	1	-	

Order	**Family**	**Latin name**	**English name**	**Most frequent answer**	***n***	**2nd most frequent answer**	***n***
Carnivora (cont.)	Mustelidae (cont.)	*Mustela frenata*	Long-tailed weasel	Beautiful (aesthetic value)	11	Predator (animals/crops)	10
	Felidae	*Herpailurus yagouaroundi*	Jaguarundi	Beautiful (aesthetic value)	9	Predator (animals/crops)	2
		Leopardus pardalis	Ocelot	Beautiful (aesthetic value)	16	Predator (animals/crops)	6
		Leopardus wiedii	Margay	Beautiful (aesthetic value)	16	Beneficial/not harmful	4
				-		Predator (animals/crops)	4
		Panthera onca	Jaguar	Beautiful (aesthetic value)	14	Predator (animals/crops)	7
		Puma concolor	Puma	Beautiful (aesthetic value)	11	Predator (animals/crops)	6
Cetartiodactyla	Cervidae	*Mazama pandora*	Yucatán brown brocket deer	Source of food for people	20	Beautiful (aesthetic value)	7
		Mazama temama	Central American red brocket deer	Source of food for people	20	Beautiful (aesthetic value)	6
		Odocoileus virginianus	White-tailed deer	Source of food for people	17	Beautiful (aesthetic value)	8
	Tayassuidae	*Pecari tajacu*	Collared peccary	Source of food for people	21	Beautiful (aesthetic value)	9
CLASS AVES							
Galliformes	Cracidae	*Crax rubra*	Great curassow	Beautiful (aesthetic value)	16	Source of food for people	9
		Ortalis vetula	Plain chachalaca	Source of food for people	17	Beautiful (aesthetic value)	9
	Phasianidae	*Meleagris ocellata*	Ocellated turkey	Source of food for people	19	Beautiful (aesthetic value)	13
CLASS REPTILIA							
Crocodylia	Crocodylidae	*Crocodylus moreletii*	Morelet's crocodile	Beautiful (aesthetic value)	4	Unpleasant/harmful	3
Testudines	Kinosternidae	*Kinosternon creaseri*	Creaser's mud turtle	Beneficial/not harmful	11	Beautiful (aesthetic value)	10

Interviewees believed that the main cause of increases in wildlife species in their communities was because they benefit from killing domestic animals and eating crops ('Eats crops/livestock/domestic animals'), while the main cause of declines was hunting by humans ('People kill/eat it'). Large-felid predation ('Large felids kill/eat it') was identified as the third main cause of wildlife species declines in the area (Fig. 3.4; Questions 10 and 11 in Appendix 3).

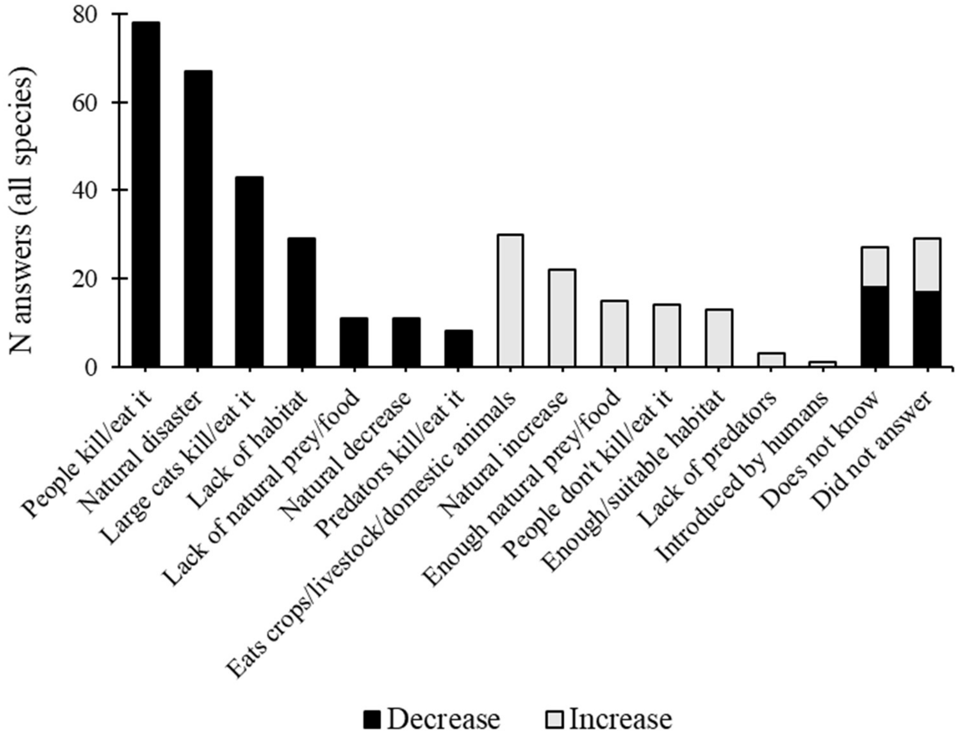


Figure 3.4. Reasons of local decrease and increase of wildlife species (n = 401).

Livestock management, hunting and human-large felid conflict

Properties owned by interviewees were small (<100 ha), and in most cases not larger than 0.2 ha (n = 9 of 12 properties; Question 2 in Appendix 3). Chicken, domestic pigs, goats, sheep and cattle were kept mostly to eat (meat, eggs and milk), and in lower proportion to sell. Sheep and pigs were also considered as a form of insurance (Fig. 3.5) against financial hardship, requiring sale of the animal to raise funds or its consumption for sustenance (Questions 3 and 4 in Appendix 3). They kept their animals in their backyards or inside fenced cowsheds/chicken coops, which were surrounded by wooden n = 6), barbwire (n =

3), chicken wire and concrete fences (*n* = 1, respectively). Only one interviewee reported keeping their animals in an open pasture (Questions 5, 6 and 7 in Appendix 3).

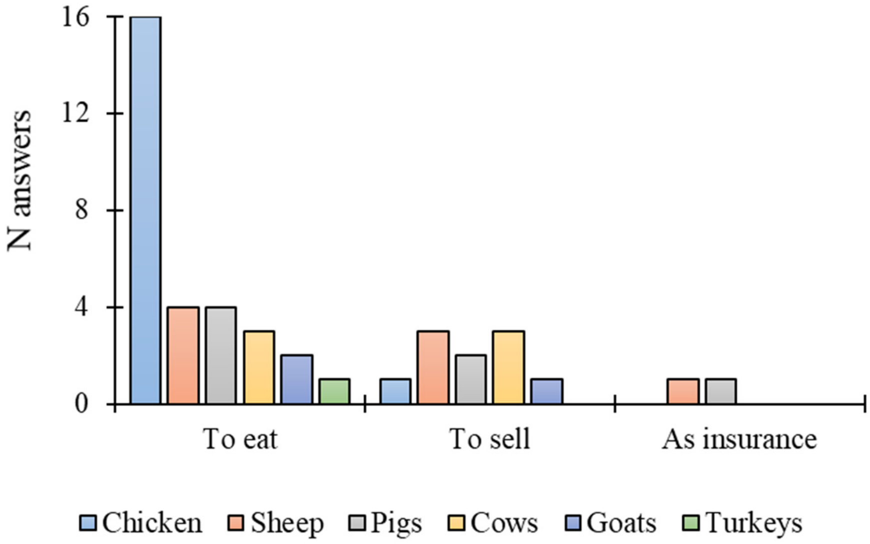


Figure 3.5. Livestock owned by local ranchers and purpose of ownership.

Most interviewees (87%, *n* = 26) reported that subsistence hunting took place in their community (Question 14 in Appendix 3). Of the 26 reporting hunting, a large proportion estimated that less than 10% of adult males hunt (69%, n = 18); minor proportions estimated that 11 – 20% and more than 20% of adult males hunt (8%, *n* = 2 for each category). The remaining 15% (*n* = 4) declared no knowledge of the proportion of adult males who hunt in their community (Question 15 in Appendix 3).

Of the 26 interviewees who reported that hunting takes place in their communities, 92% (*n* = 24) said that it occurs mainly on their plots of private land, and the remaining 8% (*n* = 2) said that it takes place everywhere in the forest (8%, *n* = 2; Question 16 in Appendix 3). A large proportion of interviewees reported decreases over the last 10 years in hunting events (58%, *n* = 15) and in participants (69%, *n* = 18), whereas a minor proportion declared no changes (hunting events 35%, *n* = 9, and participants 27%, *n* = 7), or increases (hunting events 8%, *n* = 2, and participants 4%, *n* = 1; Question 17 in Appendix 3). There was consensus on the fate of the meat from the hunted animals. For hunting events involving many people, the meat had to be distributed amongst the people who take part in the event (62%; *n* = 16); when hunting alone it became a family decision (38%, *n* = 10; Question 21 in Appendix 3).

The main purpose of hunting in these communities was to increase their dietary protein, and to a lesser extent to sell the wild meat, or to protect their crops from predators (Fig. 3.6; Question 19 in Appendix 3). The species most frequently reported as hunted were deer, collared peccary, medium-sized carnivores (white-nosed coati and Northern raccoon), large birds (ocellated turkey, greater curassow and plain chachalaca), nine-banded armadillo and Central American agouti. The three species most favoured to eat were Yucatán brown brocket deer, collared peccary and Central American red brocket deer. White-nosed coati was the single most hunted species for crop protection (Fig. 3.6; Question 18 in Appendix 3).

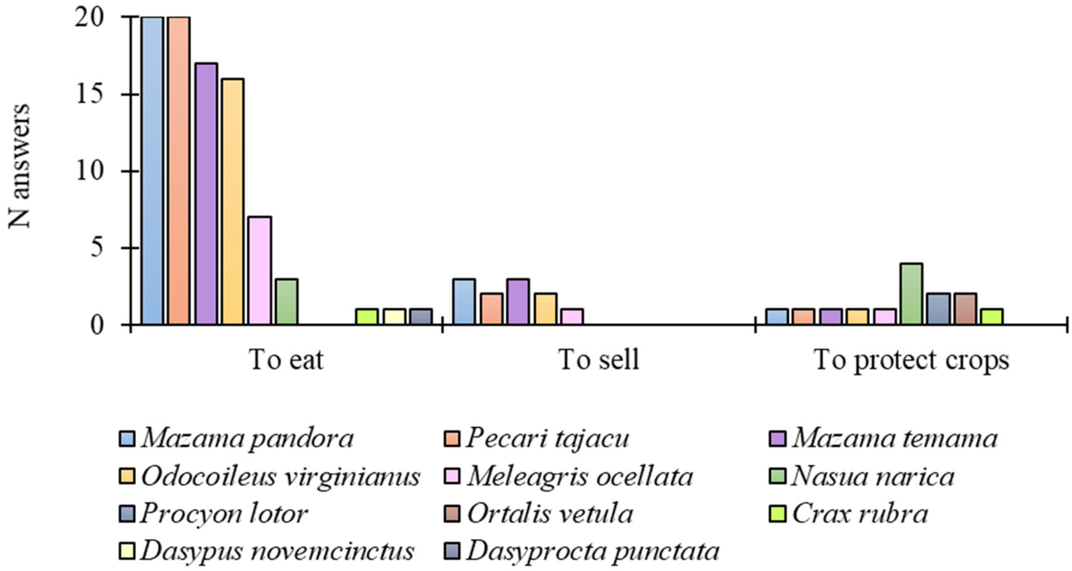


Figure 3.6. Purpose of hunting, and hunted species. See Table 3.1 for English names of species.

More than half of all 30 interviewees believe jaguars and pumas do not attack humans if they are left unprovoked (59%, n = 17 of 29 answers), whereas a lesser proportion believe they do (38%, n = 11). One interviewee reported they did not know (Question 22 in Appendix 3). This perception did not depend on whether or not they own a ranch ($\chi^2 = 0.006$; d.f. = 1; $p = 0.94$, Questions 1 and 22 in Appendix 3) or on whether or not they have experienced livestock losses by large felids ($\chi^2 = 0.65$; d.f. = 1; $p = 0.42$, Questions 22 and 25 in Appendix 3).

A small proportion of all interviewees (10%, *n* = 3) reported previous hunting of a jaguar on their property (ca. 20-30 years ago), and nobody reported previous killing of a puma (Questions 23 and 24 in Appendix 3). Eight interviewees reported experiencing predation on their own livestock by large felids (nine attacks by jaguars, three by pumas). Three interviewees reported more than one attack, with gaps of five and eight years between predation events. Sheep was the preferred domestic prey species taken by large felids (*n* = 64 individuals taken), with three cattle calves taken in one incident only (Question 25 in Appendix 3). Amongst the 8 interviewees who reported livestock predation incidents by large felids, 50% believe attacks have increased in the past ten years, whereas 25% believe they have declined and 12% believe attacks have remained the same (Questions 25 and 26 in Appendix 3).

Four interviewees declared that, in order to reduce livestock attacks, they had moved their livestock to a safer site, and one had sought assistance from local NGO Pronatura (Question 27 in Appendix 3). One interviewee who had still not made changes in their husbandry practices showed willingness to make changes in their management practices to prevent future attacks (build paddocks; Questions 27, 28 and 30 in Appendix 3). In addition, the two interviewees who had already made changes in their husbandry practices (e.g. by keeping animals inside chicken coops and fenced pastures) declared they were willing to make other changes (e.g. building paddocks) to prevent attacks (Questions 27 and 30).

Interviewees (*n* = 30 interviewees, 35 answers) believed that their best options for reducing human-wildlife conflict were: 1) to seek livestock payments from the Livestock Insurance Fund (*n* = 13 answers); 2) to get monetary support from the government (subsides for paddock fencing and payments for protection of jaguars in their properties; *n* = 11 answers); 3) to obtain advice on available practices to mitigate livestock losses by large felids (*n* = 5 answers); 4) better fulfilment of the law (*n* = 2 answers); and 5) game gardening (‘breed natural prey or livestock and give them to the jaguars’; *n* = 1 answer; Fig. 3.7; Question 31 in Appendix 3).

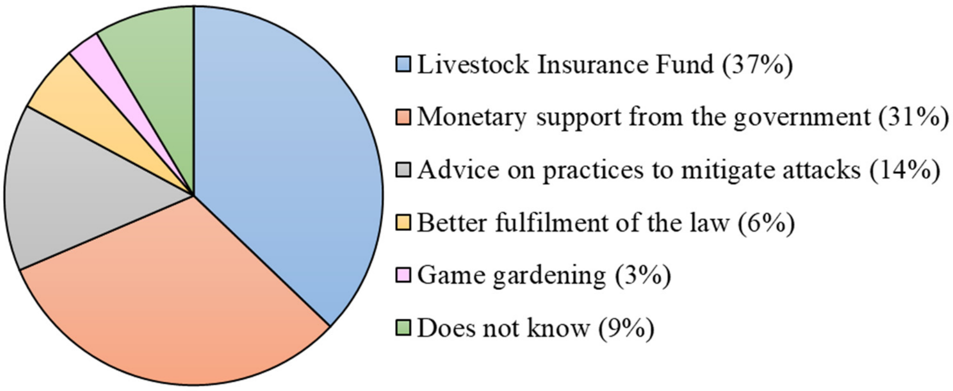


Figure 3.7. Best options for reducing human-large felid conflict. The annotated lists show segments clockwise from the top.

Two interviewees complained that payments for the Livestock Insurance Fund have not been paid (Question 32 in Appendix 3), or that they usually take a long time to arrive. This information was given outside the interview (hereon distinguished with an asterisk in brackets). One interviewee reported government officials were untruthful about requirements to obtain payments (*).

Two interviewees reported that attacks on livestock by large felids made them feel afraid (*) or angry (Question 32 in Appendix 3). Livestock losses by large felids triggered major economic issues for them. Their livestock acted as their main source of income for the present, or as an insurance for the future (*).

They had mixed opinions about using lethal control on large felids in response to livestock predation (Question 33 in Appendix 3). They believed it was their right to eliminate the predator (because it killed their animals and they need to protect themselves); however, they are aware this is against the law (*; NOM-059-SEMARNAT-2010; SEMARNAT 2010; Ley General de Vida Silvestre; SEMARNAT 2018a; Ley General de Equilibrio Ecológico y Protección al Ambiente; SEMARNAT 2018b). The majority of interviewees declared that they believed current law helps to reduce human-wildlife conflict (70%, n = 21), whereas smaller proportions declared it does not help (14%, n = 4) or did not know/did not answered (16%, n = 5; Question 34 in Appendix 3).

Discussion

The results of the questionnaire survey revealed a wide knowledge about local wildlife amongst people living in rural communities in the northern Yucatán Peninsula. A total of 36 out of 37 wildlife species were recognised by at least two interviewees as being present in their communities. The only species considered absent by all the interviewees was Baird's tapir. However, some interviewees reported that it was formerly present in their communities (*), and in fact, the species might actually be extirpated from the area (IUCN SSC Tapir Specialist Group 2016). Rural communities in the Yucatán Peninsula and Southern Mexico have good knowledge of biological and behavioural aspects of their local wildlife species, especially mammals and birds linked to agricultural practices, home gardening and hunting, and this has led to specific purposes, strategies and techniques of hunting (Santos-Fita *et al.* 2012). However, their beliefs and knowledge shape the ways they perceive nature, and this impacts how they use and manage their natural resources (Barrera-Bassols & Toledo 2005). For this reason, we structured the questionnaire to cover several categories of questions: their knowledge, their beliefs, their hunting practices and their perceptions about interactions with large felids.

Hunting was practised for subsistence purposes in the three study communities. This is usually the main type of hunting in rural communities from the Yucatán Peninsula. Many types of subsistence hunting have been reported in this region, which usually depend on the target species. These include: 1) bush beating or *batida*, which is practised in the daytime, when a group of hunters seek and 'herd' the prey with the use of trained dogs, towards another group of hunters who wait and shoot the prey; 2) stalking, practised in the late-afternoon and at night time; 3) night-light hunting; 4) opportunistic hunting, which people practice in-transit to their workplaces; 5) wild turkey hunting, specifically targeting this species; 6) hunting with bicycles and motorbikes (to get to hunting and fishing locations; C. Chávez, pers. comm.); and 7) hunting with traps and springs, which targets smaller prey species, such as gophers, small birds and squirrels (Montiel *et al.* 2000; Quijano-Hernández & Calmé 2002; Ramírez & Naranjo 2005; León & Montiel 2008; Rodríguez *et al.* 2012; Santos-Fita *et al.* 2012).

In the communities we studied, subsistence hunting was practised mainly to eat, and in minor proportion to control pests of crops. This type of hunting is practised throughout the Yucatán Peninsula (Escamilla *et al.* 2000; Montiel *et al.* 2000; Quijano-

Hernández & Calmé 2002; Ramírez & Naranjo 2005; Rodríguez *et al.* 2012; Santos-Fita *et al.* 2012; Oliva *et al.* 2014), and has been practised since pre-Hispanic times. Besides providing low-income people with substantial animal protein, has become part of their culture, being present in their myths and religious ceremonies (Aguilera 1985; Santos-Fita *et al.* 2012).

In these communities, hunters generally use .22 bolt-action rifles, and 12- to 20-gauge single-barrel shotguns, depending on the target species and the habitat (*). Rifles are usually preferred in forests, because the relatively open vegetation allows precise aim, often from an ambush position in a tree. Shotguns are generally preferred in savannahs, where the low and shrubby foliage requires tracking prey and aiming for an approximate target (*). The greater cost (x4) of shotgun cartridges over rifle bullets may influence where hunters choose to hunt (*).

Hunting preferences by interviewees in this study seemed to rely on a reduced number of game species. Similar findings have been found in a previous study in nearby rural communities from Central and Southern Yucatán Peninsula, where people did not rely on wild meat as their primary source of animal protein, and consumed only a relatively small set of large and medium-sized species. Instead, they purchased meat and raised livestock and poultry to complement their diet (Santos-Fita *et al.* 2012). This might be an indication of a regional effect.

The main hunted species in the studied communities were ungulates (red and brown brocket, white-tailed deer, and collared peccary). Similar hunting preferences have been found in several Maya communities throughout the Yucatán Peninsula. White-tailed deer, Yucatán brown brocket deer and collared peccary were amongst the main hunted species in 14 nearby communities from the Northern Yucatán Peninsula, including two of the three communities we studied (Santa María and San Pedro Bacab; Hernández 2009). Likewise, white-tailed deer was the main preferred prey species in the community of Árbol de Alacrán, also in the Northern Yucatán Peninsula (Montiel *et al.* 2000). White-tailed deer and collared peccary were the main prey in Los Petenes, in North-western Yucatán Peninsula (Rodríguez *et al.* 2012; Oliva *et al.* 2014). Lastly, collared peccary was the preferred prey species hunted in the community of Tres Reyes (Quijano-Hernández & Calmé 2002), in Eastern Yucatán Peninsula, and white-tailed deer was the most extracted species (biomass extracted) in the community of Petacab, also in Eastern Yucatán Peninsula (Ramírez & Naranjo 2005).

Ungulates were also found to be the preferred prey of large felids in nearby private reserves of El Edén Ecological Reserve and El Zapotal Conservation Area (detailed in Chapter 2). Thus, these species are of particular concern, because they remain an important source of animal protein for Maya communities (Mandujano & Rico-Gray 1991; Naranjo *et al.* 2004). Collared peccaries might be especially sensitive to hunting, given their social nature (March & Mandujano 2014), and because hunting of one group could largely affect its local abundance by reducing group size, or even eliminating complete groups (Reyna-Hurtado *et al.* 2009). If large felids compete for a limiting supply of prey, a reduced prey base for these top predators caused by human hunting may trigger livestock predation by the felids and aggravate human-wildlife conflicts in the area (Escamilla *et al.* 2000). This seems to be happening in other areas of the Yucatán Peninsula (Foster *et al.* 2014).

Interviewees reported that the main (1st and 3rd) reasons for local wildlife declines are hunting by humans and large felids, which suggests people have started to notice they compete with jaguars and pumas for the same prey. Interviewees also reported they have noticed local declines in their potential prey. Perceptions of declines of potential wildlife prey species have also been reported in other communities in the Yucatán Peninsula. This points out the need for demographic studies, to determine the conservation status of traditional hunting species in the region (Oliva *et al.* 2014).

According to interviewees, large felids preferred to prey on medium-sized domestic prey. Similar findings were reported by Hernández (2009), conducted more than a decade ago, assessing livestock attacks by large carnivores (jaguars, pumas and coyotes). In our questionnaire survey, however, the number and proportion of interviewees who reported livestock attacks by large felids (*n* = 8, 27% of interviewees) was smaller compared to findings from Hernández (*n* = 17, 33% of interviewees). This difference suggests the effectiveness of the Livestock Insurance Fund, which was established in late 2009 (CNOG 2016), after the study Hernández was published, along with the subsequent contribution of Pronatura at providing local communities with technical assistance about this programme, and on good husbandry practices.

Perceptions of increase of attacks on livestock by large felids might have been weighted by recent livestock predation events caused by one ‘problem’ jaguar during 2013

– 2015. All the interviewees who reported increases in livestock attacks lived in the community of San Pedro Bacab, which experienced several attacks by this individual. Local people sought assistance from local NGO Pronatura, which deployed camera traps in paddocks and monitored the individual. Eventually, the individual was identified as a male that was previously translocated into this region by PROFEPA government personnel (Abraham Puc, pers. comm.), and that had a previous history of livestock predation. During the period of conducting the questionnaire survey, it was captured by Government officials (PROFEPA), personnel from Pronatura and personnel from local NGO Anta Balam A. C.). This case illustrates how a single individual can cause economic hardship. For the same reason, its removal can immediately relieve conflict issues. A problem then arises about where the individual should be translocated so it will not become an issue elsewhere. In order for the translocation to be successful, a large area without potential conflict needs to be available in order for the individual can survive (Linnell *et al.* 1997).

There is also a need for further study on the perceptions of large-felid attacks on livestock, to assess whether they are indeed increasing in the area, or if such perceptions are heavily weighted by particular incidents. This is an important area of study, because communities may use lethal control against large felids in response to perceptions of threat as well as the threat itself (Marchini & Macdonald 2012).

As well as mitigating livestock losses by large felids in the area, local government and NGOs need to address perceptions of risk. This should be done before promoting strategies of tolerance to wild predators (Naughton-Treves *et al*. 2003; van Eeden *et al.* 2017). In order to reduce large-felid killings, it is necessary to understand the underlying causes for this behaviour. Propensity to kill large carnivores might be more closely associated with fear, personal and social motivations, and internal and external barriers, such as lack of skills and inefficient enforcement of the law (Naughton-Treves *et al*. 2003; Marchini & Macdonald 2012). The causal link of attitudes to behaviours might not be clear-cut, however, and it can be easy to overlook factors involved in the decision to kill a predator that are not directly related to its impact on human livelihood (Treves *et al.* 2006; Marchini & Macdonald 2012). As an example, a framework developed using the Theory of Planned Behaviour makes use of factors that are not directly related to the impact of jaguars on people. It has been used to explore the relationships between landowners' perceptions of jaguar impacts on human livelihood, and the jaguar-killing behaviour of people (Ajzen 1985; Marchini & Macdonald 2012). These tools could enlighten future explorations of the motivations for killing large felids in communities from the Northern Yucatán Peninsula. In a future questionnaire survey, questions regarding perception on jaguar impact on livestock and human safety, jaguar killing behaviour (past events) and intention to jaguar killing (future events), should be asked along with questions about group identity (sense of belonging with fellow stakeholders), descriptive norms (number of fellow stakeholders who kill jaguars), subjective norms (social agreement or disagreement about killing jaguars), and perceived behavioural control (internal and external factors that limit jaguar killing; Marchini & Macdonald 2012).

When local people experience felid attacks on livestock, personnel from Pronatura assist them in obtaining compensation from the Livestock Insurance Fund. Pronatura also makes camera traps available to rural communities and provides technical support in using them to monitor their natural resources, and to obtain funds from the Mexican programme of Payment for Ecosystem Services (PES; SEMARNAT 2013; Pronatura 2018a, b; pers. obs.). During the past decade, the communities analysed here have received technical assistance from the Program for Sustainable Rural Development by local NGO Pronatura, which has help them promote sustainable development and conservation of their ecosystems, and encouraged changes in livestock husbandry to reduce the human-wildlife conflict in the area (Pronatura 2018a). The low number of reports of large-felid killings by local people and livestock attacks by large felids in the communities studied here might be an indication of the success of the NGO's work in the area (García-Alaniz & Naranjo 2010; Peña-Mondragón *et al.* 2017; pers. obs.). However, it could also be an indication of low large-felid population densities in the area. This seems unlikely, since the communities studied here are interspersed with large areas of forest habitat contiguous with several natural protected areas that contain healthy populations of large felids (detailed in Chapter 2 for El Zapotal Conservation Area and El Edén Ecological Reserve; also Yum Balam Biosphere Reserve and Ría Lagartos Biosphere Reserve). The low attack rate could also be due to interviewees choosing not to report incidents to the interviewer because of the sensitive nature of some of the questions asked in the questionnaire, in particular questions relating to wild meat consumption and human-wildlife conflict. Questions relating to jaguar hunting are especially problematic, because this activity is illegal in Mexico (SEMARNAT 2010; Marchini & Macdonald 2012). In future studies, it would be relevant to consider the positionality of the interviewer at the beginning of the study, since the way they are perceived (e.g. legitimacy, prior involvement with population of study, institutional base, nationality, gender, age, social status, ethnicity, etc.) is likely to influence the information derived from it (Walt *et al.* 2008).

The Livestock Insurance Fund implemented by the Mexican government could be an efficient alternative to manage the human-large felid conflict in the communities we studied. The majority of interviewees believe this is the best option to minimise human-large felid conflict in their communities. This view might be related to the fact that some ranchers obtained payments for livestock losses by large felids while this study was being conducted. However, if this scheme is indeed working in the area, it has certainly been facilitated by the assistance provided by Pronatura. In Mexico, information related to government programmes is unavailable to many people in remote rural communities due to a lack of government resources for disseminating it, the poor education levels of people from rural areas, and the lack of internet access or computer skills (pers. obs.). Although compensation programmes are well received, they are also susceptible to multiple challenges imposed by community-specific contexts. These might include processing delays, corruption, and award rates that do not match market values (Dickman *et al.* 2011; Krafte Holland *et al.* 2018). In the communities we studied, some interviewees reported that payments from the Livestock Insurance Fund have taken too long to arrive, and they tend not to trust government officials. This agrees with findings made a decade earlier by Hernández (2009), who reported that people in nearby communities with livestock attacks also declared lack of effective response from government officials (SEMARNAT, SAGARPA and PROFEPA). In that study, delays by Pronatura were also perceived, although they were unlikely to be true because Pronatura has no influence on the process. No such delays were reported in the current study. Involvement from Pronatura only relies on providing technical assistance to the communities, and is not involved in the payment process.

Previous implementations of the Livestock Insurance Fund have not been successful in the Yucatán Peninsula due to the lack of assistance, and limited economic and human resources (Chávez & Zarza 2009). Effective and prompt implementation is therefore crucial, in order to ensure the utility of this scheme in the area. The majority of local people have no bank account or savings, and their livestock acts as an immediate source of capital for them (Moreno & Olmos 2008). The ongoing presence of Pronatura, as well as other NGOs, is essential for these communities, and much required by many others that have no aid from government, wherever there is a prevalence of human-large felid conflict. There is a need for further unbiased and systematic assessment of the utility of the Livestock Insurance Fund, and the effectiveness of the work that Pronatura conducts in the area (Inskip & Zimmermann 2009; Eklund *et al.* 2017; Krafte Holland *et al.* 2018).

Effective mitigation of human-large felid conflict is more likely to succeed if it uses a combination of strategies and applications that are able to adjust to changing conditions. In particular, compensation schemes are more likely to succeed if they are tied in with community participation and good livestock husbandry practices (Madden 2004). Our results suggest this could be the case here. Some interviewees indicated they have already made changes to their husbandry management practices, such as keeping their animals inside fenced paddocks and chicken coops, or relocating them to areas that are closer to the community, and some of them are using noise deterrents, provided by Pronatura Peninsula de Yucatán. The combination of these tools is likely to improve mitigation of human-large felid conflict in the area.

The questionnaire survey reported here has a scope of inference that is limited to small forest communities lying between the El Edén Ecological Reserve and El Zapotal Conservation Area. We obtained a lower sample size of interviewees than originally planned, due to limited access to communities and restricted use of their inhabitants. We could only work with communities where Pronatura has established a previous link, since it was unsafe for the (female) researcher to approach communities alone. If the safety of the researchers could be ensured in other areas, however, and suitable links established, we recommend further surveys in communities that have not yet received any technical assistance from Pronatura (e.g. San Angel, Solferino or Chiquilá). In the communities where we worked, it was common for many people to share the same household. In planning the study, we decided to avoid duplication by interviewing only one member of each household, which eventually restricted our access to people who otherwise might have been eligible for participation.

Four unforeseen shortcomings in the design of the questionnaire mean that its results must be interpreted with caution. Firstly, some interviewees had to be continuously guided through Section 2 (Perceptions towards wildlife), which made it problematic for them to complete this section. This is likely to be the result of the large the number of species used. Secondly, some questions proved to be too elaborate for some interviewees and it took the interviewer additional time to clarify the question; even with clarification, the interviewee might have not understood the question correctly. Thirdly, there were inconsistencies in the records of answers provided by some interviewees, although these could usually be rectified by reference to previous information in the questionnaire. Lastly, for some questions in Section 4 (Human-wildlife conflict) related to changes in husbandry practices, we only had a very limited number of answers, because these questions depended on answers to previous questions. In future studies, questionnaire design should be done more cautiously. Questions should be preferably kept short, especially the ones about opinions and attitudes (Bradburn *et al.* 2004; Bryman 2012). Cognitive interviewing technique could be used when conducting survey pilots to ask the interviewees to restate, in their own words, what they think the meaning of a question is (Belson 1968; Bradburn *et al.* 2004). After interviewing has been completed, an analysis of interviewer report forms, and interviewer debriefing, should be conducted to identify areas that could cause issues in analysis. This will minimise inconsistencies in the records of answers. Lastly, a good questionnaire design coupled with a low amount of 'branching' (question or series of questions being asked or not asked, depending on the answer to a previous question) will minimise skip errors, and to maximise information collected in the questionnaire (Bradburn *et al.* 2004).

The communities of study, as well as many other nearby communities, will soon start to suffer pressures from the rising tourism business in nearby communities of Solferino and Chiquilá, and will need suitable and effective incentives to preserve their traditional way of living, along with the conservation of their biodiversity. Therefore, the generation of such incentives is much needed. One step forward is the recent publication of the Management Plan for the Yum Balam Flora and Fauna Protection Area (published after 24 years of the creation of the protection area; SEMARNAT 2018c). This will help regulate exploitation activities in the area. However, effective and constant monitoring from the government will be essential if both communities and biodiversity are to be preserved.

People from the communities studied here showed eagerness to use the acoustic loggers we have been developing for the last 4 years (see Chapter 4) in their protected forests. These communities, like others in the region, have benefits from the programme of Payments for Ecosystem Services (PES) developed by the Mexican government (SEMARNAT 2013; Pronatura 2018a, b). If their forest areas covered by this programme are lost or damaged, the benefits that these people obtain from this programme will stop.

Likewise, forests will be more likely to disappear if there are no PES in this region (Ramírez-Reyes *et al.* 2018). These communities struggle to patrol their lands, however, because they do not have the human or economic resources necessary to do so. They are aware, moreover, of hunting and logging on their land by people from neighbouring communities and urban areas. They therefore see an urgent need for monitoring their wildlife and forest exploitation, which could be facilitated by acoustic monitoring. We are currently seeking grant funding to pursue this option.

Conclusion

The communities we studied have a wide knowledge of their wildlife, and hunt it to complement their diet to support their subsistence. They prefer medium-sized game species, and mainly ungulates, which are also the preferred natural prey species of large felids in the area. This likely exacerbates human-large felid conflict in the area. Conversely, work by Pronatura seems to be effective at mitigating this conflict, at least for now, by promoting good husbandry practices, and by providing assistance and making the Livestock Insurance Fund available to local people. Such work needs continuous assessment, however, in order to ensure its cost-effectiveness. In addition, detailed assessments of hunting pressure by local people, and in particular on ungulates, need to be conducted in order to determine its effects on local prey. Our results provide useful insights on human-wildlife conflict in these communities, which will aid the development and implementation of future policy and management actions to manage conflict to the benefit of sustainable coexistence of people with wildlife. In this study, we assessed a central part of the livelihoods of rural Maya communities in the Northern Yucatán Peninsula in Mexico. These people have the best chance of anybody on Earth of living in harmony with nature, and they play a vital role in the conservation of wildlife and the habitats where they inhabit. They also have some of the highest levels of poverty and they largely depend on external aid. However, they have been largely ignored and excluded from conservation efforts of their own natural resources. We can no longer see conservation and people as separate entities. Instead, we need to seek cross-disciplinary and cross-cultural understanding between distinct disciplines of ecology and sociology if we want efforts for the conservation of natural resources to be successful, and to improve quality of life (Fa *et al.* 2007; Díaz *et al.* 2015). Civil organisations such as Pronatura thus have a vital role to play.

Chapter 4 - Optimisation of sensor deployment for acoustic detection and localisation in terrestrial environments

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Contributions

All authors conceived and designed the study. PhD students (University of Southampton) Andrew P. Hill and Peter Prince, and Professor Alex Rogers (Department of Computer Science, University of Oxford) led the development of the AudioMoth acoustic sensors and classification algorithm. Alex Rogers developed the probabilistic theory from my initial work on detection radii within SPreAD-GIS maps; co-supervisor Professor C. Patrick Doncaster implemented the probabilistic theory with R scripts that developed from my initial scripts. I led the design of all field trials in collaboration with C. Patrick Doncaster and Dr Jake L. Snaddon. I led the implementation of all field trials, in collaboration with Jake L. Snaddon, Andrew P. Hill, Peter Prince and C. Patrick Doncaster. I led the sound propagation analysis with SPreAD-GIS software. All authors contributed to writing the manuscript, coordinated by C. Patrick Doncaster. Access to Pook's Hill and Tapir Mountain Nature Reserve was managed by Dr. Jake L. Snaddon. Field assistance was provided by Pook's Hill staff Vicky and Ray Snaddon, and James Vincent. Adam Lloyd supplied the digital elevation map of Tapir Mountain Nature Reserve. The manuscript was much improved by suggestions from R. Whytock and an anonymous referee. Fieldwork was conducted with resources obtained by my Mexican CONACyT Studentship (202650), a Rufford Small Grant to me (17047-1) and two SEP beca complemento studentships to me (2014: BC-3606; 2015: BC-4118).

Abstract

A rapid evolution in miniaturisation, power efficiency and affordability of acoustic sensors, combined with new innovations in smart capability, is vastly expanding opportunities in ground-level monitoring for wildlife conservation at a regional scale, using massive sensor grids. Optimal placement of environmental sensors and probabilistic localisation of sources have previously been considered only in theory, and not tested for terrestrial acoustic sensors. Conservation applications conventionally model detection as a function of distance. We develop probabilistic algorithms for near-optimal placements of sensors, and for localisation of the sound source as a function of spatial variation in sound pressure. We employ a principled GIS tool for mapping soundscapes to test the methods on a tropical-forest case study using gunshot sensors. On hilly terrain, near-optimal placement halves the required number of sensors compared to a square grid. A test deployment of acoustic devices matched predicted success in detecting gunshots, and traced them to their local area. The methods are applicable to a broad range of target sounds. They require only an empirical estimate of sound-detection probability in response to noise level, and a soundscape simulated from a topographic habitat map. They allow conservation biologists to plan cost-effective deployments for measuring target sounds, and to evaluate impacts of sub-optimal placements imposed by access or cost constraints, or multipurpose uses.

KEYWORDS: AudioMoth; biodiversity monitoring; ecosystem management; listening devices; optimization; submodularity.

Introduction

Emerging technologies for small, low-cost, power-efficient and smart monitoring devices are rapidly changing the scope of possibilities for monitoring cryptic human exploitation activities as well as biodiversity (Pimm *et al.* 2015; Cressey 2017; Kwok 2017; Berger-Tal & Lahoz-Monfort 2018). Sizes and costs of acoustic monitoring devices have reduced 20-fold in the last two years with the emergence of fit-for-purpose and customisable alternatives to commercial options (Browning *et al.* 2017; Whytock & Christie 2017; Wrege *et al.* 2017), and collective purchasing schemes (Wheat *et al.* 2013). The development of smart acoustic devices that store information only in the event of a target sound triggering the device has the potential to vastly increase the autonomy of devices. This has particular relevance to monitoring in tropical forests, which often have difficult access. For example, the AudioMoth acoustic sensor is programmable with classification algorithms that trigger event logging (Hill *et al.* 2018). This open-source smart device combines low-energy acoustic detection with small size (58×48×4 mm, 10 g without batteries) and low cost (US$43 per unit). Price is minimised by collective purchasing (GroupGets 2017). The combination of these attributes has the potential to revolutionise acoustic monitoring by making it affordable and logistically feasible to flood large areas of inhospitable ecosystems with sensors.

Given the new possibilities for grid deployments using numerous acoustic devices to monitor a large contiguous area, the question arises as to where best to place them to maximise the chance of detecting rare events, such as gunshots, chainsaws or animal calls. Optimal placement will depend on a complex combination of topography, vegetation and weather, as well as the acoustic characteristics of the target sound, the number of devices available for deployment, and their detection capability. Sensor placement problems of this type have previously been studied theoretically and they typically involve utility functions (in this case the probability of detecting a rare sound) that exhibit diminishing returns with increasing numbers of deployed sensors (Krause *et al.* 2008a). Technically, this property is known as submodularity, and it allows efficient optimisation using a greedy-heuristic algorithm. This algorithm places the first device at the location that maximises the probability of detection, and then the second device at the next location to maximise the probability of detection given the location of the first. It continues through to placement of all available devices, or to attainment of a desired overall probability of detection. Sensor placements that result from this greedy heuristic are provably close to optimal (Krause *et al.* 2008a). They have been shown to out-perform more computationally expensive alternatives in a number of challenging problems, including detecting contaminated water in a large water distribution network (Krause *et al.* 2008b). To date, however, such probabilistic approaches have not progressed beyond theoretical studies; they have neither been tested with field deployment of sensors, nor applied to acoustic sensors. Indeed, simulation tools capable of modelling the spread of sound across topographically complex landscapes have only recently become widely available for generic applications (Keyel *et al.* 2017).

Here we develop probabilistic methods for determining near-optimal placement of acoustic devices for monitoring wildlife resources, and for localisation of sound sources. We describe a case study of a deployment of AudioMoth devices (Hill *et al.* 2018) in Tapir Mountain Nature Reserve, Belize (TMNR, 17° 07′ N, 88° 54′ W). TMNR is a 25-km^2 area of mature tropical moist forest on undulating topography of 100-400 m elevation (Fig. 1), which suffers from illegal hunting. To our knowledge, this is the first field test of optimisation theory and first deployment for a terrestrial application.

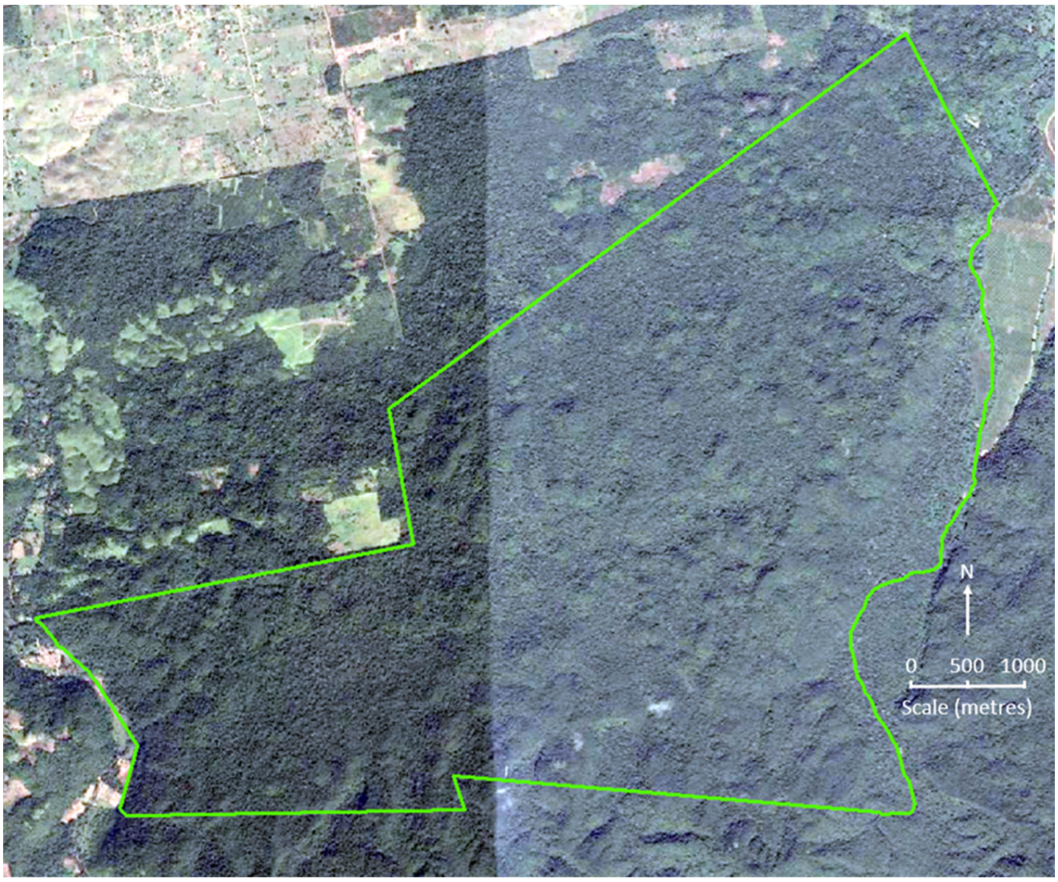


Figure 4.1. Satellite image of the Tapir Mountain Nature Reserve (TMNR), showing the Reserve encompassing homogeneous mature forest on hillocky terrain, and rectilinear patches of agricultural land only outside its boundaries. Source: Google Earth image dated 24/3/2017.

We start by developing the probabilistic theory for optimisation of device placement and localisation of detected gunshots. The Methods section describes the design of data collection in the field for calibrating and testing the procedure. The Results section gives the prediction for near-optimal number and placement of devices, and analyses its sensitivities. The results of field deployment and testing demonstrate the sensitivities of the gunshot localisation procedure.

Theory of detector placement and gunshot localisation

Greedy heuristic for near-optimal placement of detectors

We consider a landscape with a set of possible gunshot locations, $\mathcal{G}$, and a set of possible detector locations, $\mathcal{D}$. We assume that the probability of a gunshot occurring at any location $i \in \mathcal{G}$ is given by P_G^i normalised such that $\sum_{i \in \mathcal{G}} P_G^i = 1$. This probability will typically be the same for all locations such that $P_G^i = 1/|\mathcal{G}|$.

We have an acoustic propagation model that predicts the sound pressure level when a gunshot occurs at location $i \in \mathcal{G}$ and is received at detector location $j \in \mathcal{D}$. This sound pressure level is given by $SPL^{i,j}$.

The effectiveness of the acoustic sensor device is assumed to depend on the sound pressure level received at the detector location. The probability of a device actually detecting a gunshot of given received sound pressure level is described by function *g*, such that the probability of the detector at location $j \in \mathcal{D}$ detecting the gunshot that occurs at location $i \in \mathcal{G}$ is given by $P_D^{i,j} = g\left(SPL^{i,j}\right)$. This function may take any form, such as a step or a logistic, illustrated in Fig. 4.2a.

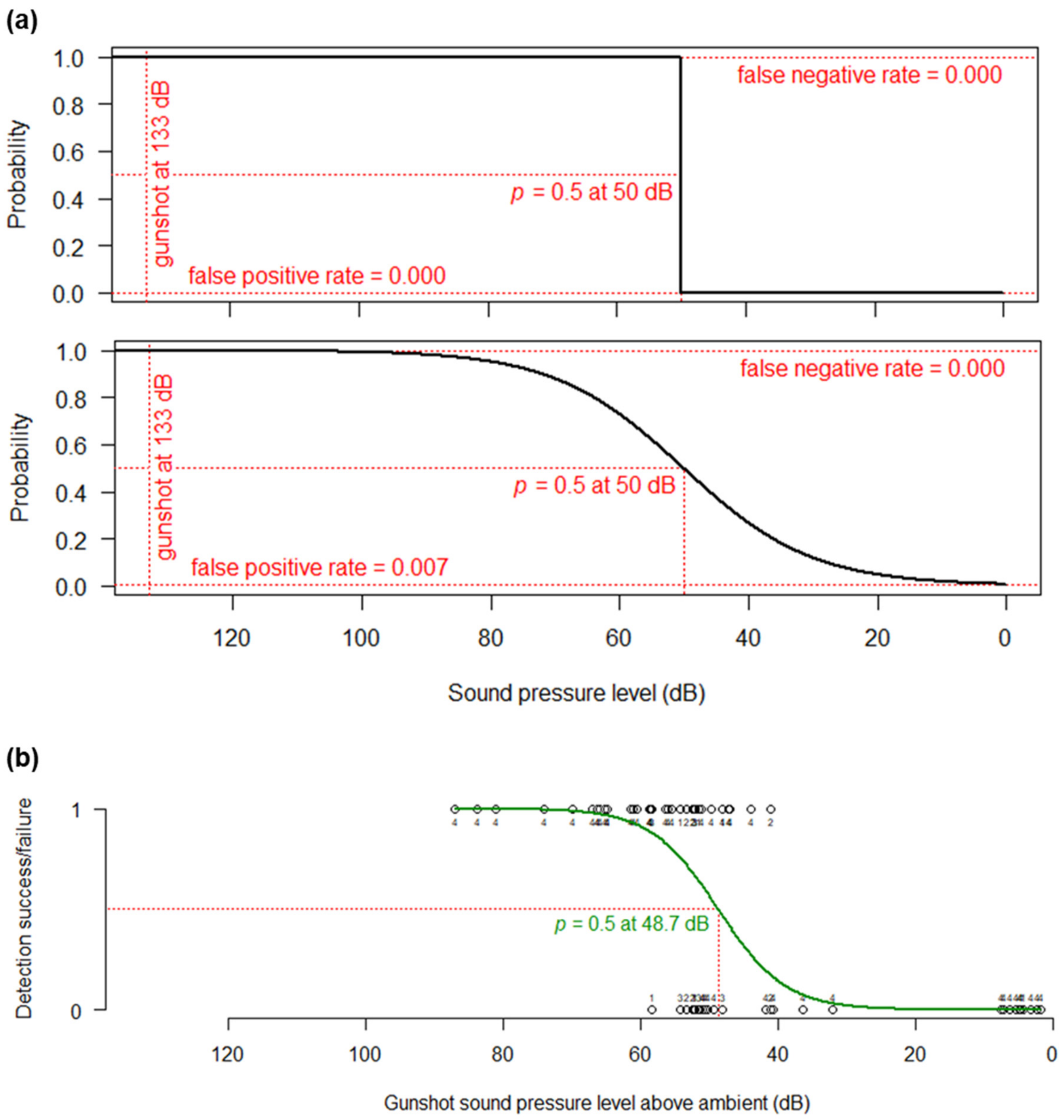


Figure 4.2. Alternative forms of the detection-probability response of an acoustic sensor to declining sound pressure level. Responses all take the form: $P_D^{i,j} = 1\Big/\Big(1 + \exp\Big(\big(SPL_{P=0.5} - SPL^{i,j}\big)\Big/decay\Big)\Big)$. (a) A simple step function with *decay* → 0, and logistic function with *decay* = 10, both with $SPL_{P=0.5}$ = 50 dB. (b) Logistic regression (green trace) fitted to empirical detection successes/failures by AudioMoth devices (open circles with frequencies). Recorded gunshot (*G* dB) and ambient (*A* dB) sound levels at each device yield the gunshot SPL above ambient as $10\times\log_{10}(10^{G/10} - 10^{A/10})$, reflecting the log scale of decibels as a measure of SPL. The best-fitting model had parameter values $SPL_{P=0.5}$ = 48.7 dB and *decay* = 4.868 ($z = 5.88$, $N = 57$, $P < 0.001$).

The probability of detecting a gunshot that occurs at any location in $\mathcal{G}$ when a single device is deployed at location j is given by:

$$P_D^j = \sum_{i \in \mathcal{G}} P_G^i P_D^{i,j} . \tag{1}$$

The probability of detecting a gunshot that occurs at any location in $\mathcal{G}$, when $|\mathcal{N}|$ devices are deployed at the set of locations $\mathcal{N}$, is given by:

$$P_D^{\mathcal{N}} = 1 - \sum_{i \in \mathcal{G}} P_G^i \prod_{j \in \mathcal{N}} 1 - P_D^{i,j} . \tag{2}$$

Note that Equation (2) expresses the probability of at least one device detecting the gunshot, and that this probability equals one minus the probability of all devices failing to detect it. Equation (2) further assumes independent detection by each sensor. Although beyond the scope of this paper, it would be straightforward to relax this constraint. The expression reduces to Equation (1) when $|\mathcal{N}| = 1$.

Given the model above, our aim is to deploy $|\mathcal{N}|$ devices to maximise $P_D^{\mathcal{N}}$. When $|\mathcal{N}| = 1$ this is easily done by choosing the single location, $j \in \mathcal{D}$, that maximises P_D^j. This case permits an optimal algorithm. When $|\mathcal{N}| > 1$ the problem is combinatorial in that we must choose $|\mathcal{N}|$ locations from a possible $|\mathcal{D}|$ locations. Large landscapes preclude an optimal algorithm. We can note, however, that this optimisation problem is submodular (Nemhauser *et al.* 1978). A real-valued function F defined on subsets $\mathcal{A}$ and $\mathcal{B}$ of a finite set $\mathcal{V}$ is called submodular if for all $\mathcal{A} \subseteq \mathcal{B} \subseteq \mathcal{V}$ and for all $s \in \mathcal{V}$, it holds that $F(\mathcal{A} \cup \{s\}) - F(\mathcal{A}) \geq F(\mathcal{B} \cup \{s\}) - F(\mathcal{B})$. Submodularity reflects the property that adding another member s to the smaller subset $\mathcal{A}$ has greater impact on F than adding it to the larger subset $\mathcal{B}$. Submodularity often occurs in problems involving sensor coverage, due to the form of Equation (2), where $P_D^{\mathcal{N}_1 \cup \{s\}} - P_D^{\mathcal{N}_1} \geq P_D^{\mathcal{N}_2 \cup \{s\}} - P_D^{\mathcal{N}_2}$ for $\mathcal{N}_1 \subseteq \mathcal{N}_2 \subseteq \mathcal{D}$, $s \in \mathcal{D}$ and $s \notin \mathcal{N}_1$, $s \notin \mathcal{N}_2$. It results in a proof that solving the optimisation problem using a greedy heuristic achieves at least a proportion $1 - 1/e \approx 63\%$ of the optimal solution (Krause *et al.* 2008a). Experimental tests *in silico* support the greedy heuristic as providing near-optimal solutions for a range of real-world competitive sensor placement challenges (Krause *et al.* 2008b). The greedy heuristic in our setting takes the following form as an algorithm:

```
Data: $P_G^i$ and $P_D^{i,j}$ for $i \in \mathcal{G}$ and $j \in \mathcal{D}$
Result: Set of device locations $\mathcal{N}$
$\mathcal{N} \leftarrow \varnothing$
while $|\mathcal{N}| < N$ do
    $s^* \leftarrow \arg\min_{s \in \mathcal{D}, s \notin \mathcal{N}} \sum_{i \in \mathcal{G}} P_G^i \prod_{j \in \mathcal{N} \cup \{s\}} 1 - P_D^{i,j}$
    $\mathcal{N} \leftarrow \mathcal{N} \cup \{s^*\}$
end
```

ALGORITHM 1 Greedy placement of devices

Algorithm 1 allocates the first of N devices optimally, and then greedily places subsequent devices. At each iteration it finds the optimal location to add one additional device given the locations of the devices that have already been placed. The algorithm has complexity $\mathcal{O}\left(N^2 \times |\mathcal{D}| \times |\mathcal{G}|\right)$ when directly implemented. This can be improved by a factor of N by caching the values of $\prod_{j \in \mathcal{N}} 1 - P_D^{i,j}$ at each iteration.

Algorithm 1 can accommodate a number of simple extensions. For example, the expected distribution of the gunshots need not be uniform over the set $\mathcal{G}$ of all possible locations. Rather, it could reflect a reality of gunshot having higher likelihood at some locations than others. The only requirement is that the distribution is appropriately normalised such that $\sum_{i \in \mathcal{G}} P_G^i = 1$. Similarly, the stopping condition of the greedy algorithm need not be based on a predetermined number of devices. The algorithm can be stopped when the marginal decrease in detection-failure probability from an additional sensor does not suffice to warrant its extra cost.

Gunshot localisation

Given a record of gunshot detections it is possible to calculate the most likely source of the gunshot. Consider the case that a subset of the deployed sensor devices at locations $\mathcal{N}_D \in \mathcal{N}$ detect a gunshot within some time period, while the others at locations

$\mathcal{N} \setminus \mathcal{N}_D$ fail to do so. The likelihood that this set of observations resulted from a gunshot at location $i \in \mathcal{G}$ is given by:

$$\mathcal{L}_D^i = \prod_{j \in \mathcal{N}_D} P_D^{i,j} \times \prod_{j \in \mathcal{N} \setminus \mathcal{N}_D} 1 - P_D^{i,j} . \tag{3}$$

The posterior probability that the gunshot occurred at location i is thus given by Bayes theorem:

$$P_G'^{i} = \frac{P_G^i \mathcal{L}_D^i}{\sum_{i \in \mathcal{G}} P_G^i \mathcal{L}_D^i} . \tag{4}$$

This describes a normalised discrete probability distribution over all possible gunshot locations such that $\sum_{i \in \mathcal{G}} P_G'^{i} = 1$.

If more than one sensor detects the gunshot, and we have access to the time that each detection occurred, we can extend the analysis to further refine this distribution. Consider that the gunshot actually occurred at unknown time t_G at location $s \in \mathcal{G}$. Each sensor at location $j \in \mathcal{N}_D$ will detect the gunshot at a later time t_D^j due to the propagation of the sound from the source of the gunshot to the location of the sensor. This detection time is given by:

$$t_D^j = t_G + \frac{d_{s,j}}{c_{\text{air}}} + \epsilon_j , \tag{5}$$

where c_{air} is the speed of sound in air, $d_{s,j}$ is the distance between gunshot location s and sensor location j, and ϵ_j is a random variable that represents noise in this observation. This noise results from two sources: (*i*) the drift of the real-time clock within the sensor, and (*ii*) uncertainty in the exact propagation path and speed of the sound.

Both sources of noise can be addressed through the same formalism by imposing an arbitrary order over all sensor locations $j \in \mathcal{N}_D$ such that the noise can be considered to have been drawn from a multivariate Gaussian distribution given by:

$$\boldsymbol{\epsilon} \sim \mathrm{Normal}\left(\mathbf{0}, \boldsymbol{\Sigma}\right), \tag{6}$$

where $\boldsymbol{\Sigma}$ defines an $|\mathcal{N}_D| \times |\mathcal{N}_D|$ covariance matrix.

Now, for any individual possible gunshot location $i \in \mathcal{G}$, we can impose the same order as above to define a vector of times, $\mathbf{t}_i$, whose elements are given by:

$$t_i^j = t_D^j - \frac{d_{i,j}}{c_{\mathrm{air}}} - t_G . \tag{7}$$

It only remains to choose the appropriate noise model and define $\boldsymbol{\Sigma}$ accordingly. In the case of noise resulting from drift of the real-time clock within each sensor, the noise is independent between sensors, and $\boldsymbol{\Sigma}$ is a diagonal matrix given by:

$$\Sigma^{j,k} = \begin{cases} \sigma_{\mathrm{drift}}^2 & \text{if} \, j = k \\ 0 & \text{otherwise} \end{cases}, \tag{8}$$

where $\sigma_{\mathrm{drift}}^2$ is a variance describing the typical accuracy of the real-time clock. Note that in this case, the covariance matrix is identical for all possible gunshot locations $i \in \mathcal{G}$.

In the case of additional noise due to uncertainty in the exact propagation path and speed of the sound we consider an additional term given by:

$$\sigma_{i,j}^2 = d_{i,j} \sigma_{\mathrm{prop}}^2 , \tag{9}$$

which is proportional to the distance between gunshot location i and sensor location j. This noise is not independent between sensors. Two sensors that are close together will likely be similarly affected by the same propagation uncertainties. Those that are far apart will not. Thus, we define the correlation between the noise at sensor locations j and k as $\mathrm{cor}_{j,k}^i$ such that each element of the covariance matrix is now given by:

$$\Sigma_i^{j,k} = \begin{cases} \sigma_{\mathrm{drift}}^2 + \sigma_{i,j}^2 & \text{if} \, j = k \\ \sigma_{i,j} \sigma_{i,k} \mathrm{cor}_{j,k}^i & \text{otherwise} \end{cases}, \tag{10}$$

where the correlation function expresses the fact that sensor locations close together are more correlated than those that are further apart, and is given by:

$$\mathrm{cor}^{i}_{j,k} = 1 - \frac{d_{j,k}}{d_{i,j} + d_{i,k}} . \tag{11}$$

Finally, the likelihood that the observed time differences, $\mathbf{t}_i$, were generated by a gunshot occurring at location $i \in \mathcal{G}$ is given by:

$$\mathcal{L}^{i}_{T} = \max_{\mathbf{t}_G} \rho(\mathbf{t}_i; \mathbf{0}, \boldsymbol{\Sigma}_i) , \tag{12}$$

where we maximise over the unknown time at which the actual gunshot occurred, and where $\rho(\mathbf{t}_i; \mathbf{0}, \boldsymbol{\Sigma}_i)$ is the standard multivariate Gaussian density function:

$$\rho(\mathbf{x}; \boldsymbol{\mu}, \boldsymbol{\Sigma}) = \frac{1}{\sqrt{|2\pi\boldsymbol{\Sigma}|}} \exp\left(-\frac{1}{2} (\mathbf{x} - \boldsymbol{\mu})^T \boldsymbol{\Sigma}^{-1} (\mathbf{x} - \boldsymbol{\mu}) \right) , \tag{13}$$

Combining this result with that of Equation 3, and again using Bayes theorem, gives the posterior probability that the gunshot occurred at location i as:

$$P'^{i}_{G} = \frac{P^{i}_{G} \mathcal{L}^{i}_{D} \mathcal{L}^{i}_{T}}{\sum_{i \in \mathcal{G}} P^{i}_{G} \mathcal{L}^{i}_{D} \mathcal{L}^{i}_{T}} . \tag{14}$$

Note that the values of σ^2_{drift} and σ^2_{prop} determine the balance of evidence between the probability of detection and the timings of the detections. Reducing the drift of the real-time clocks within the sensors, or deploying an external time signal that can be used to re-synchronised them, will reduce the value of σ^2_{drift} improving the accuracy of the estimate of the source of the gunshot. Similarly, we would expect more homogenous deployment environments to exhibit smaller values of σ^2_{prop}.

Materials and methods

Characterisation of detection probability

AudioMoth sensors were prepared for deployment by programming the on-board software with a classification algorithm to record an event upon each detection of a gunshot (Hill *et al.* 2018; Prince *et al.* 2019). Field tests at the deployment site characterised the decay in detection probability with diminishing sound pressure level (SPL) in decibels (dB) away from a gunshot.

The field tests used three independent transects in April 2018 in forest contiguous with TMNR (Fig. S1). At each transect, four AudioMoths were placed at one end with a SPL meter (Peaktech 8005). A 12-gauge shotgun (Baikal MP-18EM-M) was fired in a perpendicular orientation to the devices at approximately 200-m intervals along each transect, up to a distance of about 1 km from the devices. This procedure was repeated in daylight and nocturnal conditions. A total of 57 records of gunshot detection success/failure were obtained with associated SPL of the gunshot and ambient noise at the device, in A-weighted decibels (Data S1). A logistic model was fitted to the data on gunshot noise above ambient, shown in Fig. 4.2b. Its parameter estimates defined the form of the function *g* underpinning the greedy-heuristic algorithm.

Characterisation of sound spread

For the characteristic loudness of a gunshot at source, we used data from 167 replicate outdoor shots given in Murphy & Tubbs (2007) for a 12-gauge shotgun (Remington model 11-87). They obtained an average SPL of 132.6 dB at 1 m from the gun, in the 1250-Hz one-third octave bandwidth. This frequency is closest to the centre of the 400-2000 Hz bandwidth detected by the AudioMoth sensor.

In order to characterise the spread of gunshot sound from a gun that might be fired anywhere within the boundary of TMNR, we simulated a grid of gunshots at 200-m intervals covering the entire reserve. This was done with the SPreAD-GIS tool contained in the Sound Mapping Tools package (Keyel & Reed 2017) and implemented in ArcGIS. SPreAD-GIS modelled sound spread in a raster stack of 829 gunshots, using 132.6 dB for the SPL at source. The simulation assumed a background ambient noise of 45 dB, based on empirical nocturnal measures within TMNR taken from the transects. Most background noise was attributable to orthopterans. It also assumed an average nocturnal temperature of

25 °C, humidity of 60%, and wind speed of 5 km/hr from due East, based on yearly average meteorological conditions at the nearest weather centre, 70-km to the SE in the city of Dangriga (National Meteorological Service of Belize 2016). For each gunshot, the simulation produces a raster map of sound spread from the source under the given weather conditions, for a vegetation of mature deciduous broadleaf forest covering a topography given by an elevation map of TMNR (Technology Transformation Service 2016). In the homogeneous forest of TMNR, sound spread depends most sensitively on topography and wind speed and direction (Fig. S2).

To test the sensitivity of predictions to SPreAD-GIS input parameters, further runs replicated all its input parameter values, except (1) changing the gunshot grid from 200 m to 150 m; or (2) changing wind speed from 5 km/hr to 0 km/hr; or (3) changing the generic ‘seasonal condition’ parameter from ‘clear, calm summer night’ to ‘clear, windy summer night’.

Simulation of gunshot detection probability with distance

The logistic model shown in Fig. 4.2b was applied to the raster stack of 829 simulated gunshots across TMNR, to translate its soundscape into a detection probability landscape. The predicted distribution of SPL in decibels as a function of distance from source, collated across all gunshots, converts to a distribution of detection probabilities that is conditional on topography, and reflects local weather and vegetation (Fig. 4.3; example of a contributing gunshot in Fig. S3). The probability distribution predicts that detection within TMNR is frequently possible up to 500 m distance from a gun, but much rarer above 1000 m. This distribution aligned with our wider experience of testing gunshot detectability in the forest habitat of this region (Fig. S4).

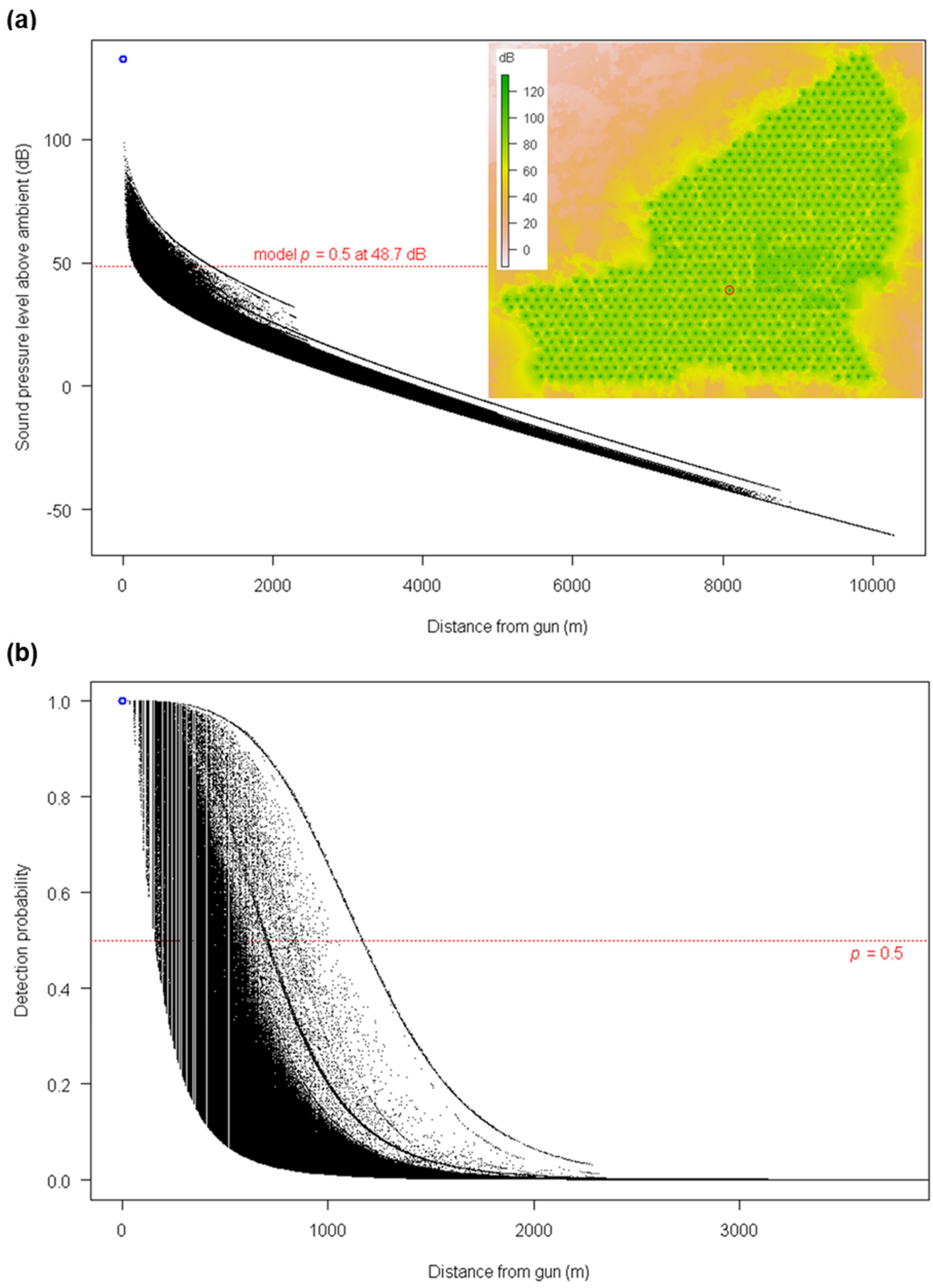


Figure 4.3. Collated output from the grid of 829 gunshots at 200-m intervals, simulated in SPreAD-GIS using inputs given in the second section of the Methods. (a) Distribution of SPL above ambient as a function of distance from the sound source; blue circle highlights 132.6 dB at source. Inset map shows the grid, with ringed gunshot analysed in Fig. S3 (b). Conversion of SPL to detection probability using the logistic algorithm parameterised in Fig. 4.2b; blue circle highlights probability = 1.0 at source.

The greedy-heuristic algorithm derived above was applied to the detection probability landscape. This was done in the R environment (R Core Team 2017) using the script listed in Data S2. The algorithm calculates the number and location of devices for near-optimal placement, given a logistic function for detection probability and a gunshot soundscape. It assumes equal probability of gunshots occurring anywhere within TMNR. It places devices only within the boundary of TMNR, which is also the boundary of the gunshot grid that generates the soundscape. The algorithm ceases to add more devices when the marginal decrease in detection-failure probability from an additional sensor becomes less than 0.001.

Test deployment and localisation of gunshots

A total of 10 AudioMoth devices were deployed in the NE sector of TMNR in April 2018, at all near-optimal locations in that sector predicted by the greedy-heuristic algorithm. The hilly terrain and hurricane-damaged forest impeded access to the extent that some devices could only be placed to within 100 m of the target location. The efficiency of the deployment was tested by firing nine gunshots within the sector. The 12-gauge shotgun was oriented in a range of directions over the nine shots, under clear and calm daytime weather conditions with ambient noise levels varying between 33 and 52 dB (median 36 dB). Current AudioMoths log events only to the nearest second. We therefore tested the accuracy of gunshot localisation based on actual detection successes/failures and the detection time-lags between devices imputed from knowledge of actual gunshot locations.

Results

Placement of devices

The greedy-heuristic algorithm predicted a requirement for 79 devices within TMNR when applied to the soundscape from 829 gunshots on a 200-m grid (Fig. 4.4a). The near-optimal placements were distributed throughout the reserve, mostly on local high ground or slopes overlooking valleys (Fig. 4.4b). The actual deployment of 10 devices targeted the ten placements in the north-easternmost corner of TMNR (ringed in Fig. 4.4b).

Further simulations with a finer-scale grid of 1486 gunshots at 150-m intervals across TMNR produced the same predicted number of devices and similar ordering, but took 79 hrs to create the raster stack in SPreAD-GIS compared to 44 hrs for the 200-m grid, on a PC with 12Gb RAM and 3.20 GHz processor. Differences in predicted locations were deemed insufficient to warrant the extra time requirement.

The near-optimal placement of 79 devices across the full extent of TMNR was predicted to achieve a residual detection-failure probability of 0.013 (Fig. 4.5a, right-most end of blue trace). In effect, this deployment would miss less than 2% of any gunshots fired anywhere within TMNR. Even in the event of all five highest ranking devices failing, the probability would rise only to 0.025, with lower-ranked devices tending to compensate for failed neighbours. In putative alternative placements of 79 devices across the full extent of TMNR, residual detection-failure probabilities rose to a predicted 0.110 for regular spacing on a 600-m grid, and 0.171 for random spacing (Figs S5 and S6). Detection-failure probabilities no greater than these magnitudes were achieved with near-optimal placements of only 40 and 32 devices respectively. The near-optimal placements can therefore halve the number of devices required to achieve a given detection efficiency for a deployment. These savings are robust to the threshold level of detection efficiency. Thus the residual detection-failure probability of 0.013 that requires 79 near-optimal placements would need 143 regular placements (on a 450-m grid). For a more relaxed threshold or more limited availability of devices, regular placements of 50 devices within TMNR (on a 750-m grid) would achieve a residual detection-failure probability of 0.237, which is just bettered by near-optimal placement of only 26 devices.

In the absence of wind, only 46 devices were required to achieve a predicted detection-failure probability of 0.013. Using the SPreAD-GIS simulation of seasonally windy instead of calm conditions, and 5 km/hr wind, near-optimal placement required 90 devices to achieve a residual detection-failure probability of 0.017. The larger number of devices reflects the noisier background induced by wind. Under these conditions, the placement of 79 devices that was near-optimal for seasonally calm conditions would achieve a residual detection-failure probability of 0.04 (Fig. S7). The difference in detection probability is negligible for the first 30 devices, which tend to get placed at, or close to, the same locations for both conditions.

The actual deployment of 10 devices in the NE sector of TMNR had a predicted residual detection-failure probability of 0.874 for gunshots occurring all across TMNR (Fig. 4.5a, right-most magenta dot). This probability would have dropped to 0.858 if we had managed to place the devices precisely at predicted near-optimal locations, instead of 3 to 100 m distant (Fig. 4.5a, inset map). The detection-failure probability diminishes to 0.045 for gunshots occurring only in the NE sector (Fig. 4.5b, right-most magenta dot). It would have dropped to 0.001 if we had placed 16 devices precisely at predicted near-optimal locations for gunshots only in this NE sector (Fig. 4.5b, right-most end of blue trace), instead of 2 to 453 m distant from these placements (Fig. 4.5b, inset map).

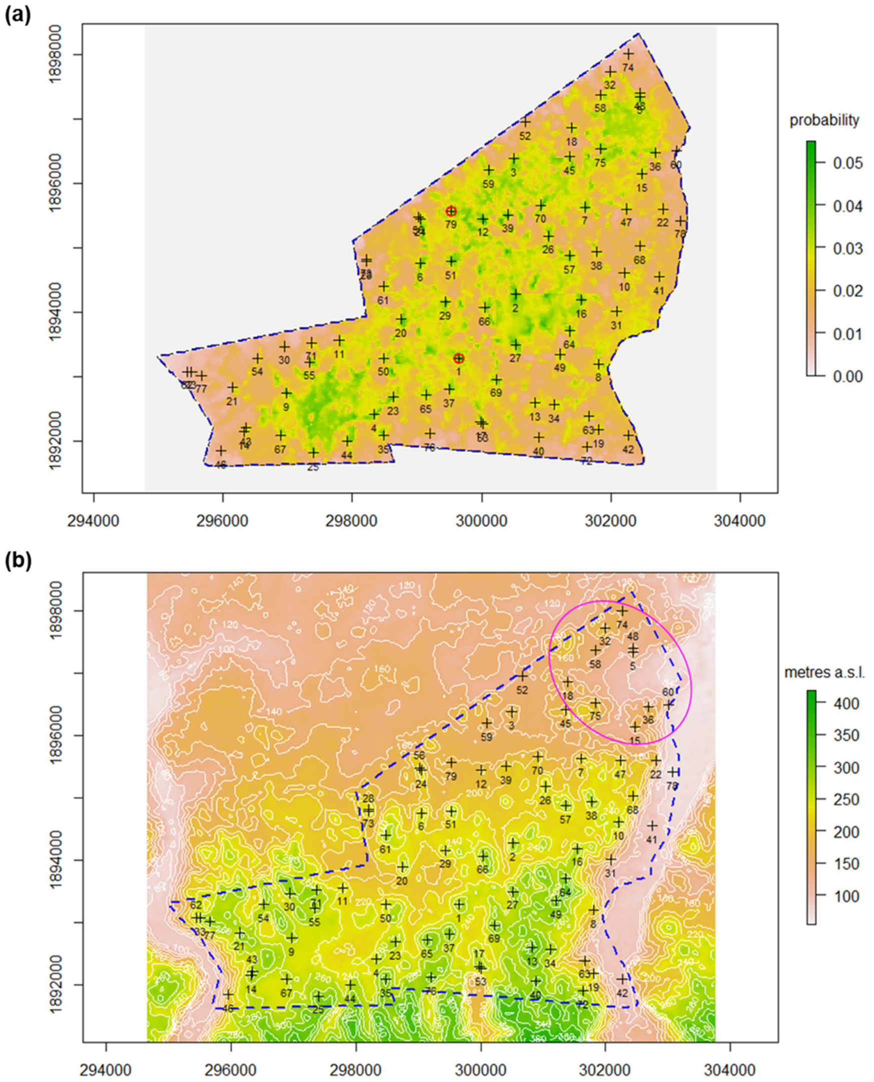


Figure 4.4. Near-optimal placement of AudioMoths within TMNR predicted by the greedy-heuristic algorithm, given function g (Fig. 4.2b) and a gunshot soundscape (Fig. 4.3a). Sites are ranked from 1 (most marginal drop in probability of detection failure) to 79 (least marginal drop). Placement is set against (a) the foundational landscape of: the probability of a single AudioMoth detecting a gunshot at any grid location, and (b) the underlying topography. The dashed blue line shows the boundary of TMNR, and the magenta oval in the top corner encompasses the 10 locations targeted for deployment of devices in April 2018. Axis labels show UTM 1-m coordinates.

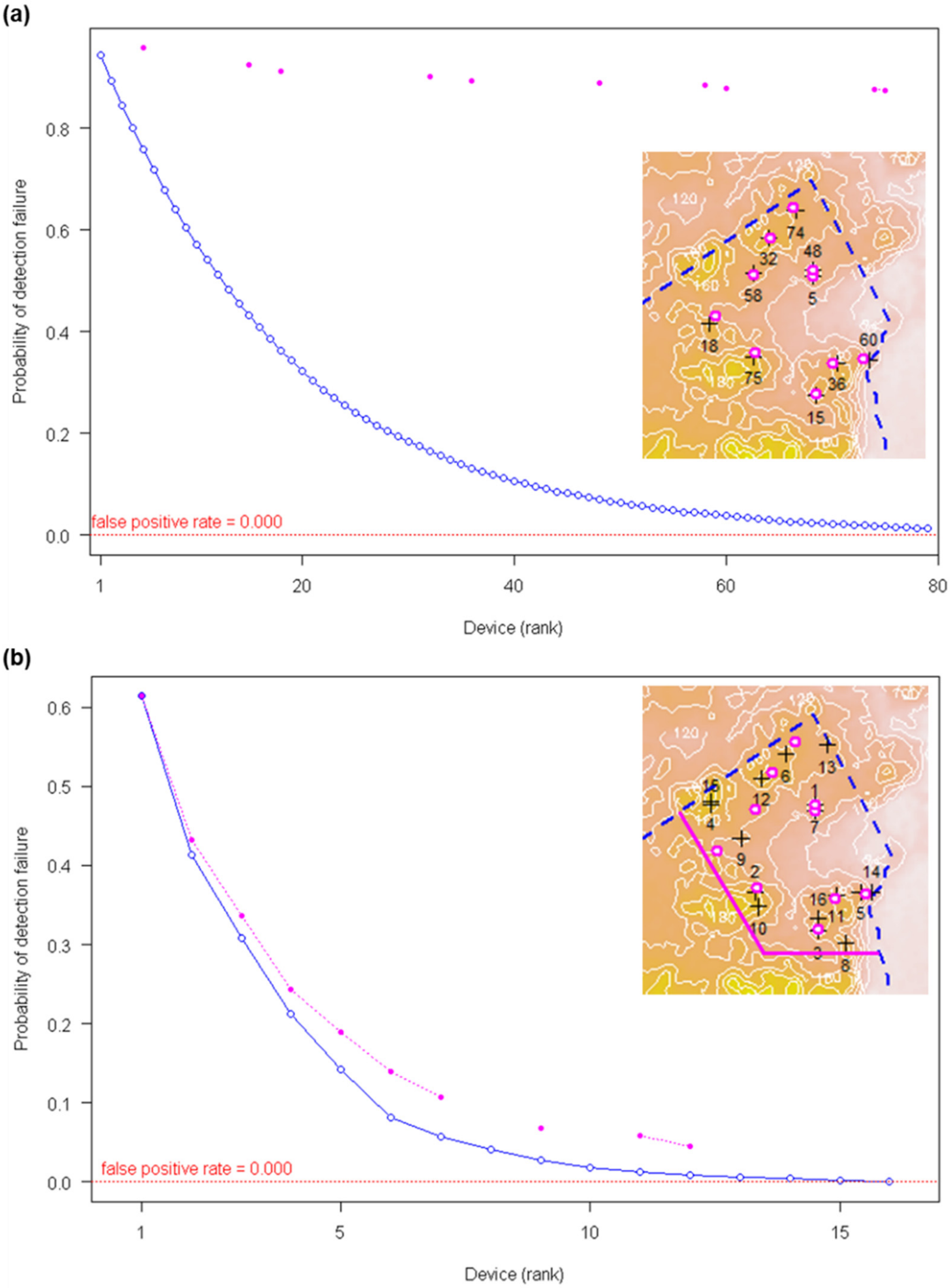


Figure 4.5. Declining probability of detection failure ($1-P_D^{\mathcal{N}}$) as a function of number of devices $|\mathcal{N}|$. (a) Near-optimal placements (Fig. 4.4) have a decreasing marginal drop with each additional device (blue trace), until the 80th device has no detectably lower probability than the 79th. Magenta dots show the declining probabilities for the 10 devices actually deployed in April 2018, at their locations near to ranked placements (inset map, magenta circles). (b). For simulated gunshots occurring only above the magenta line in the inset map, ranked crosses and graphed blue trace show the predicted near-optimal placement of 23 devices; magenta circles and graphed dots show the actual deployment of 10 devices.

Detection and localisation of gunshots

Of the nine trial gunshots in the NE sector, all triggered at least one of the 10 deployed AudioMoths, with four shots triggering two devices and one shot triggering three devices (Fig. 4.6a). The number of detecting devices had no apparent relation to ambient sound level. Regardless of gun orientation, gunshots tended to trigger the closest AudioMoth(s), at distances of 168 to 370 m, except for gunshot #9 which triggered a device at 872 m (Fig. 4.6a). Each detected gunshot could be located to the Dirichlet tile(s) of its detecting AudioMoth(s), on the assumption that no other devices lay closer to the gunshot (Fig. 4.6a). This held true for most trial gunshots; however, potential for error is illustrated by the northernmost AudioMoth, which detected gunshot #9 from further away than four other devices, only one of which also detected the gunshot.

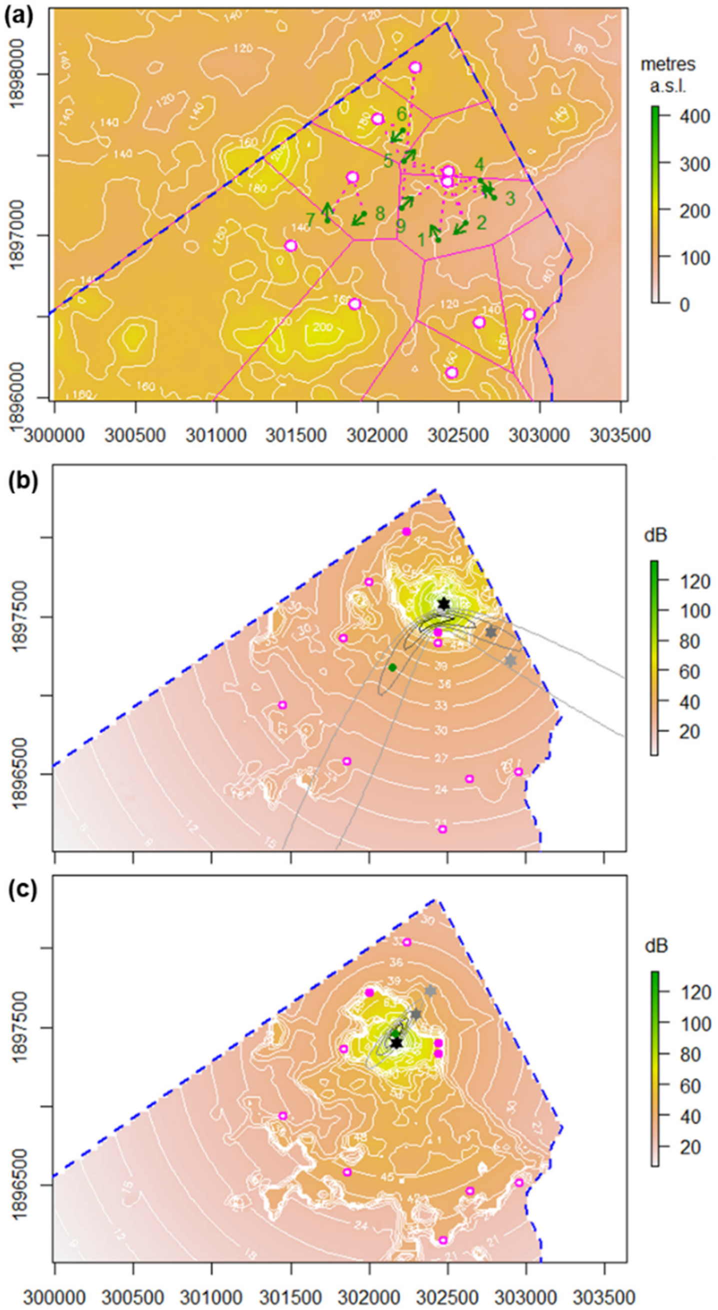


Figure 4.6. Detection of nine trial gunshots by ten devices in TMNR. (a) Gunshot locations (green dots, arrow indicating gun orientation), and deployed AudioMoths (magenta circles, dotted lines linking to detected gunshot(s)). Dirichlet tiles (magenta tessellations) each contain all points within TMNR that lie closer to the device at its centroid than to any other device. (b) Actual gunshot #9. (c) Actual gunshot #5. Plots show actual gunshot (green dot), detection success/failure by devices (closed/open magenta circles), the best estimate of gunshot location (black star, Equation 14), and decay in its SPL away from this source (white contours at 3-dB intervals, each equivalent to halving loudness). Dark- and light-grey stars show 2nd and 3rd best estimates of gunshot location. Grey contours show 20% intervals in likelihood of gunshot location based only on detection time-lag(s) between detecting devices (Equation 12, $\sigma^2_{\mathrm{drift}}$ = 0.001, equivalent to 0.03 s drift in device clocks; σ^2_{prop} = 0.000045, equivalent to 10% drift in ~1.5 s propagation time over 500 m).

The accuracy of gunshot localisation by the probabilistic method depended on the number of detecting devices and the availability of time-lag data. For example, if the northernmost device had detected gunshot #9 later than the only other detecting device by 1.457 s, this would indicate that the gunshot occurred 506 m further from the northernmost device than from the other device, assuming unimpeded sound travel at 347.3 m/s through air at 25 °C and 60% humidity. Grey contours in Fig. 4.6b identify the region of highest likelihood of gunshot location based only on this information, and estimates of timing uncertainty. With negligible error in timings, the region resolves into a hyperbola, familiar in 'hyperbolic navigation' by detection time-lags in audio or radio signals (detailed in Fig. S8; Li *et al.* 2016). The best estimate of gunshot location is given by the simulated gunshot that maximizes $P_G^{\prime i}$ in Equation 14, with a best-matching probability of replicating the observed set of detection successes and failures and observed time-lag. In this case, the estimated gunshot lay 519 m from the actual location, (Fig. 4.6b, showing its sound spread; R script for the procedures in Data S3). The magnitude of separation probably reflects influences on detection success by time-specific and local ambient conditions that deviated from the modelled conditions.

Timed detection of a gunshot by more than two devices allows triangulation of relative distances, which greatly improves location power. For example, small time differences in the event logs of the three devices detecting gunshot #5 localises the gunshot to a small region in Fig. 4.6c, geometric analysis in Fig. S9). The estimated gunshot lies 60 m from the actual gunshot (black star), and 87 m closer than the best estimate without time-lag data.

Applications of the probabilistic method to other gunshots obtained locations to within 170 m of the actual gunshots even when two detecting devices lie in close proximity to each other (Fig. S10). The method also works for gunshots picked up by only a single device, or not picked up by any device (Fig. S11). In these cases, the data contain no time-lags with which to maximise the likelihood. It is then based only on the simulated gunshot that best replicates the single observed detection success, or absence of any success, and the detection failure of all other, or all, devices (Equation 4). The case of no detections usefully identifies the area of weakest coverage by devices (Fig. S11b).

Discussion

The methods established here, of sensor deployment and sound source localisation, address one of the major challenges to the promise of non-invasive monitoring, of collecting ecologically relevant data suitable for hypothesis-testing science (Pimm *et al.* 2015). To date, almost no systematic records exist anywhere on hunting frequency in tropical forests, other than indirectly sourced estimates from questionnaire surveys (Foster *et al.* 2014). Monitoring in the Korup National Park in Cameroon using 12 passive acoustic devices continuously recording for 2 years detected a high level of shooting within a 54-km^2 grid (Astaras *et al.* 2017). The study was able to quantify an increase in gunshot frequency between years that was not detected in foot patrols of the area, and a prevalence of nocturnal over diurnal hunting. Such studies are rare because until now monitoring devices have been expensive to purchase, and bulky to deploy in areas of interest that often encompass remote habitat. The Korup study used SM2+ acoustic loggers (Wildlife Acoustic Inc, Maynard, MA) each weighing 680 g without batteries (200×200×64 mm) and costing over US$800. Their passive acoustic listening requires quarterly battery changes, and monitoring applications require analysis of thousands of hours of audio data. The new availability of cheaper, more power-efficient and smart devices opens up new options for monitoring large contiguous areas with massive grids of devices.

Our probabilistic method of device placement quantifies the sensitivities of acoustic monitoring to topography, wind, and distribution of sound sources. Analyses of alternative scenarios allow conservation biologists to measure impacts of sub-optimal deployment, imposed by access or cost constraints, or by using deployments to serve multiple purposes (e.g., to detect gunshots and chainsaws). For a desired threshold of detection efficiency, near-optimal placement on hilly terrain can halve the number of devices otherwise needed for square or random grids, thereby more than halving monitoring costs. The method is applicable to any of the habitats modelled by current sound-spread packages (Keyel & Reed 2017), to passive as well as smart sensors, and to biotic as well as anthropogenic sounds (Blumstein *et al.* 2011). It advances substantially on the current recommended practice of modelling the detection probability as a function of distance, or using a fixed detection radius for conservation applications (Thompson *et al.* 2010; Browning *et al.* 2017). The probabilistic method of localising the sound source makes use of whatever data may be available on detection timings or simply on detection successes and failures, and also allows prior beliefs about the most likely sources of gunshot to be incorporated within the same principled framework.

The closest work to our own is a desktop study of gunshot sensors by González-Castaño *et al.* (2009), developed for the different setting of externally powered acoustic sensors. This required a multi-objective optimisation, which was solved by searching for solutions on the Pareto front, where no other solution has both higher coverage and lower cost in terms of distance to a power line. Our battery-powered sensors present the simpler task of optimising detection with a cost that is proportional only to the number of deployed sensors. González-Castaño *et al.* (2009) modelled detection with a step-function (cf. Fig.-4.2 fitted smooth function) and sound propagation over 2-dimensional habitat (cf. Fig.-4.3 SPreAD-GIS 3-dimensional habitat). For gunshot localisation, they assumed independent uncertainties in detection timings caused by both clock drift and propagation path, which ignores the reality of correlated propagation paths (Equations (9)-(11)). Their resulting least-squares estimate of gunshot location equates to our maximum likelihood estimate from timings alone (Equation (12)) with zero propagation noise. Our probabilistic framework additionally incorporates a prior over possible locations, and evidence from detection itself (Equation (4)). This facilitates extension to more complex settings, for example localising the most likely single source of rapid fire, or a repeating chainsaw or biotic signal, even when each repeat may trip different sets of sensors.

The probabilistic methods described here have limitations common to any environmental detection system, in soundscape modelling, sensor design, and detection capability, which all require evaluation by site-specific ground truthing. The SPreAD-GIS soundscape that underpins detection probabilities requires significant processing times for deployments across complex topography. This is a one-off cost for a given environment, however, as the same soundscape is used for both device placement and sound localisation. We recommend that users trial alternative mesh sizes for modelling sound grids, which largely dictate processing time. In our tests, we constructed the soundscape from regionally averaged values of background noise, wind speed and direction, and influence of habitat type on sound spread. With more local-scale knowledge, these could be set to specific values for each modelled gunshot. Although the orientation of the shotgun made little difference in our localisation tests using a dense network of devices, the source amplitude will vary with the direction and elevation of the barrel. The omnidirectional sound dispersion modelled by SPreAD-GIS means that sensor placement assumes an absence of directional bias in gunshots, and gunshot localisation will be greatly improved by accurate measurement of time-lags. Sensor clocks will typically have crystals giving an accuracy of 20 parts per million, equivalent to 2 s/day. Clock synchronisation can be achieved on AudioMoths using external plugin modules, such as a GPA receiver with accurate satellite timing, or a radio transmitter synced to a receiving base-station clock. The benefit of synchronisation needs weighing against the extra cost and power consumption of the plugin. The same probabilistic algorithm can be used either with or without clock synchronisation, however, and without it the evidence for the gunshot location is derived from the detection events only, rather than their timings. Any sound-detection algorithm programmed into sensors requires thorough validation against continuous recording within the monitored habitat, and manual review. The advantage of smart detection in reducing power consumption and data storage nevertheless remains set against the inherent limitation that target sound detection cannot be validated with respect to concurrent background noise at each sensor. This trade-off will have particular relevance to target sounds with less easily calibrated signal attenuation, such as wild animal calls.

Sound-source localisation across tens of metres, for example of bird calls, may be too fine-scale for soundscape mapping by GIS or localisation based on detection probability. In such cases an array of networked sensor nodes, each containing a sub-array of multiple microphones can be used to detect direction as well as time of arrival of sounds from continuously synchronised clocks. Collier *et al.* (2010) deployed this system in a 2-d landscape with a sufficiently small array of nodes to localise bird calls from the sum of cross-correlations between microphones, achieving accuracies to well within a metre.

Our empirical tests constituted the first stage in a planned deployment for near-optimal detection of gunshots across the full extent of TMNR, at the invitation of the Belize Forest Department. Their interest is in sustainable exploitation of the tropical forests that still cover 40% of Belizean land mass. A shortage of rangers for patrolling forests puts a high premium on automated monitoring. Ongoing developments in equipping devices with classification algorithms for detecting chainsaws and animal calls (Prince *et al.* 2019) raise the prospect of efficient multipurpose deployments. New advances in radio communication promise future capability for real-time detection and localisation of exploitation activity, by linking networked devices to a base station. Commercial systems of this sort already exist for camera trapping (e.g., Cuddelink product page 2018), and are undergoing development for open-source AudioMoth sensors (Hill *et al.* 2018).

Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Data S1. Empirical data for trials and deployment.

Data S2. R script for near-optimal placement of acoustic sensors.

Data S3. R script for localisation of sound source.

Figures S1 to S11. Supplementary figures illustrating estimation of sensor detection capability, sensor placement, and gunshot localisation (also see Appendix 6 of this volume).

Chapter 5 - General discussion

Can large felids coexist with people? My thesis has addressed several aspects of this issue. I have provided evidence that human activities threaten forest biodiversity in the Northern Yucatán Peninsula, but also that the wellbeing of rural communities, who are custodians of the unprotected communal forests, depends on conservation of biodiversity. The ecology of jaguars and pumas evaluated in Chapter 2 suggested that these felids share much the same niche inside the small private reserves of EEER and EZCA, and that their continued persistence depends on prey remaining available in the surrounding unprotected forests. The structured interviews and discussions with local people reported in Chapter 3, however, suggested that the conservation of these communal forests is jeopardised by constant pressures from overhunting and logging by outsiders as well as locals, largely unpoliced by the communities which lack resources to patrol their lands or monitor rates of resource extraction. The analysis in Chapter 4 delivers a new cost-effective option for these communities to monitor resource extraction from their forests. In this general discussion, I will attempt a synthesis of these results in terms of their conservation and societal values.

The main outcomes of Chapter 2 included an evaluation of the density of jaguars, and the availability and selection of prey for jaguars and pumas in NYP, and within the private reserves of EEER and EZCA. Densities of jaguars were estimated robustly with spatially explicit capture-recapture models that for the first time in this region recognised sex-specific capture probabilities. The availability of natural prey species was assessed from their presence in camera-trap photos and in felid scats, and from associations between daily activity patterns of jaguars and pumas and their prey. Jaguars and pumas were widespread and abundant in the study area, as were potential prey species, such as collared peccaries, Yucatán brown brocket deer, ocellated turkeys and ocelots. Jaguars and pumas in NYP had largely similar activity patterns, with pumas being more active during the day. Activity patterns of felids were more nocturnal from those of their preferred prey. Both felids preferred to eat collared peccary, deer and white-nosed coati, and both selected against ocellated turkey. Pumas ate a higher proportion of deer compared to jaguars, and jaguars also consumed nine-banded armadillo and Northern tamandua. We found no evidence of consumption of domestic prey species by these felids. Overall, despite dietary niche breadth being more species rich for pumas and more evenly distributed for jaguars, dietary niche overlap exceeded random expectation. Both jaguars and pumas selected the same prey species as those hunted by local communities, which will likely intensify human-wildlife conflicts in the area when prey become scarce for both felid and human predators. Differential use of jaguar and puma habitat in space might be a mechanism that drives coexistence for these two felids in NYP. Neither species, however, showed strong or consistent evidence of excluding the other from any areas of the trapping grid. There was some indirect evidence of jaguars excluding pumas from one part of one reserve in one year, suggesting the possibility of coexistence by dominance hierarchy in competition for the same resource niche. Overall, the ecology of jaguars and pumas suggests these felids are pushed together inside the private reserves of EEER and EZCA, also that these protected forest habitats will not suffice alone to support local populations of either species, and that surrounding communal forests play a vital role for felid conservation in this area.

The main outcomes of Chapter 3 included an evaluation of interactions between local Maya communities and large felids in the Northern Yucatán Peninsula, by recording livestock management practices, wild meat consumption, hunting habits and experiences of human-wildlife conflict. This was assessed by structured interviews with villagers using a questionnaire survey. Results showed that interviewees owned small, fenced plots of land and that they kept domestic animals predominantly for consumption. They had a wide knowledge of wildlife present in their local area. They showed perception bias with respect to estimating higher abundances of game species than other species, and perception preference for wild herbivores over carnivores. Interviewees had concerns about perceived decreases in the abundances of local wildlife over recent years, and attributed these reductions mainly to regular subsistence hunting by their own communities. Only a small proportion of interviewees reported large-felid attacks on their livestock. Interviewees believed that current law facilitates a reduction in wildlife conflicts, and that the Livestock Insurance Fund is the best mitigation tool. The principal game species in the area, as identified by the survey, were also the main prey for jaguars and pumas in the two nearby natural protected areas of EEER and EZCA. Survey results suggested a valuable contribution in technical assistance by local NGO Pronatura, aimed at reducing conflicts with large felids in these communities. The presence of this NGO provides an important bridge between local communities and government policy. Overall, it was clear from these discussions that Pronatura did an effective job of mitigating impacts of large felids on local people, but these people in their roles as custodians of communal forests needed empowering to manage the wildlife resources within their forests.

The main outcome of Chapter 4 was a potential solution to some aspects of the conservation issues raised in chapters 2 and 3. The chapter reported on the development of a novel approach to monitoring human agents of disturbance in protected and unprotected forests of the Yucatán Peninsula, using a grid of low-cost, high-tech acoustic loggers to quantify hunting rates in the forest. We developed probabilistic algorithms for near-optimal placements of gunshot sensors, and for localisation of the sound source as a function of spatial variation in sound pressure. On hilly terrain, near-optimal placement reduced by half the required number of sensors compared to a square grid. A test deployment of acoustic devices matched predicted success in detecting gunshots, and traced them to their local area. These techniques will allow conservation biologists to plan cost-effective deployments for measuring target sounds, and to evaluate impacts of sub-optimal placements imposed by access or cost constraints, or multipurpose uses. Acoustic monitoring of these cryptic human agents of disturbance constitutes a tool that could have substantial impacts on forest conservation in tropical forests. In the longer term, we hope to work with local communities, through the intermediary of Pronatura, in exploring their willingness to use such tools to help police their communal forests.

The study has provided new insights into jaguar and puma ecology and their local relationship with the people who inhabit this area. Its findings are applicable to the social context of the Northern Yucatán Peninsula. Different ecologies and relationships may apply in the Southern Yucatán Peninsula, which contains the Calakmul Biosphere Reserve. The Calakmul reserve covers 7,230 km^2, constituting the largest tropical rainforest reserve in Mexico and Central America (Chávez *et al.* 2007a). It lies within the Selva Maya forest, which stretches south into Belize and Guatemala over a total area of 40,000 km^2, and forms the best-conserved continuous tropical forest north of the Amazon in the Western Hemisphere (Goodell *et al.* 2006; García-Anleu *et al.* 2015). The Calakmul reserve is managed by the Mexican government (SEMARNAT 2000). It is structured as core zones, which only permit conservation and scientific activities, and buffer zones, which permit activities such as forestry and agriculture by local people (Gómez-Pompa & Dirzo 1995). No communities are allowed to live within either core or buffer zones of the reserve. Small towns surround its outer edges, however, and large-scale agriculture and cattle ranching is practised in the south-eastern area of the reserve, which suffers degradation (Chávez 2010). This region will have threats to biodiversity and human-wildlife conflicts that differ from those of our study area in the Northern Yucatán Peninsula. Nonetheless, the area-specific scope of knowledge that we have generated in this study will facilitate opportunities for local-scale solutions to the global-scale problems of biodiversity loss on an overcrowded planet. Many such studies (including for example the CONACyT-funded PhD thesis in preparation by C. Argudín-Violante on social-ecology in the Southern Yucatán Peninsula), will ultimately make fundamental contributions to the bulk of understanding necessary to address the global-scale issue of living sustainably with nature (Madden 2004; Brooks *et al.* 2006; Díaz *et al.* 2015).

This study has documented the vital contribution of a local NGO to socio-ecological harmony, with Pronatura Península de Yucatán as an example of an organisation that understands the necessity of linking the conservation of natural resources to the wellbeing of local communities. We have reported how this NGO delivers technical assistance to local communities by providing access to the Livestock Insurance Fund, by providing camera-traps to monitor natural resources in rural communities, and by providing assistance in obtaining funds from the Mexican programme of Payment for Ecosystem Services (PES; SEMARNAT 2013; Pronatura 2018a, b; pers. obs.), which facilitates opportunities for local communities to profit from the conservation of their natural resources. The NGO plays a vital role in the conservation of jaguars and pumas, and their prey, by leading continuous camera-trap monitoring programmes in the NYP (Pronatura 2017). More generally across the Yucatán Peninsula, it also contributes to the conservation of birds, whale sharks and sea turtles, and it provides assistance in sustainable rural development, including ecotourism, and in welfare, including the management of forest fires (Pronatura 2019). Other NGOs in the Yucatán Peninsula also recognise the importance of coupling conservation with social welfare. For example, Ya'axché Conservation Trust in Belize has a mission to empower local communities to take a greater leadership in the sustainable use of their forests and rivers (Ya'axché Conservation Trust 2019).

El Edén Ecological Reserve and El Zapotal Conservation Area constitute part of the 'Red de Reservas Privadas y Sociales de la Península de Yucatán' (RRPSPY). This network of four reserves, covering ca. 5,360 km^2, is governed by an alliance of four owners (Pronatura Península de Yucatán A. C., Kaxil Kiuic A. C., Amigos de Sian Ka'an A. C. y Reserva Ecológica El Edén, A. C.) of private lands, who wish to promote the conservation of ecosystems and biodiversity within their domains, and the cultural diversity that they maintain, for the benefit of local communities (Gasse-Margat 2019).

From our understanding of the continuity of biodiversity between two small reserves in NYP, and the dependence of local communities on this biodiversity, we believe that the long-term effective operation of this reserve network will contribute substantially to strengthening the role of biodiversity conservation in poverty alleviation. The value of small private reserves across Mexico would be enhanced by expansion of this network to the national scale, yet no such national-scale network currently exists in Mexico. Elsewhere, a successful example is Natura 2000, the flagship conservation programme of the European Union, and the largest coordinated network of protected areas in the world, which stretches over 10% of the land area of the EU. It is managed by the governments of EU member countries, coordinated through EU parliamentary directives, and it includes strictly protected nature reserves, covering lands that are mostly in private ownership. Its approach centres on people working with nature, and its members must ensure that the sites are managed in a sustainable manner, both ecologically and economically (European Commission 2019). Natura 2000 demonstrates that a shared goal of conserving representative habitats and species can be tackled at large scale by cooperation across member states that have very different levels of economic wealth and diversity of natural resources. The nation state of Mexico, which takes the official title of Estados Unidos Mexicanos (the United Mexican States), could perhaps take inspiration from this initiative of the European Union.

Although the government of Mexico has no plans – to our knowledge – for networking private nature reserves at a national scale, Mexico does lead the world in its system of Payments for Ecosystem Services (PES). Mexico’s national PES programme pays rural landholders for hydrological services, carbon sequestration, biodiversity conservation, and sustainable agroforestry (SEMARNAT 2013; Shapiro-Garza 2013). It was implemented in 2003 and is now one of the largest PES programmes in the world. The original intention was to introduce efficiency into environmental policy by creating a market for healthy ecosystems. Almost all attempts to create markets for ES failed, however, and the programme has subsequently evolved into a hybrid of market-like mechanisms, state regulations, and subsidies (McAfee & Shapiro 2010). It now has much of the character of a federal subsidy for rural poverty alleviation (Bulte *et al.* 2008; Shapiro-Garza 2013). Other countries, including the United Kingdom, could perhaps build on this initiative by Mexico, yet the UK government policy on PES (DEFRA 2013) omits to draw on any of the many critical appraisals of the Mexican experience.

We documented the value of two small, protected areas and their surrounding communal forests in the conservation of species with large biotic boundaries that exceed reserve boundaries. Losing them would trigger significant conservation issues for jaguars and pumas, and their prey. It has been recognised that small, protected areas act like stepping-stones for jaguars moving across highly modified landscapes, providing safe sites and breeding areas (Luja *et al.* 2017), and corridors allow migration between protected areas (Beier 1993). Reserve managers lack funds and personnel to patrol and safeguard the natural resources in the reserves. There is an opportunity to direct Payments for Ecosystem Services towards this funding need, but currently Federal Government lacks the financial capital to do so.

We also documented the value of unprotected forests for the conservation of biodiversity, and the awareness by local people of the richness of their natural resources. We found that they recognised and appreciated the value of forest mammal species, and that they recognised a lack of knowledge about their abundances and a lack of resources to manage their sustainable exploitation to police current threats to their forests. The conservation of communal forests within the Mexican system of 'ejidos' nevertheless offers a very valuable opportunity for biodiversity conservation in Mexico. Ejidos are parcels of land entrusted by government to rural communities for tenure as farmland, either communally or partitioned amongst individual members. Although the principle dates back to the Aztec era, it only became a federal system in the early 20th Century, as a key part of efforts to address the landlessness and rural inequity that had contributed to the outbreak of the Mexican Revolution of 1910-1920. Legal status was granted to ejidos in Article 27 of the 1917 Mexican Constitution, the currently used constitution in Mexico. Since then, the ejido has been recognised as legally owned communal land, where collective exploitation can only happen with prior approval of the 'ejidal' assembly (Congreso de la Unión 2008). Half of the nation's land is contained under this land-property type (Perramond 2000), which emphasises both the importance of, and opportunity for, preserving natural resources inside these communal lands.

In this thesis, I have presented first tests of an acoustic technique for monitoring natural forest resources. We believe that this methodology, and further developments in the fast-evolving field of conservation technology, will ultimately provide underfunded reserves and local communities, such as the ones we have studied here, with viable options for policing their forests. Many challenges still need addressing before such technologies can function to the benefit of forest rangers and local communities. Future studies must work with local communities in evaluating their needs and wishes, and the real and perceived usefulness of technology, and potential issues and misuses in its applications. We need to evaluate effective ways to empower people with capacities to police their own resources. Collaborative monitoring involving local data interpretation should be addressed before making our system of acoustic sensors available to reserves and local communities. Locally-based monitoring will require the participation of local stakeholders at all stages from the design of monitoring grids to collection of datasets, their analysis, and decision making. Scientists should input their expertise in providing advice and training, and in-depth analysis. The ultimate goal of local ownership of this technique and its results should be reinforced by leaving the collected data in the local area (Danielsen *et al.* 2009).

Tropical forests in the Yucatán Peninsula, and their constituent biodiversity, face enumerable conservation issues. Population trends in this region sustain an annual average growth rate of 1.5% for the state of Yucatán and 2.7% for Quintana Roo (INEGI 2019), and rural communities face constant pressures to sell their lands in an escalating drive by the tourism industry to connect tourist hotspots of Cancún, Mérida and Holbox (Escamilla *et al*. 2000; León & Montiel 2008). A reduction of 32% in the national budget for the environmental sector, announced by the recently elected government of President Andrés Manuel López Obrador (Enciso 2018), and the construction of the Maya Train (‘Tren Maya’), which the President has personally endorsed to run the length of the Yucatán Peninsula (traversing the Calakmul Biosphere Reserve, Tren Maya 2019), will likely have profound impacts on regional biodiversity and ecosystems, and on the welfare of poor Maya communities who subsist directly on these ecosystems.

In addition to these threats, subsides by the Secretariat for Agriculture and Rural Development (previously ‘SAGARPA’; SADER 2019) that promote shifts from arable agriculture to livestock ranching amongst communities of the Yucatán Peninsula, where crops are failing in the increasingly frequent droughts, will only escalate the conversion of forests lands to pasture in this region. For local communities, this is likely to prove a missed opportunity to supplement their income with profits from sustainable forest products, including honey, peppercorns, chilli peppers and cacao. All of these products have global markets, and indeed the largely artisanal production of Maya honey is third in volume of global honey export, after China and Argentina (Güemez Ricalde 2017). A current study is exploring this issue of alternative livelihoods (Argudín-Violante, PhD thesis in preparation). An example of an effective programme to improve the quality of life of local people, through a diversified system of production, is the partnership between Toledo Cacao Growers Association and Green & Black's chocolate company, which has provided sustainable livelihoods for an entire district in Belize (Steinberg 2002).

The Intergovernmental Panel on Climate Change report: 'Global Warming of 1.5 ºC' (2018) has documented that current rates of human activities will increase global temperatures from 1.5 to 2 °C above pre-industrial levels at some time between 2030 and 2052. If the increase reaches 2 °C, it will substantially deepen the effects of climate change on ecosystems and biodiversity above the effects that we will experience with almost certain warming of 1.5 ºC. With the extra half a degree, it has estimated that 50% more species will lose half their geographic range, that twice the global terrestrial land area will experience a transformation of its ecosystems, and that there will be more risks of forest fires and spread of invasive species. In addition, climate-related risks will increase for health, livelihoods, food security, water supply, human security, and economic growth (IPCC 2018). One of the main aims of this report was to emphasise the value in urgent and concerted collaborative international action now, to prevent the extra half a degree of temperature rise over the next 12 to 34 years. Climate change is already affecting the forests of the Yucatán Peninsula, however, with economically and culturally damaging impacts on the communities that inhabit it, including increased frequencies of hurricanes and droughts (Audefroy & Cabrera Sánchez 2017; Comisión Regional de Cambio Climático 2019). For the Maya communities of the Yucatán Peninsula, disastrous climate change is not a new phenomenon in their history. A previous episode of climate change very likely contributed directly to the total collapse of the Classic Maya civilization, which happened during the driest period of the middle to late Holocene epoch (Hodell *et al.* 1995; deMenocal 2001). It is unfortunate for modern Mayas that they predominantly live in the poor rural and forest communities that are most sensitive to current climate change.

Can large-felids and people coexist together? They can, but we need to provide the jaguars and pumas with opportunities to survive, by creating habitat refuges from the threats that endanger their survival. In human dominated landscapes, one way to envisage these refuges is as 'game gardens', which provision human and animal hunters with sustainable stocks of wild meat (Smith 2005). The landmark 2018 IPCC report has recognised that reducing the impacts of climate change will require planting millions of square-kilometres of forest (IPCC 2018: key finding C.2.5). Even the chief executive officer of the Shell multinational oil conglomerate has expressed support for this need. CEO Ben van Beurden admitted, in an unpublished speech, that a massive afforestation effort, as large as the Amazon forest, will be needed to meet the tougher 1.5 °C global warming target, and that more renewable energy alone will not suffice (Vaughan 2018; Shell Corp. 2019). The internationally recognised need for massive afforestation represents an unprecedented opportunity for reversing global biodiversity loss and bringing forest services to bear on poverty alleviation. In addition, the need to ensure the integrity of mature and diverse high-quality forests and other terrestrial habitats, such as grasslands, peatlands, wetlands, mangroves and agricultural lands, has been recognised as crucial to maintain ecosystem services and to reach the CO_2 mitigation target needed to slow down global warming (Seddon *et al.* 2019). If this ambition is adopted in the Yucatán Peninsula, it will provide jaguars and pumas and the rural communities that live amongst them with a much more stable future.

Appendix 1 - Photographic key of jaguars identified in NYP

F01_EEER_2016_R2_C26-I__00026

F02_EEER_2015_R1_C29-I__00022

F03_YB_2016_R1_C04-I__00027

F04_EZCA_2016_R2_ZAP_1-478

F05_EZCA_2015_R1_SITIO_3-I__00001

F06_EZCA_2016_R2_ZAP_1_2-587

M01_EEER_2016_R2_C27-I__00031

M02_EEER_2015_R2_C29-I__00011

M03_EEER_2015_R2_C22-I__00017

M04_EEER_2016_R1_C29-I__00061

M05_EEER_2016_R1_C01-I__00012

M06_EEER_2016_R1_C16-I__00005

M07_YB_2015_R2_C09-EK000075

M08_EZCA_2015_R1_SM_3-Cdy00014

M09_EZCA_2016_R2_CENOTE_1_2-Cdy00004

M10_EZCA_2015_R1_SITIO_8-Cdyi0004

U01_EEER_2016_R1_C42-I__00005

U02_EEER_2016_R1_C35-I__00016

NOTE: First letter in names indicates sex: F = females; M = males; U = Undetermined.

U03_EEER_2015_R1_C09-I__00035

U04_YB_2016_R1_C04-I__00012

U05_YB_2015_R2_C09-EK000117

NOTE: First letter in names indicates sex: F = females; M = males; U = Undetermined.

Appendix 2 - Supporting information for Chapter 2

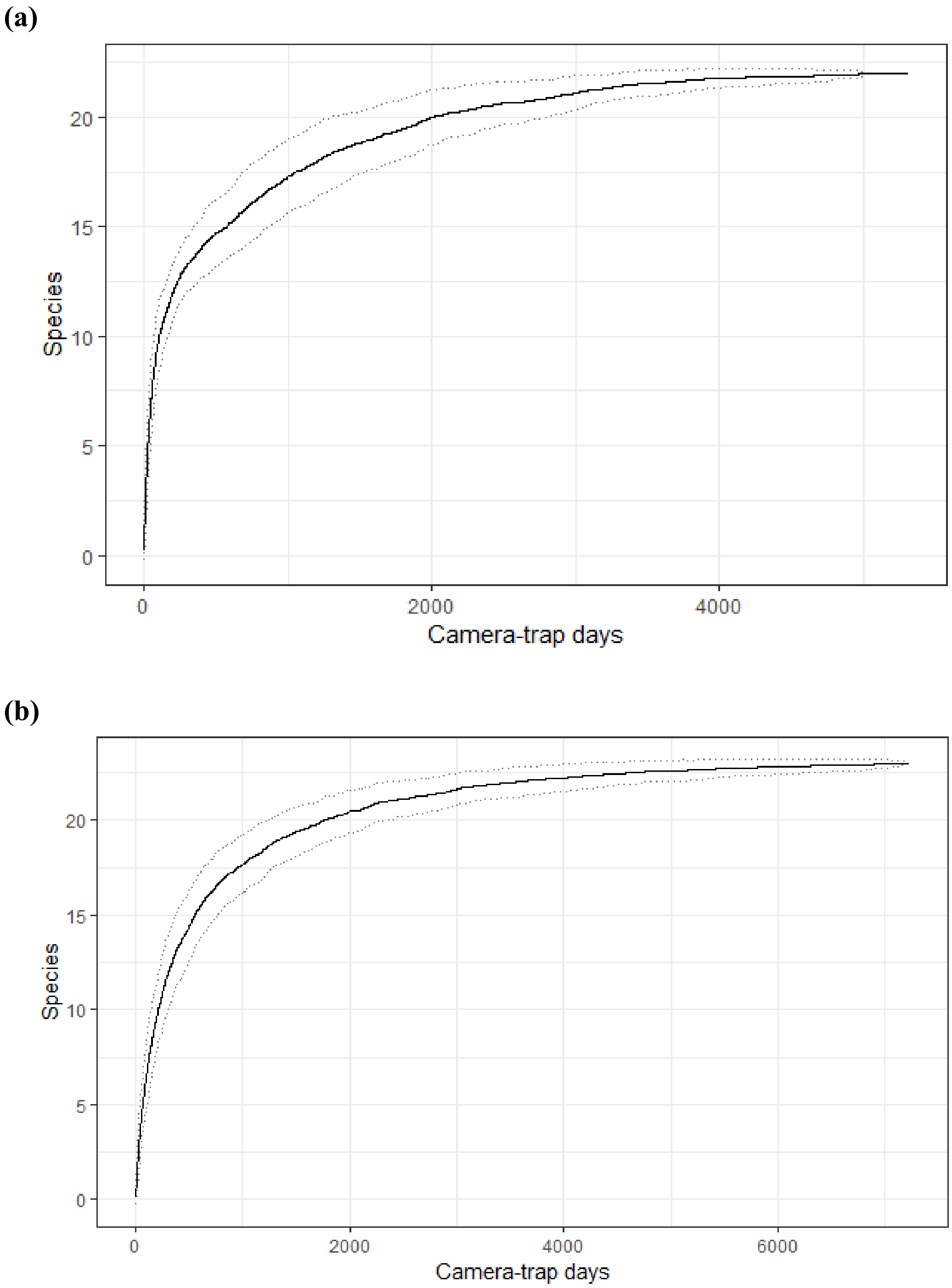


Figure A2.1. Randomised species accumulation curve (solid line) for camera-trap sampling effort, and confidence intervals (dashed lines), in (a) EEER (5,228 camera days) and (b) EZCA (7,151 camera days). Data pooled across years. Species captured in EEER: 22 (both years), 21 (2015) and 19 (2016), and in EZCA: 23 (both years), 19 (2015) and 23 (2016).

Table A2.1. Naïve occupancy (NO) and relative abundance index (RAI) of large felids and their potential prey species captured in EEER. Largest values are shown in bold.

Order	Family	Latin name	Common name	NO (2015)	NO (2016)	RAI (2015)	RAI (2016)
CLASS MAMMALIA							
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	Common opossum	-	0.04	-	0.07
		Didelphis virginiana	Virginia opossum	0.03	0.04	0.04	0.15
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	0.05	-	0.08	-
Pilosa	Myrmecophagidae	*Tamandua mexicana*	Northern tamandua	-	-	-	-
Rodentia	Cuniculidae	*Cuniculus paca*	Lowland paca	0.13	0.04	2.24	1.64
	Dasyproctidae	*Dasyprocta punctata*	Central American agouti	0.05	-	0.08	-
Lagomorpha	Leporidae	*Sylvilagus floridanus*	Eastern cottontail	-	-	-	-
Carnivora	Canidae	*Canis latrans*	Coyote	0.08	0.09	0.12	0.15
		Urocyon cinereoargenteus	Grey fox	0.24	0.23	0.63	1.19
	Procyonidae	*Nasua narica*	White-nosed coati	0.24	0.21	0.63	0.60
		Procyon lotor	Northern raccoon	-	-	-	-
	Mephitidae	*Conepatus semistriatus*	Striped hog-nosed skunk	0.03	0.06	0.04	0.11
	Mustelidae	*Eira barbara*	Tayra	0.03	0.09	0.04	0.15
	Felidae	*Herpailurus yagouaroundi*	Jaguarundi	0.05	-	0.08	-
		Leopardus pardalis	Ocelot	0.47	0.51	1.57	2.20
		Leopardus wiedii	Margay	0.03	0.09	0.04	0.15
		Panthera onca	Jaguar	0.55	0.55	2.48	2.31
		Puma concolor	Puma	0.63	**0.81**	2.32	4.95
Cetartiodactyla	Cervidae	*Mazama pandora*	Yucatan brown brocket deer	0.58	0.70	3.66	**5.21**
		Mazama temama	Central American red brocket deer	0.03	0.09	0.04	0.22
		Odocoileus virginianus	White-tailed deer	0.03	0.15	0.04	0.41
	Tayassuidae	*Pecari tajacu*	Collared peccary	0.29	0.55	0.83	2.50
CLASS AVES							
Galliformes	Cracidae	*Crax rubra*	Great curassow	0.29	0.40	1.26	1.86
		Ortalis vetula	Chachalaca	0.14	0.18	0.20	1.64
	Phasianidae	*Meleagris ocellata*	Ocellated turkey	**0.70**	0.63	**6.06**	3.61

Table A2.2. Naïve occupancy (NO) and relative abundance index (RAI) of large felids and their potential prey species captured in EZCA. Largest values are shown in bold.

Order	Family	Latin name	Common name	NO (2015)	NO (2016)	RAI (2015)	RAI (2016)
CLASS MAMMALIA							
Didelphimorphia	Didelphidae	*Didelphis marsupialis*	Common opossum	0.09	-	0.12	-
		Didelphis virginiana	Virginia opossum	0.16	0.03	0.37	0.03
Cingulata	Dasypodidae	*Dasypus novemcinctus*	Nine-banded armadillo	0.09	0.03	0.12	0.07
Pilosa	Myrmecophagidae	*Tamandua mexicana*	Northern tamandua	0.02	-	0.02	-
Rodentia	Cuniculidae	*Cuniculus paca*	Lowland paca	0.18	0.03	0.32	0.03
	Dasyproctidae	*Dasyprocta punctata*	Central American agouti	0.07	0.13	0.20	0.59
Lagomorpha	Leporidae	*Sylvilagus floridanus*	Eastern cottontail	0.05	0.03	0.10	0.10
Carnivora	Canidae	*Canis latrans*	Coyote	0.09	-	0.10	-
		Urocyon cinereoargenteus	Grey fox	0.16	0.08	0.22	0.13
	Procyonidae	*Nasua narica*	White-nosed coati	0.30	0.28	0.39	0.39
		Procyon lotor	Northern raccoon	-	-	-	-
	Mephitidae	*Conepatus semistriatus*	Striped hog-nosed skunk	0.16	0.20	0.22	0.42
	Mustelidae	*Eira barbara*	Tayra	0.05	-	0.05	-
	Felidae	*Herpailurus yagouaroundi*	Jaguarundi	-	-	-	-
		Leopardus pardalis	Ocelot	0.41	0.38	0.88	1.01
		Leopardus wiedii	Margay	0.09	0.05	0.10	0.10
		Panthera onca	Jaguar	0.50	0.63	0.86	2.70
		Puma concolor	Puma	0.27	0.28	0.49	1.14
Cetartiodactyla	Cervidae	*Mazama pandora*	Yucatan brown brocket deer	0.41	0.48	1.01	1.66
		Mazama temama	Central American red brocket deer	0.07	0.08	0.07	0.10
		Odocoileus virginianus	White-tailed deer	0.02	0.03	0.07	0.03
	Tayassuidae	*Pecari tajacu*	Collared peccary	0.23	0.30	0.44	1.01
CLASS AVES							
Galliformes	Cracidae	*Crax rubra*	Great curassow	0.25	0.28	0.42	0.75
		Ortalis vetula	Chachalaca	0.14	0.10	0.15	0.23
	Phasianidae	*Meleagris ocellata*	Ocellated turkey	**0.80**	**0.80**	**6.48**	**6.50**

Table A2.3. Classification activity of large felids and their potential prey species captured from our camera-trap sampling data in EEER and EZCA.

Order	**Family**	**Latin name**	**Common name**	**EEER**	**EZCA**
CLASS MAMMALIA					
Didelphimorphia	Didelphidae	*Didelphis virginiana*	Virginia opossum	-	Nocturnal
Rodentia	Cuniculidae	*Cuniculus paca*	Lowland paca	Nocturnal	Nocturnal
	Dasyproctidae	*Dasyprocta punctata*	Central American agouti	-	Cathemeral
Carnivora	Canidae	*Urocyon cinereoargenteus*	Grey fox	Mostly nocturnal	Cathemeral
	Procyonidae	*Nasua narica*	White-nosed coati	Mostly diurnal	Mostly diurnal
	Mephitidae	*Conepatus semistriatus*	Striped hog-nosed skunk	-	Nocturnal
	Felidae	*Leopardus pardalis*	Ocelot	Nocturnal	Nocturnal
		Panthera onca	Jaguar	Cathemeral	Mostly nocturnal
		Puma concolor	Puma	Cathemeral	Cathemeral
Cetartiodactyla	Cervidae	*Mazama pandora*	Yucatan brown brocket deer	Mostly diurnal	Mostly diurnal
		Odocoileus virginianus	White-tailed deer	Diurnal	-
	Tayassuidae	*Pecari tajacu*	Collared peccary	Mostly diurnal	Mostly diurnal
CLASS AVES					
Galliformes	Cracidae	*Crax rubra*	Great curassow	Mostly diurnal	Mostly diurnal
		Ortalis vetula	Chachalaca	Diurnal	Diurnal
	Phasianidae	*Meleagris ocellata*	Ocellated turkey	Diurnal	Mostly diurnal

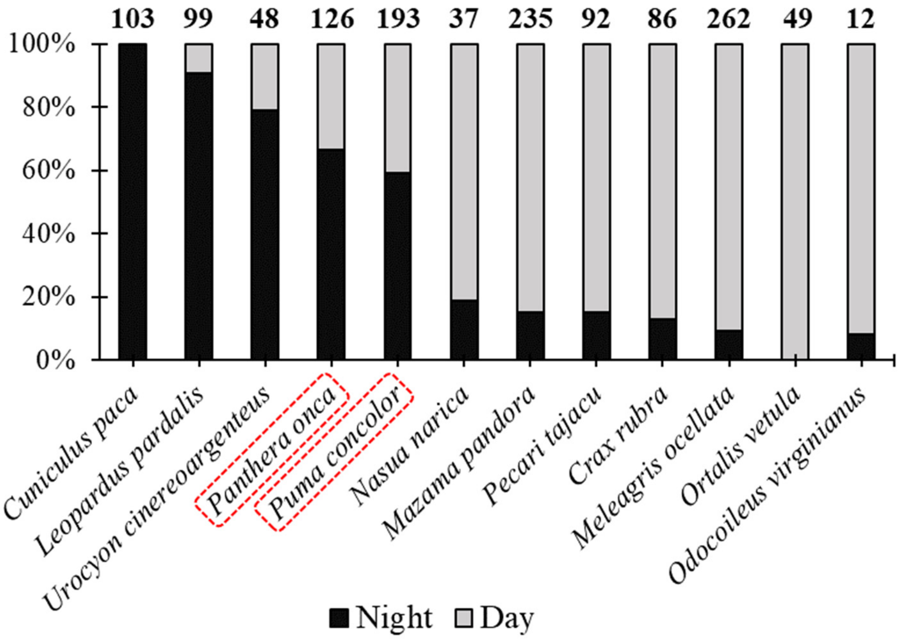


Figure A2.2. Activity records of large felids and their potential prey species (> 10 records) found in EEER. Order by proportion of night-time and daytime records (number of observations on top of bars).

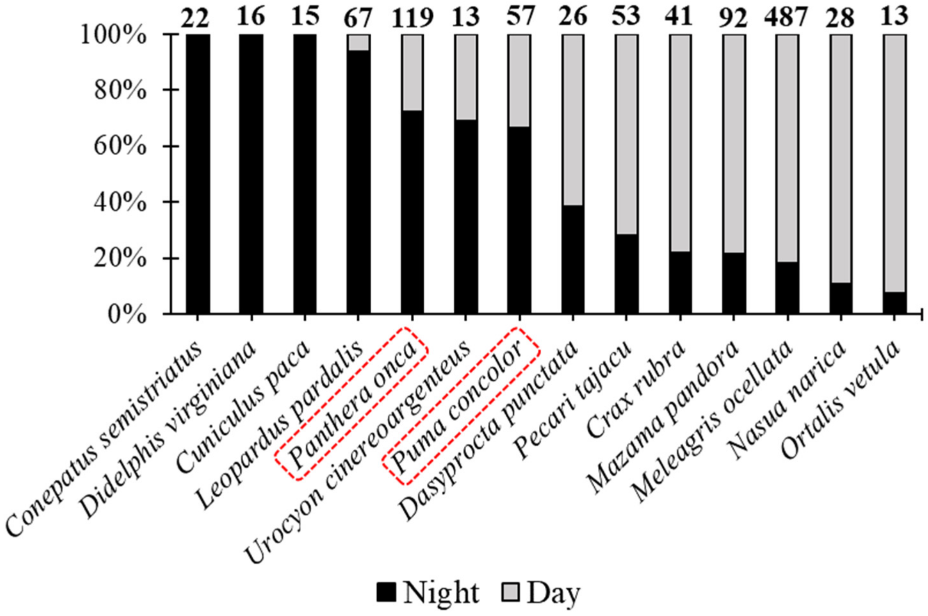


Figure A2.3. Activity records of large felids and their potential prey species (> 10 records) found in EZCA. Order by proportion of night-time and daytime records (number of observations on top of bars).

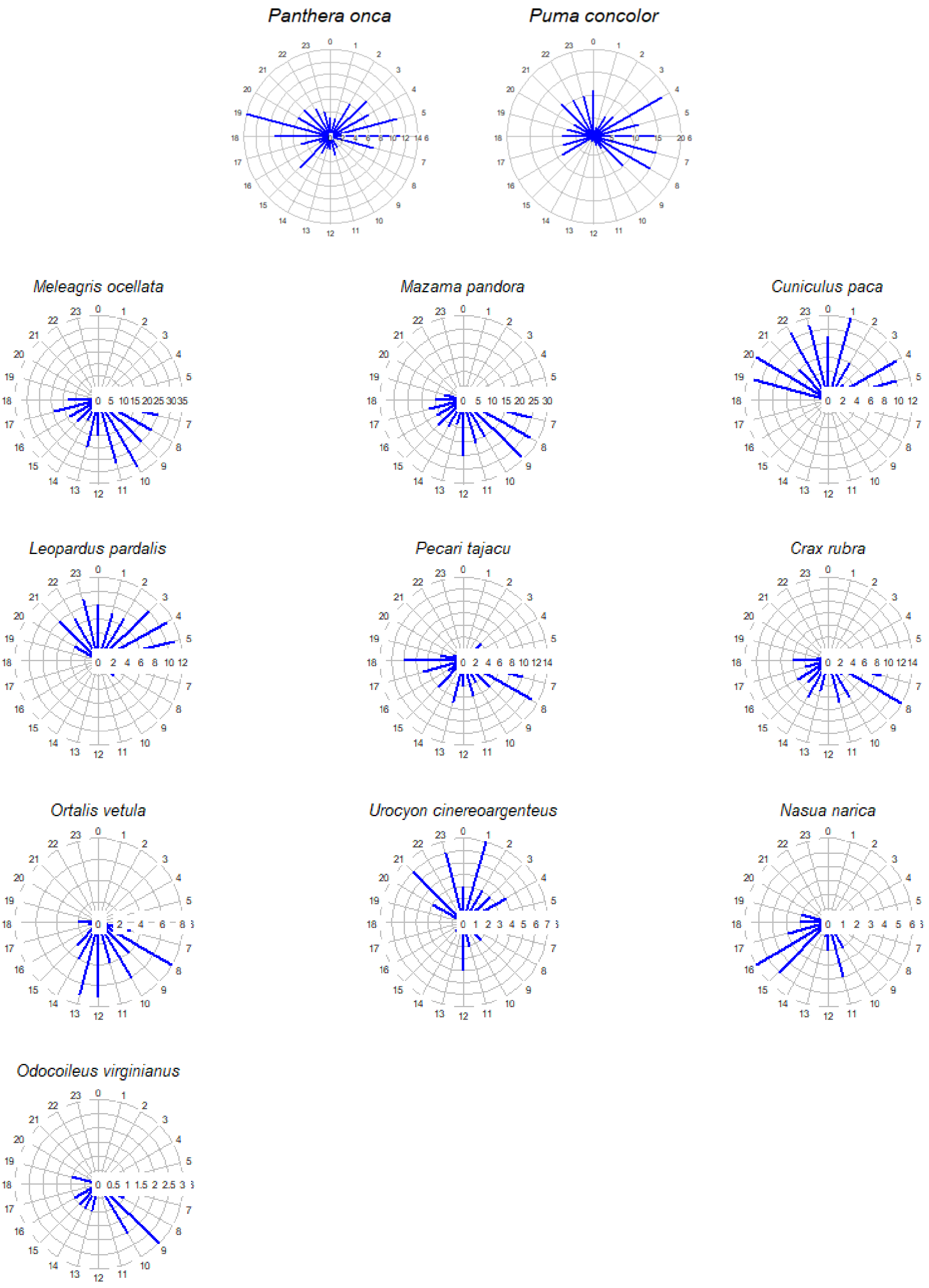
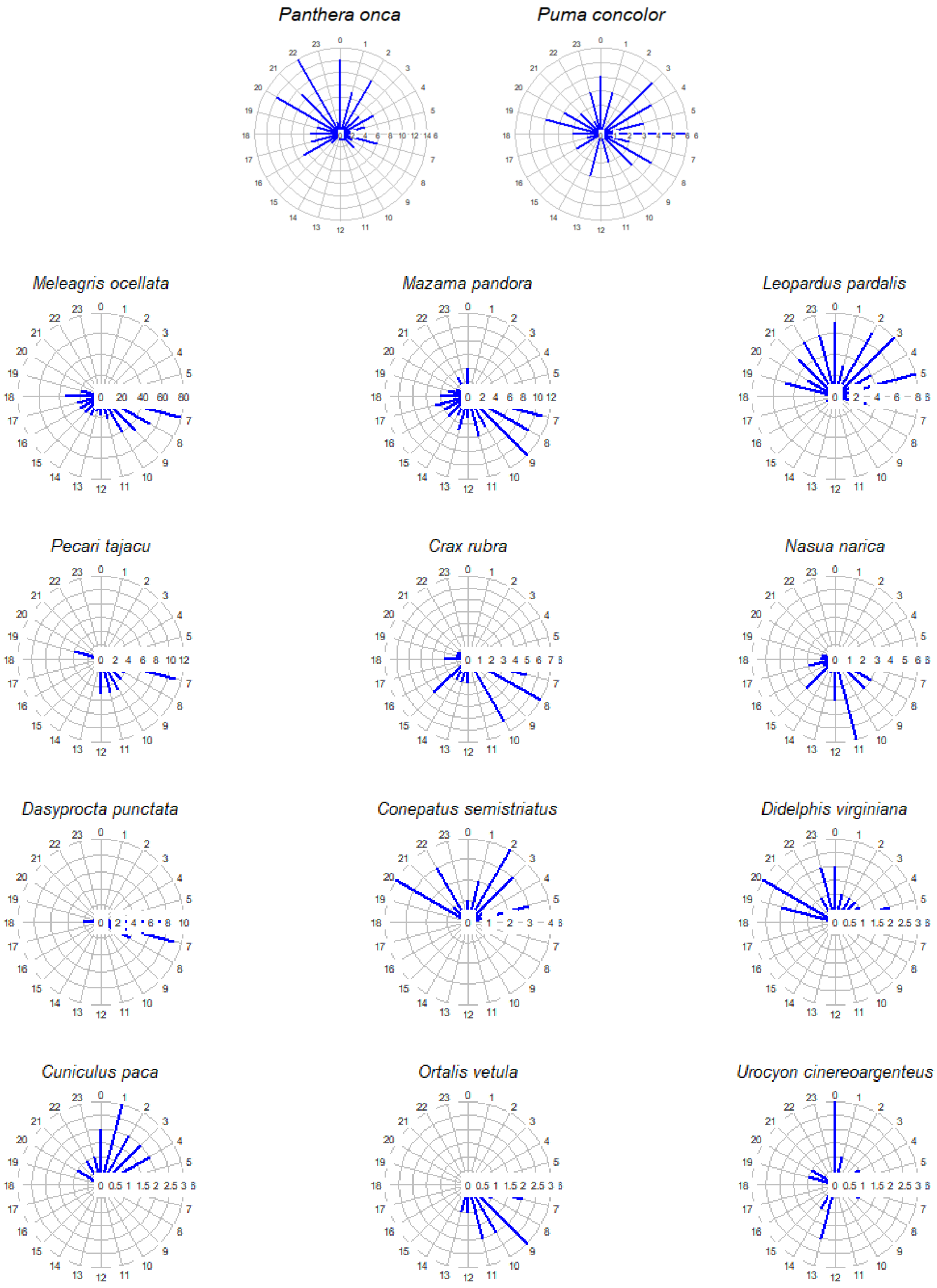


Figure A2.4. Radial plots of activity for jaguar and puma, and their potential prey species, in EEER. The length of each line signifies number of hourly events. Jaguar and puma are shown at the top of the figure. Below, their potential prey species are ordered by Latin name.



Panthera onca

Puma concolor

Meleagris ocellata

Mazama pandora

Leopardus pardalis

Pecari tajacu

Crax rubra

Nasua narica

Dasyprocta punctata

Conepatus semistriatus

Didelphis virginiana

Cuniculus paca

Ortalis vetula

Urocyon cinereoargenteus

Figure A2.5. Radial plots of activity for jaguar and puma, and their potential prey species, in EZCA. The length of each line signifies number of hourly events. Jaguar and puma are shown at the top of the figure. Below, their potential prey species are ordered by Latin name.

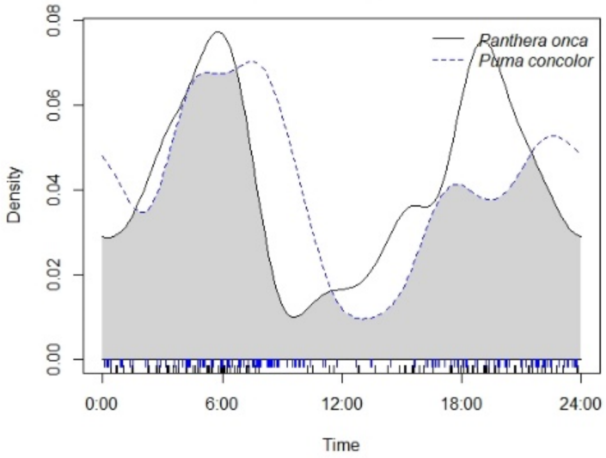
Table A2.4. Overlap in activity patterns between jaguars and pumas, and between large felids and their potential prey species, in EEER. Wald statistic (W), p < 0.05 (bold) signifies less than 5% chance of the two samples coming from the same activity pattern. Jaguar and puma are shown at the top of the table. Below, their potential prey species are ordered by overlap (*W*) with jaguars.

Species	***n***	**Coefficient of overlapping (± C. I.)** ***Panthera onca***	**W**	***p***	**Coefficient of overlapping (± C. I.)** ***Puma concolor***	**W**	***p***
Panthera onca	125	-	-	-	0.81 (0.72 - 0.89)	0.34	0.56
Puma concolor	192	0.81 (0.72 - 0.89)	0.34	0.56	-	-	-
Urocyon cinereoargenteus	48	0.67 (0.50 - 0.74)	0.88	0.35	0.71 (0.55 - 0.78)	2.53	0.11
Nasua narica	35	0.57 (0.42 - 0.68)	1.38	0.24	0.58 (0.44 - 0.69)	2.88	0.09
Pecari tajacu	84	0.58 (0.44 - 0.65)	2.69	0.10	0.59 (0.48 - 0.66)	5.25	**0.02**
Leopardus pardalis	99	0.68 (0.56 - 0.75)	3.00	0.08	0.71 (0.60 - 0.78)	6.06	**0.01**
Cuniculus paca	100	0.64 (0.53 - 0.72)	3.13	0.08	0.63 (0.51 - 0.68)	6.50	**0.01**
Mazama pandora	235	0.53 (0.42 - 0.59)	3.82	0.05	0.59 (0.50 - 0.65)	7.42	**0.01**
Meleagris ocellata	255	0.47 (0.36 - 0.52)	3.99	**0.04**	0.52 (0.43 - 0.57)	7.89	**0.01**
Odocoileus virginianus	10	0.40 (0.19 - 0.61)	4.31	**0.04**	0.44 (0.27 - 0.65)	6.68	**0.01**
Ortalis vetula	49	0.38 (0.21 - 0.43)	5.81	**0.02**	0.44 (0.29 - 0.50)	10.16	**<0.005**
Crax rubra	81	0.51 (0.39 - 0.58)	6.16	**0.01**	0.55 (0.44 - 0.60)	10.08	**<0.005**

Table A2.5. Overlap in activity patterns between jaguars and pumas, and between large felids and their potential prey species, in EZCA. Wald statistic (*W*), p < 0.05 (bold) signifies less than 5% chance of the two samples coming from the same activity pattern. Jaguar and puma are shown at the top of the table. Below, their potential prey species are ordered by overlap (*W*) with jaguars.

Species	***n***	**Coefficient of overlapping (± C. I.)** ***Panthera onca***	**W**	***p***	**Coefficient of overlapping (± C. I.)** ***Puma concolor***	**W**	***P***
Panthera onca	120	-	-	-	0.77 (0.64 - 0.89)	0.44	0.51
Puma concolor	56	0.77 (0.64 - 0.89)	0.44	0.51	-	-	-
Urocyon cinereoargenteus	13	0.71 (0.47 - 0.88)	0.43	0.51	0.78 (0.55 - 0.93)	1.20	0.27
Leopardus pardalis	67	0.80 (0.70 - 0.90)	1.39	0.24	0.70 (0.57 - 0.82)	2.41	0.12
Didelphis virginiana	16	0.78 (0.61 - 0.92)	1.45	0.23	0.65 (0.47 - 0.81)	2.48	0.12
Pecari tajacu	53	0.43 (0.31 - 0.56)	3.74	0.05	0.65 (0.51 - 0.79)	4.46	**0.03**
Nasua narica	28	0.38 (0.24 - 0.49)	3.83	0.05	0.50 (0.34 - 0.65)	4.68	**0.03**
Mazama pandora	93	0.48 (0.38 - 0.59)	4.10	**0.04**	0.64 (0.51 - 0.76)	4.78	**0.03**
Conepatus semistriatus	20	0.73 (0.57 - 0.87)	5.71	**0.02**	0.62 (0.46 - 0.77)	5.98	**0.01**
Crax rubra	41	0.36 (0.23 - 0.46)	7.84	**0.01**	0.54 (0.40 - 0.68)	7.92	**<0.005**
Cuniculus paca	14	0.59 (0.39 - 0.76)	11.60	**<0.005**	0.53 (0.32 - 0.70)	10.36	**<0.005**
Ortalis vetula	13	0.21 (0.07 - 0.30)	12.90	**<0.005**	0.38 (0.22 - 0.55)	11.25	**<0.005**
Meleagris ocellata	482	0.37 (0.29 - 0.45)	15.93	**<0.005**	0.54 (0.42 - 0.65)	11.51	**<0.005**
Dasyprocta punctata	26	0.24 (0.11 - 0.31)	45.13	**<0.005**	0.35 (0.23 - 0.47)	26.61	**<0.005**

(a)



(b)

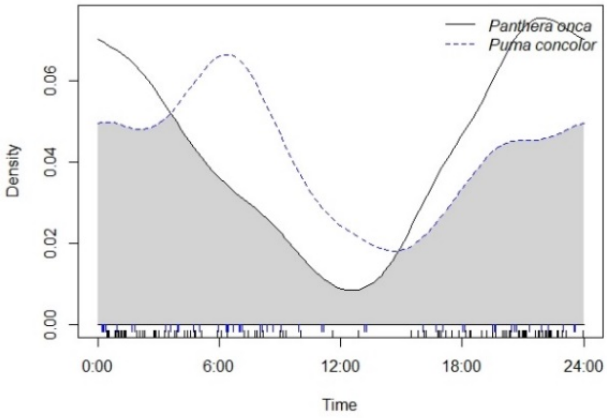
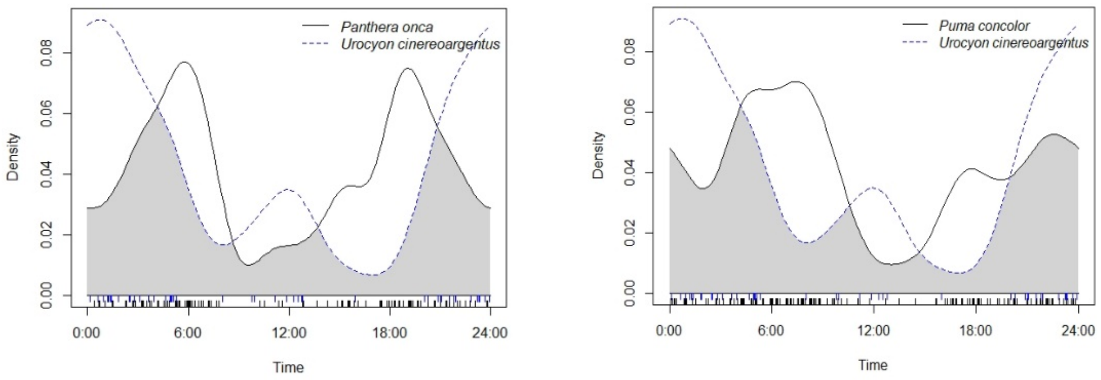


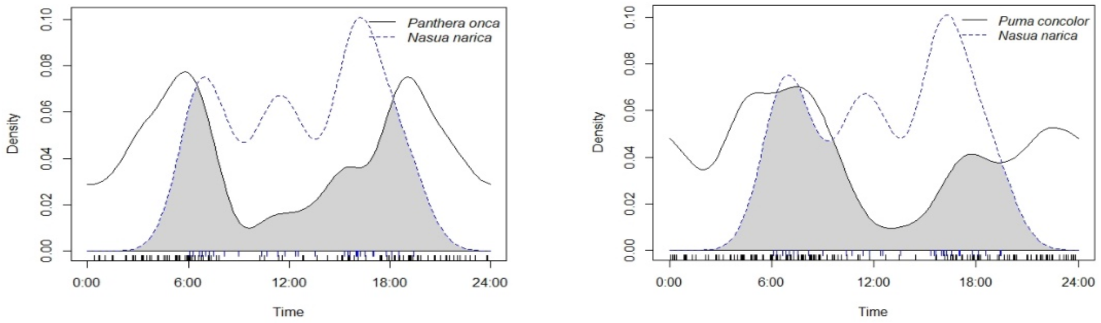
Figure A2.6. Activity curves and overlap between jaguar (black, continuous line) and puma (blue, dotted line) in (a) EEER and (b) EZCA. The coefficient of overlapping equals the area in grey below both curves. The original records for jaguar (black) and puma (blue) are shown at the foot of the chart as a ‘rug’.

Jaguar
(*Panthera onca*)

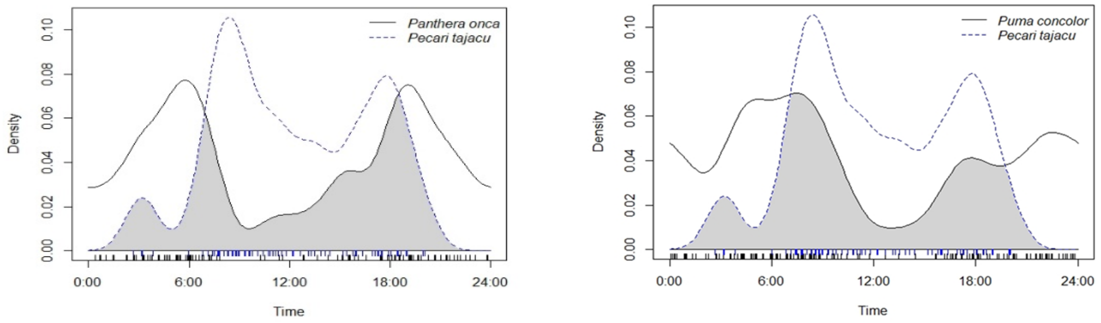
Puma
(*Puma concolor*)



Grey fox
(*Urocyon cinereoargenteus*)



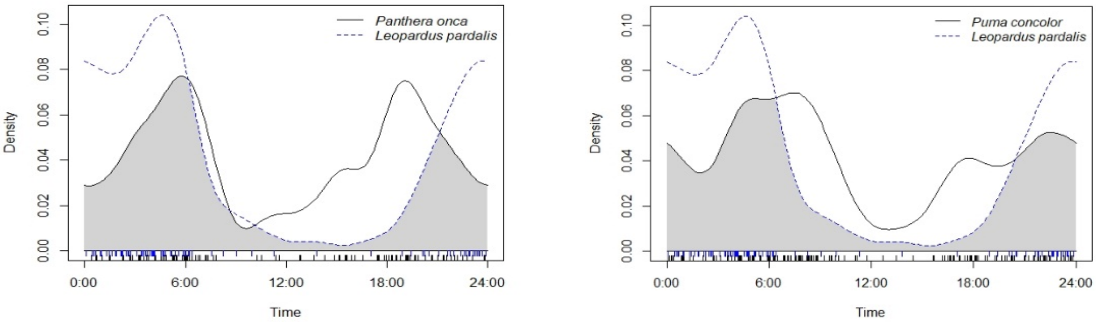
White-nosed coati
(*Nasua narica*)



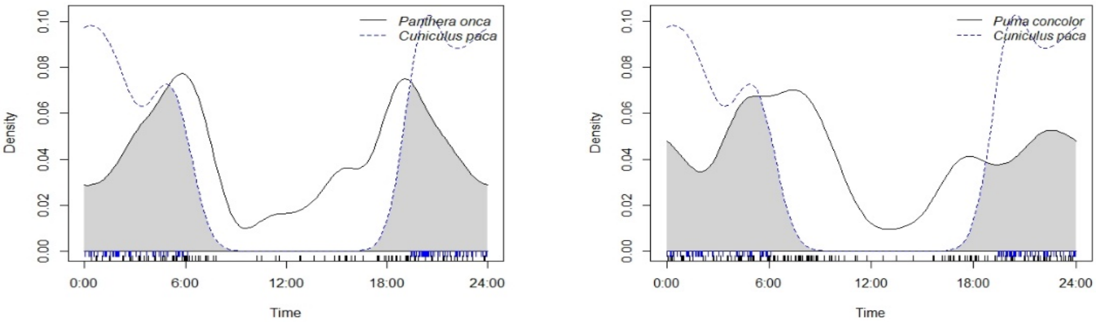
Collared peccary
(*Pecari tajacu*)

Figure A2.7. Activity curves and overlap between jaguars (black, continuous line on the left-hand side) and pumas (black, continuous line on the right-hand side), and their potential prey species (blue, dotted line) in EEER. The coefficient of overlapping equals the area in grey below both curves. The original records for jaguar (black) and puma (blue) are shown at the foot of the chart as a 'rug'. Ordered from the highest to the lowest Coefficient of overlapping between jaguars and prey.

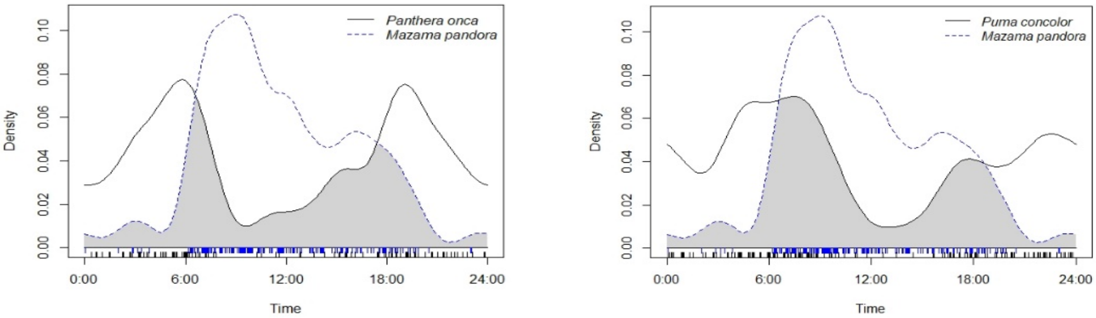
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



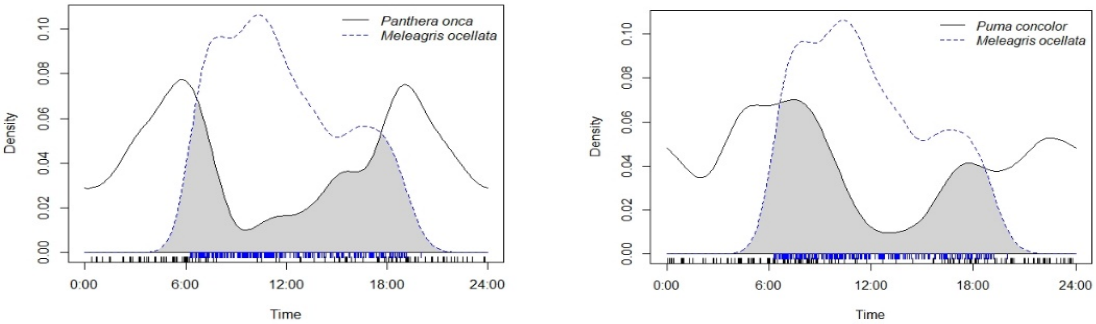
Ocelot
(*Leopardus pardalis*)



Lowland paca
(*Cuniculus paca*)



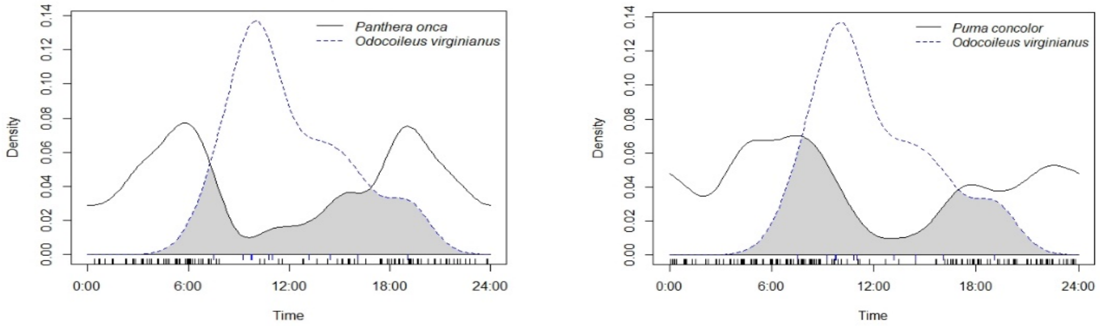
Yucatán brown brocket deer
(*Mazama pandora*)



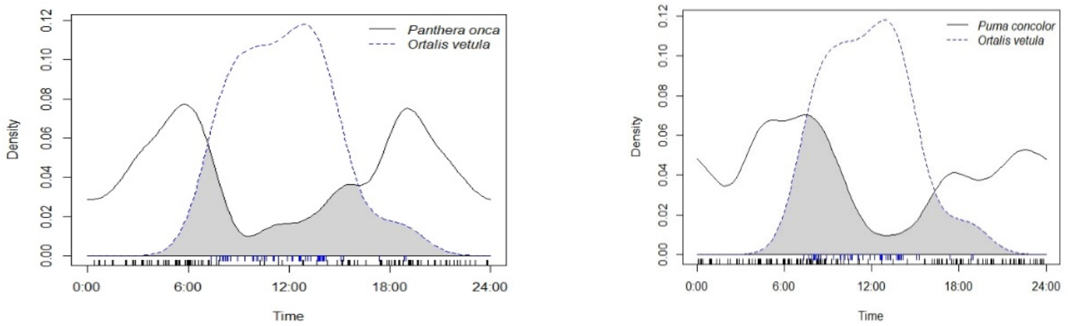
Ocellated turkey
(*Meleagris ocellata*)

Figure A2.7 (Cont.).

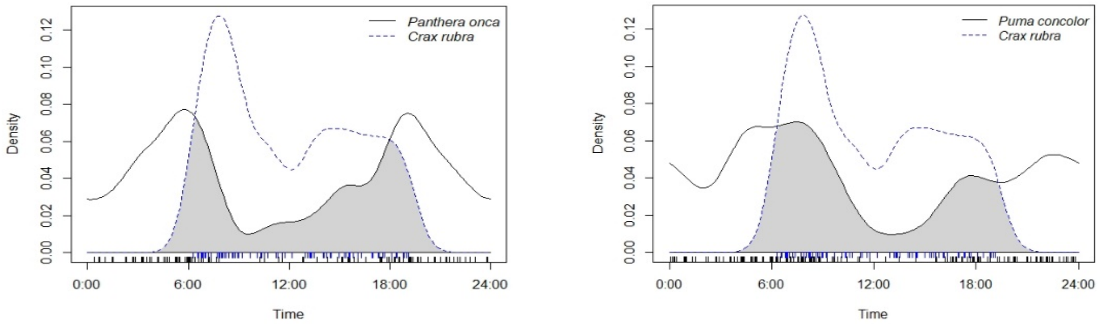
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



White-tailed deer
(*Odocoileus virginianus*)



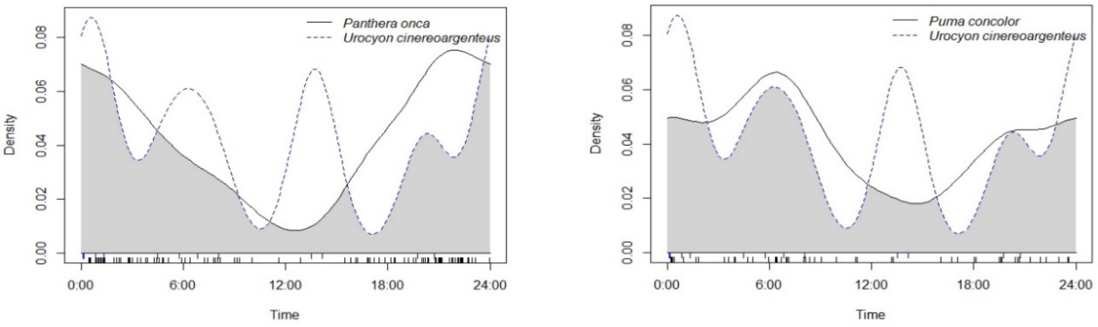
Plain chachalaca
(*Ortalis vetula*)



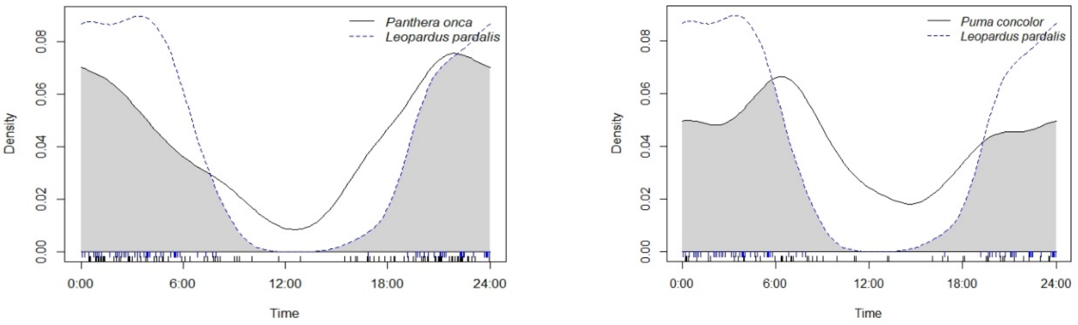
Great curassow
(*Crax rubra*)

Figure A2.7 (Cont.).

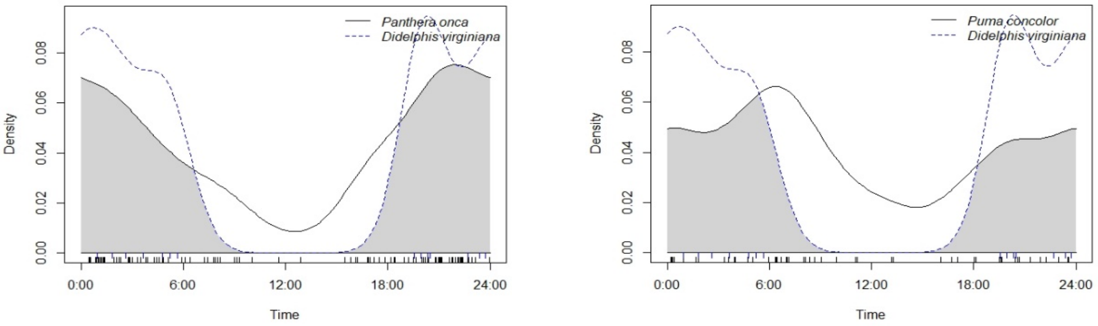
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



Grey fox
(*Urocyon cinereoargenteus*)



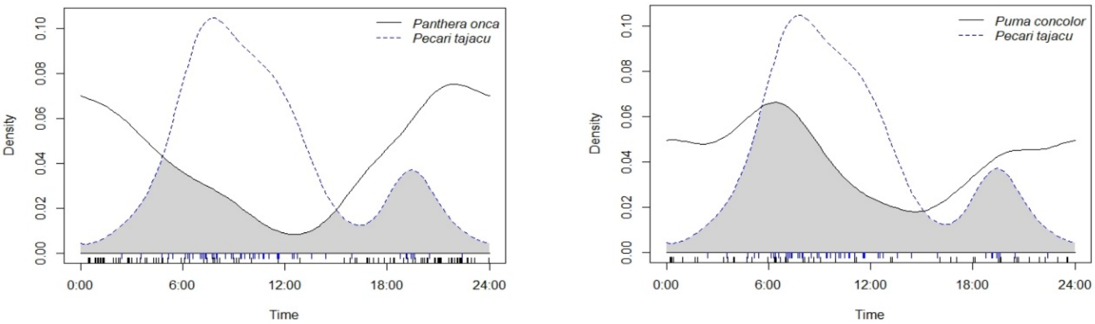
Ocelot
(*Leopardus pardalis*)



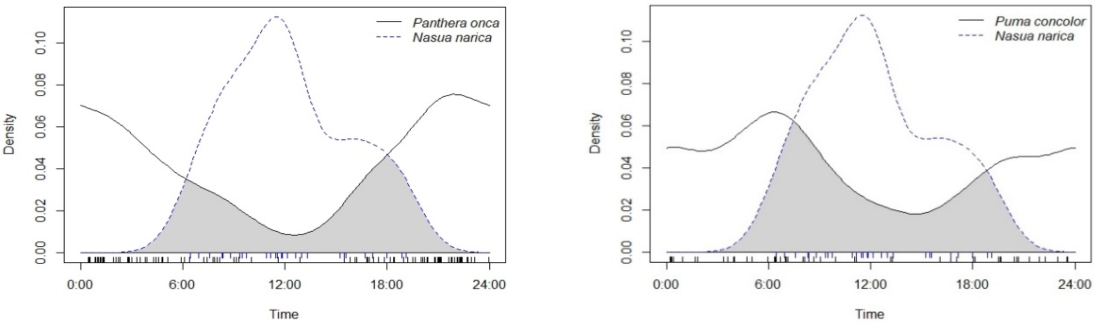
Virginia opossum
(*Didelphis virginiana*)

Figure A2.8. Activity curves and overlap between jaguars (black, continuous line on the left-hand side) and pumas (black, continuous line on the right-hand side), and their potential prey species (blue, dotted line) in EZCA. The coefficient of overlapping equals the area in grey below both curves. The original records for jaguar (black) and puma (blue) are shown at the foot of the chart as a ‘rug’. Ordered from the highest to the lowest Coefficient of overlapping between jaguars and prey.

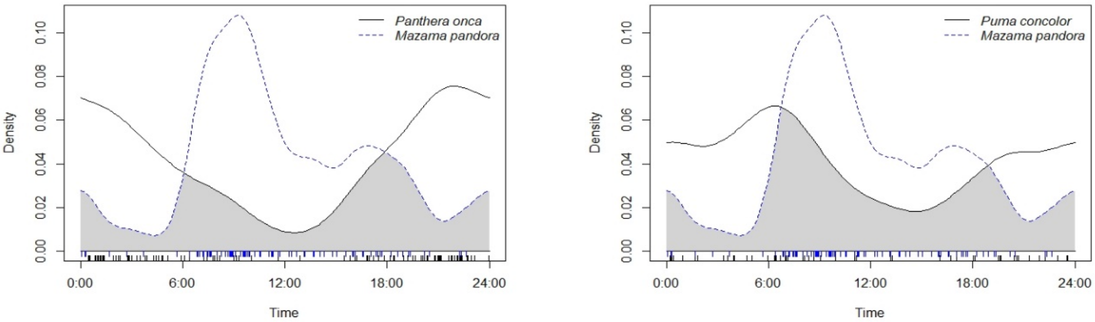
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



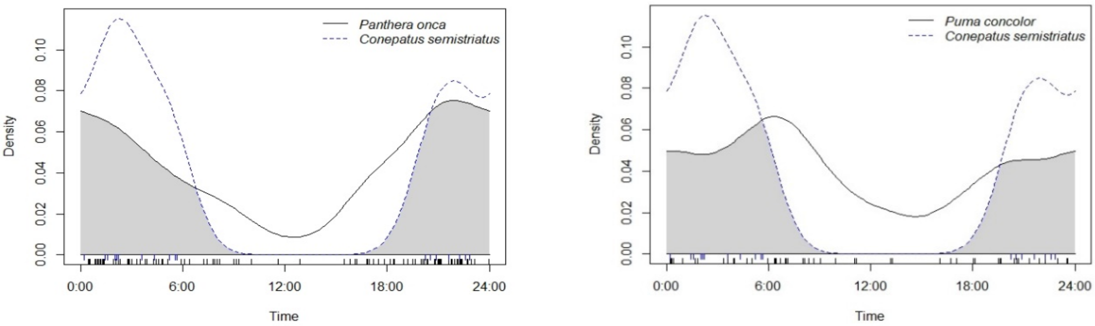
Collared peccary
(*Pecari tajacu*)



White-nosed coati
(*Nasua narica*)



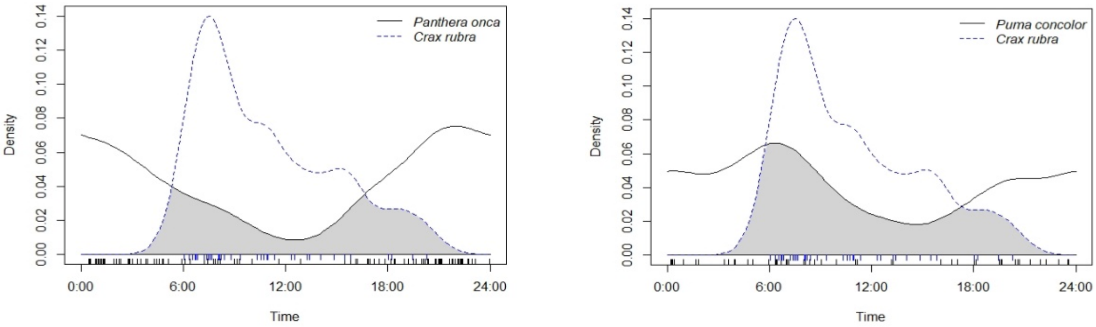
Yucatan brown brocket
(*Mazama pandora*)



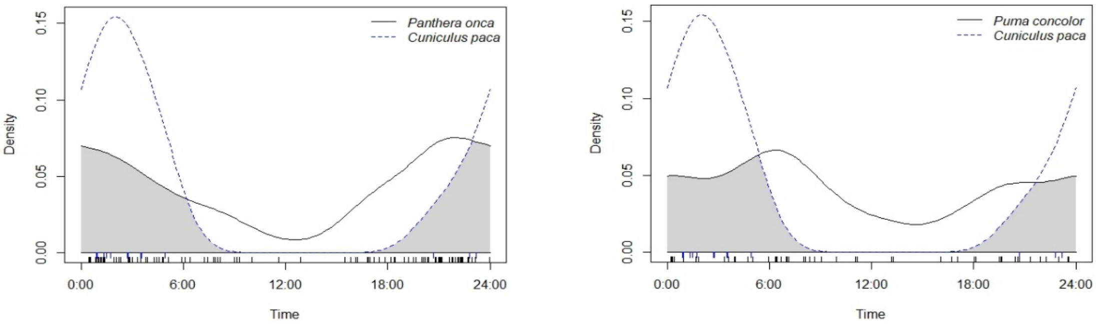
Striped hog-nosed skunk
(*Conepatus semistriatus*)

Figure A2.8 (Cont.).

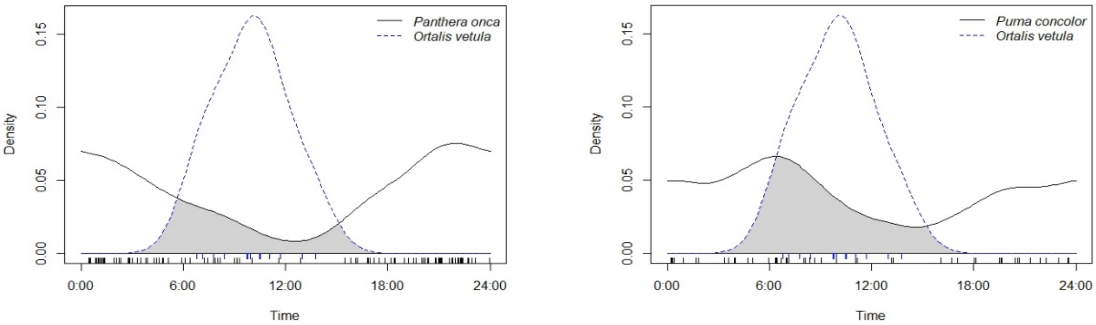
Jaguar (*Panthera onca*)	Puma (*Puma concolor*)



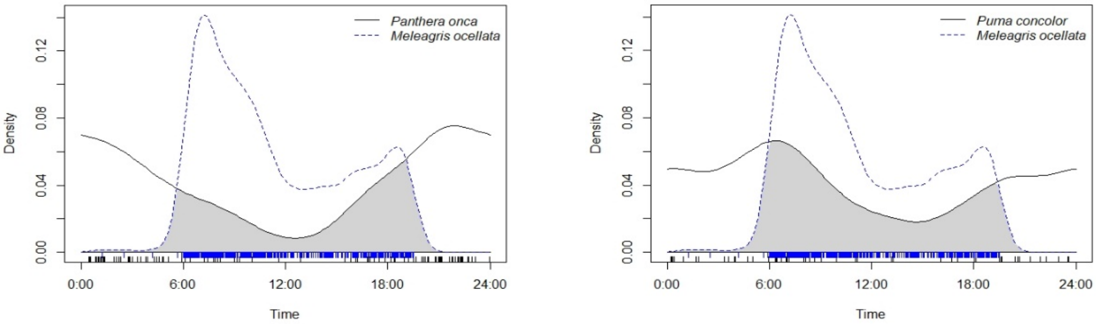
Great curassow
(*Crax rubra*)



Lowland paca
(*Cuniculus paca*)

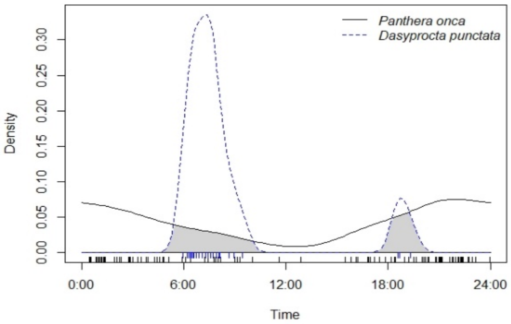
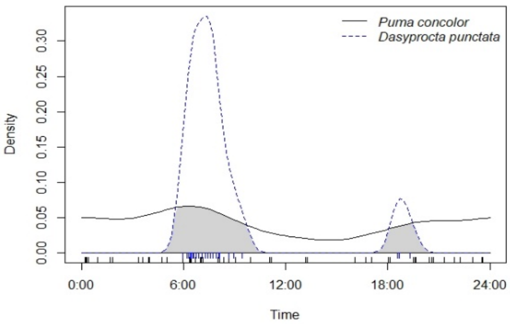


Plain chachalaca
(*Ortalis vetula*)



Ocellated turkey
(*Meleagris ocellata*)

Figure A2.8 (Cont.).

Jaguar (*Panthera onca*)	Puma (*Puma concolor*)
	

Central American agouti
(*Dasyprocta punctata*)

Figure A2.8 (Cont.).

Appendix 3 - Survey questionnaire used to assess perceptions about wildlife, wild meat consumption, livestock management practices and human-wildlife conflict in the Yucatán Peninsula

Questionnaire to evaluate livestock management practices, perceptions of wildlife, wild meat consumption and human-wildlife conflict in the Yucatán Peninsula, Mexico

Implemented by Evelyn Piña Covarrubias

PhD research student

ERGO ID number: 13836

[English translation]

Participant number: ________ Date: ______/___________/_______

I have read the *Participant information sheet* to the participant. S/he has understood their rights, has had an opportunity to ask questions, and has consented to take part in this study:

____

Evelyn Piña Covarrubias

Research in charge of study

Section 1. Livestock management.

1. Do you own a livestock ranch, work in a livestock ranch or do you keep domestic livestock on your property?
    a. Yes.
    b. No…go to Question 8.
2. What is the size of the property?
    a. Small (< 100 ha): ______ ha.
    b. Medium (100 – 500 ha): _________ ha.
    c. Large (> 500 ha): __________ ha.
3. What kind and how many livestock animals do you own?
4. What do you own them for?

Species	3	4 –What for?						
	# Ind.	Meat	Milk	Eggs	Wool/ leather	Work in farm	To sell	Other
Cows				■		■		
Sheep			■	■		■		
Pigs			■	■	■	■		
Goats				■	■	■		
Horses		■	■	■	■			
Donkeys		■	■	■	■			
Chicken			■		■	■		
Turkey			■	■	■	■		
Other:								

5. Which is the main type of livestock management on the property?
    a. Extensive (free ranging).
    b. Intensive (contained in cowshed/barn).
    c. Backyard.
    d. Other: __________________.
6. Does the property have a fence to hold the livestock in? If so, what is the main material it is built of?
    a. No
    b. Wooden.
    c. Concrete.
    d. Barbed wire.
    e. Electrified.
7. Which is the main livestock-birthing place in the property?
    a. Fenced maternity pasture.
    b. Fenced paddock.
    c. Open pasture.
    d. Other: __________________.

Section 2. Perceptions towards wildlife

8. Do these animals live in your community?
9. How many do you think there are in your community?
10. For the last 10 years, do you think their numbers have increased, remained the same or decreased?
11. Why?
12. What do you think about having these animals in your community?
13. What is their purpose in nature?

Species	8	9 – Abundance				10 – Changes				11 – Reason for changes?	12 - Opinion				13 – Purpose in nature?
	Yes	A lot	Mem	A few	Do not know/NA	More	The same	Less	Do not know/NA		I like it	Do not care for it	I do not like it	Do not know/NA	
Common opossum															
Nine-banded armadillo															
Northern tamandua															
Geoffroy's spider monkey															
Black howler monkey															
Coyote															
Grey fox															
Northern raccoon															
Kinkajou															
Cacomistle															
White-nosed coati															
Striped hog-nosed skunk															
Spotted skunk															
Long-tailed weasel															
Neotropical river otter															
Greater grison															
Tayra															
Ocelot															
Margay															
Jaguarundi															
Puma															
Jaguar															
White-tailed deer															
Central American red brocket deer															
Yucatan brown brocket deer															
Collared peccary															
Baird's tapir															
Eastern cottontail															
Mexican porcupine															
Spotted paca															
Central American agouti															
Hispid pocket gopher															
Great curassow															
Ocellated turkey															
Plain chachalaca															
Morelet's crocodile															
Creaser's mud turtle															

Section 3. Hunting habits and wild meat consumption

14. To your knowledge, is there hunting in your community?

    a. Yes.
    b. No…go to Question 22.

15. What proportion of adult males (> 18 years old) hunt?

    a. ________ %.
    b. Do not know/prefer not to say.

16. Where do these people hunt the most?

    a. Inside their properties.
    b. Inside the properties of family and friends.
    c. Inside natural reserve areas.
    d. Everywhere.
    e. Do not know/prefer not to say.

17. In the last 10 years, have you noticed changes in the intensity of the hunting events/participants?

	Hunting events	**Participants**
Increased greatly		
Increased slightly		
Remained the same		
Decreased greatly		
Decreased slightly		
Do not know/prefer not to say		
Other:		

18. What species are hunted the most in your village?

19. What for?

18	**19**			
Hunted species	To sell	To eat	For fun	Does not know/NA

20. How often do people go to hunt (times per week/month/year)? _______________

21. In your village, who decides what happens with the hunted meat?

a. Head of household.
b. Wife.
c. Husband.
d. Joint decision between wife and husband.
e. Depends on the circumstances.
f. The entire community decides.
g. Other: ____________________.

Section 4. Human-carnivore conflict

22. Do you think large felids would attack humans without being provoked?

	Yes	No
Jaguars		
Pumas		

23. Have large felids ever been killed on/near your property or in the forest?

	Yes	No…Question 25
Jaguars		
Pumas		

24. What happened?

	Event 1	Event 2	Event 3
Date			
Felid species			
Sex and age			
Circumstances			

25. Have you ever experienced livestock loss occasioned by large felids?

a. No…go to Question 31.
b. Yes. How many times?: _________ events. Describe the last three events:

	Event 1	Event 2	Event 3
Date			
Livestock species attacked			
Number of individuals killed			
Predator species			
Action against predator			
Evidence to identify predator			
Circumstances			

26. In the last 10 years, the livestock loss due to large felid predation has:
    a. Increased greatly.
    b. Increased slightly.
    c. Remained the same.
    d. Decreased greatly.
    e. Decreased slightly.
    f. Do not know/prefer not to say.

27. Have you made something to minimise predation by large felids on your livestock?
    a. Yes. What? ___________________________________. Go to question 31.
    b. No.

28. Would you make any changes in your husbandry practices in order to minimise predation by large felids?
    a. Yes…Go to question 30.
    b. No.

29. Why you do not want to make any changes in your husbandry practices to minimise predation on your livestock?...Go to Question 30
    a. Do not have enough money/human resources to make/follow up the changes.
    b. Do not believe any changes will make a difference.
    c. Do not know what changes I could make to minimise predation.
    d. Other: ____.
    e. Prefer not to say.

30. What changes would you make? Choose one/multiple.
    a. Avoid livestock from entering the forest.
    b. Moving animals away from the forest.
    c. Managing calving seasons.
    d. Establish maternity pastures.
    e. Protect calves.
    f. Keeping records of livestock losses from all causes.
    g. Use of nocturnal paddocks near the village/with dogs.
    h. Electric fences.
    i. Incorporate other species of livestock with defensive behaviour to predation into the paddock (i.e. donkeys).
    j. Correct disposal of dead individuals (any cause).
    k. Protection of the natural prey species of large felids in your property.
    l. Other: ____.
    m. Do not know/prefer not to say.

31. Which policy change(s) would be the best to help reduce this conflict? Select one/multiple.
    a. Subsides for paddock fencing (e. g. electric fences).
    b. Tighter enforcement of the law (people and government officials).
    a. Livestock Insurance Fund.
    b. Payment for protection of jaguars in the property.
    c. Better
    d. Advice on the practices available to mitigate livestock losses by large felids.
    e. Involvement in decision making of local people.
    f. Other: ____.
    g. Nothing.
    h. Do not know/prefer not to say.

32. In your community, what problems have been caused by the attacks to livestock by large felids?

____

33. What do people in your village/community think about control of jaguar and puma in response to livestock predation?
    a. In favour.
    b. Against.
    c. Depends of the circumstances.
    d. Do not know/prefer not to say.

34. Does current law facilitate or impede the reduction of this conflict?
    a. Yes.
    b. No.

Section 5. Socio-demographic characteristics of interviewee

35. Sex:
    a. Female.
    b. Male.

36. Age:
    a. 18 - 24 years.
    b. 25 - 34 years.
    c. 35 - 44 years.
    d. 45 - 54 years.
    e. 55 – 64 years.
    f. 65 – 74 years.
    g. > 74 years.

37. What is your educational level?

a. No reading or writing skills.
b. Home schooling.
c. Primary school incomplete.
d. Primary school complete.
e. Secondary school incomplete.
f. Secondary school complete.
g. High school incomplete.
h. High school complete.
i. Undergraduate course incomplete.
j. Undergraduate course complete.
k. Other: ________________

Appendix 4 - Participant information sheet for survey questionnaire used to assess perceptions about wildlife, wild meat consumption, livestock management practices and human-wildlife conflict in the Yucatán Peninsula

Questionnaire to evaluate livestock management practices, perceptions of wildlife, wild meat consumption and human-wildlife conflict in the Yucatán Peninsula, Mexico

Implemented by Evelyn Piña Covarrubias

PhD research student

ERGO ID number: 13836

Participant information sheet

IMPORTANT: This information will be read out to you before deciding to take part in this study. If you are happy to participate you will be asked to provide express verbal approval to the researcher conducting the questionnaire.

Purpose of the study: This survey is part of a research study conducted by Evelyn Piña Covarrubias for her PhD programme at the University of Southampton, in collaboration with Pronatura Península de Yucatán, A. C. The purpose of the study is to evaluate jaguar, puma and prey population health, as well as the predator-prey relationship between jaguars and pumas and their prey and the human-felid conflict in the Yucatán Peninsula, Mexico.

Purpose of the survey: The purpose of this survey is to interview adult (≥18 years old) livestock owners, ranch managers and villagers from the Yucatán Peninsula, to collect information on local livestock management practices, the human perceptions of wildlife, wild meat consumption and the human-wildlife conflict in the Yucatán Peninsula, Mexico, with the aim to explore ways of reducing livestock predation by jaguars and pumas, crop losses to their wild prey, and ultimately to contribute with the conservation of these felids and the welfare of the local communities.

What will be done: You will answer a questionnaire, which will take 20-30 minutes to complete. You will be asked to answer questions about the characteristics, the management methods and the type/number of the domestic livestock in the property that you own or where your work (if applicable). You will also be asked about your perceptions about local mammals, wild meat consumption and human-felid conflict experiences.

Benefits of this study: With the completion of this questionnaire, you will be contributing to our efforts to develop best practice recommendations of good practice to minimize conflicts with wild predators, through reduction of livestock predation, and living sustainably with wildlife.

Confidentiality and protection of your identity: Your responses will be treated in confidence. It is important for you to know that no information will be asked about your personal identity or domicile. The "Participant number" will only be used to recognise questionnaires. It is important for you to understand that some of the questions concern sensitive information that involves hunting of wildlife and consumption of wild meat. Upon completion of the analysis, information that involves livestock management practices will be separated from information related to wild meat.

Discomforts and decision to quit: Your participation is voluntary. If you feel uncomfortable with a question, you have no obligation to answer it. You are free to withdraw your participation from this study at any time. If you do not want to continue, you can communicate this to the interviewer and the survey will stop immediately, being destroyed in front of you.

How the findings will be used: Results from this study will be shared with Pronatura Península de Yucatán, A. C. after conduction of analysis. Information derived will be used only for educational purposes, and will be presented in educational settings, at conferences and they will be published in scientific journals in the field of biological sciences, ecology and conservation. These findings will potentially contribute to the design of mitigation strategies for the human-felid conflict in the area.

Contact information: If you have further concerns about this study, please contact:
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Extension 101

By beginning this survey, you acknowledge that you have understood this information and agree to participate in this research, with the knowledge that you are free to withdraw your participation at any time.

Evelyn Piña Covarrubias
Researcher in charge of this study

Appendix 5 - Pilots of experiments to detect human exploitation

Pilot experiments were conducted in El Edén Ecological Reserve (EEER) and El Zapotal Conservation Area (EZCA), both in Mexico, and in Pook's Hill (PH; Pook's Hill Lodge 2014), in Belize, during 2015 and 2016, and using three Song Meter SM3+ acoustic recorders (32x21x6 cm, 3,200 g, £800; Fig. A5.1a; Wildlife Acoustics 2015) as surrogates to develop a network of pilot AudioMoth cryptic acoustic loggers (5x4x1 cm, 32 g, £10; Fig. A5.1b; Rogers 2015; Hill *et al.* 2018). Replicate locations were sampled in each of the main habitats in the study areas: (i) secondary growth tropical semi-deciduous forest and (ii) savannah (Mexico), and (iii) tropical rainforest (Belize). Replicates were chosen for their accessibility with a motorized vehicle.

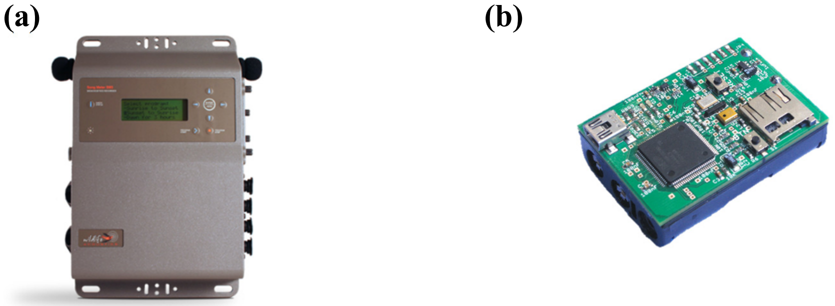

Figure A5.1. Commercial high-fidelity Song Meter SM3+ acoustic recorder (a) and pilot AudioMoth acoustic logger (b).

Four sound types associated to sources of anthropogenic disturbance were tested:

a) Chainsaw: A small (Homelite CSP3314, 102 dBA) and large (Stihl [EZCA] and Husqvarna 455 Rancher [PH]; 114 dBA) chainsaws were activated cutting through a medium-sized log (Fig. A5.2).

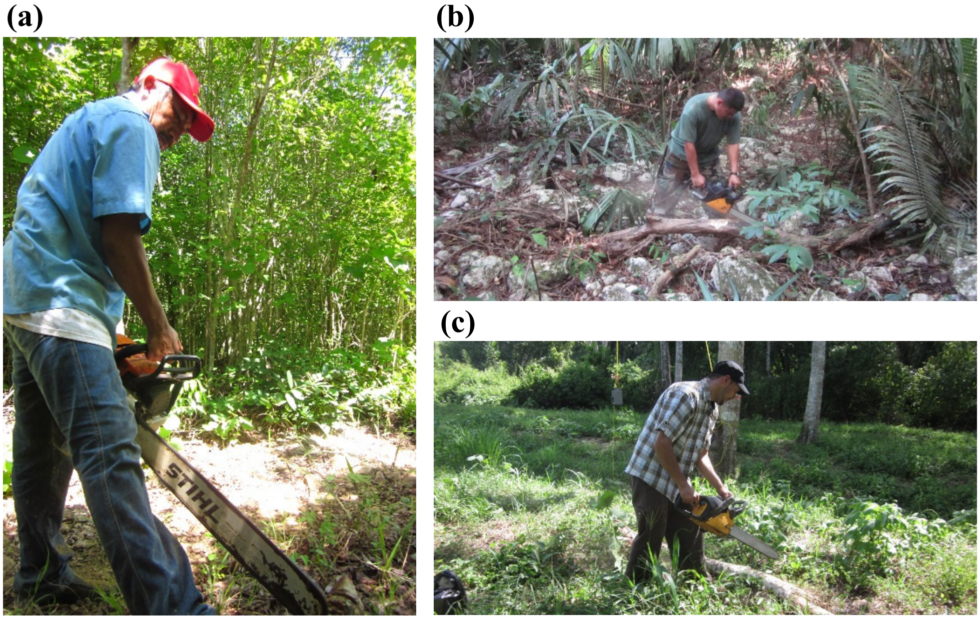

Figure A5.2. Chainsaws used in (a) EZCA and (b, c) PH, cutting a medium-sized log.

b) Human voice: Two different procedures were conducted to record human voices. In EEER, a ca. 30-second dialog (in Spanish) was recited by one adult male in a neutral tone at the volume of conversation (Fig. A5.3):

P1 - Hola Manuel, ¿Cómo estás?	*P2 - Bien, Pablo, ¿Qué dice la familia?*
P1 - Pues los niños bien, la que ha estado enferma es mi esposa.	*P2 - ¿Qué tiene?*
P1 - Pues parece que le dio dengue, pero no estamos seguros.	*P2 - ¿Ya la llevaste al doctor?*
P1 - No, mañana vamos a ir a la clínica de San Rafael.	*P2 - Pues ojalá no sea dengue.*
P1 - Sí, pues ojalá.	*P2 - Por cierto, ayer me encontré a tu suegro.*
P1 - ¿Qué te cuenta?	*P2 - Pues que sembró maíz, frijol y calabaza en su parcela este año.*
P1 - Sí, yo le dije que sembrara calabaza, porque ya viene día de muertos.	*P2 - Pues yo le dije que, si quiere, que yo las vendo en el mercado.*
P1 - Ah, mira, pues qué bien, así no tiene que andar de aquí para allá con la mercancía.	*P2 - Ya vámonos, parece que va a llover.*

Figure A5.3. Adult male reciting speech to record human voice.

In EZCA, a person walked away for 100 m in opposite directions (back and forth) from the acoustic recorders, counting the steps (≈ 1 m each), using a neutral tone at the volume of conversation.

c) *Motorized vehicle:* A 6-cylinder 4×4 motorized Jeep Grand Cherokee Laredo model 2002 vehicle (ca. 50 dB level at idle) was used to test the sound of a car engine (Fig. A5.4).

Figure A5.4. Motorized vehicle used to record a car engine.

d) Guns: A .22 mm rifle (one gauge bullets) and a shotgun (16 gauge bullets), both used for hunting, were fired (Fig. A5.5).

Figure A5.5. Rifle, shotgun .22 bullets and shotgun pellet used in (a, c) EZCA and in (b, d) PH.

Experiments to create soundscapes of human and wildlife activity proceeded in three stages:

Pilot trials

Pilot trials were designed to determine the maximum distance and optimal height for detecting each sound type in each habitat. Replicate locations were sampled in the two main habitats of EEER (secondary growth sub-deciduous forest and savanna).

In EEER, three Song Meter SM3+ acoustic recorders were activated at increasing distances and heights from sound sources to find the limits of detectability in relation to sound type and habitat. These rapid trails were conducted to inform the full experimental designs by setting the maximum distance d_{max} and height range h_{max} for detecting various sound types (water pump, chainsaw, human voice, and car) under different conditions. In addition, a third experiment was conducted in EEER to calibrate the sound level, using the sound Check Tone Generator (Völker 2011), playing a 1 kHz tone, on an iPhone 4 mobile phone, and walking away at opposite directions and variable distances from an acoustic recorder hanging in a tree at height of 2 m. Every 10 paces the mobile phone was rotated 360° horizontally.

Sound attenuation experiment

This experiment was designed to enumerate how sound carries with distance and height. Sampling was carried out in tropical secondary-growth semi deciduous forest (EZCA) and primary-growth tropical semi-deciduous rainforest (PH). Secondary-growth semi deciduous forest is the most prevalent habitat in the area and has a taller and denser canopy than savanna; tropical rainforest is rarer in Mexico, with the tallest and most dense canopy.

Three Song Meter SM3+ acoustic recorders were positioned in a tree at $h = 2$ m, 4 m and 6 m, one above the other. Four types of sounds were tested: human voice (only EZCA, counting steps), car engine (only EZCA), chainsaw (large chainsaw in EZCA, small/large in PH) and shotgun (rifle in EZCA, shotgun in PH). The shotgun and the chainsaw were carried in the motorized vehicle and these two sound types were triggered one after the other at distances $d = 250$ m, 500 m, 750 m and 1 km (Fig. A5.6).

Each replicate was tagged with the date, time, coordinates and current weather. This experiment was replicated in a) EZCA (four replicate locations in the secondary growth tropical semi-deciduous dry forest) and b) PH (four replicate locations in tropical rainforest). In PH, two gunshots were triggered in each distance location, one towards the acoustic readers, and another away from them.

The procedures in each study area were as follows: (i) in each replicate, the devices were fixed at three heights (2, 4 and 6 m) in a tree of known position, using marked ropes to measure height; (ii) run through the 4 sound types (only EZCA) at each distance (rifle/shotgun and chainsaw: 250 m, 500 m, 750 m and 1 km, EZCA and PH); and (iii) replicate with the devices fixed to a tree in different locations.

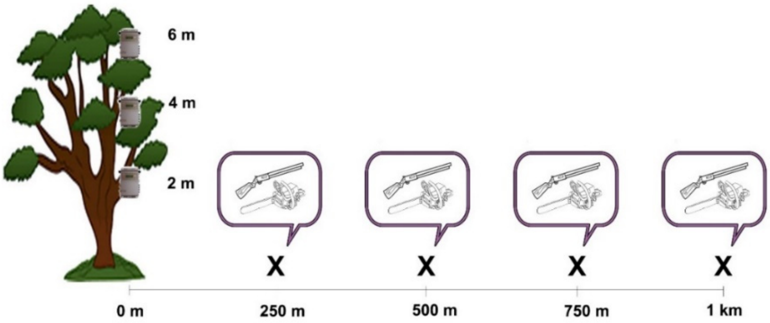

Figure A5.6. Design for sound attenuation experiment.

Sound location experiment

The sound location experiment was designed to test the capacity for a network of devices to locate sound sources. Results from the previous experiment dictated the separation of the three acoustic recorders at each vertex of an approximately equilateral triangle, and their height above ground, to locate the source of a sound. In each triangle the 'sound sources' (only shotgun/rifle and chainsaw) were positioned at different locations in the triangle. The rifle/shotgun and the chainsaw were carried in the motorized vehicle or by foot, the rifle/shotgun being triggered before the chainsaw (Fig. A5.7). Each trial was tagged with date, time, coordinates and weather. This experiment was conducted at two replicate locations in El Zapotal (secondary growth tropical semi-deciduous forest) and two in PH (tropical rainforest).

The procedures per study area were as follows: (i) the devices were fixed at three trees (vertices) with known positions of an approximately equilateral triangle, and run through the 2-sound types at each of the locations; and (ii) replicate once more with the devices fixed to triplets of trees in different locations.

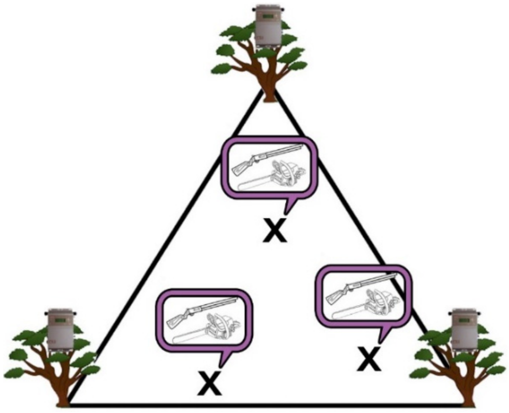

Figure A5.7. Design for sound location experiment.

Appendix 6 - Supporting information for Chapter 4

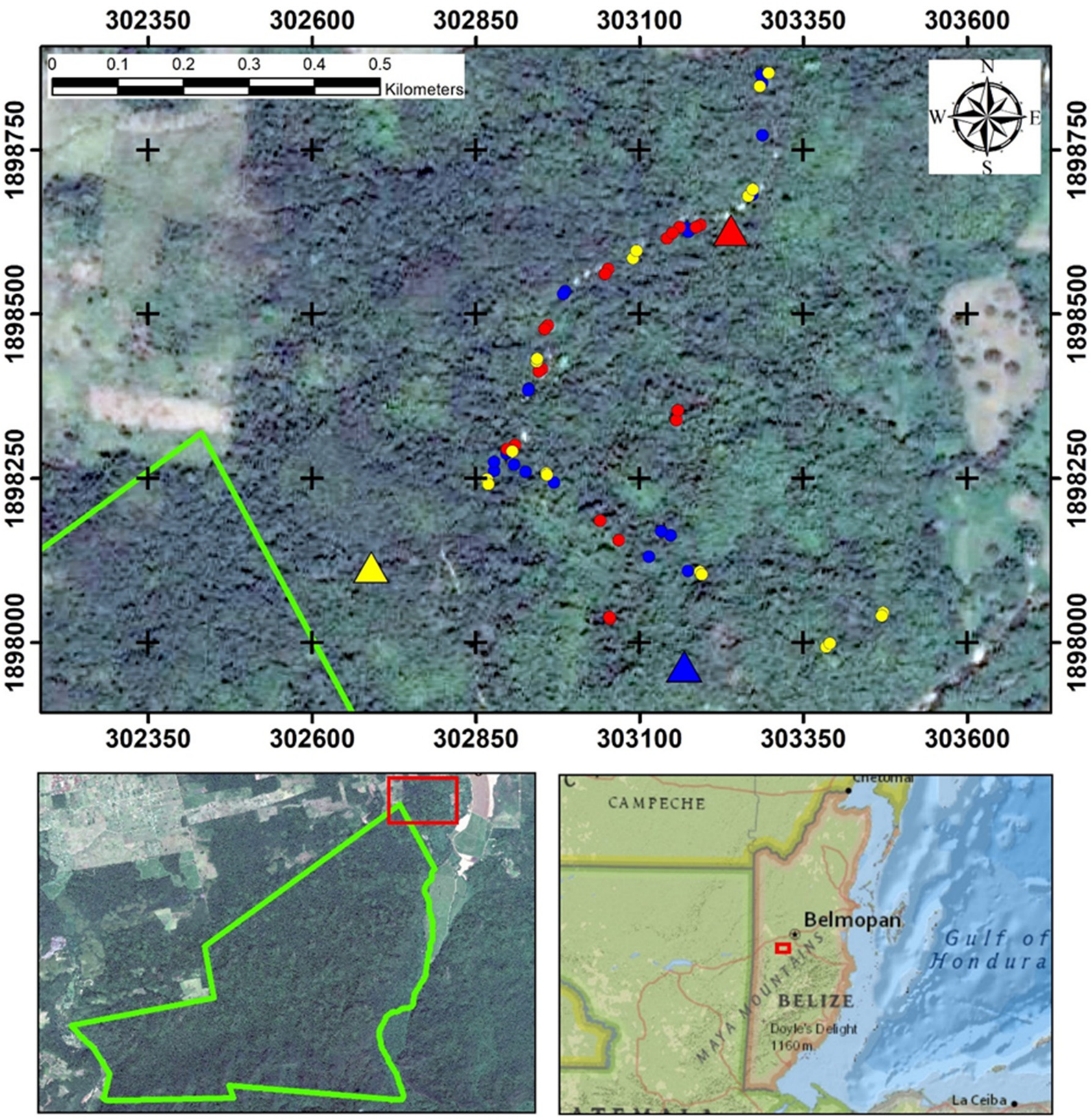

Figure S1. Map of transects for gunshot-detection trials (Google Earth 23 March 2017). Maps below main map show location of trials relative to TMNR, and Maya Mountains of Belize (Esri – National Geographic World Map). Main map symbol colours yellow, red and blue distinguish trials 1, 2 and 3 respectively. Triangle = location of AudioMoth for the trial, circles = gunshot locations for the trial.

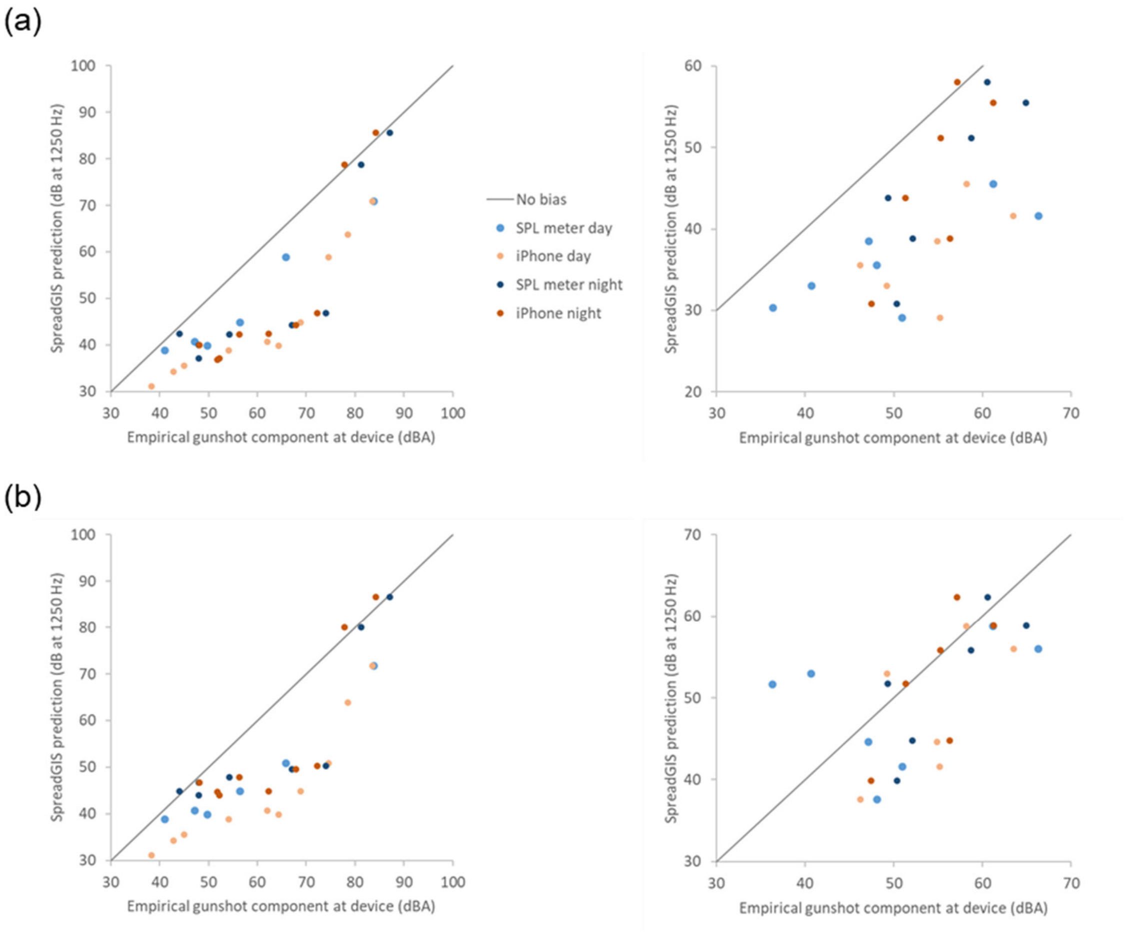

Figure S2. Predicted sound spread from SPreAD-GIS, ground-truthed against empirical data from two transects (trials 1 and 2 in Data S1) measuring gunshot SPL above ambient. (a) SPreAD-GIS prediction from input parameters described in main-text Section 3.2; (b) prediction from identical input parameters except generic seasonal conditions changed from ‘calm’ to ‘windy’. Main-text analyses use (a) in preference to (b) in order to ensure conservative estimates of sound spread.

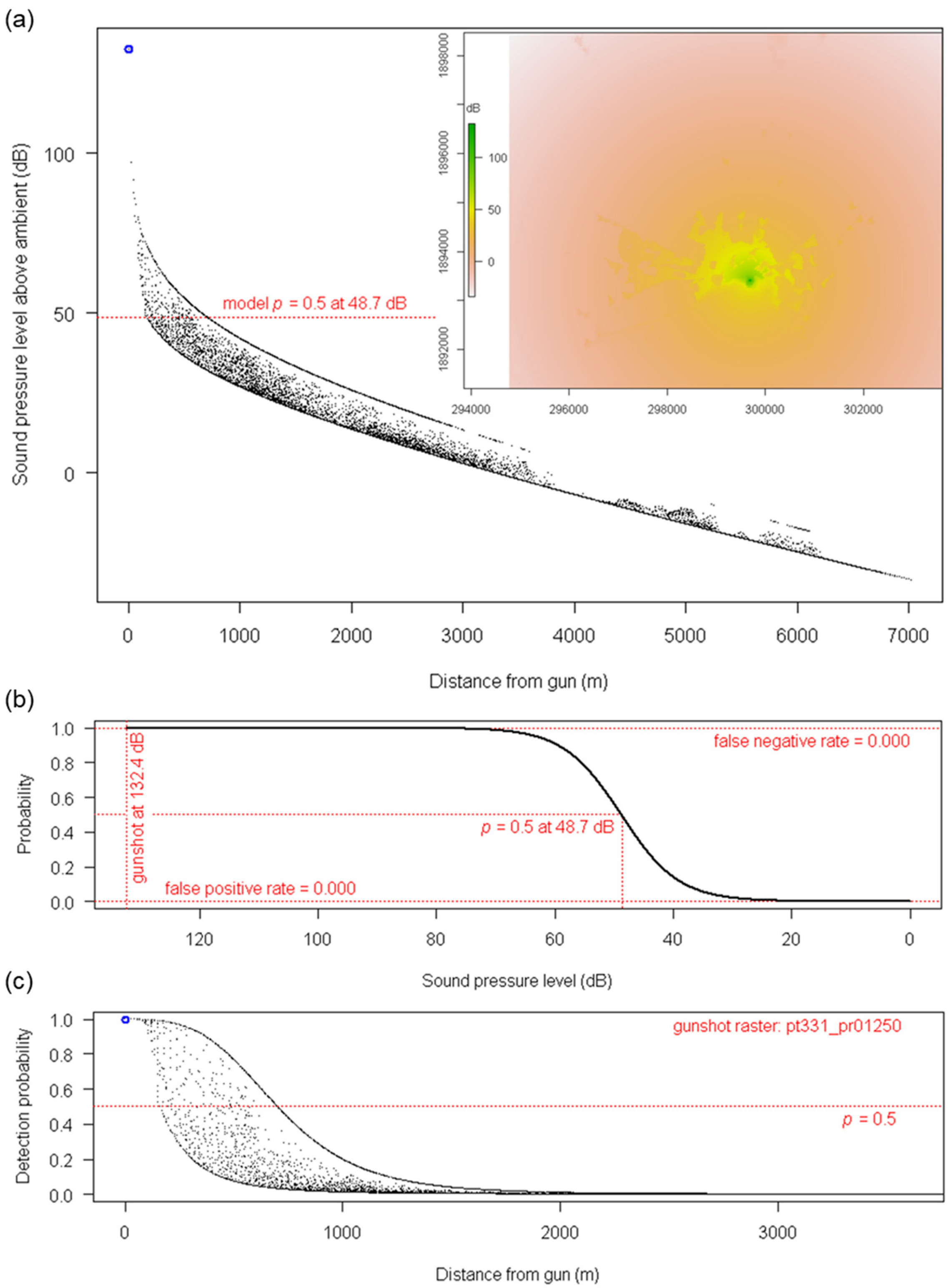

Figure S3. Example of soundscape and corresponding detection probability for the gunshot ringed in the inset map to main-text Fig. 4.3a. (a) Distribution of SPL above ambient for all map pixels; note the uneven spatial distribution and westward drift in the inset map, dictated by topography and 5 km/hr East wind. (b) Function *g*, obtained from the logistic regression in main-text Fig. 4.2b. (c) Application of *g* to the SPL data, to obtain a distribution of detection probabilities with distance from this source for all map pixels.

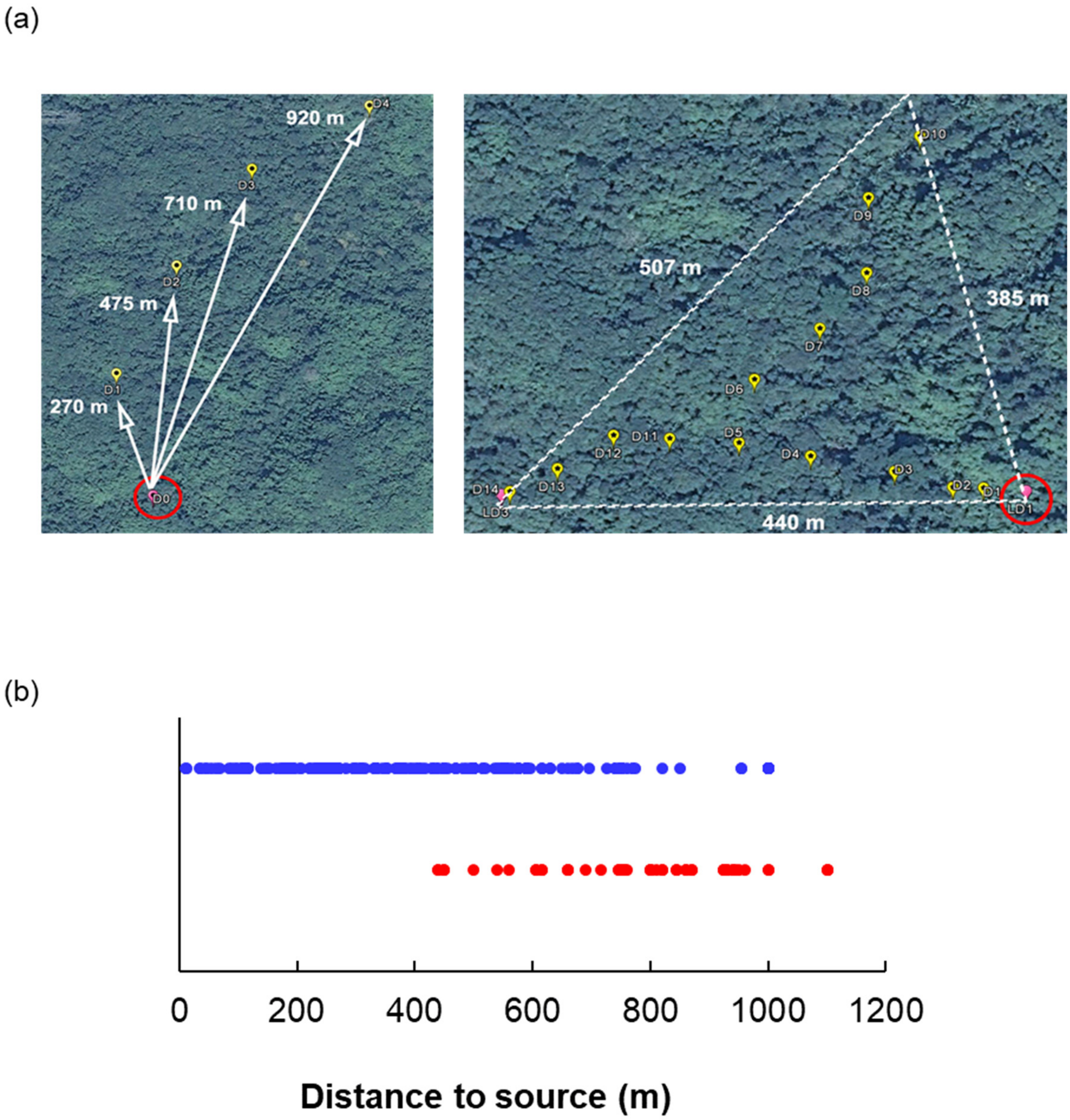

Figure S4. Success/failure in gunshot detection by ear with distance from source. (a) Example transects in 2015 and 2016 using SM3+ devices and prototype AudioMoths, and a 12-gauge shotgun. Devices inside the red ring picked up shotguns at all yellow dots. (b) Summary results from all 318 gunshots (success = 261; failure = 57) on 10 transects in the NE region of main-text Fig. 4.1 during 2015 and 2016.

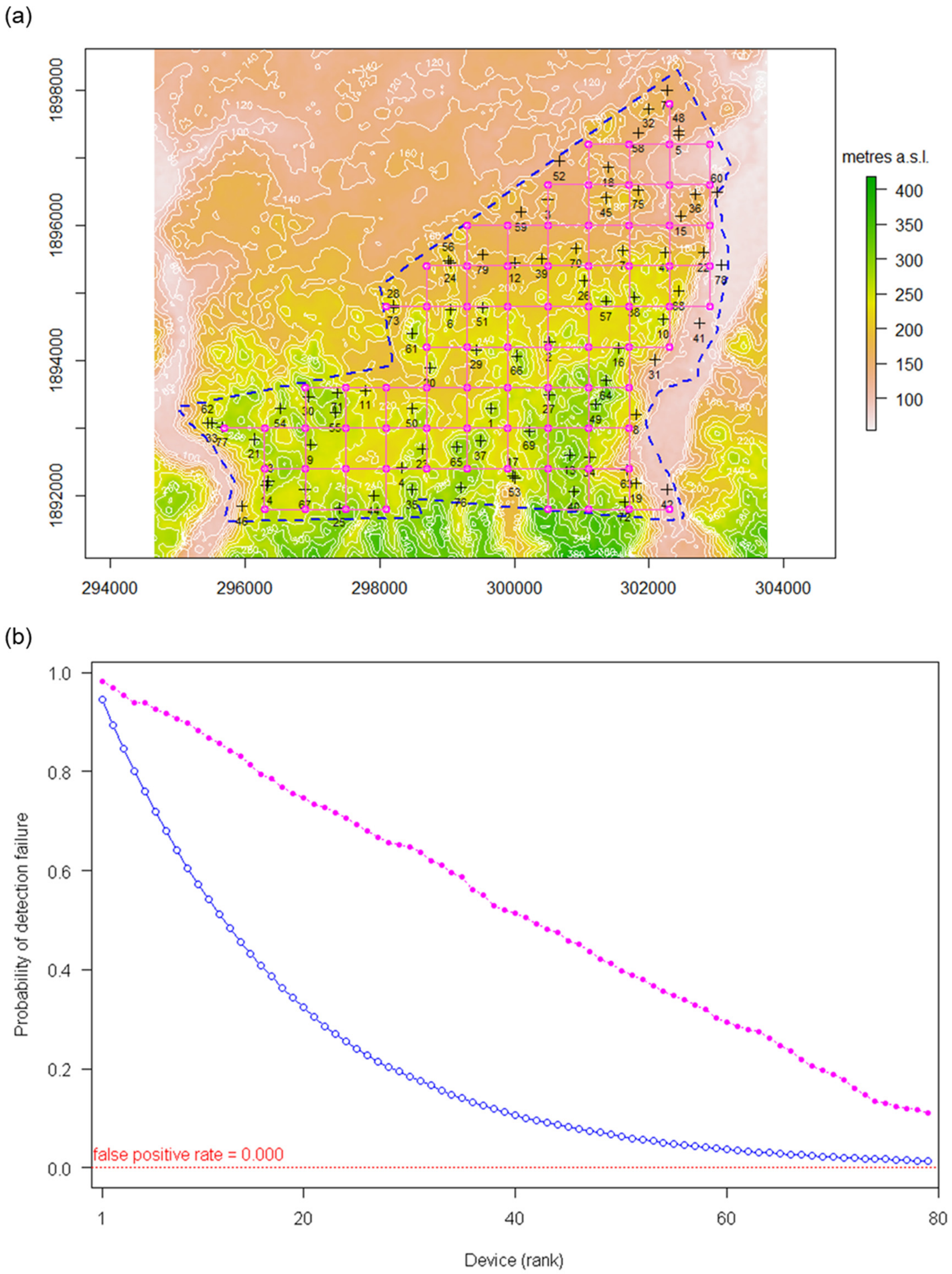

Figure S5. Performance of near-optimal placements, compared to regular placements of an equal number of devices, on a 600-m grid. (a) Near-optimal (ranked crosses) and regular (magenta circles) placements of 79 devices. (b) Declining probability of detection failure as a function of number of devices, for near-optimal (blue circles) and regular (magenta dots) placements.

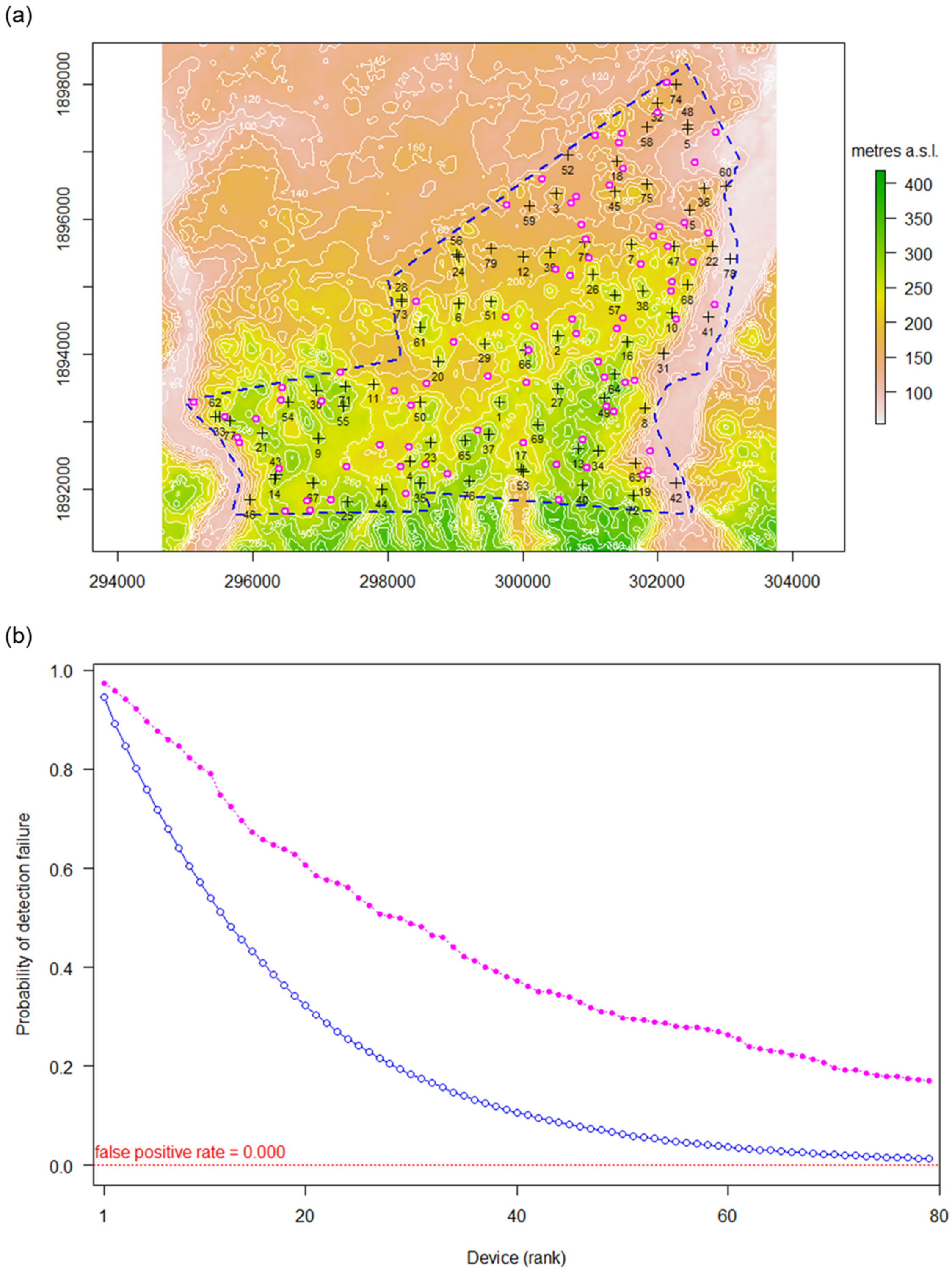

Figure S6. Performance of near-optimal placements, compared to random placements of an equal number of devices. (a) Near-optimal (ranked crosses) and random (magenta circles) placements of 79 devices. (b) Declining probability of detection failure as a function of number of devices, for near-optimal (blue circles) and random (magenta dots) placements.

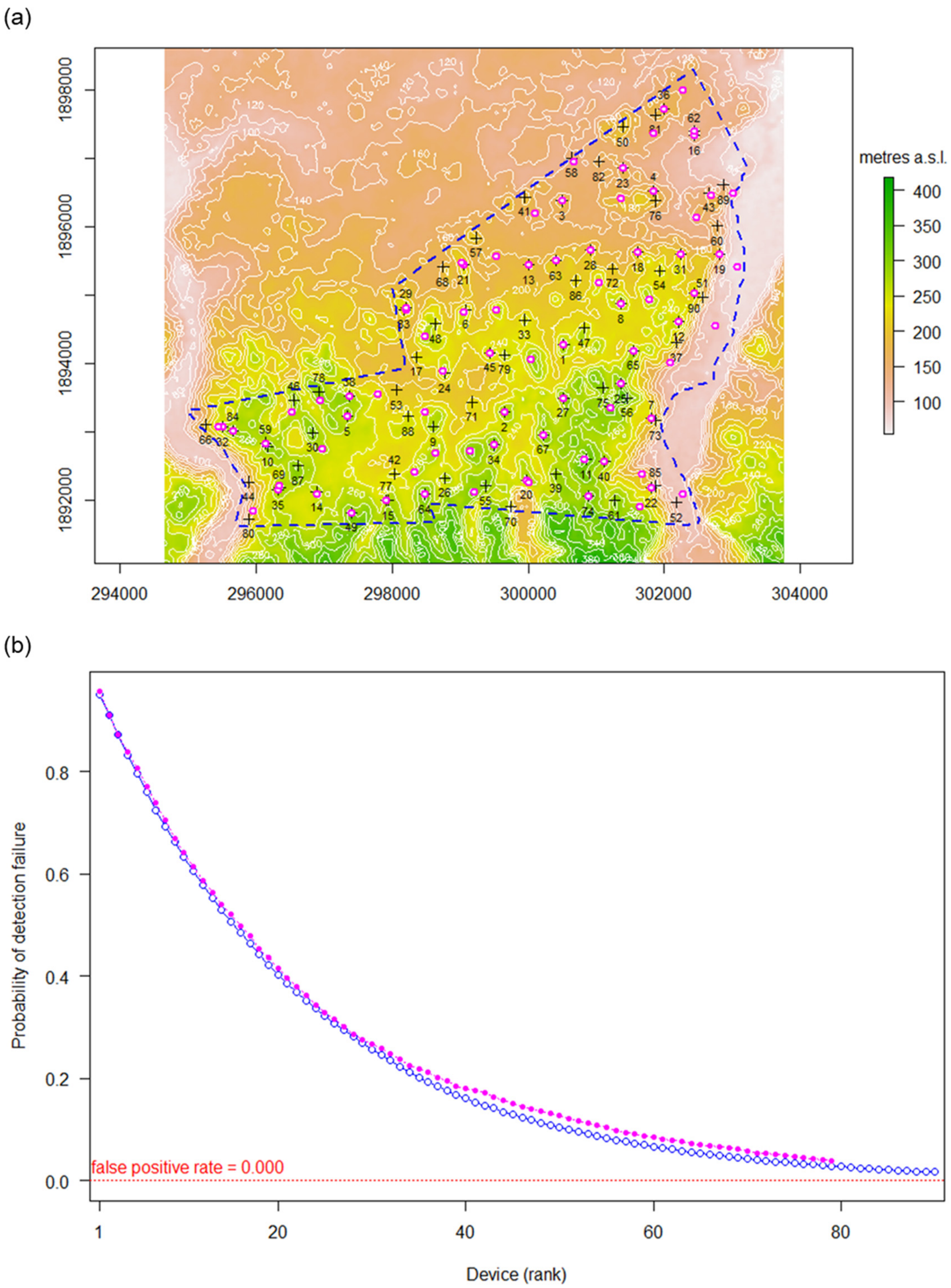

Figure S7. Performance of near-optimal placements for seasonally windy and calm conditions. (a) Placement of 90 devices for windy (ranked crosses) and 79 devices for calm (magenta circles). (b) Declining probability of detection failure as a function of number of devices, for windy placement under windy conditions (blue circles) and calm placement under windy conditions (magenta dots).

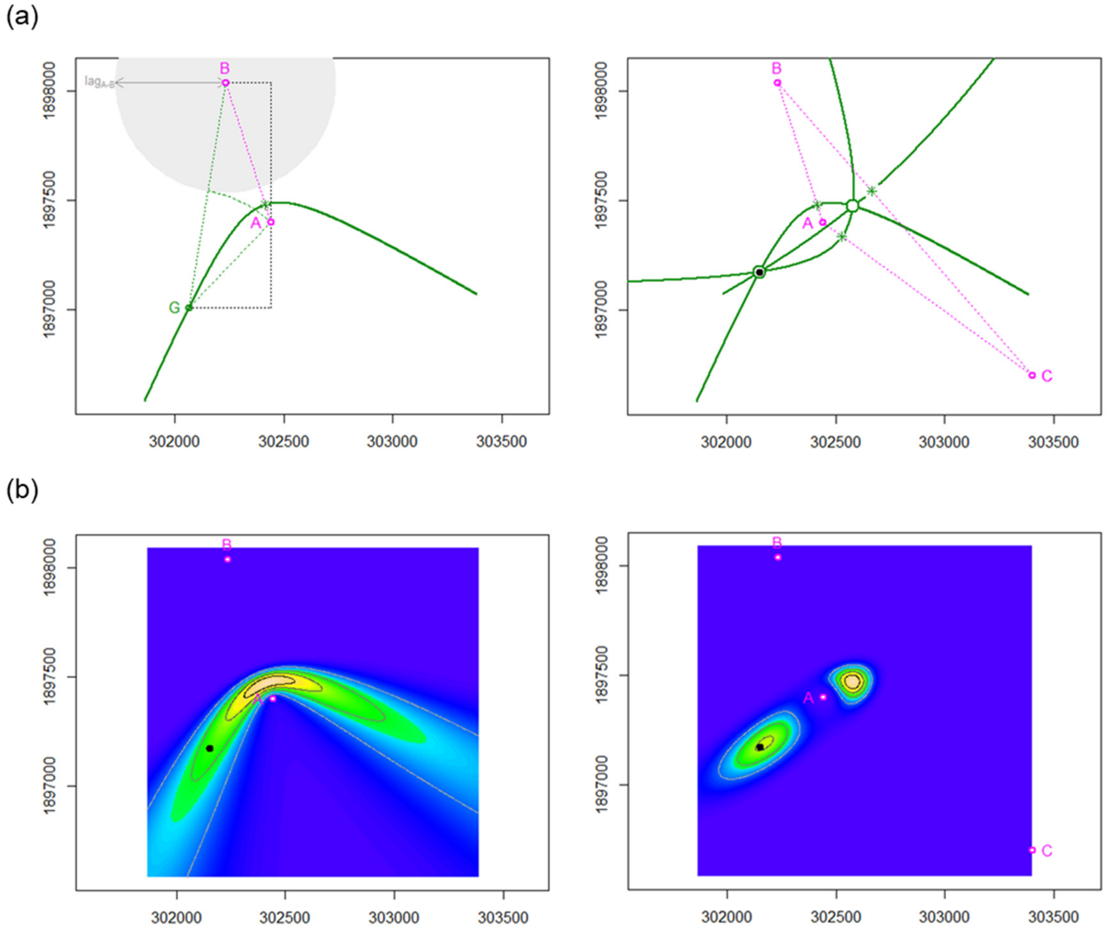

Figure S8. Localisation of gunshot #9 solely from detection time-lag(s) between devices. (a) Hyperbolic navigation in the absence of uncertainty in timings. Left-hand graph: calculation of the hyperbola of equal difference in distance of gunshot to device B relative to gunshot to device A, given the detection time-lag at B after A and speed of sound, here 1.457 s and 347.3 m/s. Every point on the green hyperbola, for example at G, has the property that distance G-B equals distance G-A plus lag$_{A-B}$, where lag$_{A-B}$ is the distance travelled by sound over the lag time, here 506 m. Angle G-A-B is then a cosine function of the side lengths of its triangle, from which obtain the coordinates of G. Right-hand graph: detection time-lags to a hypothetical third device C, here 2.787 s after A and consequently 1.329 s after B, fixes the gunshot to two possible locations, including gunshot #9 at the black dot. (b) Gunshot likelihood in the presence of uncertainty due to drift in device clocks and to variation in sound propagation path (Equation 12, σ^2_{drift} = 0.001, equivalent to 0.03 s drift in device clocks; σ^2_{prop} = 0.000045, equivalent to 10% drift in ~1.5 s propagation time over 500 m). Contours show 20% likelihood intervals above purple region of lowest likelihood. Left-hand graph: two detecting devices (corresponding to (a) left-hand graph), showing the error in propagation path exerting more influence with greater distance from detectors; right-hand graph: three detecting devices (corresponding to (a) right-hand graph).

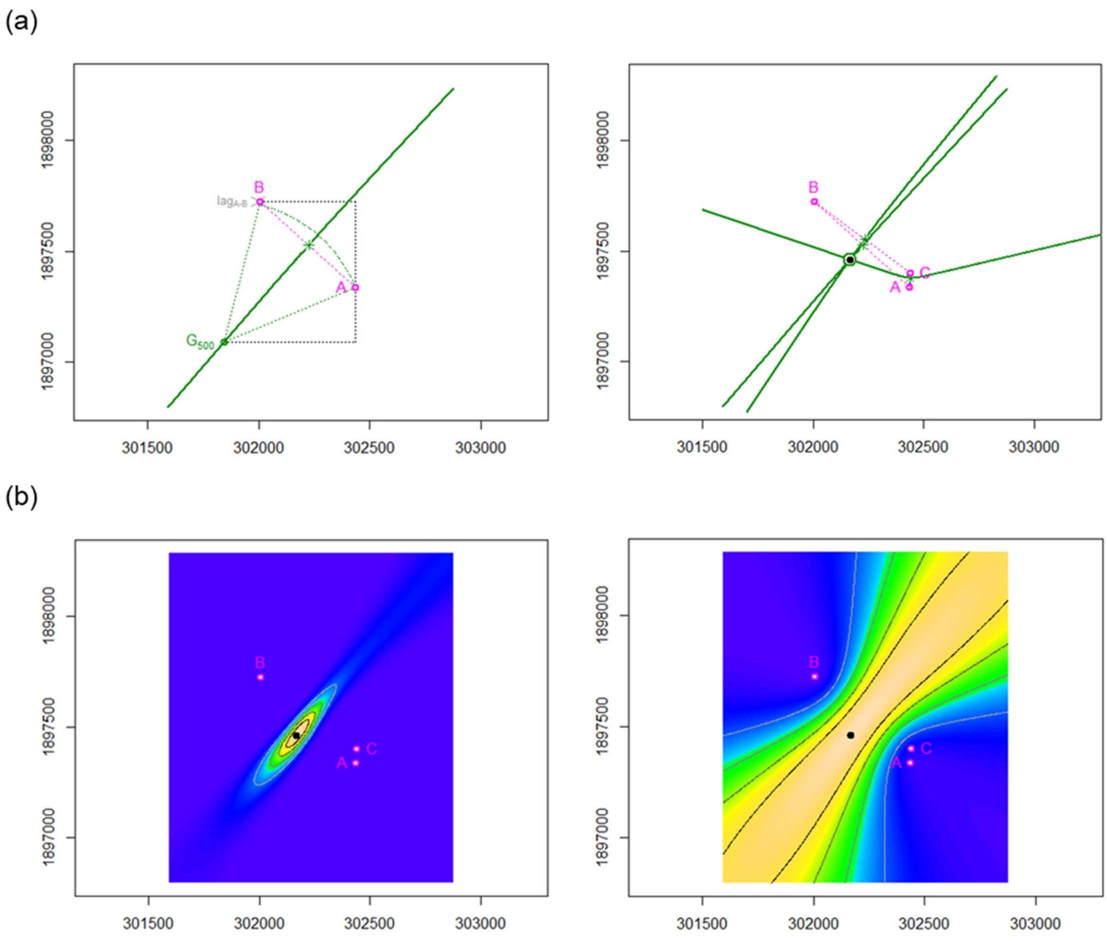

Figure S9. Localisation of gunshot #5 solely from detection time-lags between three detecting devices. Labelling as for Fig. S8. (a) Hyperbolic navigation in the absence of uncertainty in timings. Left-hand graph shows the flat hyperbola set by a small time-lag of 0.035 s in detection by device B after A. Right-hand graph shows the intersection of hyperbolas given detection by device C, 0.049 s before A. (b) Gunshot likelihood given detections by devices A, B and C, and uncertainty due to variation in sound propagation path and drift in device clocks (Equation 12, σ^2_{prop} = 0.000045, equivalent to 10% drift in ~1.5 s propagation time over 500 m). Left-hand graph has σ^2_{drift} = 0.001, equivalent to 0.03 s drift in device clocks; right-hand graph has σ^2_{drift} = 0.25, equivalent to 0.5 s drift in device clocks. The larger uncertainty in timings greatly diminishes the value of the time-lag between closely-spaced devices A and C relative to the time-lags to the more distant device B. With clock drift dominating the noise term, the paired devices A and C act as one, due to highly correlated propagation noise and averaged clock drift.

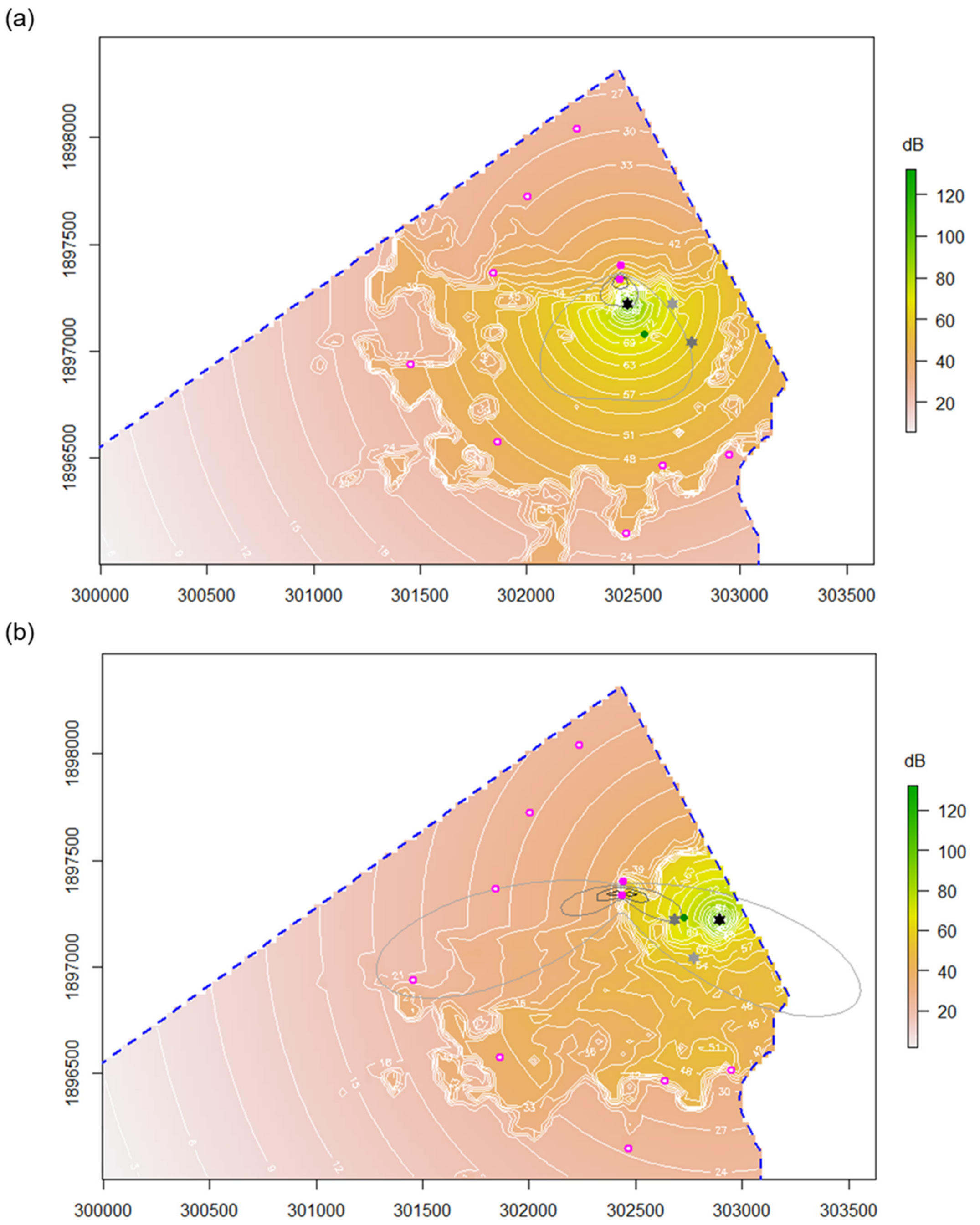

Figure S10. Estimated location (black star, Equation 14) of a gunshot, and decay in its SPL away from this source (white contours at 3 dB intervals), given only a set of timed detections and failures by AudioMoths (closed/open magenta circles). Green closed circle shows (a) actual gunshot #2 (162 m from its best estimate, with the most southerly detecting device recording the gunshot 0.164 s before the closely neighbouring device), and (b) actual gunshot #3 (164 m from its best estimated location, with the most southerly detecting device recording the gunshot 0.069 s before the closely neighbouring device). Dark- and light-grey stars show 2nd and 3rd best estimates of gunshot location. Grey contours at 20% intervals show likelihood of gunshot location based only on the detection time-lag between detecting devices (Equation 12, $\sigma^2_{\text{drift}} = 0.001$; $\sigma^2_{\text{prop}} = 0.000045$).

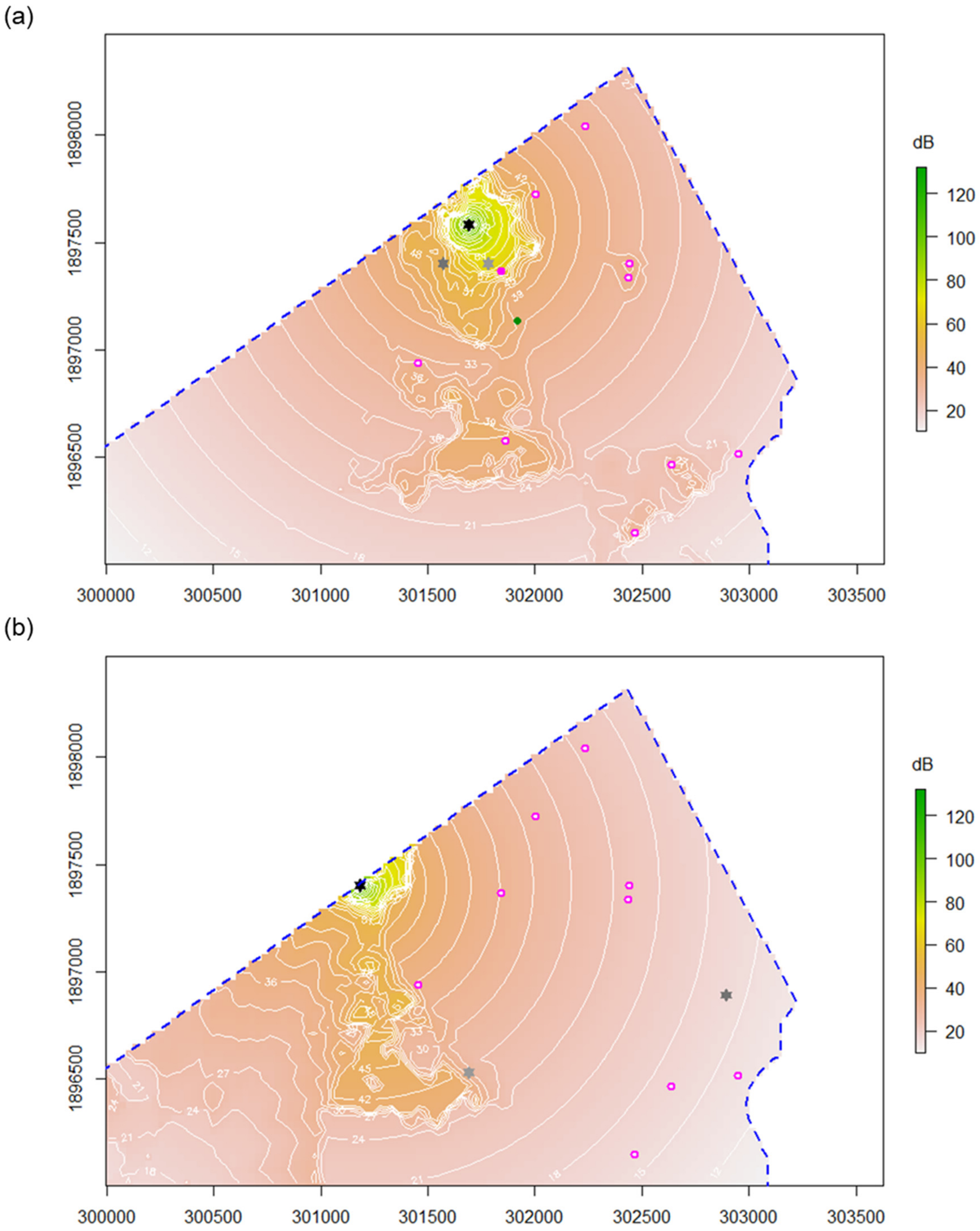

Figure S11. Estimated location (black star, Equation 4) of a gunshot, given only a single AudioMoth detection or no detections amongst 10 devices. (a) Green closed circle shows actual gunshot #8 (500 m from its best estimated location) detected by one device (closed magenta circle). (b) Most likely location of a gunshot undetected by all nine devices (open magenta circles). Other symbols as for Fig. S9 and main-text Fig. 4.6.

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