The nine lives of a threatened felid in a human-dominated landscape: assessing population decline drivers of the guiña (*Leopardus guigna*)

Nicolás Gálvez

Durrell Institute of Conservation and Ecology (DICE)

School of Anthropology and Conservation

University of Kent, UK

November 2015

Thesis submitted for the degree of

Doctor of Philosophy in Biodiversity Management “hasta aquí vamos bien dijo el gato,

que venía cayendo desde el séptimo piso

cuando pasaba frente al segundo”

Nicanor Parra

Acknowledgements

First and foremost I would like to dedicate this thesis to and acknowledge the support and unconditional love of my wife Claudia Ríos and my children Tineo Gálvez and Violeta Amancay Gálvez. All this work would not have been possible had it not been for their patience, understanding, and most of all their hugs and kisses. Secondly, all my parents at some stage of my life (you know what I mean), especially my Mom and Carter for all their support and love throughout the years. My deepest appreciation to my family Meyra Scarneo, Arturo Robinson, Antonio Gálvez, Liliana Castro, Cristián Gálvez and Francisco Gálvez. Also to Cecilia Gajardo, Tito Pollack and Alicia Aguiló. A special mention to Cristian Bonacic, Alberto Dittborn, Jerry Laker, Benito González, José Luis Riveros, and Juan Gastó who have in one way or another supported and inspired my work. Also, to José Tomás Ibarra, Tomás Altamirano, Omar Ohrens, Isabel Rojas, Robert Petitpas, Felipe Hernandez, Pelayo Benavides, Gonzalo Valdivieso, Antonio Hargreaves, Nichola Beukes, Giri Varahtarajan, Nelson Follador, Elke Schüttler and Jake Bicknell for being important support during my work and overall professional development.

My deepest gratitude extends to my supervisor, Zoe G. Davies, for the immense support of my work and for constantly pushing my limits to improve my writing and scientific frame of mind. Also for continued support by David W. Macdonald at WildCRU-Oxford who believed in this project and allowed it to reach its destination; I am forever grateful. I also want to express my gratitude to Bob J. Smith and Freya St. John for their valuable guidance and support on various topics. Last but not least, I am very grateful to Byron T. Morgan and Guruzeta Guillera-Arroita for their patience in our statistical discussions and for always being available and supportive. A big thank you goes to Mira Fleutchz for her patience and hard work in getting the first season of survey done. Most importantly to all landowners who kindly permitted my work on their land.

I also want to thank our funders at the Chilean Ministry of the Environment (FPA 9-I-009-12), the Robertson Foundation, the Recanati-Kaplan Foundation, Marie Curie Fellowship Program (POIF-GA-2009-252682) and PANTHERA, especially Lisanne Petracca for providing satellite imagery and her work on the landcover classification. Many more things are still to come from this highly relevant baseline work. I am deeply grateful for having received a post-graduate scholarship from the Chilean National Commission for Scientific and Technological Research (CONICYT-Becas Chile).

Author's declaration

All chapters in this thesis were written by N. Gálvez. Comments and editorial suggestions were made by my supervisor Z.G. Davies (all chapters). Chapters 2-4 include collaborations with other researchers, both internal and external to University of Kent. All fieldwork was conducted by N. Gálvez, with the exception of the first camera-trap season, which was overseen by N. Gálvez but undertaken by M. Fleutchz.

Chapter 2: was conceived by N. Gálvez. The online questionnaire was developed by N. Gálvez with support by Z.G. Davies. All data analyses were done by N. Gálvez. Statistical insights and R code programming support were provided by G. Guillera-

Arroita and B.J.T. Morgan. N Gálvez wrote the paper with collaborative input from all co-authors.

Chapter 3: was conceived N Gálvez. The sampling design and questionnaire were developed by N. Gálvez with support from F.V.A. St. John and Z.G. Davies. Landcover maps were developed by L. Petracca and N. Gálvez, with methodological feedback given by R.J. Smith and Z.G. Davies. Extraction of landcover variables from the map and all data analyses were carried out by N Gálvez. N. Gálvez wrote the paper with collaborative input from all co-authors.

Chapter 4: was conceived by N. Gálvez. The sampling design and questionnaire were developed by N. Gálvez with input from F.V.A. St. John and Z.G. Davies. All data analyses were conducted by N. Gálvez, who also wrote the paper, with collaborative input from all co-authors.

Abstract

The world's human population and an expanding agricultural frontier are exerting increasing pressure on the Earth's systems that sustain life resulting in unprecedented levels of biodiversity loss. Carnivores, which play a key role in ecosystem function and integrity, are also particularly threatened by habitat loss and killing by humans in response to livestock predation. At the same time carnivores, particularly felids show a paucity of studies that suggests population assessments and long-term monitoring is an urgent matter. This thesis looks the how habitat loss, fragmentation and human persecution affects predators in an agricultural landscape with particular focus on a species of conservation concern: the small felid guiña (Leopardus guigna) considered vulnerable with a declining population trend. A cost-effective survey framework was developed, which shows existence of trade-offs for researchers and managers to improve population assessments. The drivers of decline of the guiña are assessed with an extensive camera-trap data set showing that the guiña can tolerate a high degree of habitat loss in agricultural land but requires the existence of large farms and high number of forest patches. Retribution killing does not seem to be a significant extinction driver, although there is uncertainty regarding the impact on the population. However, killing behaviour by farmers is predicted by encounters suggesting that poultry management is an effective mitigation measure. Predator specific predictors of killing by farmers were observed but a commonality to all is that knowledge of legal protection does not explain killing suggesting other measures must be taken. Integrating ecological and social knowledge allows us to tease apart the relative importance of different potential extinction pressures effectively and make informed recommendations as to where future conservation efforts should be prioritised.

Contents

Table of figures

Table of tables

1. Introduction

1.1. Species extinction drivers

The human population across the world, currently estimated at seven billion people, is thought to increase between two to four billion by 2050 (United Nations 2015). Undoubtedly, this will underpin a range of serious threats to ecosystems and species already in crisis. Human activities are currently driving the sixth mass extinction of species in geological history (Barnosky et al. 2011), with rates up to 1,000 times higher than estimated background rates (Pimm et al. 2014). Human activities on earths systems are on such a scale that recent work provides evidence of the existence, starting in the 17th century, of a new geological era the "Anthropocene" (Steffen et al. 2011). Degradation of ecosystems and the subsequent loss of species by human activity during the last 50 years is unprecedented (Millennium Ecosystem Assessment 2005).

Biodiversity is measured at different scales such as genes, species, community and ecosystem diversity. Although there is still on-going research and debates regarding how diferent ecosystem functions influence ecosystem services, biodiversity is deemed as key for many ecosystem processes or functions which in turn provide some important ecosystem services for humanity such as provision of food and fuel (e.g. wood) and regulating functions such as soil formation, pest control, resistence to plant invasions, carbon sequestration, amongst others (Cardinale et al. 2012). Biodiversity has been stated as necessary to sustain humanitys' wellbeing and economic development but is at risk if urgent measures are not taken to reverse and mitigate degradation (Millennium Ecosystem Assessment 2005). The levels of biodiversity loss we are witnessing today are beyond a “safe operating space” for the future outlook of humanity (Rockström et al. 2009). In general, intrinsic species traits such as having a slow life history (e.g. low reproductive rate), being situated at the top of the food chain (e.g. predators), occurring at low density and having a small geographical range are associated with higher extinction risk (Purvis et al. 2000).

Species specific traits predispose extinction risk and human-induced environmental modifications and direct resource use are also driving species losses. A suite of factors are responsible, including habitat destruction, degradation and fragmentation, overexploitation (e.g. unsustainable use), pollution, invasive species and climate change (Millennium Ecosystem Assessment 2005). They can have varying effects on a species and usually interact in complex ways that exacerbate the impacts (Brook, Sodhi & Bradshaw 2008). In general, growing human pressure from land-use change or intensification are predicted to be the biggest threats faced by biodiversity over the coming century (Sala et al. 2000). Land intensification can involve an increase in all the extinction drivers such as clearing of forest habitat for agriculture (e.g. Morton et al. 2006), creating road networks which give access to poachers or loggers to previously inaccessible areas (Laurance, Goosem & Laurance 2009). Furthermore, the spread of generalist invasive species can be increased by changes in habitat structures (e.g. Pauchard & Alaback 2004) or even the increase of domestic animals which compete and transmit disease to wildlife (e.g. Hughes & Macdonald 2013).

1.2. Agricultural landscapes and drivers of forest conversion

Habitat loss and fragmentation, particularly of forest cover, is driven by the expansion of agricultural lands. The extent of crop land and pastures are now reaching ~ 40% of terrestrial landscapes (Foley et al. 2005). Furthermore, it is estimated that 40% to 70% of biodiversity rich biomes will be converted to cultivated land by 2050 (Millennium Ecosystem Assessment 2005). Subsequently, threats to species and ecosystems will continue to increase; mainly due to human demand for agricultural commodities (Hambler & Canney 2013). For example, the increasing demand for oil palm products that are used in an array of products for human consumption (e.g. food stuffs, toiletries, biofuels) is driving deforestation in Southeast Asia for the need to increase cultivated areas (Fitzherbert et al. 2008). Demand for meat and increasing livestock production is the main source of greenhouse gases and a major driver in clearing of forests to enable agricultural crops such as soy for livestock feed (McMichael et al. 2007). In biodiversity rich tropical areas, the expansion of agricultural lands in detriment to forest cover is driven by complex synergies of economic and development policies, infrastructure, social drivers and expansion of "cash crops" that provide greatest benefit per unit of investment (Geist & Lambin 2002). To prevent further forest loss nations must implement efficient and sustainable use of existing landscapes (Lambin & Meyfroidt 2011) together with a network of protected areas (Hambler & Canney 2013).

1.3. Monitoring landscape change and populations

Monitoring is defined as a "process of gathering information about some system variable of state" (e.g. abundance, habitat cover) that may be of interest for the evaluation of management decisions or scientific inquiry (Yoccoz, Nichols & Boulinier 2001). The extinction crisis of species and the increasing pressure of human induced landscape change requires long-term monitoring as an important step to propose timely conservation interventions, as well as enabling the evaluation of targets set by the Convention of Biological Diversity (CBD) at a global scale (Collen et al. 2013b). One important monitoring scheme is the Global IUCN Redlist Index that measures changes in extinction risk based on the IUCN Redlist of species which can provide necessary data for the evaluation on how effective conservation efforts have been. For example Hoffmann et al. (2010) showed that the extinction risk of vertebrates since 1980 would have been much higher if there had not been conservation measures in place. Monitoring of species with the Redlist Index can be assessed at local levels as well as at global scales. Both scales are assessed with equal threshold values and, due to the scale, national level assessments can provide more specific guidelines for conservation action (Collen et al. 2013a). An additional monitoring scheme that has been used globally to monitor biodiversity is the Living Planet Index (LPI), which uses data from vertebrate abundance trends at local or regional scales. The LPI can be robust and useful to monitor conservation efforts however some limitations are apparent such as data deficiency and an over representation of bird data (Collen et al. 2009). There are also several proposed monitoring methods to evaluate increasing human pressure on biodiversity such as the use of satellite imagery to monitor change in land use, effects of climate change on species and landscapes, impacts of invasive species, and ecological footprints amongst others (see Collen et al. 2013b).

Monitoring schemes that aim to gather data on specific taxa or areas of interest often lack clear statements regarding three fundamental questions: why are you doing it (i.e. clear aim and objectives), what is your target state variable that will tell you something useful about the system in order to fulfil aims and objectives, and lastly how you will go about doing it (Yoccoz, Nichols & Boulinier 2001). The definition and explicit account of the first two questions (i.e. why and what) are fundamental so that monitoring schemes can be effective, focused and scrutinized. In turn the how question (i.e. survey effort allocation) will ultimately ensure that the investment in monitoring provides accurate and precise returns in data quality, particularly in detecting trends of change (Jones 2013). For example higher precision targets or power to detect change could be established a priory dependant on specific goals of surveys (i.e. why and what questions) which will result in increasing survey effort. For example, to evaluate the decline of a critically threatened species there would be a need for higher precision of parameters compared to an abundant species of conservation concern for which less precise estimates might suffice (Guillera-Arroita & Lahoz-Monfort 2012). Any monitoring scheme must ensure that the sampling design and effort can account and correct for biases given spatial variation and imperfect detection (Yoccoz, Nichols & Boulinier 2001). For example, occupancy as a state variable is a useful metric to monitor species trends (i.e. dynamics) since it is cheaper than abundance based schemes, it corrects for imperfect detection and it can accommodate for spatial variation and environmental relationships (MacKenzie & Reardon 2013).

1.4. Habitat loss and fragmentation

Habitat destruction, arising from the processes of loss (e.g. clearance for agriculture) and degradation (e.g. selective logging), poses the greatest threat to species and ecosystems (Hambler & Canney 2013). It is first important to understand what 'habitat' is. Habitat refers to all the conditions that enable a species to occur in a particular area (Lindenmayer & Fischer 2007).

Habitat loss occurs when continuous habitat (e.g. forest) is reduced in overall size, whereas fragmentation occurs when an area of habitat is subdivided into smaller units (Fahrig 2003; Lindenmayer & Fischer 2007). The differences between these two processes can be illustrated with the following example. A continuous patch of habitat can be either reduced by half its area but remain a single patch (i.e. loss) or subdivided into multiple patches with an equivalent area extent. The latter scenario represents habitat fragmentation, in addition to loss. These processes occur simultaneously when continuous habitats are modified and can have different impacts on the landscape configuration and species. Fragmentation studies show variable results because either fragmentation has not been well defined in the study design (Fahrig 2003) or they may be confounded by whether the focal species is a specialist or generalist, how it responds to habitat edges and ranging behaviour or dispersal patterns through the matrix (the non-habitat which surrounds patches) (Ewers & Didham 2006).

In general terms, fragmentation will increase the number of patches in the landscape, reduce the mean size of the patch, and increase the isolation of patches (Fahrig 2003). By reducing the size of remnant patches, there can be an impact on the carrying capacity of the habitat to sustain the original population particularly if the species is a habitat specialist and requires core habitat area away from the edge (Bender, Contreras & Fahrig 1998). The subdivision in many patches increases the edge of the habitat, which is the ecotone or transition between the original habitat and the surrounding new habitat (e.g. forest and grassland transition). For example, reproductive rates of specialist species may decrease due to increased nest predation at edges (Lahti 2001), or the penetration of the edge can lead to an increase in generalist species that increase competition with specialist species (Marvier, Kareiva & Neubert 2004). Furthermore, fragmentation can increase the isolation of patches which has negative implications for species that are restricted in movement but less so for ones that are able to cross surrounding habitat or the matrix (Fahrig 2003). For those species able to cross the matrix, favourable conditions might foster movement (e.g. refuge sites on route) and or provide resources (e.g. increased abundance of rodents due to grain production in agricultural lands) which can mitigate the impacts of fragmentation (Ewers & Didham 2006).

Fragmented landscapes can support source-sink population dynamics. Large populations in larger patches or higher productivity areas (i.e. higher abundance of prey, reproductive success, higher density) in the case of wide ranging territorial species (e.g. carnivores) can act as a source of individuals (i.e. sink) to smaller populations in smaller patches or to less productive areas; potentially structured as a metapopulation and fostering species persistence (Hambler & Canney 2013). Habitat connectivity could mitigate impacts of land conversion and possibly increase the carriying capacity of those landscapes (Fischer & Lindenmayer 2007). Not only connectivity of good-quality habitat is relevant but also the focus on poor-quality habitat as they could significantly improve movement and persistence of populations in fragmented landscapes (Wiegand, Revilla & Moloney 2005). However, human induced extinction drivers such as hunting, illegal logging, fires, invasive species, competition from domestic animals, may all increase and act synergistically in fragmented landscapes as a result of making habitats more accessible (Brook, Sodhi & Bradshaw 2008). Hence, fragmented landscapes may also act as ecological traps, where species are drawn to them because of suitable habitat conditions (e.g. forest patches in agricultural lands) but their reproductive success and abundance is significantly lower than in non fragmented landscapes (Robertson & Hutto 2006). Finally, observable species richness or persistence in a fragmented landscape may be due to an "extinction debt" where there is a lag time between current patterns and the long-term impacts (Hambler & Canney 2013).

1.5. Human behaviour and biodiversity

The activities of human communities can have great impacts on relevant habitats or species of conservation concern in agricultural landscapes. For example poaching of wildlife within protected areas, by the surrounding communities, can drive local extinctions and reduce the effective size of the parks (Dobson & Lynes 2008) or degrade them by hunting, fires, logging and grazing of domestic livestock (Bruner et al. 2001). Hence it is widely recognised that without engagement and participation of local communities the fate of many species and habitats is even more uncertain. There are some examples where strict legal structures, based on scientific knowledge and empowerment of local communities, can foster sustainable extraction of resources (Castilla & Fernandez 1998) or incorporating local stakeholders in decision making processes and implementation to safe-guard predators and livestock can provide improved conservation outcomes outside protected areas (Treves et al. 2006).

Engaging with local communities to implement effective conservation measures ultimately requires a robust understanding of human behaviour (St John, Keane & Milner-Gulland 2013). Social-psychology models of behaviour provide frameworks that suggest that an individual’s action is influenced by social norms or what is the socially expected behaviour, personal beliefs and attitudes, and the level of control people perceive they have over performing a particular act such as having the skill and tools (Manfredo & Dayer 2004). Research of attitudes towards environmental issues in conservation abound, but can be misleading because there is evidence that what people say can be different to what people do, hence assessing behaviour is warranted (Herberlein 2012). Unfortunately, resource use by communities can in many cases be illegal proving further difficulties in monitoring or understanding the prevalence of the overexploitation of resources. When activities are illegal respondents will sometimes tend to conceal their activities because of fear of punishment. However there are now methods that can provide information for key conservation questions such as what is being exploited, where, who and what are the behavioural drivers influencing the illegal activity. The choice of method will depend on the type of activity, prevalence, monitoring budget, and ability to detect the activity (Gavin, Solomon & Blank 2010).

1.6. Integration of social and ecological data for conservation

Ultimately, biodiversity conservation requires not only understanding the ecological effects of habitat modifications and impacts on species but also the human dimension given the impact that our activities are having on the earth´s systems. Natural science is important but not enough to tackle the social and political complexities that surround conservation problems (Macdonald & Wills, 2013). It is imperative that social sciences be included in study programmes of conservation biology and also in conservation oriented research (Mascia et al. 2003). Biological conservation must integrate natural and social science if we are to find effective solutions of, for example, protected area effectiveness, resolve environmental conflicts such as land rights and generally guide decision making processes together with those communities directly involved so that conservation can have a real impact on reversing environmental degradation (Mulder & Coppolillo 2005). For example in resource management, there is an important body of evidence that a “systems” approach which relies on adaptive management that can link socio and ecological knowledge, can provide better outcomes in terms of resilience of human communities to unexpected circumstances and to the sustainable use of natural resources (Folke, Berkes & Colding 1998). For example, the management of an invasive species that has economic value to local stakholders can be most effective and accepted when general views of local stakeholders are taken into account (e.g. Marshall et al. 2011). Conservation planning excercises – where cost-effective priority targets such as representative habitats and species are identified in a landscape of conservation concern - can benefit from incorporating social data and the empowerment of communities in the decision making process to ensure a feasible plan for the implementation stage (Knight et al.

2013). Conservation targets will ultimately be driven or constrained by societal values and priorities regarding desirable outcomes or identified problems which, if oriented by scientific rigour and systematically assessed, can be greatly benefitial to establish cost-effective strategies (Pullin et al. 2013).

In many instances conservation complexities arise from conflict between human groups (human-human conflict) that have different objectives regarding the managment of a particular species and or landscape (Redpath et al. 2013). There is an increasing trend of these type of conflicts worldwide which require new strategies, particularly involving social science, to foster long-term solutions of co-existence (Dickman 2010). The link between social and ecological data is particularly relevant when a species or guild of conservation concern comes into conflict with human communities, either from direct threat (e.g. Leopards killing people in India) or indirectly through economic losses (e.g. crop raiding by elephants). Managing wildlife conflict requires, not only the evaluation of mitigation measures, but an integration across disciplines to link risk factors of social (e.g. inequality and power, beliefs, distrust) and environmental (e.g. land use and management, human behaviour to protect assets) dimensions that can lead to different intensities of conflict which can ultimately provide knowledge for effective conflict reduction and co-existence strategies (Dickman 2010).

1.7. Carnivores pose complex conservation challenges

Mammalian Carnivores (Order Carnivora) are particularly vulnerable to extinction from direct human action by killing of predators and also from habitat degradation.

Carnivores personify the main problems that challenge conservation effectiveness (Gittleman et al. 2001).

Carnivora comprises 287 extant species in 123 genera and 16 families (Ullas Karanth & Chellam 2009), including Felidae (cat family), Ursidae (bear family), Canidae (dog family), and Mustelidae (weasel family) amongst others. Body size can vary considerably, from very large Ursids such as brown bears (Ursus arctos), which weigh >160 kg, to very small felids, such as the rusty spotted cat (Prionailurus rubiginosus) at just 1 kg. Likewise, carnivores display a diverse range of traits and behaviours; they are distributed across all major continents (except non-native to Australia) and occupy a varied number of ecosystems, showing large variability in home range size and social structure (Gittleman et al. 2001).

Carnivores occupy high trophic levels and can impact ecosystem processes. For instance, large carnivores can regulate herbivory by predation of large herbivores and also lower abundances of meso-carnivores which, in the absence of large carnivores, can have unexpected and sometimes negative ecological effects (Ripple et al. 2014). Furthermore, the elimination of predators from landscapes may cause unwanted effects in ecosystem integrity and function such as increase in herbivores with subsequent impacts on vegetation (Sekercioglu 2006; Bruno & Cardinale 2008) and the local extinction of a few predators can have comparable effects on ecosystem functioning to a large reduction in the diversity of plant species (Duffy 2003).

The extinction risk of carnivorous species is relatively high due to life history traits, environmental requirements and interaction with human communities. Predators in human-dominated landscapes, such as carnivorous mammals and birds of prey, are particularly prone to extinction because they are at the top of the food chain and have predominately slow life histories such as low reproductive rates (Purvis et al. 2000). Biological traits of carnivores, in general, predict to a large extent extinction risk of species but become more relevant in explaining variation when species are subject to higher human activity; suggesting an increase in extinction risk with expanding human density (Cardillo et al. 2004). Human density can reduce persistence of many species and even put at risk populations within protected areas due to wide-ranging behaviour of carnivores outside boundaries (Woodroffe 2000). Carnivorous mammals are particularly vulnerable in human dominated landscapes because of negative interactions with local communities, triggered by livestock predation (i.e. livelihood) and/or attacks on human lives (Treves & Karanth 2003; Inskip & Zimmermann 2009; Ullas Karanth & Chellam 2009; Inskip et al. 2014). Furthermore, retribution killing, defined as the elimination of carnivores in retaliation for livestock predation or attacks on people, is particularly worrisome if the species is of conservation concern given the potential population impacts of non-natural mortality (Chapron et al. 2008; Liberg et al. 2012).

The fate of carnivores will ultimately depend on management and interventions in human-dominated landscapes aimed to ensure habitat suitability and reducing negative human interactions. Conservation must strive to find ways to establish co-existence between carnivores and people, under the premise that some level of predation and retribution killing will always occur (Treves & Bruskotter 2014). Mitigation measures can take many forms. Conflict areas can be identified, so targeted mitigation actions can be undertaken (Treves et al. 2004). These could include the use of predator deterrents (Shivik 2006), such as guard-dogs to reduce predation of livestock (Andelt & Hopper 2000), improving night holding facilities (Tumenta et al. 2013) or grazing water buffalo alongside cattle to protect against puma and jaguar predation (Hoogesteijn & Hoogesteijn 2008).

An in-depth qualitative understanding of the motivations and underlying political situations driving conflict is necessary for effective measures (Inskip et al. 2014) or finding ways to empower local communities to be part of the solution and not the problem (Sillero-Zubiri & Laurenson 2001; Treves et al. 2006). Most importantly, and specifically when retribution killing or just plain killing of carnivores is occurring, identifying the drivers of killing behaviour by individuals can be most useful for the implementation of conservation measures such as targeting specific social segments or orientate mitigation measures to be included in policy or behavioural change campaings(St John et al. 2012).

The research undertaken on carnivores has been biased towards big cats and canids within the order, with relatively little attention having been paid to small cats, mustelids, civets and mongooses (Ginsberg 2001). Indeed, only around 15% of species have been the subject of serious scientific scrutiny (Ginsberg 2001), with those characterised by small geographic ranges and body size having received significantly less research (Brooke et al. 2014). This trend is exemplified by the felidae family, from which 14 threatened species have had less than three in-situ studies published (Brodie 2009). In general, carnivores are hard to study due to their elusive behaviour, low density and nocturnal habits (Long 2008). Although this makes population status assessments a difficult tasks to undertake, such monitoring and research is important across geographic areas where threat levels are high, if we are to prevent further loss of species (Balmford, Green & Jenkins 2003).

1.7.1. Methods to study carnivores

Carnivores can be studied using a variety of ecological techniques and the choice of method will ultimately depend on the ecological question being evaluated and/or management objectives of the particular project. Survey methods can be can either be classified as ‘invasive’, where individuals are captured (e.g. to take biometric measurements, be tagged for future identification, or fitted with a radio-collar for monitoring purposes, tissue or blood samples for DNA), or ‘non-invasive’, where individuals are assessed remotely. Invasive methods tend to provide very detailed and high resolution data about individuals or, in some cases where sample sizes are large enough, species populations. For example, DNA from tissue or blood samples can be used to assess population structure (e.g. Napolitano et al. 2014) and telemetry can yield fine-scale information on habitat use (e.g. Dunstone et al. 2002). Although invasive methods provide high quality data, they are generally very expensive and difficult to carry out over large geographical areas.

A detailed description of non-invasive methods is provided in Long et.al. (2008). Techniques include surveys using scats (i.e. faeces; which can provide non-invasive

DNA and diet information), tracks (either on natural terrain or artificial tracks plates), hair samples (again, providing DNA) and camera-traps. Camera-traps are now widely deployed in mammal surveys (Rowcliffe & Carbone 2008; O'Connell, Nichols & Karanth 2010; Burton et al. 2015). They are particularly valuable for surveying elusive species because they can work independently in remote areas and perform effectively in comparison to alternative detection methods such as track plates (Gompper et al. 2006; Long et al. 2007; Long 2008; Balme, Hunter & Slotow 2009).

Camera-trap data can be used to study presence/absence, occupancy, abundance (where individuals can be identified via distinguishing features such as coat pattern), behaviour (using video settings) and activity patterns (O'Connell, Nichols & Karanth 2010). In particular, the number of camera-trap occupancy studies is growing rapidly, with the majority of focal species being carnivores or ungulates (Burton et al. 2015). 'Capture histories' describe the detection pattern of species at a site over repeated sampling occasions within a particular season. Occupancy models can then use this information to estimate the maximum likelihood of occupancy and detection probability parameters.

Recent advances in occupancy modelling have improved the utility of presence-absence data substantially, allowing the true proportion of the landscape that is occupied by a species to be quantified (Vojta 2005). The mathematical techniques allow researchers to correct for imperfect detection, which occurs when the species is present but not found and recorded (MacKenzie et al. 2006). Occupancy estimates are scale dependant, so it is important to determine what the size of the sample unit should be, ensuring that it is biologically meaningful for the species (e.g. home range size). If a sample unit is too large, occupancy will be underestimated, and if it is too small, the area of occupancy will be overestimated (MacKenzie et al. 2006). Multi-season models also exist, which can be used to estimate occupancy dynamic parameters, describing how sample units change in status through time. This is a useful tool for monitoring of threatened species because survey methods to obtain data can be deployed over large geographical areas (Guillera-Arroita, Ridout & Morgan 2010).

1.8. The guiña as a study species

There are many global prioritization schemes that look at how to focus conservation efforts at a large scale (Brooks et al. 2006); however, conservation science needs to build on empirical studies to provide evidence in benefit of effective measures for threatened species at a local scale (Ginsberg 2001). The wild felid guiña (Leopardus guigna) is such an example.

The guiña (Leopardus guigna) is a threatened wide-ranging forest dwelling felid. It is the smallest Neotropical cat at <2 kg and occurs in two distinct morphs, spotted and melanistic (Fig. 1.1). It is categorised as Vulnerable, with a declining population trend, by the International Union for Conservation of Nature (IUCN) as a result of habitat loss, retaliatory killings by people in response to poultry predation, increasing incidences of roadkill and disease transmission by domestic cats (Napolitano et al. 2015). The IUCN Red List criteria used to classify the species as Vunerable were A2abc, C2a(i) ver 3.1, representing population decline, area of occupancy reduction, four of the six subpopulations having less than 1,000 mature individuals and the fact that overall threats are predicted to increase in the future.

Figure 1.1 Camera-trap photos of spotted (top left and bottom) and melanistic (top right) guiña (Leopardus guigna), including a unique capture of a mother and cub (lower left). The photo on the lower right demonstrates how well the species is camouflaged and the relative scale of the felid in comparison to the understory vegetation (< 1 m).

The guiña is a solitary species thought to require forest habitat with dense understory and the presence of bamboo (Chusquea spp.) (Nowell & Jackson 1996; Acosta-Jamett & Simonetti 2004). However, it is known to occupy remnant patches of fragmented forest remaining within agricultural areas (Sanderson, Sunquist & W. Iriarte 2002;

Acosta-Jamett & Simonetti 2004; Gálvez et al. 2013) and can use grassland or shrub for movement between habitats and perhaps foraging on habitat edges (Dunstone et al. 2002). The main prey base of guiña are small mammals (<1 kg) and birds, particularly from the flightless endemic tapaculo family (Freer 2004; Sanderson, Sunquist & Iriarte 2002). Guiña are skilled tree climbers, where it can take refuge during the day (Sunquist & Sunquist 2002), as well as predating on bird nests (Altamirano et al. 2013) or small arboreal mammals such as the long-tailed colilargo (Oligoryzomys longicaudatus), Chilean climbing mouse (Irenomys tarsalis), and the marsupial Monito del Monte (Dromiciops gliroides) (Moreira-Arce et al. 2015). As is true for many wild felids and carnivores in general, guiña activity patterns relate to activity of its prey (Delibes-Mateos et al. 2014). The guiña is mainly nocturnal, with increased activity during crepuscular periods (Delibes-Mateos et al. 2014; Hernandez et al. 2015). Although not much is known regarding fecundity, it is estimated that a female can have between 1-4 cubs (Nowell & Jackson 1996). There is no basic information available on reproductive success, survival or independence of cubs and dispersal to new territories. However, from my camera traping experience, I have only documented 1 cub from three distinct and independent events (large geographical separation) within the study area.

The home range of the species has been estimated at 1.3-2.5 km^2, based on information from seven individuals (Sanderson, Sunquist & W. Iriarte 2002), 0.3-2.2 km^2 from ten individuals (Dunstone et al. 2002) and 1.3- 4 km^2 from five individuals within the study area of this thesis (Schüttler et al. unpublished data). Common to most felids, there is some overlap between smaller home ranges of females with larger areas for males (Dunstone et al. 2002).

The güiña is considered a pest by local human communities as it can predate on chickens (Silva-Rodríguez, Ortega-Solís & Jiménez 2007; Herrmann et al. 2013). Consequently, retribution killings have been recorded (Sanderson, Sunquist & W. Iriarte 2002; Gálvez et al. 2013), although the extent of persecution has never been formally assessed. Furthermore, household domestic dogs in rural areas have also reportedly killed guiñas (Sepúlveda et al. 2014). These sources of non-natural mortality, together with evidence of an historic population and genetic variability reduction (i.e. bottleneck), could eventually be a significant issue for the long-term persistence of the species (Napolitano et al. 2014).

1.8.1. Study system

The study was conducted in the Tolten catchment of the Araucanía region in southern Chile, at the northern limit of the South American temperate forest ecoregion (39º15´S, 71º48´W) (Armesto et al. 1998). The area falls within several global biodiversity conservation prioritisation schemes. It is part of the Chilean winter rainfall-Valdivian forests biodiversity hotspot, meaning that >50% of plants are endemic and habitat has been historically reduced to less than 30% of its original extent (Myers et al. 2000). In addition, it is also identified in conservation priorotization schemes such as last of the wild, frontier forests, endemic bird areas, centres of plant diversity and the Global 200 ecoregions of importance (Brooks et al. 2006). The temperature of the study area has a yearly average of 11.5 °C and the rainfall spans from 1000 and 3000 mm (Luebert & Pliscoff 2006). The natural forest vegetation of the study area is deciduous southern beech forest, characterized by Nothofagus obliqua, Laurelia sempervirens, Eucryphia cordifolia, Podocarpus saligna and Aextoxicon punctatum in lowland forests. As the altitude increases, the Nothofagus dombeyi, Nothofagus alpina, Laureliopsis philippiana and Araucana araucana become more dominant (Luebert & Pliscoff 2006).

In particular, the system was chosen because it comprises two distinct geographical sections common throughout Southern Chile and guiña distribution: the Andes mountain range and central valley. Land-use in the central valley is primarily intensive agriculture (e.g. cereals, livestock, fruit trees) and urban settlements (Fig. 1.2), whereas farmland (which occurs < 600 m.a.s.l) in the Andes is less intensively used (e.g. unimproved grasslands) and is surrounded by tracks of continuous forest on steep slopes (Fig. 1.3). These two areas also represent variation with regards to habitat loss and fragmentation from the Andes Mountains to the Central valley where the status of the guiña is largely unknown (Sunquist & Sunquist 2002). In addition, I have previous research experience in the study area (Galvez et al. 2013) and it is part of long-term research plans of my local research institution.

Figure 1.2 Central valley part of the study area in the Araucanía region of southern Chile, showing remnant patches of native vegetation surrounded by intensive agricultural crops and livestock grazing.

Native vegetation remains as a patchy mosaic in agricultural valleys. In fact, only 5% of forest vegetation remains after human colonisation from the late 19th century (Miranda et al. 2015). In the Andean valleys the same patchy mosaic vegetation is present, but mostly at elevations below 600 m.a.s.l. Continuous forests only persist on steep slopes at higher elevations not suitable for agricultural activities and climatic restrictions. All of the protected areas are located above 800 m.a.s.l. They are very important for delivering ecosystem services (e.g. protecting the water catchment) but contribute less to biodiversity conservation because endemic species rich areas are within lowland areas with native vegetation (Armesto et al. 1998).

Figure 1.3 Andean mountain range study area in the Araucanía region of southern Chile, showing the narrow agricultural valleys surrounded by continuous tracks of native forest on higher elevation slopes.

1.8.2. Landcover classification

A lack of high quality landcover data is usually a limiting factor in ecological studies that look at relationships between habitat and species. For our study region, landcover maps were only available for the Andean agricultural valleys. Classification of the central valley was therefore needed. The study region (i.e. large area) delimination took into account bioclimatic similiarity and study areas in particular (i.e. smaller areas) to represent the Central valley and Andean agricultural valleys.

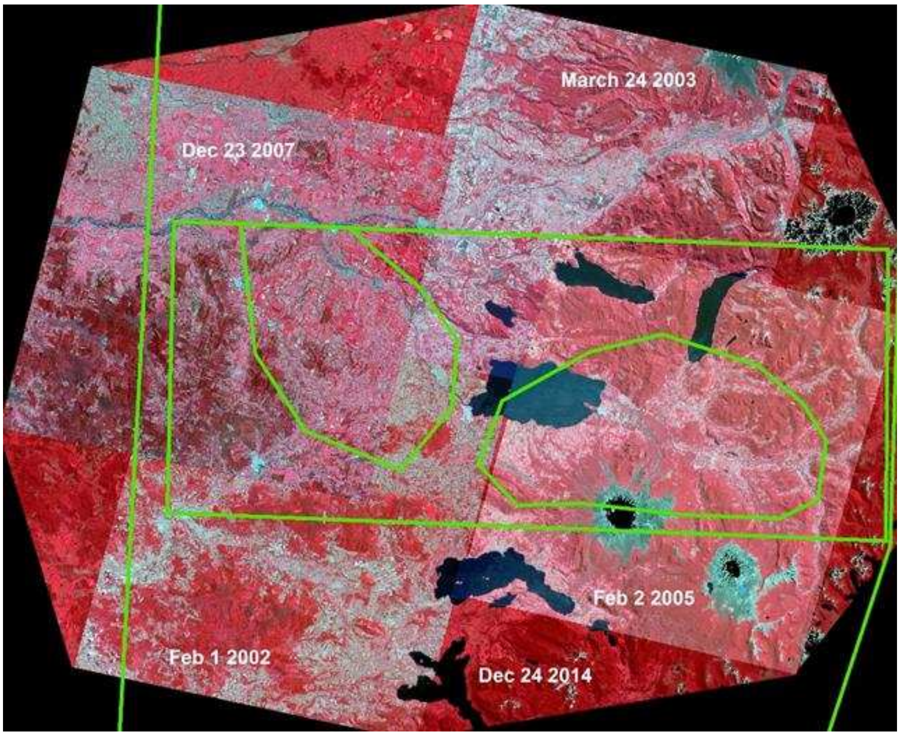

Figure 1.4 The spatial extent of the five satellite images (four Aster 15m resolution, 2002, 2003, 2005, 2007 and one Landsat 8 at 30m resolution 2014) used to derive the supervised classification of landcover across the study region. Green lines and polygons were used as references to delimit study area.

For studies investigating the impacts of fragmentation and habitat loss on species, the resolution of the map must be sufficiently high to pick up on the variation in the landscape at a scale which is biologically meaningful (Gustafson 1998). We classified landcover using a composite of four Aster images at 15 m resolution, from 2002-2007 (downloaded from http://glovis.usgs.gov/), and a single Landsat 8 image of 30-m resolution, from 2014, for the few small areas of the study region not covered by the Aster images (Fig. 1.4). A pixel resolution of 15 m equates to less than 0.0075% of the estimated average guiña home range size for the study area (MCP 95% mean = 270 ±137 ha; Schüttler E. unpublished data). All the sample units used in our surveys were covered by the Aster images. Moreover, the landcover configuration across the sample units in the study region derived from the Aster images is not noticeably different from that in 2014 Google Earth images.

Table 1.1 Extent and relative percentage of each landcover class across the study region in southern Chile.

Landcover	Area (km^2)	Percentage (%)
Forest	5742.4	38%
Shrub	2163.1	14%
Agricultural land	4458.9	30%
Exotic forest plantations	1309.5	9%
Water	612.7	4%
Bare ground	627.7	4%
Urban	100.3	1%

The resulting land cover shows how forest and agricultural land are the predominant landcover and forests increase towards the east in the Andes (Table 1.1 and Fig. 1.5).

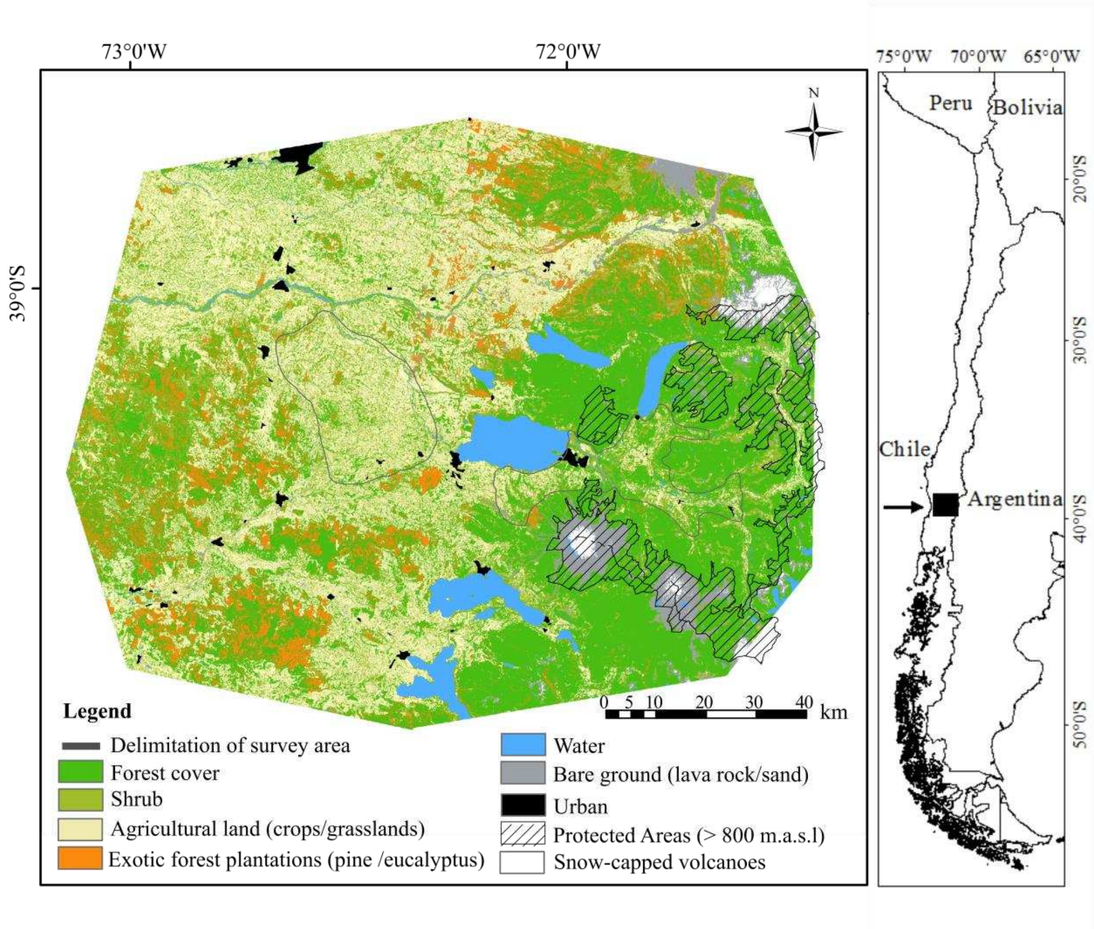

Figure 1.5 Landcover classification of study area in southern Chile showing delimination of where our sample units were surveyed and protected areas in the Andes Mountains. The grey polygon to the left represents the central valley and the one to the right valleys within the Andes Mountains. For detailed methods on the land cover classification see Chapter 3.

1.9. Outline of this thesis and research questions

The issues faced by carnivores require an integrated view of ecological and social processes over large geographical areas, so a robust evidence-base can be established and used to inform effective conservation action. Furthermore, the elusive nature of carnivores, and paucity of data for many species, means that improvement into how economic resources are used to survey threatened species is of utmost importance.

The aim of this thesis was to investigate how the threats of habitat loss, fragmentation and human-wildlife conflict act and/or interact on the population dynamics of forest dwelling carnivores within human modified landscapes. Furthermore and for a particular species, the guiña, predict future conservation scenarios, practical management of landscapes, and contribute to necessary methods for long-term assessment of populations. A better understanding of how the species survives in the heavily modified anthropogenic landscapes of southern Chile will provide an evidence-base to support the development of future conservation interventions.

In this thesis, I developed a mathematical cost function which can be used to improve survey effort allocation within an occupancy modelling framework. In addition, I explored the interaction between habitat loss, fragmentation and retribution killing as drivers of decline of the guiña. The thesis is composed of the three chapters, written as stand-alone independent research papers.

Chapter 2 contributed to the literature on occupancy survey effort allocation for terrestrial mammals. Particularly, I tested whether the inclusion of specific camera trapping costs to survey effort allocation of occupancy estimates - not done previously - provide relevant trade-offs associated to the number of sites, number of repeat surveys (i.e. sampling occasions), and number of camera-traps needed to achieve statistical precision. Specifically, does survey effort allocation advice change for species of diferent características such as abundance (i.e. rare versus common), detectability and home range areas? For this purpose a detailed camera-trap survey cost function was developed, linked to the statistical precision of parameters. The guiña, together with other elusive mammal case study species, are used as empirical examples of how the framework can be applied to data deficient and threatened species.

Chapter 3 investigated the relative effects of habitat loss, fragmentation, and anthropogenic pressure on the guiña, species considered a forest specialist, by integrating ecological and social data into a common modelling framework. Specifically, I asked whether there is a level of habitat loss or fragmentation at which the occupancy dynamics (i.e. changes in occupied or unoccupied status) are negatively impacted (i.e. high turnover of occupied sites) and alternatively is human pressure having a neutral, equal or larger impact? The paper analyses a substantial camera-trap occupancy dataset, collected over four seasons, as well as data derived from remote-sensed imagery and householder questionnaires. The study demonstrated the importance of taking an interdisciplinary approach to conservation in order to identify the key threats to mammals inhabiting a human-dominated landscape.

Chapter 4 explored the prevalence of livestock predation experienced by householders (i.e. reported predation) across the study region, and aimed to identify factors that can predict when a farmer might proactively seek to kill a species as a consequence. Particularly whether socio-economic, knowledge of rules, reported predation, frequency of encounters, responses to hypothetical predation scenarios are associated with killing species, under the expectation that different species will produce varying outcomes. To investigate human behaviours that are sensitive and/or illegal, we use the random response technique (RRT) method to question our human study participants. The findings highlight that knowledge of rules does not deter illegal behaviour and that predator-specific strategies must be undertaken to reduce persecution.

1.10. References

Acosta-Jamett, G. & Simonetti, J.A. (2004) Habitat use by Oncifelis guigna and Pseudalopex culpaeus in a fragmented forest landscape in central Chile. Biodiversity & Conservation, 13, 1135-1151.

Altamirano, T.A., Hernandez, F., De La Maza, M. & Bonacic, C. (2013) Güiña (Leopardus guigna) preys on cavity-nesting nestlings. Revista Chilena de Historia Natural, 86, 501-504.

Andelt, W.F. & Hopper, S.N. (2000) Livestock guard dogs reduce predation on domestic sheep in Colorado. Journal of Range Management, 53, 259-267.

Armesto, J., Rozzi, R., Smith-Ramírez, C. & Arroyo, M. (1998) Conservation targets in South American temperate forests. Science, 282, 1271-1272.

Balme, G.A., Hunter, L.T. & Slotow, R. (2009) Evaluating methods for counting cryptic carnivores. The Journal of wildlife management, 73, 433-441.

Balmford, A., Green, R.E. & Jenkins, M. (2003) Measuring the changing state of nature. Trends in Ecology & Evolution, 18, 326-330.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L. & Maguire, K.C. (2011) Has the Earth's sixth mass extinction already arrived?. Nature, 471, 51-57.

Bender, D.J., Contreras, T.A. & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology, 79, 517-533.

Brodie, J.F. (2009) Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodiversity and Conservation, 18, 2927-2939.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J. (2008) Synergies among extinction drivers under global change. Trends in ecology & evolution, 23, 453-460.

Brooke, Z.M., Bielby, J., Nambiar, K. & Carbone, C. (2014) Correlates of research effort in carnivores: body size, range size and diet matter. PloS one, 9, e93195.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S. (2006) Global biodiversity conservation priorities. Science, 313, 58-61.

Bruner, A.G., Gullison, R.E., Rice, R.E. & da Fonseca, G.A. (2001) Effectiveness of parks in protecting tropical biodiversity. Science, 291, 125-128.

Bruno, J.F. & Cardinale, B.J. (2008) Cascading effects of predator richness. Frontiers in Ecology and the Environment, 6, 539-546.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004) Human population density and extinction risk in the world’s carnivores. PLoS Biology, 2, e197.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D. & Wardle, D.A. (2012) Biodiversity loss and its impact on humanity. Nature, 486, 59-67.

Castilla, J.C. & Fernandez, M. (1998) Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. Ecological Applications, 8, 124-132.

Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S. & Clobert, J. (2008) The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology, 45, 1667-1674.

Collen, B., Griffiths, J., Friedmann, Y., Rodriguez, J.P., Rojas-Suàrez, F. & Baillie, J.E.M. (2013a) Tracking Change in National-Level Conservation Status: National Red Lists. Biodiversity Monitoring and Conservation: Bridging the Gap between Global Commitment and Local Action (eds B. Collen, N. Pettorelli, J.E.M. Baillie & S.M. Durant), pp. 17–44. John Wiley & Sons, London..

Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R. & Baillie, J.E.M. (2009) Monitoring change in vertebrate abundance: the Living Planet Index. Conservation Biology, 23, 317–327.

Collen, B., Pettorelli, N., Baillie, J.E.M. & Durant, S.M. (2013b) Biodiversity monitoring and conservation: bridging the gap between global commitment and local action. John Wiley & Sons, London.

Delibes-Mateos, M., Díaz-Ruiz, F., Caro, J. & Ferreras, P. (2014) Activity patterns of the vulnerable guiña (Leopardus guigna) and its main prey in the Valdivian rainforest of southern Chile. Mammalian Biology, 79, 393-397.

Dickman, A.J. (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal conservation, 13, 458–466.

Dobson, A. & Lynes, L. (2008) How does poaching affect the size of national parks?. Trends in ecology & evolution, 23, 177-180.

Duffy, J.E. (2003) Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters, 6, 680-687.

Dunstone, N., Durbin, L., Wyllie, I., Freer, R., Jamett, G.A., Mazzolli, M. & Rose, S. (2002) Spatial organization, ranging behaviour and habitat use of the kodkod (Oncifelis guigna) in southern Chile. Journal of zoology, 257, 1-11.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews, 81, 117-142.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics, 34, 487-515.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecology & Biogeography, 16, 265–280.

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F. & Phalan, B. (2008) How will oil palm expansion affect biodiversity?. Trends in ecology & evolution, 23, 538-545.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. Science, 309, 570-574.

Folke, C., Berkes, F. & Colding, J. (1998) Ecological practises and social mechanisms for building resilience and sustainability. Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience, First (eds F. Berkes & C. Folke), pp. 414–437. Cambridge Univ Press, Cambridge.

Freer, R.A. (2004) The spatial ecology of the Guina (Oncifelis guigna) in Southern Chile. PhD thesis. University of Durham.

Gálvez, N. & Bonacic, C. (2008) Filling gaps for guiña cat (kodkod) conservation in southern Chile. Wild Felid Monitor: Newsletter of Wild Felid Research and Management Association (WFA), 1, 13.

Gálvez, N., Hernández, F., Laker, J., Gilabert, H., Petitpas, R., Bonacic, C., Gimona, A., Hester, A. & Macdonald, D.W. (2013) Forest cover outside protected areas plays an important role in the conservation of the Vulnerable guiña Leopardus guigna. Oryx, 47, 251-258.

Gavin, M.C., Solomon, J.N. & Blank, S.G. (2010) Measuring and monitoring illegal use of natural resources. Conservation Biology, 24, 89-100.

Geist, H.J. & Lambin, E.F. (2002) Proximate Causes and Underlying Driving Forces of Tropical Deforestation Tropical forests are disappearing as the result of many pressures, both local and regional, acting in various combinations in different geographical locations. Bioscience, 52, 143-150.

Ginsberg, J.R. (2001) Setting priorities for carnivore conservation: What makes carnivores different?. (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & Wayne R.K.), pp. 498-523. Cambridge University Press.

Gittleman, J.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. (2001) Why carnivore conservation?. Carnivore Conservation (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & Wayne R.K.), pp. 1-7. Cambridge University Press, Cambridge.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin, 34, 1142-1151.

Guillera-Arroita, G. & Lahoz-Monfort, J. (2012) Designing studies to detect differences in species occupancy: power analysis under imperfect detection. Methods in Ecology and Evolution, 3, 860–869.

Guillera-Arroita, G., Ridout, M.S. & Morgan, B.J.T. (2010) Design of occupancy studies with imperfect detection. Methods in Ecology and Evolution, 1, 131-139.

Gustafson, E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art?. Ecosystems, 1, 143-156.

Hambler, C. & Canney, S.M. (2013) Conservation. Cambridge University Press. Cambridge.

Herberlein, T.A. (2012) Navigationg Environmental Attitudes. Conservation Biology, 26, 583-586.

Hernandez, F., Galvez, N., Gimona, A., Laker, J. & Bonacic, C. (2015) Activity patterns by two colour morphs of the vulnerable guiña, Leopardus guigna (Molina 1782), in temperate forests of southern Chile. Gayana, 79, 102-105.

Herrmann, T.M., Schüttler, E., Benavides, P., Gálvez, N., Söhn, L. & Palomo, N. (2013) Values, animal symbolism, and human-animal relationships associated to two threatened felids in Mapuche and Chilean local narratives. J Ethnobiol Ethnomed, 9, 4269-4269.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B. & Cox, N.A. (2010) The impact of conservation on the status of the world’s vertebrates. Science, 330, 1503–1509.

Hoogesteijn, R. & Hoogesteijn, A. (2008) Conflicts between cattle ranching and large predators in Venezuela: could use of water buffalo facilitate felid conservation?. Oryx, 42, 132-138.

Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming domestic dogs and wildlife. Biological Conservation, 157, 341-351.

Inskip, C., Fahad, Z., Tully, R., Roberts, T. & MacMillan, D. (2014) Understanding carnivore killing behaviour: Exploring the motivations for tiger killing in the Sundarbans, Bangladesh. Biological Conservation, 180, 42-50.

Inskip, C. & Zimmermann, A. (2009) Human-felid conflict: a review of patterns and priorities worldwide. Oryx, 43, 18-34.

Jones, J.P.G. (2013) Monitoring in the real world. Biodiversity monitoring and conservation: bridging the gaps between global commitment and local action. (eds B. Collen, N. Pettorelli, J.E.M. Baillie & S.M. Durant), pp. 335–347. John Wiley & Sons, London.

Knight, A.T., Rodrigues, A.S.L., Strange, N., Tew, T. & Wilson, K.A. (2013) Designing effective solutions to conservation planning problems. Key Topics in Conservation Biology 2 (ed D.W.Macdonald.& K.J. Willis), pp. 362–383. Blackwell Publishing, Oxford.Lahti, D. (2001) The “edge effect on nest predation” hypothesis after twenty years. Biological Conservation, 99, 365-374.

Lambin, E.F. & Meyfroidt, P. (2011) Global land use change, economic globalization, and the looming land scarcity. Proceedings of the National Academy of Sciences of the United States of America, 108, 3465-3472.

Laurance, W.F., Goosem, M. & Laurance, S.G. (2009) Impacts of roads and linear clearings on tropical forests. Trends in Ecology & Evolution, 24, 659-669.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012) Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proceedings of the Royal Society, 279, 910-915.

Lindenmayer, D.B. & Fischer, J. (2007) Tackling the habitat fragmentation panchreston. Trends in Ecology and Evolution, 22, 127-132.

Liu, J., Daily, G.C., Ehrlich, P.R. & Luck, G.W. (2003) Effects of household dynamics on resource consumption and biodiversity. Nature, 421, 530–533.

Long, R.A., MacKay, P., Ray, J. & Zielinski, W. (2008) Noninvasive survey methods for carnivores. Island Press. Washington D.C.

Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J. & Buzas, J.S. (2007) Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. The Journal of Wildlife Management, 71, 2018-2025.

Luebert, F. & Pliscoff, P. (2006) Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria. Santiago.

Macdonald, D.W. & Willis, K.J. (2013) Key Topics in Conservation Biology 2 (eds DW Macdonald and KJ Willis). John Wiley & Sons, Oxford.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press. London.

MacKenzie, D.I. & Reardon, J.T. (2013) Occupancy methods for conservation management. Biodiversity Monitoring and Conservation: Bridging the Gap Between Global Commitment and Local Action (eds B. Collen, N. Pettorelli, J.E.M. Baillie, & S.M. Durant), pp. 248–264. John Wiley & Sons, London.

Manfredo, M.J. & Dayer, A.A. (2004) Concepts for exploring the social aspects of human–wildlife conflict in a global context. Human Dimensions of Wildlife, 9, 1-20.

Marvier, M., Kareiva, P. & Neubert, M.G. (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk analysis, 24, 869-878.

Marshall, N.A., Friedel, M., Van Klinken, R.D. & Grice, A.C. (2011) Considering the social dimension of invasive species: the case of buffel grass. Environmental science & policy, 14, 327–338.

Mascia, M.B., Brosius, J.P., Dobson, T.A., Forbes, B.C., Horowitz, L., McKean, M.A. & Turner, N.J. (2003) Conservation and the social sciences. Conservation Biology, 17, 649-650.

McMichael, A.J., Powles, J.W., Butler, C.D. & Uauy, R. (2007) Food, livestock production, energy, climate change, and health. The lancet, 370, 1253-1263.

Millennium Ecosystem Assesment (2005) Ecosystems and human well-being. Island Press, Washington, DC.

Miranda, A., Altamirano, A., Cayuela, L., Pincheira, F. & Lara, A. (2015) Different times, same story: Native forest loss and landscape homogenization in three physiographical areas of south-central of Chile. Applied Geography, 60, 20-28.

Moreira-Arce, D., Vergara, P.M., Boutin, S., Simonetti, J.A., Briceño, C. & Acosta-Jamett, G. (2015) Native forest replacement by exotic plantations triggers changes in prey selection of mesocarnivores. Biological Conservation, 192, 258-267.

Morton, D.C., DeFries, R.S., Shimabukuro, Y.E., Anderson, L.O., Arai, E., del Bon Espirito-Santo, F., Freitas, R. & Morisette, J. (2006) Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon. Proceedings of the National Academy of Sciences, 103, 14637-14641.

Mulder, M.B. & Coppolillo, P. (2005) Conservation: linking ecology, economics, and culture. Princeton University Press. New Jersey.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. Nature, 403, 853-858.

Napolitano, C., Gálvez, N., Bennett, M., Acosta-Jamett, G. & Sanderson, J. (2015a) Leopardus guigna. The IUCN Red List of Threatened Species 2015. URL http://www.iucnredlist.org/details/15311/0. [accessed 11 September 2015].

Napolitano, C., Johnson, W.E., Sanderson, J., O'Brien, S.J., Hoelzel, A.R., Freer, R., Dunstone, N., Ritland, K., Ritland, C.E. & Poulin, E. (2014) Phylogeography and population history of Leopardus guigna, the smallest American felid. Conservation Genetics, 15, 631-653.

Nowell, K. & Jackson, P. (1996) Wild cats: status survey and conservation action plan. IUCN Gland. Switzerland.

O'Connell, A.F., Nichols, J.D. & Karanth, K.U. (2010) Camera traps in animal ecology: methods and analyses. Springer Science & Business Media. London.

Pauchard, A. & Alaback, P.B. (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. Conservation Biology, 18, 238-248.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science, 344, 1246752.

Pullin, A.S., Sutherland, W., Gardner, T., Kapos, V. & Fa, J.E. (2013) Conservation priorities: identifying need, taking action and evaluating success. Key Topics in Conservation Biology 2 (eds DW Macdonald and KJ Willis)..pp. 3–22. Blackwell, Oxford.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. Proceedings .of the Royal Society, 267, 1947-1952.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D.C. & Watt, A. (2013) Understanding and managing conservation conflicts. Trends in Ecology & Evolution, 28, 100–109.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. Science, 343, 1241484.

Rockström, J., Steffen, W., Noone, K., Persson, Å, Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C. & Schellnhuber, H.J. (2009) A safe operating space for humanity. Nature, 461, 472-475.

Robertson, B.A. & Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology, 87, 1075–1085.

Rowcliffe, J.M. & Carbone, C. (2008) Surveys using camera traps: are we looking to a brighter future?. Animal Conservation, 11, 185-186.

Sala, O.E., Stuart, C., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. Science, 287, 1770-1774.

Sanderson, J., Sunquist, M.E. & Iriarte, A. (2002) Natural history and landscape-use of guignas (Oncifelis guigna) on Isla Grande de Chiloé, Chile. Journal of mammalogy, 83, 608-613.

Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. Trends in ecology & evolution, 21, 464-471.

Sepúlveda, M.A., Singer, R.S., Silva-Rodríguez, E., Stowhas, P. & Pelican, K. (2014) Domestic dogs in rural communities around protected areas: conservation problem or conflict solution?. PLoS ONE 9, e86152.

Shivik, J.A. (2006) Tools for the edge: what's new for conserving carnivores. Bioscience, 56, 253-259.

Sillero-Zubiri, C. & Laurenson, M.K. (2001) Interactions between carnivores and local communities: Conflict or co-existence?. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 282-312. Cambridge University Press, Cambridge.

Silva-Rodriguez, E., Ortega-Solis, G.R. & Jimenez, J.E. (2010) Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile. Austral Ecology, 35, 765–777.

Silva-Rodríguez, E.A., Ortega-Solís, G.R. & Jiménez, J.E. (2007) Human attitudes toward wild felids in a human-dominated landscape of southern Chile. Cat News, 46, 19-21.

Silva-Rodríguez, E.A. & Sieving, K.E. (2011) Influence of care of domestic carnivores on their predation on vertebrates. Conservation Biology, 25, 808–815.

Silva-Rodríguez, E.A. & Sieving, K.E. (2012) Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. Biological Conservation, 150, 103–110.

St John, F.A., Keane, A.M. & Milner-Gulland, E.J. (2013) Effective conservation depends upon understanding human behaviour. Key Topics in Conservation Biology, 2nd ed (eds D. Macdonald & K.J.Willis), pp 344-361. Blackwell, Oxford.

St John, F.A.V., Keane, A.M., Edwards-Jones, G., Jones, L., Yarenell, R.W. & Jones, J.P.G. (2012) Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. Proceedings of the Royal Society, 279, 804-812.

Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011) The Anthropocene: conceptual and historical perspectives. Philosophical transactions.Series A, Mathematical, physical, and engineering sciences, 369, 842-867.

Sunquist, M. & Sunquist, F. (2002) Wild Cats of the World. University of Chicago Press.

Treves, A. & Bruskotter, J. (2014) Tolerance for predatory wildlife. Science, 344, 476-477.

Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology, 17, 1491-1499.

Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A. & Wydeven, A.P. (2004) Predicting human-carnivore conflict: A spatial model derived from 25 years of data on wolf predation on livestock. Conservation Biology, 18, 114-125.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. (2006) Co-managing human–wildlife conflicts: a review. Human Dimensions of Wildlife, 11, 383-396.

Tumenta, P.N., de Iongh, H.H., Funston, P.J. & Udo de Haes, Helias A (2013) Livestock depredation and mitigation methods practised by resident and nomadic pastoralists around Waza National Park, Cameroon. Oryx, 47, 237-242.

Ullas Karanth, K. & Chellam, R. (2009) Carnivore conservation at the crossroads. Oryx, 43, 1-2.

Vojta, C.D. (2005) Old dog, new tricks: innovations with presence-absence information. Journal of Wildlife Management, 69, 845-848.

Wiegand, T., Revilla, E. & Moloney, K.A. (2005) Effects of habitat loss and fragmentation on population dynamics. Conservation Biology, 19, 108–121.

Woodroffe, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation, 3, 165-173.

Woodroffe, R. & Ginsberg, J.R. (2000) Ranging behaviour and vulnerability to extinction in carnivores. Behaviour and Conservation (eds L.M. Goslin & W.J. Sutherland), pp. 125–140. Press Syndicate of the University of Cambridge.

Yoccoz, N.G., Nichols, J.D. & Boulinier, T. (2001) Monitoring of biological diversity in space and time. Trends in Ecology & Evolution, 16, 446–453.

2. Cost-efficient effort allocation for camera-trap occupancy surveys of mammals

Authors

Gálvez, N., Guillera-Arroita, G., Morgan, B.J.T. and Davies Z.G. Cost-efficient effort allocation for camera-trap occupancy surveys of territorial mammals. Submitted to Biological Conservation.

2.1. Abstract

1. Camera-traps are an important tool for estimating occupancy for unmarked mammals. Cost-efficient effort allocation recommendations for occupancy surveys have focused on the trade-off between the number of sample units and sampling occasions, with simplistic accounts of associated costs which do not reflect well the reality of camera-trap based surveys.
2. Here we describe realistic camera-trap survey costs as a function of number of sample units, sampling occasions and camera-traps per sample unit, and link them to precision in occupancy estimation. We evaluate survey effort trade-offs for hypothetical species representing different levels of occupancy (ψ) and detection (p) probability to identify optimal design strategies. We apply our cost function to three threatened species as working examples with parameters from existing literature. Additionally, we use an extensive camera-trap data set to evaluate independence between additional camera traps per sampling unit.
3. The optimal number of sampling occasions that result in minimum cost decrease as detection probability increases irrespective if the type of species as rare (ψ <0.25) or common (ψ >0.5). Elusive species (p <0.25) with large home ranges (>10 km^2) show the most expensive survey scenarios. A large number of combinations for different species types show realistic cost options with fewer sampling occasions and additional cameras. Camera-trap independence can be obtained when more than one camera trap is installed per sample unit.
4. We identify trade-offs and provide managers and researchers with cost-efficient guidance for occupancy surveys based on camera-traps of unmarked territorial

mammals. Efficient use of survey budgets ultimately contributes to the conservation of threatened and data deficient mammal species.

Key-words: elusive species, imperfect detection, species management, threatened species, wildlife monitoring

2.2. Introduction

To conserve threatened species effectively, conservationists must first assess the status of populations to evaluate current or future decline trends. With financial resources generally in short supply, wildlife researchers and managers need to adopt cost-efficient monitoring survey protocols to gather baseline data to inform appropriate conservation interventions (Fryxell, Sinclair & Caughley 2014). Terrestrial mammals can be a particular challenge to survey due to their elusive nature, the fact that they often occur at low densities and, in many cases, are difficult to distinguish individually. As such, population status inferences where individuals are undistinguishable or unmarked rely frequently on presence-absence data. The value of presence-absence data has increased markedly in recent years as a result of significant developments in occupancy modelling techniques (Vojta 2005) including, for example, being able to account explicitly for the imperfect detection of elusive species (MacKenzie et al. 2006).

Camera-traps are a widely used tool in ecology and conservation (Rowcliffe & Carbone 2008; O'Connell, Nichols & Karanth 2010; Burton et al. 2015). They are particularly valuable for surveying elusive mammals because they are non-invasive, can work independently, compared to other methods such as telemetry, in remote areas and perform effectively in comparison to alternative detection methods (Gompper et al. 2006; Long et al. 2007; Long 2008; Balme, Hunter & Slotow 2009). Camera-traps have therefore been deployed in a broad array of circumstances, ranging from monitoring species populations and constructing mammal inventories in tropical forests (Tobler et al. 2008), through to evaluating the importance of logged forests for an elusive forest dwelling bear (Linkie et al. 2007) and assessing the impacts of habitat loss on carnivore guilds (Long et al. 2011). Additionally, the number of occupancy studies based on camera-trap data is growing rapidly, with the majority of focal species being carnivores or ungulates (Burton et al. 2015), possibly due to their elusive behaviour.

Despite the abundance of camera-trap occupancy studies being conducted and published globally; there is a paucity of research examining how survey effort allocation to optimize statistical precision can be influenced by operational costs. In the context of occupancy modelling, survey effort guidelines have been developed to address the trade-off between the number of sample units (hereafter SUs) and sampling occasions (i.e. number of repeat visits to detect the species at a SU) (MacKenzie & Royle 2005; Field, Tyre & Possingham 2005; Bailey et al. 2007; Guillera-Arroita, Ridout & Morgan 2010; Guillera-Arroita & Lahoz-Monfort 2012). All these studies imply a very simplistic cost function, where total survey cost is proportional to the total number of survey visits (i.e. number of SUs x survey visits/SU). The underlying assumption in each case is that a field team member revisits an SU during each sampling occasion. MacKenzie & Royle (2005) go further and account for extra initial set-up costs at each SU, acknowledging that the first sampling occasion at a SU may be more expensive than subsequent visits. This previous work, whilst useful, does not provide accurate recommendations for camera-trap surveys where the length of a survey can be extended (i.e. more “sampling occasions” conducted) without directly adding costs. This is because, once installed, camera-traps can work independently for periods of time between installation, maintenance checks and/or retrieval without a specific associated cost.

Other important effort allocation trade-offs must be considered when surveying wide-ranging territorial mammal species. Species with large home ranges might be difficult to detect due to non-random movement across a large area. In theory, additional independent camera-traps could reach the same level of detection probability with fewer sampling occasions (Long 2008), meaning a balance needs to be struck between the number of sampling occasions and number of camera-traps per SU. Similarly, species with low detection probability require longer surveys to achieve precise estimates (Shannon, Lewis & Gerber 2014) thus, where length of survey might need to be restricted by some user-defined criteria (e.g. 100 days maximum survey of all SUs), additional camera-traps may be required to compensate. The impact on survey costs of the trade-off between sampling occasions and number of detection devices (e.g. camera-traps) is yet to be evaluated in the literature.

Here we provide effort allocation guidelines for cost-efficient occupancy studies of terrestrial mammals using camera-traps. We develop a detailed cost function for camera-trap surveys, which we parameterise with operational installation efficiency values (e.g. minutes to install a camera-trap) provided by practitioners (e.g. wildlife managers, researchers). This is then used to consider trade-offs in survey effort allocation in terms of the optimal number of sampling occasions and number of camera-traps within a SU needed to achieve occupancy precision targets at minimum costs. We assess a range of occupancy and detection probability scenarios for species with different home range sizes, as well as considering two types of transport between SUs: vehicular and walking. We also discuss survey design alternatives, using three threatened mammals as working examples, illustrating how our cost function can be employed to identify cost-efficient strategies. For one of the case study species, for which an extensive camera-trap survey dataset exists, we additionally evaluate the deployment of multiple camera-traps per SU in terms of the similarity of their detection histories and how this varies with distance between devices.

2.3. Methods

2.3.1. Sample unit definition and survey length

SU size directly influences the amount of time spent in the field, by increasing field team member movement time both within and between SUs. The size of the home range should determine the area of, and distance between, independent SUs so that interpretation of the occupancy parameter is useful for monitoring populations of territorial mammals over large geographic areas (MacKenzie et al. 2006). We can define a minimum distance between SUs D_s as the diameter of the circular area representing the typical home range size of the species R:

$D_s = \sqrt{\frac{4R}{\pi}}(1 + \alpha)$ eqn 1, where α is an additional buffer (a proportion of home range size) that can be used as a conservative approach to account for home range size uncertainty and or extra space to facilitate variable camera placement within the SU (e.g. not in exact center) in order to maintain distance between adjacent units.

The duration or length of a particular survey has several implications with respect to occupancy model assumptions. The total survey length L can be defined as the number of days over which all SUs are surveyed. A maximum length of survey, L_{max}, should be set a priori and must be clearly justifiable based on the camera-trap survey objectives (Burton et al. 2015) and relevant modelling assumptions (e.g. compliance with population closure criteria, occupancy model assumptions where sites do not change in status for the duration of the survey; MacKenzie et al. 2006). In practice, to fit camera-trap data to the occupancy framework, the continuous data collected by the camera-traps can be divided into discrete replicate segments considered as sampling occasions K (but see Guillera-Arroita et al. 2011 for alternative ways to analyse continuous data in occupancy modelling). By defining the number of days per segment, we restrict the survey design to a maximum number of sampling occasions or K_{max}, per SU, which complies with L_{max}:

$K_{max} = \frac{L_{max}}{O}$ eqn 2,

where O is the number days that are collapsed into a single sampling occasion.

2.3.2. Accounting for survey costs

The total cost of a camera-trap survey is a function of the number of SUs (S), the duration of the survey (and hence of the number of sampling occasions K), and the number of camera-traps per SU (n). We can write the cost function in a general form as:

$C_T(S, K, n) = C_O + S \cdot C_v(K, n)$ eqn 3,

where C_o represents fixed costs and C_v is the cost of surveying one SU, which is dependent on K and n. By fixed costs we refer to those which are not associated with in-situ operations and particular to each project (e.g. maintenance of a field station or field vehicle, salaries of permanent staff and international flights). To be realistic, we assume that the survey team needs transport via a field vehicle (e.g. truck, boat). Hereafter we do not consider fixed costs because they do not affect the determination of the optimal design strategy (they are independent of the choice of K and n).

In building our cost function C_v, we consider four types of costs:

$C_v(K, n) = C_1(K, n) + C_2(K, n) + C_3(n) + C_4(K, n)$ eqn 4,

where $C_1(K, n)$ is camera-trap operational cost within the SU (e.g. instalment, maintenance, retrieval), $C_2(K, n)$ relates to field logistics during the survey (e.g. travel to survey area, break times), $C_3(n)$ comprises camera-trap equipment cost and $C_4(K, n)$ is post-survey image processing cost.

Operational cost C_1 consists of all the financial outlay connected with installing i, retrieving r and conducting maintenance service checks c for the camera-traps in a single SU, including costs associated with fuel consumption and personnel salaries. To calculate C_1, we compute the time spent at a particular SU during installation H_i, retrieval H_r or maintenance checks H_c:

$$H_x = \left\{ tn + \frac{d(n-1)}{V_w} + \frac{D_s}{V_y} \right\} \text{eqn 5,}$$

where $t(i, r, c)$ is the time (hours) spent handling the cameras, d is the travel distance between cameras within the SU (km), V_w is walking speed through habitat (km/h) to camera-traps within an SU, and V_y is the speed of travel between SUs (km/h), which can either be by vehicle ($V_y = V_v$) or walking ($V_y = V_w$). To account for distance walked when operations are entirely done on foot, we correct the last term in eqn 5 by multiplying by twice the diameter of the SU walked $\frac{2D_s}{V_w}$. This assumes that a field vehicle is left at the initial SU, the camera-traps are set up sequentially and then the same distance has to be walked again on the return journey back to the field vehicle, after the last SU has been installed. We also assume that i involves the preparation of a single camera-trap (i.e. loading batteries, memory card and checking overall function) and positioning of the camera-trap (i.e. placement in appropriate location within the SU) for the duration of the survey. Checking/changing batteries, lures, baits and memory cards with the camera-traps are in position equates to c, whereas r consists of data collection (e.g. downloading the memory card), note-taking and removal of camera-trap after the survey is complete.

Once these times have been computed, the total operational cost is:

$$C_1(K, n) = m \left\{ H_i + H_r + \left\lfloor \frac{KO}{z} - 1 \right\rfloor H_c \right\} \text{eqn 6,}$$

where m is the combined salary per hour of a qualified field officer and a non-qualified field assistant. To reflect real-world security and work efficiency considerations, we assume that a field team is composed of at least two people: one qualified field officer (i.e. researcher, park ranger) who can work independently setting up camera-traps, and a non-qualified field assistant (e.g. guide, tracker) who cannot set up camera-traps independently. The camera-traps may need to be checked more than once during the survey, hence the factor multiplying H_c, where z is the time interval in days between maintenance checks (we use $\lfloor . \rfloor$ to denote that the term $\frac{KO}{z}$ is rounded down to the nearest whole number and minus the last sampling occasion as that cost is included in retrieval). In addition, if $V_y = V_v$, then a term must be added to eqn 6 to account for fuel costs $\frac{D_s F_l}{F_e}$, where F_l is the fuel cost per litre and F_e is the fuel efficiency (km/l).

Field logistics cost C_2 includes costs associated with travel from accommodation in the vicinity of the fieldwork region to the survey area and daily consumables (e.g. meals, break times). Before we can determine this value, we need to consider the total number of days working at a SU across the duration of the survey and then sum the daily fuel, food, and salary costs. First we compute the number of days spent working at a particular SU:

$$H_{SU} = \frac{\left\{H_i + H_r + \left\lfloor \frac{KO}{z} - 1 \right\rfloor H_c\right\}}{(W-B)E} \text{ eqn 7,}$$

which includes amount of actual working time (hours) (from eqn 6) corrected for efficiency and net available work time during a particular day. W is the number of hours in a working day. B is the number of hours per day spent travelling and taking breaks, which we calculate as $1 + D_t/V_m$, where D_t is the daily return distance travelled between the field accommodation and survey area and V_m is the travel speed on a motorway or main road plus a break for an hour for lunch and rest. E is the estimated efficiency given normal field setbacks (a factor from 0 to 1). We can now compute the field logistic costs as:

$C_2(K,n) = H_{SU}\left\{\frac{D_t F_l}{F_e} + G + Bm\right\}$ eqn 8,

where G is the cost of food and daily consumables, m is the combined salary of the fieldwork team members and $\frac{D_t F_l}{F_e}$ is the fuel cost to the survey area.

Camera-trap equipment cost C_3 accounts for the expenditure related to purchasing camera-traps, batteries and memory cards:

$C_3(n) = nC_a$ eqn 9,

where C_a is the cost of a single camera-trap unit, with its memory card plus batteries for the entire survey.

Post-survey image processing cost C_4 is calculated as:

$C_4(K,n) = \frac{n \cdot I_d \cdot K \cdot O \cdot I_c}{I_h}$ eqn 10,

where I_d is the average number of images taken by a camera-trap per day, I_c is the cost per hour of a trained researcher to process images and I_h is number of images processed per hour (including the identification of species and data entry into a database).

2.3.3. Linking survey costs to estimator precision

To evaluate survey design trade-offs, we need to link survey costs to estimator quality. This way we can identify the most cost-efficient survey effort allocation to achieve a given level of precision (or, alternatively, identify the best way to allocate a given amount of effort to maximize estimator precision). MacKenzie & Royle (2005) provide the following approximation for the variance of the occupancy estimator, ψ:

$var(\psi) = \frac{\psi}{S}\left\{1 - \psi + \frac{1-p^*}{p^* - Kp(1-p)^{K-1}}\right\}$ eqn 11,

where p is the probability of detection in a sampling occasion at a SU where the species is present, and $p^* = 1 - (1-p)^K$ is the cumulative probability of detection after K sampling occasions. For our camera-trap survey scenario, the probability p refers to the combined detectability of the n camera-traps per SU. Assuming independence among the cameras, we have:

$p = 1 - (1 - p_1)^n$ eqn 12,

where p_1 is the probability of detection with a single camera-trap.

The variance in eqn 11 reflects the precision that we can expect in our estimation of occupancy, and is a function of the number of SUs S, number of survey occasions K and number of camera-traps per site n. From eqn 3, and excluding fixed costs, we can write the number of SUs as:

$S = \frac{C_T}{C_v}$ eqn 13.

By substituting S of eqn 13 into eqn 11 we are able to relate survey design (i.e. S, K, n) and estimator precision (i.e. var(ψ)) to total costs as follows:

$C_T = \frac{\psi C_v}{var(\psi)}\left\{1 - \psi + \frac{1-p^*}{p^* - Kp(1-p)^{K-1}}\right\}$ eqn 14,

and from here then calculate the required number of SUs within eqn 13.

2.3.4. Final cost: standard design and vehicle hire.

Equations 13 and 14 provide us with the number of SUs required for estimator precision. We assume a standard design where all SUs are surveyed for the same amount of sample occasions across the duration of the survey (MacKenzie et al. 2006). For simplicity we assume that cameras are installed simultaneously in the survey area. In some circumstances the number of SUs which need to be surveyed (eqn 13) might exceed what is feasible with just one field vehicle (a fixed cost) which we assume can only accommodate the transportation of two field teams (four individuals). The employment of extra teams does not affect C_1, C_2, C_3, C_4 because these are calculated on a per SU basis. Nevertheless, it does impact on the number of field vehicles required to move multiple field teams around the study area to achieve a standard design. We therefore incorporate this into the cost-function as vehicle hire, rather than purchase, and treat it as a variable cost. For simplicity, we assume that the amount of time between the first and last visit to a camera-trap (for i, c or r) can be estimated as a proportion of L_{max}. For example, to achieve a standard design where all SUs are sampled simultaneously there might be a need to limit the time between the first and last camera installation to no more than 10 days. We can then determine the total amount of fieldwork days L as:

$L = L_{max}\{L_i + \left\lfloor \frac{KO}{z} - 1 \right\rfloor L_c + L_r\}$ eqn 15,

where L_i, L_c, and L_r are defined a priori proportions of L_{max} – based on some management criteria - which ensure that all SUs are simultaneously surveyed for the same amount of time over the duration of the survey.

First we need to determine the number of field teams needed to comply with L. The number of additional teams Q will reduce fieldwork days by 2+Q, where two accounts for the number of teams with an existing field vehicle. We can express compliance of restrictions with:

$L = \frac{S \cdot 1.16 \cdot H_{SU}}{2+Q}$ eqn 16,

where S is the number of SUs determined from eqn 13, H_{SU} is the days spent at each SU (eqn 9) multiplied by 7/6 (1.16) to realistically include 1 day of rest per 6 days of work.

From eqn 16, we can estimate the number of field teams needed by solving for Q:

$Q = \frac{S \cdot 1.16 \cdot H_{SU}}{L} - 2$ eqn 17

where the solution is rounded up to the nearest whole number when Q >0. When Q<0, the solution is set to 0 because extra field teams are not required.

Hence final costs C_F can be expressed as:

$C_F = C_T + \frac{Q}{2} JL$ eqn 18,

where C_T are total costs (eqn 14), Q/2 is the number of extra vehicles and J is the cost of vehicle hire per day.

2.3.5. Cost function parameterization

We parameterized our cost function based on information acquired from experienced camera-trap surveyors (e.g. researchers, wildlife managers, park rangers, postgraduate students) via an online quantitative questionnaire with closed questions. The questionnaire consisted of seven sections (Appendix 2.S3 in supporting information) relating to respondents general experience conducting camera-trap surveys, time spent on various fieldwork operations, costs associated with fieldwork operations, costs of survey equipment and transport, post-survey processing of camera-trap data, and experience of conducting occupancy modelling using camera-trap data. A pilot exercise was carried out with seven initial respondents and, with no major modifications required to the questionnaire their responses were retained and included in the sample. The questionnaire was available online for 30 days between April and May 2015 via the Bristol Online survey platform (© University of Bristol). A link to the questionnaire was distributed in an opportunistic manner via several camera-trapping forums, social media groups, as well as being sent directly to authors of camera-trap surveys published in journal articles. All cost values and currency provided by respondents were converted to US dollars using an online currency converter (http://www.xe.com). We parameterized our cost function with the means (or medians when outliers were prevalent) of the values recorded for each parameter (Appendix Table 2.S1 in Supporting Information). Appendix 2.S2 provides R code of the cost function with the parameters used which also allows for the parameterization for specific case studies.

2.3.6. Survey design trade-off evaluation: hypothetical parameter values for species

We applied the methods above (eqn 14 and 18) to assess survey effort trade-offs for a range of hypothetical species camera-trap survey scenarios. For this purpose, we chose the occupancy estimator quality target of var(ψ) = 0.0056, which corresponds to a standard error of 0.075 in occupancy estimates. We deemed this as a reasonable general survey target for hypothetical species. We considered three levels of home range size values, R = 3, 10 and 30 km^2, to represent small (2-6 kg), medium (10-15 kg) and large (>25kg) species respectively (Gittleman & Harvey 1982; Swihart, Slade & Bergstrom 1988). Within each of those home range size levels, we evaluated all combinations of occupancy ψ and detection p probability based on the values 0.10, 0.25, 0.5, 0.75 and 0.90. All detection probability values refer to p_1 (eqn 12) which refers to the detection at one camera for one sample occasion. This range represents rare (ψ <0.25) to common (ψ > 0.50) species. Similarly, for detection, the values represent elusive (p <0.1) to conspicuous species (p >0.5). The number of days considered a sampling occasion was set at five, informed by our questionnaire results.

For each scenario, we assessed survey costs for increasing number of sampling occasions K and independent camera-traps n per SU. Based on our questionnaire results (Table S1), we considered up to four camera-traps per SU and limited our evaluation of K to a maximum of 20, to keep total survey length below 100 days (L_{max} =100) which is within the average and mode of camera trap surveys conducted by users (Table S1). To ensure costs represent a standard design we used eqn 18 and set the proportion of L_{max} for i, c and r at 0.1, 0.15, and 0.30 respectively. Meaning that, for example, installation (i) of all cameras occurs in an amount of time equal to no more than 10% of L_{max}. We considered travel between SUs both via vehicle V_v and walking V_w to examine the impact of this decision. Any survey that uses a mixture of these transport types would result in intermediate values as walking and vehicle travel represent the two extremes of a continuum. In total, 150 survey scenarios were compared (i.e. ψ, p and R). We then identifyed which pair of K and n results in minimum cost and, for all other combinations, calculated how many times greater the cost was compared to the minimum. For illustrative purposes, we classifyed these quantities into five categories: i) 1-1.5; ii) 1.5-2; iii) 2-3; iv) 3-5; and, v) over 5 times greater than minimum cost (Fig. 1 and 2). We excluded combinations of n and K where the required number of SUs to survey exceeded 400 as, in general, this would be logistically unrealistic. To evaluate the effect of p on cost per SU under different ψ scenarios, we ploted the cost per SU of the identified minimum costs. All models, analyses and graphics were conducted with R version 3.2.0 R Core Team (2015).

2.3.7. Worked examples for three case study territorial mammals

To provide working examples for territorial mammals, we applied the cost function to three threatened carnivores that have been the focus of camera-trap occupancy surveys and represent proximate values of home range size R evaluated in the cost function (i.e. 3, 10, 30 km^2): guiña (Leopardus guigna) (home range = ~3 km^2) (E. Schüttler unpublished data), marbled cat (Pardofelis marmorata) (home range = 11.9 km^2) (Grassman et al. 2005), and sun bear (Helarctos malayanus) (home range >15 km^2) (Te Wong, Servheen & Ambu 2004). All three species are associated with forest habitat, are threatened or data deficient, and have occupancy and detection probability estimates, for one camera trap, available in the literature (Linkie et al. 2007; Johnson, Vongkhamheng & Saithongdam 2009; Gálvez et al. 2013). We ran the cost function using levels of occupancy, detection probability and the number of days considered a sample occasion reported in the cited studies. All other parameters of the cost function were kept fixed.

2.3.8. Independence of detection histories within SUs: the guiña study case

To provide an empirical example of an evaluation of independence between multiple camera-trap capture histories – an assumption of eqn. 12 of the cost function – we interrogate the guiña case study in more detail, using data from a camera-trap survey which has been conducted in the temperate forest ecoregion of southern Chile (39º15´S, 71º48´W) (N. Gálvez unpublished data). A total of 145 SUs (4 km^2) across agricultural land were randomly chosen from 230 potential SUs, each equivalent to the mean observed guiña home range size (Minimum Convex Polygon 95% mean = 270 ±137 ha; Schüttler et al. in review). We conducted a total of four survey seasons (summer 2012, summer 2013, spring 2013, summer 2014), with two camera-traps installed per SU (mean distance apart =230 m ±182 SD) for 20-24 days. Sampling occasions were set to two-day blocks because individual cats do not stay longer than this in one place (Schüttler et al. in prep), meaning that each SU was surveyed for 10-12 sampling occasions.

To assess independence, we estimate a Jaccard similarity index for each pair of camera-traps in an SU via the detection and non-detection history for each sampling occasion (i.e. a binary response of “11, “01” or “10”). The Jaccard similarity coefficient was applied as we are interested in assessing similarity in detection within a SU; non-detections pairs (00 histories) were thus removed for analysis. Distance between each pair of camera-traps, and whether or not they were placed within contiguous habitat, were plotted against the index for each season.

2.4. Results

The online questionnaire was completed by 53 respondents with experience in conducting camera-trap surveys in 35 countries, spread across all continents. Respondents had, on average, completed six camera-trap surveys (SE = 0.68), and most had finished their last survey during 2014. Out of the 28 parameter values included in the cost function, 20 were derived from the questionnaires (Table S1 in supplementary information).

2.4.1. Trade-off evaluation: hypothetical species

Our evaluation reveals that, for both types of transport (vehicular and walking) between SUs and across all ψ-p scenarios, the combinations with fewest ($K < 3$) replicate survey occasions and lowest number of camera-traps per SU ($n < 2$), led to unrealistic solutions due to the large number of SUs required (>400) (Fig. 2.1 and 2. 2). Minimum cost for walking-based surveys are ~20% more expensive than those using a vehicle, when comparing ψ-p scenarios at each home range size. The expenditure per SU of minimum cost combinations decreases as detection probability rises for both types of transport between SUs and ψ scenarios (Fig. 2.3). The highest cost per SU is at low p but with large variation. Across all ψ scenarios, minimum costs per SU fell to ≤500 USD per SU when p is >0.25, and variation was negligible after mid p (i.e. <0.5). Highest cost at low p is driven mainly by the number of SUs, hence camera trap equipment costs, needed for statistical precision.

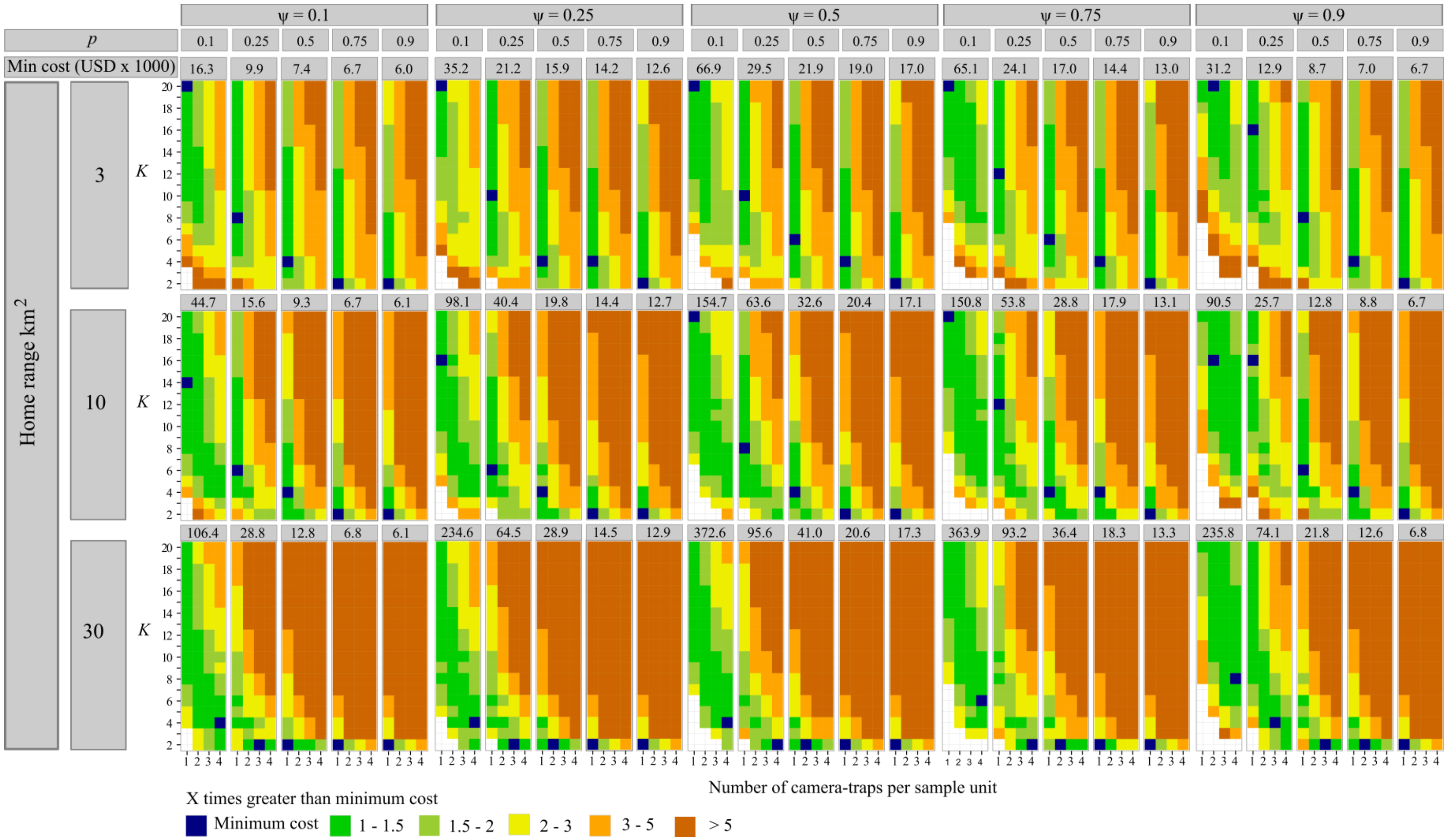

Figure 2.1 Cost (US dollars) of different camera-trap occupancy survey effort allocations, assuming vehicular transport is employed between sample units (SUs). Each tile represents a combination of number of sampling occasions K and number of camera-traps n per SU.

Tile colour reflects the cost required to achieve a target statistical precision (S.E. =0.075) in occupancy estimates (ψ) for any given combination of home range size (3, 10, 30 km^2), occupancy and detection (p) probabilities. All detection probability values refer to p_1 (eqn 12) which refers to the detection of one camera for one sample occasion. Costs are shown in relative terms, benchmarked against the cheapest combination indicated in blue: 1-1.5, green; 1.5-2, olive; 2-3, yellow; 3-5, light orange; >5 times greater, orange. Maximum number of K considered was 20 (assuming that each occasion is five days long and a maximum possible survey length is 100 days).

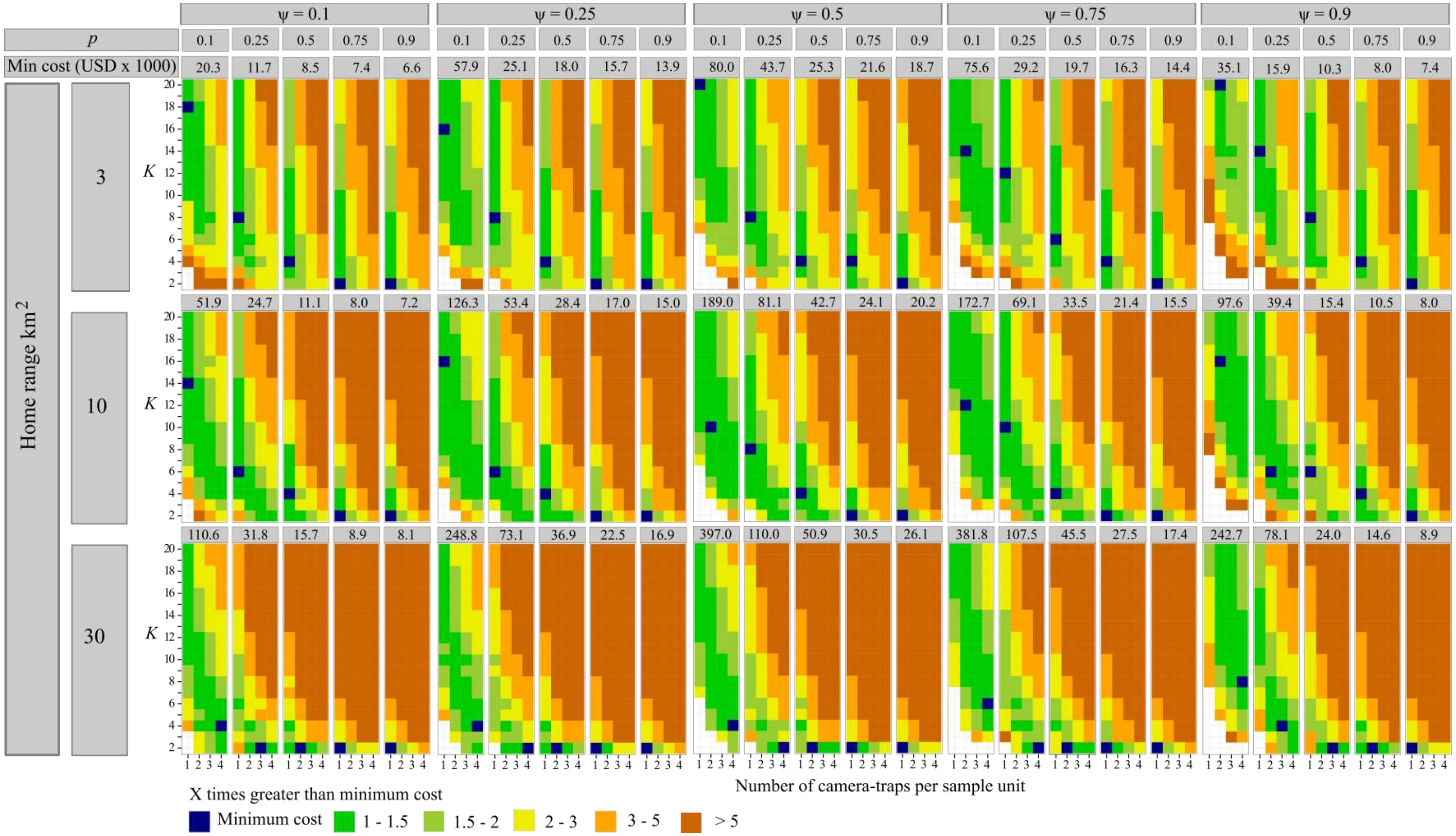

Figure 2.2 Cost (US dollars) of different camera-trap occupancy survey effort allocations, assuming the distance between sample units is walked. For details regarding the figure arrangement, please refer to the legend for Figure 1.

In general, and relative to each ψ-p scenario, particularly expensive combinations are more frequent at high levels of K and n, predominantly where p and home range are greater in size. Cheaper cost combinations tend to be less frequent for larger p values and become progressively more restricted in range as ψ increases, particularly for the 10 and 30 km^2 sized home ranges. Between ψ scenarios, values of minimum cost are highest at mid ψ (i.e. 0.5) and decrease towards 0.1 and 0.9 levels for both types of transport. In all ψ-p scenarios, the values of minimum cost rise with increasing home range size. Indeed, at p levels of 0.1 and 0.25, the largest home range scenario is on average 4.7 (SD =1.5) times more expensive to survey than the smallest. This is in comparison to the largest being 1.5 (SD =0.5) more expensive than the smallest home range size scenario for higher p levels (i.e. >0.5). Within each ψ scenario, minimum cost is negatively associated with detection probability, meaning that low p is the most expensive level. Low p, at each ψ scenario, is 4 (SD =0.9), 10 (SD =2) and 21 (SD =6.4), times more costly than high p at 3 km^2, 10 km^2 and 30 km^2 home range size respectively. Generally, the K required for minimum cost combinations decreases as p increases across all scenarios.

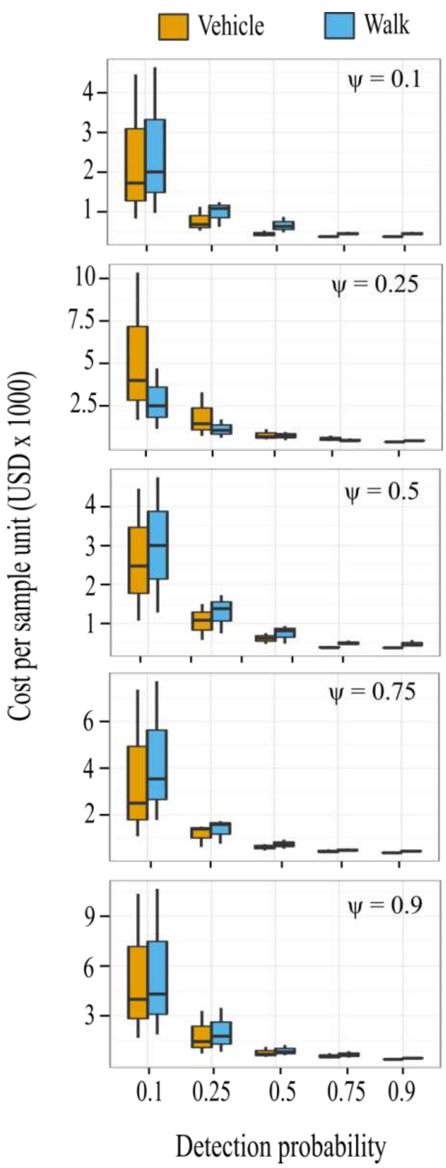

Figure 2.3 Range of costs (US dollars) per sample unit (SU) for all minimum cost occupancy (ψ) and detection (p) probability combinations. Both type of transport between SUs (walking and vehicular) are compared.

When multiple camera-traps are deployed per SU, minimum cost combinations occur for scenarios with the largest home range size and at higher ψ, and result in the most efficient design in 38 of the 150 scenarios tested, all for either 10 or 30 km^2 home range sizes (Fig. 2.1 and 2.2). At high ψ and low p, all minimum cost combinations are reached with multiple camera-traps across all home range sizes and travel types.

At 30 km^2, multiple camera-trap solutions were best across all ψ scenarios where p <0.75. Across ψ-p scenarios, cheaper combinations were, in general, reached at lower K than the specific minimum cost combination, but with multiple camera-traps.

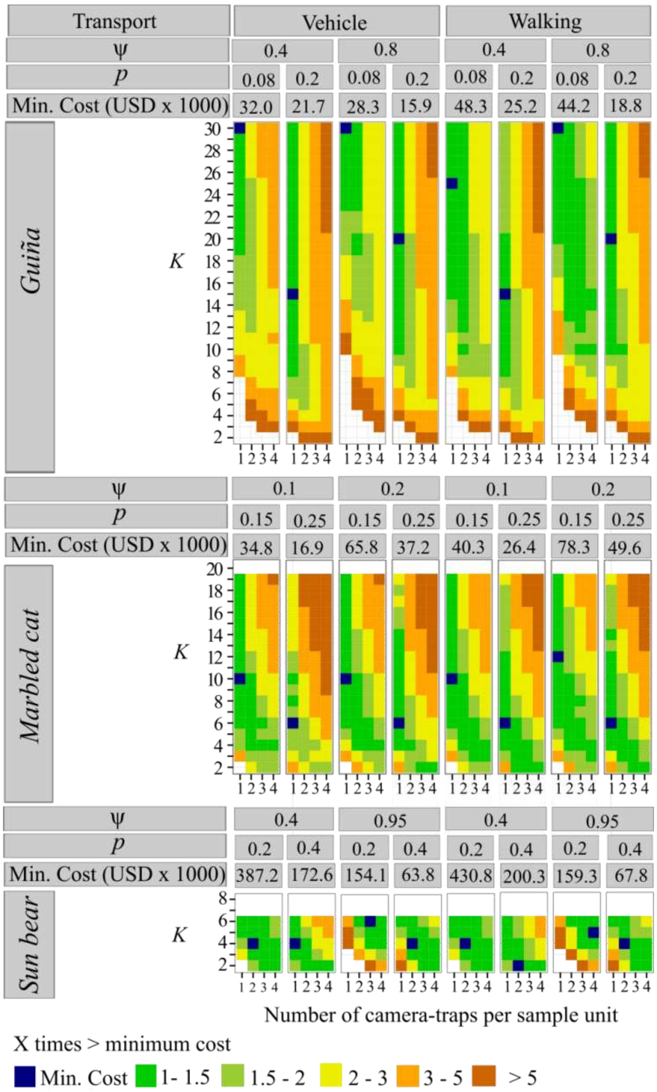

Figure 2.4 Camera-trap occupancy survey effort scenarios and combinations for three threatened case study carnivore species: guiña (Leopardus guigna), marbled cat (Pardofelis marmorata) and sun bear (Helarctos malayanus). For details regarding the figure arrangement, please refer to the legend for Figure 1. Both walking and vehicular transport between sample units are evaluated, as well as various combinations of occupancy (ψ) and detection (p) probability derived from the literature for each

species. Guiña (Leopardus guigna): 3 km^2 home range (Schüttler et al. in review); occupancy and detection parameters with two days considered a sampling occasion (Fleschutz 2013). Marbled cat (Pardofelis marmorata): 11.9 km^2 home range (Grassman et al. 2005); occupancy and detection parameters and five days considered a sampling occasion (Johnson et al. (2009). Sun bear (Helarctos malayanus): >15 km^2 home range (Te Wong, Servheen & Ambu 2004), occupancy and detection parameters and 15 days considered a sampling occasion (Linkie et al. (2007).

2.4.2. Case study: territorial mammals

Scenarios for the case study species illustrate the broad trends obtained for the hypothetical species, such as higher costs being associated with larger home range size and lower p, as well as reduction in required K with an increase in p (Fig. 2.4). The guiña and marbled cat do not yield minimum cost combinations with multiple camera-traps, but the opposite is true for the sun bear in most scenarios. Lower cost combinations are reached with multiple camera-traps at lower K across all three species.

The guiña study case reveals that most capture histories between cameras show no similarity (i.e. equal zero) and occur along the entire distance between camera-traps gradient (Fig. 2.5a). Histories which demonstrate some level of similarity (i.e. >0.00), the majority within an index of <0.5, are concentrated at distances between devices <300 m. The similarity index tends to decrease when camera-traps are >300 m apart. There is no difference in the similarity index between camera-traps positioned in contiguous and non-contiguous forest habitat (Fig. 2.5b).

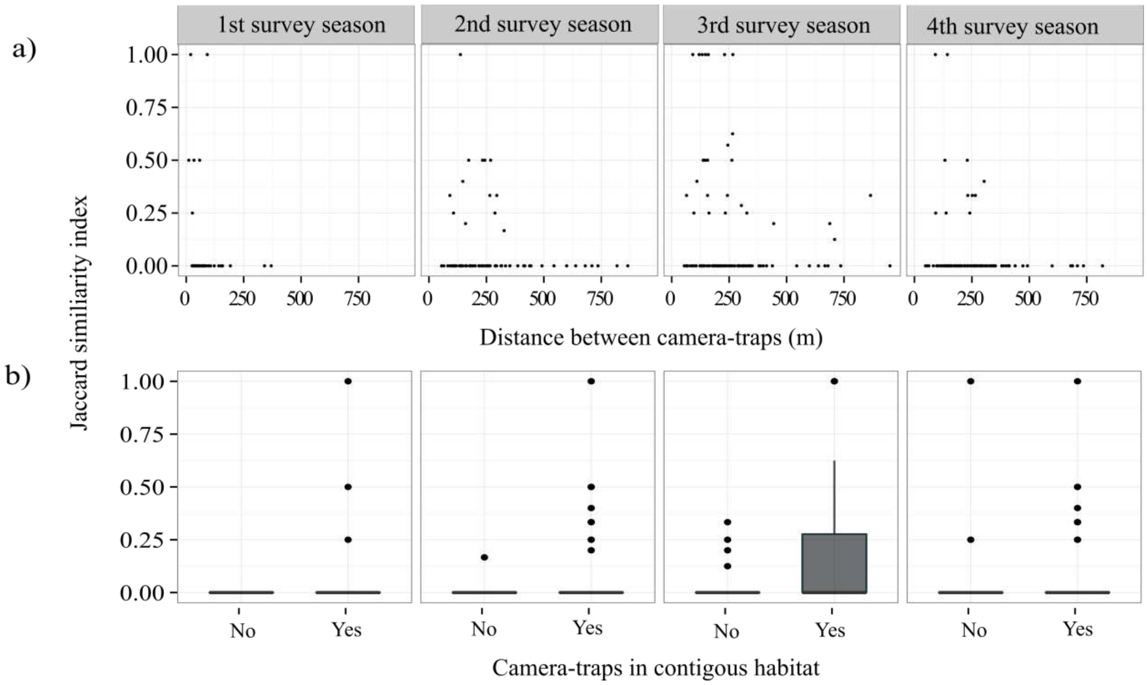

Figure 2.5 Jaccard similarity index of the camera-trap occupancy survey capture histories for two devices per sample unit (SU), used when surveying guiña (Leopardus guigna) over four seasons. The index is plotted against: (a) distance between camera-traps (m) within each SU, and; b) whether or not the two devices were set up within a contiguous habitat patch in the SU.

2.5. Discussion

Initial estimates of parameters (i.e. ψ and p) are key to informing decisions about effort allocation in camera-trap occupancy surveys (MacKenzie & Royle 2005; Guillera-Arroita, Ridout & Morgan 2010). Our work goes further, demonstrating the importance of accounting for camera-trap specific costs and species ranging behaviour to improve cost-efficiency in survey effort allocation. We have identified cost-efficient solutions with trade-offs between number of camera-traps within a SU and the number sampling occasions, particularly for wide ranging species (i.e. home range >10 km^2).

As established by the more simplistic cost functions already published in the literature (MacKenzie & Royle 2005; Guillera-Arroita, Ridout & Morgan 2010), in addition to our study, the optimal number of sampling occasions decreases as detection increases. This implies that precise occupancy estimates can be obtained with just a few sampling occasions for species which are detected easily. However, our results go on to show that the difference in the optimal number of sampling occasions between rare (ψ <0.25) and common (ψ >0.25) species is minimal.

In general, highly elusive species (p <0.1) are the most expensive to survey. When elusive (p <0.25), rare species (ψ <0.25) appear relatively cheaper to survey compared to more common ones (ψ >0.50), given the same target precision for occupancy estimation. Indeed, common species are costly to survey where they have occupancy estimates of 0.5 or 0.75 and are highly elusive (p <0.1). This pattern arises because we chose variance as our metric to represent occupancy estimator quality; the optimal number of sampling occasions drives p^* (eqn 11) near 1, meaning that the variance approximates that of a binomial proportion, which is highest at mid-levels of occupancy. Consequently, keeping a given precision target across species type (i.e. rare or common) requires a larger sample size at occupancy estimates around 0.5. Different precision target criteria for common versus rare species could be used, depending on specific goals of the survey such as evaluating the decline of a critically threatened species that would need higher precision compared to an abundant species of conservation concern which less precise estimates might suffice (Guillera-Arroita & Lahoz-Monfort 2012).

Improvements in species detectability might mitigate the high cost associated with camera-trap occupancy surveys for elusive species. The steep drop in the value of minimum cost combinations for detection probabilities 0.1 to 0.25, across all scenarios, suggest that it would be worthwhile for practitioners to conduct a pilot exercise to test alternative designs with the aim of maximising focal species detectability prior to conducting a full survey. For instance, this may involve assessing how detection probability is influenced by microhabitat characteristics surround the camera-trap position in the SU, prevailing weather conditions (e.g. O'Connell et al. 2006) or camera-trap settings (e.g. Hamel et al. 2013).

For elusive species with large home range area requirements, it is generally more cost-efficient to conduct occupancy surveys using multiple camera-traps over fewer sampling occasions, irrespective if they are rare or common. This is driven by the fact that it is more expensive in terms of extra work (i.e. time and salaries) and travel between/within larger SUs to undertake extra sampling occasions. For species with small/medium home range sizes and low detectability, a range of relatively cost-efficient design combinations are available to practitioners, providing flexibility with respect to both the number of sampling occasions and camera-traps. Occasionally, field survey teams may face certain logistical constraints, such as needing to conduct short camera-trap rotations or confine work to periods of favourable weather. This can therefore be overcome by adopting an approach where multiple camera-traps are used per SU but the overall length of the survey is decreased. Another potential constraint which might be faced is the need to reduce number of sampling occasions to ensure occupancy modelling assumptions are more comfortably met for a particular species (Rota et al. 2009).

Our guiña case study shows that achieving independence between multiple camera-traps positioned within a single SU is feasible for species with a small home range. However, we only evaluated the use of two camera-traps, and maintaining independence would become increasingly difficult with more devices. Moreover, care needs to be taken to ensure that they are not located so far apart that the camera-traps in adjacent SUs become too close, and thus loose independence (i.e. between SUs). Furthermore, an alternative function could be developed, similar to eqn 12 that relates p as a function of n, but accounts for potential dependence between additional cameras. All other methods would still apply.

The three case studies evaluated here reveal how our cost function can provide practitioners with efficient survey allocation scenarios for surveying territorial mammals. For each species there are various trade-offs that warrant consideration, depending on the conservation context. For instance, monitoring guiña in agricultural landscapes is highly pertinent for the conservation of this threatened species (Gálvez et al. 2013), but could also prove cheaper than monitoring in hard to access national parks. Furthermore, detection probably is likely to be greater within remnant habitat patches in farmland, which will significantly reduce survey length and cost. Our knowledge of how marbled cats are distributed across Asia is lacking, and hindering conservation efforts (Johnson, Vongkhamheng & Saithongdam 2009). If field conditions or logistics constraints mean that survey length must to be kept short, our cost function show that there are a wide range of cost-efficient options available, centred on fewer sampling occasions and additional camera-traps. Likewise, sun bear surveys, which are required in forested areas outside protected lands (Linkie et al.

2007), could be most cost-efficient with using multiple camera-traps per SU. One important point to note is that our framework is developed for constant occupancy models (i.e. with no covariates). In many species-specific cases, practitioners might be interested in appraising the effects of environmental covariates or the impact of management interventions, which may require sampling more SUs for statistical reasons. This would be most expensive for elusive species, due to the costs associated with each SU (Fig. 3). Our cost function can be readily incorporated in the evaluation of survey design trade-offs for more complex models via simulations.

Worldwide, around 15% of mammal species are data deficient and need urgently to have their extinction risk evaluated (Schipper et al. 2008). Our cost function provides practitioners with a valuable tool which can be used to inform the design of cost-efficient camera-trap occupancy surveys, which are required to assess the conservation status of potentially threatened unmarked territorial mammals. While the evaluation here represents average field survey parameters, as reported by practitioners, it can be readily adapted to account for specific survey conditions and objectives.

2.6. Acknowledgments

We thank the Chilean Ministry of the Environment (FPA 9-I-009-12), Robertson Foundation and Recanati-Kaplan Foundation for financial assistance. We are grateful to D.W. Macdonald, A.Dittborn, J.Laker, C.Bonacic, G.Valdivieso, N. Follador, D.Bormpoudakis, T.Gálvez and C.Ríos for their support and assistance, the researchers who commented on the pilot version of the questionnaire for their feedback, and all the survey respondents for their time and the information provided.

NG received a postgraduate scholarship from the Chilean National Commission for Scientific and Technological Research (CONICYT-Becas Chile).

2.7. References

Bailey, L.L., Hines, J.E., Nichols, J.D. & MacKenzie, D.I. (2007) Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. Ecological Applications, 17, 281-290.

Balme, G.A., Hunter, L.T. & Slotow, R. (2009) Evaluating methods for counting cryptic carnivores. The Journal of wildlife management, 73, 433-441.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology. DOI: 10.1111/1365-2664.12432. Available on-line.

Field, S.A., Tyre, A.J. & Possingham, H.P. (2005) Optimizing allocation of monitoring effort under economic and observational constraints. Journal of Wildlife Management, 69, 473-482.

Fleschutz, M. (2013) Impact of fragmentation on Leopardus guigna in the Chilean temperate rainforest. MSc thesis, Geopraphisches Institut, Johannes Gutenberg Universitat.

Fryxell, J.M., Sinclair, A.R. & Caughley, G. (2014) Wildlife ecology, conservation, and management. John Wiley & Sons, Oxford.

Gálvez, N., Hernández, F., Laker, J., Gilabert, H., Petitpas, R., Bonacic, C., Gimona, A., Hester, A. & Macdonald, D.W. (2013) Forest cover outside protected areas plays an important role in the conservation of the Vulnerable guiña Leopardus guigna. Oryx, 47, 251-258.

Gittleman, J.L. & Harvey, P.H. (1982) Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology, 10, 57-63.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildlife Society Bulletin, 34, 1142-1151.

Grassman, J., LonI, Tewes, M.E., Silvy, N.J. & Kreetiyutanont, K. (2005) Ecology of three sympatric felids in a mixed evergreen forest in north-central Thailand. Journal of mammalogy. 86, 29-38.

Guillera-Arroita, G., Morgan, B.J., Ridout, M.S. & Linkie, M. (2011) Species occupancy modeling for detection data collected along a transect. Journal of agricultural, biological, and environmental statistics, 16, 301-317.

Guillera-Arroita, G. & Lahoz-Monfort, J. (2012) Designing studies to detect differences in species occupancy: power analysis under imperfect detection. Methods in Ecology and Evolution, 3, 860-869.

Guillera-Arroita, G., Ridout, M.S. & Morgan, B.J.T. (2010) Design of occupancy studies with imperfect detection. Methods in Ecology and Evolution, 1, 131-139.

Hamel, S., Killengreen, S.T., Henden, J., Eide, N.E., Roed-Eriksen, L., Ims, R.A. & Yoccoz, N.G. (2013) Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. Methods in Ecology and Evolution, 4, 105-113.

Johnson, A., Vongkhamheng, C. & Saithongdam, T. (2009) The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. Oryx, 43, 626-633.

Linkie, M., Dinata, Y., Nugroho, A. & Haidir, I.A. (2007) Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. Biological Conservation, 137, 20-27.

Long, R.A. (2008) Noninvasive survey methods for carnivores. Island Press. Washington.

Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J. & Buzas, J.S. (2007) Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. The Journal of Wildlife Management, 71, 2018-2025.

Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J. & Buzas, J.S. (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology, 26, 327-340.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press. London.

MacKenzie, D.I. & Royle, J.A. (2005) Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology, 42, 1105-1114.

O'Connell, A.F., Nichols, J.D. & Karanth, K.U. (2010) Camera traps in animal ecology: methods and analyses. Springer Science & Business Media. London.

O'Connell, A.F., Talancy, N.W., Bailey, L.L., Sauer, J.R., Cook, R. & Gilbert, A.T. (2006) Estimating site occupancy and detection probability parameters for meso-and large mammals in a coastal ecosystem. Journal of Wildlife Management, 70, 1625-1633.

R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org [accessed 01 June 2015]

Rota, C.T., Fletcher Jr, R.J., Dorazio, R.M. & Betts, M.G. (2009) Occupancy estimation and the closure assumption. Journal of Applied Ecology, 46, 1173-1181.

Rowcliffe, J.M. & Carbone, C. (2008) Surveys using camera traps: are we looking to a brighter future?. Animal Conservation, 11, 185-186.

Schipper, J., et.al. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science, 322, 225-230.

Shannon, G., Lewis, J.S. & Gerber, B.D. (2014) Recommended survey designs for occupancy modelling using motion-activated cameras: insights from empirical wildlife data. PeerJ, 2: e532..

Swihart, R.K., Slade, N.A. & Bergstrom, B.J. (1988) Relating body size to the rate of home range use in mammals. Ecology, 393-399.

Te Wong, S., Servheen, C.W. & Ambu, L. (2004) Home range, movement and activity patterns, and bedding sites of Malayan sun bears Helarctos malayanus in the rainforest of Borneo. Biological Conservation, 119, 169-181.

Tobler, M., Carrillo-Percastegui, S., Leite Pitman, R., Mares, R. & Powell, G. (2008) An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. Animal Conservation, 11, 169-178.

Vojta, C.D. (2005) Old dog, new tricks: innovations with presence-absence information. Journal of Wildlife Management, 69, 845-848.

2.8. Supporting Information

2.8.1. Appendix 2.*S*1: Table 2.*S*1

Table 2.S1. Description of constant parameters used to estimate camera-trap survey cost provided by users obtained from an on-line questionnaire and literature reference values.

Type	Terms	Parameter	Number of respondents[a]	Average (SD)	Median	Mode	Min	Max	Value used in the cost function	Comments and units used in the cost function
User experience	Experience (years)	-	53	5 (3)	4	3	1	15	-	For reference use
	Number of completed surveys	-	53	6 (5)	4	3	1	30	-	For reference use
	Year last survey was conducted	-	53	-	-	2014	2005	2015	-	For reference use
Field operation values	Camera-trap installation time (mins)	I	53	40 (36)	30	30	5	180	0.66	Average hours
	Camera-trap retrieval time (mins)	R	53	15 (10)	15	10	2	45	0.25	Average hours
	Maintenance check time (mins)	C	53	13 (11)	10	5	1	60	0.21	Average hours
	Time between maintenance checks (days)	Z	32	17 (12)	15	15	1	50	10	
	Overall survey length (days)	L_{max}	45	128 (94)	90	90	30	540	100[c]	
	Duration of survey per sampling unit (days)	-	51	58 (56)	45	30	6	300	-	For reference use
	Time considered a sampling occasion (days)	O	20	7 (5)	6	5	1	15	5 [b]	Mode

	Length work day (hours)	W	53	8 (3)	8	8	1	15	8	Average hours
	Proportion of time spent on setbacks	E	52	0.16 (0.12)	0.10	0.10	0.00	0.50	0.84	Efficiency =1-average
	Walking speed between sampling units (km/hour)	V_w	-	-	-	-	-	-	3.5	Average km/hour
	Vehicle speed between sample units (km/hour)	V_y	37	33 (12)	30	20	15	60	33	Average km/hour
	Vehicle speed on main road (km/hour)	V_m	40	64 (27)	60	60	20	120	64	Average km/hour
	Fuel efficiency (km/l)	F_e	-	8 (0.93)	8	8	6.3	9.7	8[d]	Average km/l
	Distance between field accommodation and survey area (km)	D_t	36	50 (52)	28	20	3	200	56	Median km
Field costs ($USD)	Salary of trained personnel (USD/hour)	m_{tp}	34	10 (8)	8	25	1	30	10	Average USD per hour
	Salary of field assistants (USD/hour)	m_{fa}	29	4 (4)	2	2	0	16	4	Average USD per hour
	Food costs (USD/day)	G	44	16 (19)	10	10	1	109	16[e]	Average USD per person
	Petrol (USD/l)	F_l	36	3 (4)	1	1	0	15	3	Average USD per l
	Cost of renting field vehicle (USD/day)	J	23	86 (80)	50	50	12	350	86	Average USD per day

Camera units	Cost of camera-trap (USD/unit)	C_a	46	350 (214)	257	200	80	931	350[f]	Average USD per unit
Post-survey image processing	Number of images per camera-trap	I_d	43	21 (29)	12	17	0	144	21	Average per day
	Images processed per an hour	I_h	29	396 (532)	100	100	4	2000	396	Average per hour
	Cost of processing images (USD/hour)	I_c	27	12 (14)	6	16	1	60	12[g]	Average USD per hour
Other	Maximum time spent installing camera-traps (days)	L_i	-	-	-	-	-	-	0.10[h]	Proportion of L_{max}
	Maximum time spent maintaining camera-traps (days)	L_c	-	-	-	-	-	-	0.15[h]	Proportion of L_{max}
	Maximum time spent retrieving camera-traps (days)	L_r	-	-	-	-	-	-	0.30[h]	Proportion of L_{max}
	Extra buffer area around a sample unit (%)	α	-	-	-	-	-	-	0.25	Proportion of sample unit

a) Included for parameter values evaluated via the questionnaire

b) We use the mode of the criteria used to determine the number of days collapsed into one sampling occasion in occupancy studies

c) We use 100 days as maximum length of survey which is within the average and mode.

d) Based on fuel efficiency figures for Jeep, Land Rover, Nissan, Subaru, Toyota and Suzuki petrol sport/pickup/utility vehicles, made between 1995 and 2010. Source: US Department of Energy 2015 (http://www.fueleconomy.gov/)

e) Food cost is doubled in cost function as the field team is assumed to comprise two individuals

f) Includes the camera-trap, SD card and batteries

g) Cost of trained personnel paid to identify species and enter data into a database

h) The maximum number of days between the first and final camera-trap field activity for each operation type (i.e. installation, maintenance and retrieval), estimated as a proportion of maximum survey length (L_{max})

2.8.2. Appendix 2.S2: R code of the cost function and parameter values used for simulations

```
buff <- 0.25   # proportion of buffer size / increase of sample unit
i    <- 0.66   # hours spent installing a camera unit
r    <- 0.25   # hours spent retrieving a camera unit
c    <- 0.21   # hours spent conducting a maintenance check to a camera unit
Fl   <- 3      # cost per litre of petrol   USD/lt
Fe   <- 8      # fuel efficiency km/lt.
mtp  <- 10     # salary per unit time (hr) of a trained researcher/personnel
mfa  <- 4      # salary per unit time (hr) of a field assistant.
d    <- 0.5    # return distance between cameras within the Sampling unit (km)
z    <- 10     # number of days between maintenance checks.
Id   <- 21     # average number of images taken by a camera per day
Ic   <- 12     # cost per hour of trained personnel to process images
Ih   <- 396    # number of images processed in an hour
Ca   <- 350    # unit cost per camera (i.e. camera, batteries, memory card)
W    <- 8      # total daily working hours
Vw   <- 3.5    # walking speed (km/hr)
Vv   <- 33     # vehicle speed within study area.
Vm   <- 64     # motorway / main road velocity km/hr
E     <- 0.84   # estimated efficiency given normal field setbacks "0" no time lost to field work problems, "1"  all
of your time dedicated to normal field set backs
Dt   <- 56     # return daily distance between field station and survey area
G    <- 32     # daily cost of food and small field consumables for a team of 2 (minimum per sampling unit)
J    <- 86     # daily cost of renting vehicle
Lmax <- 100    # maximum length of survey in days
Li   <- 0.10   # proportion of time of Lmax restriction designated to installing cameras
Lc   <- 0.15   # proportion of time of Lmax restriction designated to checking/servicing cameras
Lr   <- 0.30   # proportion of time of Lmax restriction designated to retrieving cameras
varpsi <- 0.0056  # target SE of 0.075
O <- 5 # number of days considered a sampling occasion
```

 # COST EVALUATION FUNCTION

```
getHx<-function(x,n,d,Vw,Vy,D){x*n+(d*(n-1))/Vw + D/Vy}  # eqn 5: for vehicle travel (Vy=Vv and D=Ds);
                                                          #        for walking (Vy=Vw and D=2*Ds)
Ctfunction <- function (psi, p, R, K, n, isV=T) {   # parameters that must be defined: psi,p, R, K, n
  Ds <- sqrt(4*R/pi)*(1+buff) # eqn 1
  Vy <- ifelse(isV,Vv,Vw)    # component of eqn 5
  D  <- ifelse(isV,Ds,2*Ds)  # component of eqn 5
  Cf <- ifelse(isV,Ds*Fl/Fe,0) # component of eqn 6 when vehicle travel between sample units. Cost of petrol.
  Hi <-  getHx(i,n,d,Vw,Vy,D)  # component of eqn 6 for installation
  Hr <-  getHx(r,n,d,Vw,Vy,D)  # component of eqn 6 for retriaval
  Hc <-  getHx(c,n,d,Vw,Vy,D) * {ceiling(K*O/z)-1}  #component of eqn 6 for service checks
  m  <-  mtp+mfa    # combined salary paid per hour of 1 field team
  c1 <- Cf + m*(Hi + Hr + Hc)     #eqn 6
  c4 <- n*Id*K*O*Ic/Ih            # eqn 10
  c3 <-  Ca*n              # eqn 9
  B  <- 1 + (Dt/Vm) # non camera processing times   (hr)
  HSU <- (Hi + Hr + Hc)/(E*(W-B)) # eqn 7
  c2  <-  HSU*(Dt*Fl/((Fe + G + (B*m)))) #eqn 8
  pn  <-  1-(1-p)^n   # eqn 12
  pnn <- 1-(1-pn)^K    # component of eqn  11 (p*)
  Ct <- ((psi*(c1+c2+c3+c4))/varpsi)*((1-psi) + ((1-pnn)/(pnn-(K*pn*((1-pn)^(K-1))))))  # eqn 14  total cost without
extra teams
  S <- Ct/(c1+c2+c3+c4)  #eqn 13
  Kmax <- ifelse(K*O<Lmax,K*O,F) # L max is set to 100 (eqn 2)
  L <- Lmax*(Li+Lc*{ceiling(K*O/z)-1}+Lr) # eqn 15. Length of checks corrected for number of checks
  Q <- max(0,ceiling((S*1.16*HSU/L)-2))   # eqn 17 corrected when Q <0.
  Jq <- ifelse(Q/2<0,0,ceiling(Q/2))  # component of eqn 18 corrected for two teams per extra vehicle. Equivalent to
Q/2.
  CF <- Ct + Jq*J*L  #eqn 18.  Final costs considering vehicle rental for extra teams
  myfilename<-ifelse(isV,"CostVehicle.txt","CostWalking.txt")
  return (write(c(psi, p, R,  K, n, Q, Jq, S, Ct, CF, Kmax), file= myfilename, append=TRUE, ncolumns= 11))
}
```

 # SIMULATIONS

```
## for a range of values of parameters
psi <- c(0.1, 0.25, 0.5, 0.75, 0.9)
```

```
p <- c(0.1, 0.25, 0.5, 0.75, 0.9)
R <- c(3, 10, 30)
K <- 2:20
n <- 1:4
## OR for single parameter values ###
#psi <- 0.1
#p <- 0.1
#R <- 3
#K <- 20
#n <- 1
# simulate through all scenarios
for (a in psi) {
  for (b in p){
    for (c in R){
      for (y in K){
        for (j in n){
          CostV <- Ctfunction(a, b, c, y, j,isV=T)
          CostW <- Ctfunction(a, b, c, y, j,isV=F)
        }}}}}
```

2.8.3. Appendix 2.S3: Online questionnaire

Digital camera trapping survey questionnaire pilot

Page 1: Experience in digital camera trap surveys

The following questionnaire aims to quantify the **time, effort and costs** associated with **digital camera trap surveys** on medium to large mammals based on the experiences of past projects across the world.

We do not ask about project results or specific wildlife data.

The objective of our research is to produce a tool that can be used by researchers and practitioners to inform optimum effort allocation in occupancy survey design.

We invite anyone with practical experience in managing and conducting digital camera trap surveys to participate (e.g., wildlife ecologists, wildlife managers, NGO field officers, and researchers).

Please distribute the link to the questionnaire throughout your professional network.

Thank you for taking the time to complete this survey -- your contribution is highly valued. The questionnaire should take ~20-30 minutes to complete.

You can stop, save and then later return to the questionnaire should you wish to do so.

Your answers will be anonymous. No personal data is asked for or retained. You are free to stop the questionnaire at any point.

By pressing the 'Continue' button, you are indicating your willingness to participate in the research.

If you have any further queries, please contact Nicolas Galvez (ng253@kent.ac.uk)

Page 2: General personal experience

The following questions refer to your personal experience conducting digital camera trap surveys.

Most questions relate to your experience of the last survey that you completed. If you feel that it is another survey that you are more familiar with, then choose this one as the basis for your responses.

2 How many **years of experience** do you have conducting **digital camera traps surveys? (please state number in years)**

2.a If you selected Other, please specify:

3 **How many** digital camera trap surveys have you completed? (please state the **number**) We refer to completed field surveys and processing of data (if relevant), but not analysis and publication.

3.a If you selected Other, please specify:

survey? (please indicate **year**)

4.a If you selected Other, please specify:

5 In which **country or countries** did you last conduct a camera trap survey? (please **list**)

6 What **brand(s) of digital camera trap** did you use on your last survey?

- Reconyx
- Bushnell
- Cuddeback
- Scoutguard
- Moultrie
- Stealth Cam
- Other

6.a If you selected Other, please specify:

Page 3: Field operations

The following questions refer to your experience in operating digital camera trap surveys.

We refer to **1 camera station** as the deployment of **1 camera unit per sample unit.** Not facing camera stations

Most questions relate to your experience of the last survey that you completed. If you feel that it is another survey that you are more familiar with, then choose this one as the basis for your responses.

7 During your last survey, **how long was the entire survey period?** We consider entire survey period to be all the time that digital camera traps were deployed (e.g. 120 days) (please state in **days**)

7.a If you selected Other, please specify:

8 During your last survey, on average, **how long were camera stations set up for?** We refer to number of days each **camera station** was deployed (e.g. 20 days). (please state in **days**)

9 During your last survey, approximately **how long did it take you to install a single camera station?** We consider installation to include the preparation of single camera unit, **site selection** and on-site installation (please state in

minutes) We refer to **site selection** at the micro scale i.e. when in immediate point defined before hand where the camera will be set up. **Not travel time to the immediate point.**

10 During your last survey, approximately **how long did it take you to uninstall a single camera station?** We consider uninstallation to include data collection (e.g. downloading the SD card), note taking and removal of equipment (please state in **minutes**)

11 During your last survey, approximately **how long did it take you to conduct a single maintenance check to a camera station?** We consider **maintenance** to include checking/changing batteries, lures, baits, changing SD cards **(not downloading)**, etc (Please state in **minutes**)

12 During your last survey, what was the **planned number of days between maintenance check of each digital camera station?** We refer to planned number of days as that integrated into the survey design aim rather than actual frequency once fieldwork had begun (please state in **days**)

13 On average, how many **hours a day did field personnel work** during your last survey? We consider a work day to include camera trapping operations, breaks and travelling time (please provide average number of **hours per day**)

13.a If you selected Other, please specify:

14 Over the entire period of your last completed survey, **what percentage of time was spent attending to fieldwork setbacks?** We consider fieldwork set backs to include issues such as car or camera malfunctions, emergencies, illness, etc., rather than normal field work planned field work activities integrated into the survey design(please **tick the most applicable option**)

- 100% All of your time
- 90%
- 80%
- 70%
- 60%
- 50%
- 40%
- 30%
- 20%
- 10%
- 0% None of your time
- Other

14.a If you selected Other, please specify:

Page 4: Survey Operational costs

In the following section, we ask for average cost values associated with your last digital camera trap survey.

Please provide your best estimate for each question

Most questions relate to your experience of the last survey that you completed. If you feel that it is another survey that you are more familiar with, then choose this one as the basis for your responses.

15 During your last survey, what was the average **cost per day of food and other small consumable items associated with daily field operations?** (please provide **amount** and **currency** otherwise **N/A** if you do not know) We refer to the average estimated cost of **all meals per day per person.**

15.a Which currency?

- US Dollar
- Great Britain Pound
- Euro
- Indian Rupee
- Australian Dollar
- Canadian Dollar
- Japanese Yen
- Chinese Yuan
- N/A Do not know
- Other

15.a.i If you selected Other, please specify:

16 During your last survey, what was the average **cost per litre of fuel?** (please provide **amount** and **currency** otherwise **N/A** if you do not know)

16.a Which currency?

- US Dollar
- Great Britain Pound
- Euro
- Indian Rupee
- Australian Dollar
- Canadian Dollar
- Japanese Yen
- Chinese Yuan
- N/A Do not know
- Other

16.a.i If you selected Other, please specify:

17 During your last survey, what was the average **daily (inclusive of tax, if relevant) salary of personnel who worked independently** setting up camera trap stations? Here we are referring to fully trained qualified personnel, including you if applicable, paid for by the project grant. (please provide **amount** and **currency** otherwise **N/A** if you do not know)

11 / 27

17.a Which currency?

- US Dollar
- Great Britain Pound
- Euro
- Indian Rupee
- Australian Dollar
- Canadian Dollar
- Japanese Yen
- Chinese Yuan
- N/A Do not know
- Other

17.a.i If you selected Other, please specify:

18 During your last survey, **did you have field assistants?** Here we are referring to non-qualified assistants who were not working independently in the field (e.g. volunteers, trackers, guides etc.) and paid for by the project grant.

- Yes
- No

18.a What was the average **daily salary (inclusive of tax, if relevant) of personnel who were assistants** setting up camera trap stations? Here we are referring to non-qualified assistants who were not working independently in the field (e.g. volunteers, trackers, guides etc.) and paid by the project grant. (please provide **amount** and **currency** otherwise **N/A** if you do not know)

18.a.i Which currency?

- US Dollar
- Great Britain Pound
- Euro
- Indian Rupee
- Australian Dollar
- Canadian Dollar
- Japanese Yen
- Chinese Yuan
- N/A Do not know
- Other

18.a.i.a If you selected Other, please specify:

19 During your last survey, what was the **cost of one camera trap unit?** We refer to a camera unit as including the camera, SD card and batteries for entire survey period. (please provide **amount** and **currency** otherwise **N/A** if you do not know)

- US Dollar
- Great Britain Pound
- Euro
- Indian Rupee
- Australian Dollar
- Canadian Dollar
- Japanese Yen
- Chinese Yuan
- N/A Do not know
- Other

19.a.i If you selected Other, please specify:

20 During your last survey, what was the **daily cost of renting a field vehicle**? (please provide **amount** and **currency** otherwise **N/A** if you do not know)

20.a Which currency?

Page 5: Post-survey image processing

The following section includes questions regarding post-survey image processing.

Please provide your best estimate for each question.

Most questions relate to your experience of the last survey that you completed. If you feel that it is another survey that you are more familiar with, then choose this one as the basis for your responses.

21 Have you been involved in post-survey image processing?We consider post-survey image processing to include species identification and the addition of image information to a spreadsheet/database

- Yes
- No

21.a During your last survey, on average, **how many images were taken by a single digital camera trap station during the length of survey at one particular site**? We refer to correct functioning of camera trap stations in normal working conditions of your survey. (please state **number** otherwise **N/A** if you do not know)

21.b On average, **how many images were fully processed per hour** from your last survey? We consider post-survey image processing to include species identification and the addition of image information to a spreadsheet/database (please state **number** otherwise **N/A** if you do not know)

21.c During your last survey, **what was the average daily salary (inclusive of tax, if relevant) of qualified personnel who were independently**

processing camera trap images post-survey? We consider post-survey image processing to include species identification and the addition of image information to a spreadsheet/database. Please include **your own daily salary** if applicable. (please provide **amount** and **currency** otherwise **N/A** if you do not know)

21.c.i Which currency?

Page 6: Occupancy modelling

The following section relates to experience in analyzing digital camera trap data in single species occupancy modelling.

Please provide your best estimate for each question.

22 Have you analyzed camera trap data with **single species occupancy modelling?**

- Yes
- No

22.a Which **species** did you target? (please state **scientific name**)

22.b What is the estimated average **home range** of the species? (Please state in **km2**)

22.c During analysis, **how many days have you considered to be a sampling occasion?** (We consider a sampling occasion to be the number of days collapsed into one occasion) (Please state in **days**)

22.d What criteria did you use to define the number of days considered a sampling occasion?

Page 7: Travelling

The following section is intended to obtain values associated with travelling during your surveys.

Please provide your best estimate for each question.

Most questions relate to your experience of the last survey that you completed. If you feel that it is another survey that you are more familiar with, then choose this one as the basis for your responses.

23 In which type of **landscape** did you conduct your last digital camera trapping survey?

- Tropical rainforest
- Boreal forest
- Temperate forest
- Grassland/Savanah
- Shrub
- Agricultural mosaic
- Urban
- Desert
- Other

23.a If you selected Other, please specify:

24 During your last survey, what was your average **vehicle speed between camera sites within the immediate study area?** (please state in **kilometres per hour**)

25 During your last survey, what was your average **vehicle speed on a motorway or main road to the immediate study area from the accommodation?** (please state in **kilometres per hour**)

25.a If you selected Other, please specify:

25.b What was the average **distance you travelled on a motorway or main road to your immediate study area from the accommodation?** We refer to the distance between accommodation to where field sites begin. (please state in **kilometres** otherwise **N/A** if you do not know)

Page 8: Comments

Please leave any comments or suggestions that you might have.

26 Do you have any further comments or clarifications you wish to share in relation to your answers?

3. Integrating ecological and social knowledge to assess drivers of carnivore decline within a human-dominated landscape

Authors

Gálvez, N., St. John, F.S.V, Schüttler, E., Macdonald, D.W., Davies, Z.G. Submitted to Journal of Applied Ecology.

3.1. Abstract

1. Habitat loss and fragmentation as a result of land-use change are key threats to the long-term persistence of terrestrial mammals. Furthermore, some carnivorous mammals are threatened due to retribution killing by humans in response to livestock predation.
2. We use a multi-season camera-trap occupancy modelling framework to assess the dynamics of a threatened felid case study species, guiña (Leopardus guigna), over an extensive landscape representing an agricultural-use gradient. Data used in the modelling were derived from four seasons of camera-trap surveys, remote-sensed images and face-to-face household questionnaires. Specifically, we examined how habitat loss, fragmentation and human pressures impact the species. Additionally, we investigated the general prevalence of illegal retribution killing by householders across the study region using Random response technique questioning.
3. The occupancy dynamics of the case study species were mainly supported by Markov chain processes, indicating that the occupancy status of any given season depends on the previous one.
4. The felid is elusive, with a low detection probability.
5. Guiña can possibly tolerate a high degree of habitat loss as long as the landscape is not overly subdivided (i.e. land ownership) and that it may contain a high number of remnant habitat patches. Retribution killing, livestock predation events and human encounters with the species do not seem to drive species decline.
6. Synthesis and applications. Human-dominated landscapes with large intensive farms can have conservation value for elusive carnivorous mammals, as long

as an appropriate network of habitat patches exist. Despite previous indications that human persecution is a factor contributing to the decline of the guiña, it is not the case in the study region. Conservation efforts should therefore be targeted towards ensuring remnant habitat patches in agricultural areas are retained, rather than investing in campains targeting change in human behaviour to mitigate retribution killing. Our study demonstrates the value of taking an interdisciplinary approach to assessing the threats to a carnivorous mammal, by integrating ecological and social knowledge into a single modelling framework. It has allowed us to tease apart the relative importance of different potential extinction pressures effectively and make informed recommendations as to where future conservation efforts should be prioritised.

Key-words: Agriculture, camera-trap surveys, conservation, habitat fragmentation, habitat loss, human persecution, Leopardus guigna, occupancy dynamics, random response technique, retribution killing.

3.2. Introduction

Land-use change is one of the greatest threats facing terrestrial biodiversity globally (Sala et al. 2000). Long-term species persistence is being negatively influenced by habitat loss, fragmentation, degradation and isolation (Henle et al. 2004b). The impacts of these land-use change processes include, for example, declines in habitat specialist population sizes (Bender, Contreras & Fahrig 1998), increased predation and mortality due edge effects in highly fragmented landscapes (Lahti 2001), increased inter-specific competition between habitat specialists and generalists (e.g. Marvier, Kareiva & Neubert 2004) and reduced genetic variation (e.g. Napolitano et al. 2015b). In general, species with traits such as a low reproductive rate, low population density, large individual area requirements or a narrow niche are more sensitive to habitat loss and fragmentation (Fahrig 2002; Henle et al. 2004a) and, therefore, have a higher risk of extinction (Purvis et al. 2000). Consequently, many territorial mammals are particularly vulnerable to habitat modification as a result of land-use change.

Additionally, in human-dominated landscapes, mammal populations are threatened directly by the behaviour of people (Ceballos et al. 2005). For instance, larger species (i.e. mammals with a body mass >1 kg) are often persecuted because they are considered a pest, food source or a marketable commodity that can be traded (Woodroffe, Thirgood & Rabinowitz 2005). Carnivorous mammals are particularly vulnerable to retribution killing by people, normally in response to livestock predation or attacks on humans, presenting a highly complex management challenge for species of conservation concern (Treves & Karanth 2003; Inskip & Zimmermann 2009). Indirectly, mammals are also threatened by factors such as the introduction of invasive plant species, which reduce habitat complexity (Rojas et al. 2011), or domestic pets, which cause direct interference, predation or disease transmission (Hughes & Macdonald 2013).

Increasingly and under future land use change scenarios, conservation of carnivorous mammals will require novel approaches outside protected areas (Di Minin et al. 2016). To mitigate effectively the threats faced by carnivorous mammals in human-dominated landscapes, through targeted conservation interventions, practitioners and policy-makers need to understand the relative contribution that pressures such as habitat loss/fragmentation and persecution play in species population declines. This necessitates an integrated and interdisciplinary research approach (Clark et al. 2001). First of all, it is important to determine the differentiated impacts of habitat loss and fragmentation on a species, as the conservation actions required to alleviate the pressures associated with the two processes are likely to be different (Fahrig 2003; Lindenmayer & Fischer 2007). For instance, if habitat loss is the key driver then large patches may need to be protected to ensure long-term survival, whereas if fragmentation is the main threat then it might be that a certain configuration of remnant vegetation is better. Similarly, conservationists must assess whether or not human individuals/communities are having a detrimental effect on species populations, as well as quantifying the magnitude of the problem (St John, Keane & Milner-Gulland 2013). Studies which examine human wildlife 'conflict' tend to focus on understanding: (i) patterns of livestock predation (e.g. Treves et al. 2004; Bagchi & Mishra 2006); (ii) motivations and attitudes towards wildlife via in-depth qualitative methods (e.g. Inskip et al. 2014); or, (iii) ways that humans can co-exist with carnivores (Sillero-Zubiri & Laurenson 2001; Treves et al. 2006). However, despite this valuable body of work, there seems to be a paucity of interdisciplinary research that evaluates explicitly both ecological and social drivers of species decline in a single coherent quantitative framework, across a geographic scale pertinent to informing conservation decision-making and investment (Dickman 2010).

Here we consider how the prime threats to carnivorous mammals may be assessed over a human-dominated landscape using the guiña (Leopardus guigna), an International Union for the Conservation of Nature (IUCN) Red Listed felid. Specifically, we examined how habitat loss, fragmentation and human pressures may interact and impact upon this forest dwelling species, using data derived from camera-trap surveys, remote-sensed images and questionnaires with householders across the study landscape. These factors were then integrated and evaluated within multi-season occupancy dynamics models. We argue that by combining such ecological and social knowledge, we can ultimately provide a more robust evidence-base for informing conservation efforts.

3.3. Methods

3.3.1. Study system

The study was conducted in the Tolten catchment of the Araucanía region in southern Chile, at the northern limit of the South American temperate forest ecoregion (39º15´S, 71º48´W) (Armesto et al. 1998). The system comprises two distinct geographical sections common throughout Southern Chile: the Andes mountain range and central valley. Land-use in the latter is primarily intensive agriculture (e.g. cereals, livestock, fruit trees) and urban settlements, whereas farmland (which occurs < 600 m.a.s.l) in the Andes is less intensively used and is surrounded by tracks of continuous forest on steep slopes and protected areas (>800 m.a.s.l; Fig. 3.1). The natural vegetation across the study region consists of deciduous and evergreen Nothofagus forest (Luebert & Pliscoff 2006), which remains as a patchy mosaic in agricultural valleys and as continuous forest tracts at higher elevations within the mountains (Miranda et al. 2015).

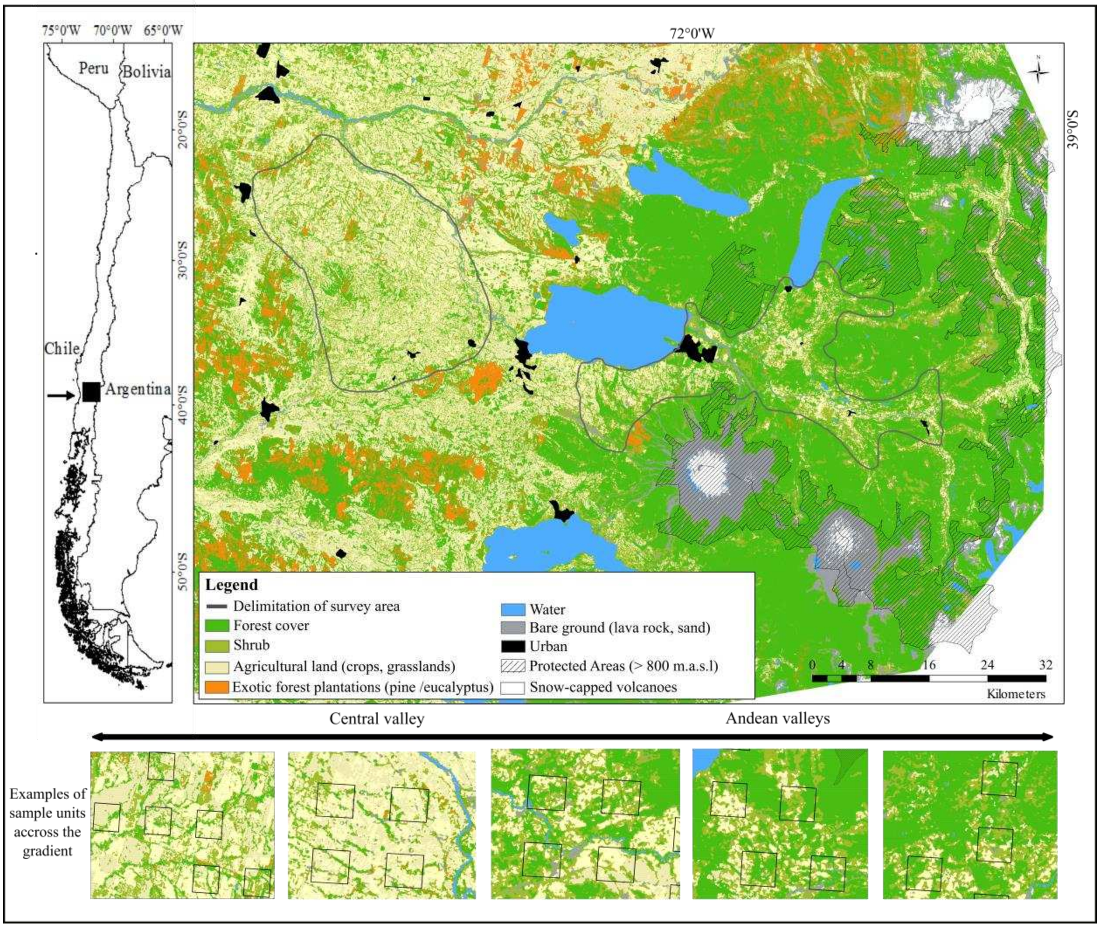

Figure 3.1 Distribution of landcover classes and protected areas across the study region in southern Chile, including the forest habitat of guiña (Leopardus guigna), our case study species. We have indicated the two zones within which the 145 sample units (SUs: 4 km^2 each) were located, with 73 SUs in the central valley (left polygon) and 72 in within the Andes (right polygon). The positions of each SU are not shown to comply with the ethical guidelines associated with studying illegal human behaviour (i.e. guiña is protected by law). Illustrative examples of the variation in landscape configuration within SUs across the human-domination gradient are provided (bottom of image).

The güiña is the smallest neotropical felid (<2 kg) and is categorised as Vulnerable by the IUCN (Napolitano et al. 2015a). The species is nearly endemic to Chile, as it is very scarce within Argentina. It is thought to require forest habitat with dense understory and presence of bamboo (Chusquea spp.) (Nowell & Jackson 1996). However, the güiña is known to occupy remnant patches of fragmented forest remaining within agricultural areas (Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004; Gálvez et al. 2013). The carnivorous felid is protected by law but considered as detrimental by rural communites as it can predate on chickens and retribution killings have been reported previously (Sanderson, Sunquist & W. Iriarte 2002; Gálvez et al. 2013), although the extent of persecution has not been formally assessed. Due to these attributes, the species makes an ideal case study to explore how habitat loss, fragmentation and human pressures may combine to influence the habitat patch occupancy dynamics of a territorial carnivorous mammal in a human-dominated landscape.

3.3.2. Survey design

3.3.3. Case study felid detection and non-detection

A grid of 4 km^2 potential sampling units (SUs) was laid at regular intervals across the study region, representing a gradient of forest habitat fragmentation due to agricultural use and human settlement below 600 m.a.s.l. The size of the SUs is equivalent to the mean observed guiña home range size (MCP 95% mean = 270 ±137 ha; Schüttler E., unpublished data). The minimum sampling effort required to achieve statistical precision (i.e. S.E. <0.075), in terms of the number of SUs and repeated sampling occasions, was estimated following Guillera-Arroita, Ridout & Morgan (2010) and using species specific parameter values from Gálvez et al. (2013). A total of 145 SUs were selected at random from the 230 in the grid, with 73 and 72 located in the central valley and Andes mountain valley respectively (Fig. 3.1). To estimate dynamic parameters for the probability of habitat patches being occupied (colonised) or unoccupied (extinct), we conducted multi-season occupancy surveys. The Andean valleys were surveyed for four seasons (summer 2012, summer 2013, spring 2013, summer 2014), while the central valley was surveyed for three (the latter three seasons). Occupancy models provide a flexible framework that can accommodate missing observations and thus the missing season (MacKenzie et al. 2006). A total of four rotations (i.e. blocks of camera-traps) were used to survey all SUs within a 100 day period each season. Detection and non-detection data were thus collected for 20-24 days per SU. Sampling occasions comprised two-day blocks, because individuals do not stay more than this time in one place (Schüttler E., unpublished data), meaning that each SU was surveyed for 10-12 sampling occasions. Two camera-traps (Bushnell ™trophy cam 2012) positioned 100-700 m apart were placed near the centre of each SU, in forest habitat, with a minimum distance of >2 km between camera-traps of adjacent SUs. Camera traps were placed at a height of 30-40 cm and a minimum distance 100 cm from detection zone. Most cameras were installed in narrow trails within forest fragments. The detection histories of both camera-traps in a SU were pooled. A few camera-trap malfunctions or thefts were treated as missing observations.

3.3.4. Habitat loss/fragmentation predictors of occupancy dynamics

The extent of habitat loss and fragmentation was evaluated using biologically meaningful metrics which have been reported in the literature as being relevant to the guiña, using either field or remote-sensed landcover data (Table 3.1, Appendix 3.S1 & Table 3.S1 in Supporting Information). The metrics were measured within a 300 ha circular buffer centred on the midpoint between both cameras in each SU. Landscape subdivision was used as a proxy for human pressure and management variability (Theobald, Miller & Hobbs 1997; Hansen et al. 2005), based on the number of properties or land parcels recorded in each SU (CIREN 1999).

3.3.5. Microhabitat predictors of occupancy dynamics

The microhabitat surrounding a camera-trap might influence species activity (Acosta-Jamett & Simonetti 2004), and was therefore surveyed within a 25 m radius around each camera-trap, as this is deemed to be area over which localised conditions may influence species detectability (Tables 3.1 & 3.S1). Five classes of percentage understory and bamboo cover (Braun-Blanquet 1965), and three classes of logging intensity and livestock activity, were recorded. In addition, we noted the presence and type of water resources during each season. The data from both camera-trap sites in each SU were pooled and median used when values differed.

3.3.6. Human encounter/pressure predictors of occupancy dynamics

We administered a questionnaire face-to-face (N = 233) with residents living in the one or two households closest to the camera-traps within each SU, from May to September 2013. The aim was to solicit information from residents of the study region regarding their socio-demographic/economic background, guiña encounters, the extent of livestock predation by guiña, tolerance of livestock predation, ownership of dogs on the land parcel and whether they had ever killed a guiña. As it is illegal to kill guiña in Chile (Law 19.473 Ministry of Agriculture) the Randomized Response Technique (RRT) method was used to ask this sensitive question (Appendix S2 in supporting information). Questionnaires were administered by NG who is Chilean and has lived in the study region for over 10 years. The questionnaire was piloted with 10 local householders living outside the SUs; feedback was used to improve the wording, order of questions and time scale that people could remember.

We ascertained the general prevalence of guiña retribution killing across the study region via analysis of the RRT data. A total of 1000 bootstraps were conducted to obtain a 95% confidence interval. As this cannot be done at the spatial resolution of each SU (i.e. RRT provides the proportion of respondents independent of where they spatially occur), other variables were used to assess human encounters/pressure towards the case study species at this scale (Table 3.1, Appendix 3.S1 & Appendix 3.S2). When more than one household was surveyed in a SU and responses were categorically different (i.e. one household report predation and the other did not) only the data from the household that report experiences was kept. When households report different values, the median between them was used. For number of dogs the median between households was used.

3.3.7. Multi-season models and selection procedure

The 15 potential model predictors were tested for collinearity and, in instances where variables were correlated (Pearson's or Spearman's $|r|>0.7$), we retained the covariate that conferred greater ecological/social meaning and ease of interpretation (Tables 3.1 & 3.S1). All continuous variables, except percentages because they are already in a relevant scale, were standardized to z-scores.

Table 3.1 Habitat loss/fragmentation, human encounter/pressure and microhabitat predictors evaluated when modelling occupancy (ψ,), colonisation (γ), extinction (ε) and detection (p) probability parameters of multi-season camera-trap surveys of guiña

(Leopardus guigna), an elusive and territorial small carnivore. Further details can be found in Appendix 3.S1, 3.S2 and Table 3.S1 in the Supporting Information.

Parameter	Predictor	Abbreviation in models
	Habitat loss/fragmentation	
ψ, ε, γ	Percent of forest cover/habitat	Forest
ψ, ε, γ	Percent shrub cover/marginal habitat	Shrub
ψ, ε, γ	Number of forest patches	PatchNo
ψ, ε, γ	Shape index forest patches	PatchShape
ψ, ε, γ	Forest patch size area[†]	PatchAreaW
ψ, ε, γ	Forest patch continuity[†]	Gyration
ψ, ε, γ	Edge length of forest land cover class	Edge
ψ, ε, γ	Landscape shape index of forest[‡]	LSI
ψ, ε, γ	Patch cohesion[†]	COH
	Human encounters/pressure	
ψ, ε	Land subdivision	Subdivision
ψ,ε	Intent to kill	Intent
ψ,ε	Predation	Predation
ψ,ε	Frequency of predation	FQPredation
ψ,ε, p	Frequency of encounters[§]	FQEncounter
ψ,ε	Number of dogs	Dogs
	Microhabitat	
p	Bamboo density (Chusquea spp.)	Bamboo
p	Density of understory	Understory
p	SU rotation	Rotation
p	Intensity of livestock activity	Livestock
p	Intensity of logging activity	Logging
p	Water availability	Water

[†]Predictor excluded due to collinearity with percent of forest cover (Pearson's │r│>0.7)

[‡]Predictor excluded due to collinearity with number of forest patches (Pearson's │r│>0.7)

[§]Predictor also fitted with detection probability

We estimated occupancy (ψ), detection (p), colonisation (γ) and extinction (ε) using maximum likelihood and multi-season models (MacKenzie et al. 2006) in the software PRESENCE (Hines 2006). Model residuals of detection/non-detection data for each season were tested for the existence of spatial autocorrelation using Moran's I (Dormann et al. 2007). We used a fixed band of 3 km from the midpoint of buffers, which amounts to an area three times larger than the home range of the case study species which we deemed a robust scale for evaluation.

The model selection procedure involved increasing the complexity of models by fitting predictors for each parameter separately and evaluating the likelihood improvement with Akaike's Information Criterion (AIC). Models that accounted for >0.8 of the AIC weight and were within <2 ΔAIC were considered to have substantial support (Burnham & Anderson 2002), and thus the predictors were selected and used in the next step in a forward manner (e.g. Kery, Guillera-Arroita & Lahoz-Monfort 2013). Firstly, we investigated whether seasonal dynamics occurred at random, followed a Markov Chain process or if there were no changes in ψ. This allowed us to define a base structure that accounted for the seasonal dynamic in competing models of habitat loss/fragmentation and human encounters/pressures. Secondly, we fitted habitat loss/fragmentation, human encounter/pressures and microhabitat predictors (Table 3.1). In order to not over fit the models and risk spurious results (Burnham & Anderson 2002), and for comparison, we kept models with only one predictor per parameter.

Univariate detection models were fitted keeping ψ, γ and ε constant (e.g. ψ(.), γ(.), ε(.)). Keeping the best p model, we evaluated models that represented habitat loss/fragmentation effects on ψ (Table 3.1), while keeping γ and ε constant. The best ψ and p models were then used to add further complexity to γ and ε probability. For ε we fitted all predictors. However, we assumed that γ is influenced by habitat loss/fragmentation predictors, not human encounters/pressure because the species would be lured to an area due to habitat conditions rather than by lower human pressure. We fitted ε followed by γ, and then vice versa, following Kery et al. (2013). A constant or null model was included in all candidate model sets. In total 38 candidate models were compared to consider all model sets. Only a few models with convergence problems or implausible parameters (i.e. very large parameter and SE estimates) were eliminated from each model set. The final AIC-best model was evaluated for goodness of fit following MacKenzie and Bailey parametric bootstrap test for dynamic occupancy models in R package "AICcmodavg" with 5,000 iterations. The predict function and derived parameter code in UNMARKED (Fiske & Chandler 2011) was used to plot significant predictors for each parameter and derived ψ.

3.4. Results

3.4.1. Habitat loss/fragmentation predictors

We excluded four habitat loss/fragmentation predictors due to collinearity with extent of forest cover and number of patches (Tables 3.1 & 3.S1). Across the study region, variation in the degree of habitat loss and fragmentation was substantial. Extent of forest cover in SU's ranged from 1.8% to 76% with a mean of 27.5% (SD= 18.9), and shrub cover followed a similar pattern (range: 9.1% to 53.1%; mean= 26%; SD=

8.3%). The number of habitat patches per SU varied between 14 and 163, with a mean of 52.9 (SD=25.7), and patch shape was diverse, from highly irregular forms at 7.8 to less irregular forms at 1.3 (mean= 3.13; SD= 1.3). Some SUs include a relatively high length of edge with 48,405 m, whereas others had as little as 4,755 m. Land subdivision also presented quite a wide range from 1 to 314 properties with an average of 41.3 (SD= 37.2).

3.4.2. Human encounter/pressure predictors and retribution killing

A total of 233 respondents completed the questionnaire across the study region. The majority were between 46 and 67 years old and had lived in their property for 25 to 50 years (average 35; SE= 0.09). Property sizes were 1-1200 ha in size, with a median of 29 ha and an average of 98 ha (SE= 0.85). Respondents, on average, received a monthly income equivalent to US$ 558 (SE= 2.81) and had received 10 years of formal schooling (SE= 0.01).

Reported encounters with the guiña were sparse. Nearly half of the respondents (N= 116) reported seeing a guiña during their lifetime. On average, the sighting occurred 17 years ago (SD= 15). However, in the last 4 and 10 years, only 10% and 21% of people respectively had encountered the case study species. Predation events were also uncommon. Only 16% of respondents (n= 37) attributed a livestock predation event in their lifetime to the guiña, with just 7% (n= 16) reporting that this had occurred in the past decade. Of the guiña predation events in the last 10 years, 81% (N= 13) were recorded in the Andes SUs. The number of people with an intent to kill the case study species was greater than those who had encountered it or suffered a livestock predation event; 38% (N= 89) of respondents stated that they would kill a guiña if two chickens were predated, increasing to 60% (n= 140) if 25 chickens were predated. Furthermore, using the RRT method, we found that the proportion of respondents who had killed a guiña was 0.09 (SE= 0.08; 95% CI= 0.02-0.16).

3.4.3. Occupancy dynamics

During the study, there were 23,373 camera-trap days and 713 sampling occasions with detections (season 1=96; season 2= 185; season 3= 240; season 4= 192). The naïve estimate of occupied sites (i.e. sites with detection/total sites) was similar across all four seasons (0.54; 0.52; 0.58; 0.59) and between the central valley and Andes SU (both areas >0.5). No spatial autocorrelation was observed among SUs during any survey season, thus a correction parameter was not needed (season 1 I= -0.03 (α = 0.74); season 2 I= 0.05 (α = 0.31); season 3 I= 0.05 (α = 0.36); season 4 I= 0.07 (α = 0.17)).

The seasonal dynamics of the guiña was mainly supported by Markov chain processes (model ID 1.0-1.6, Table 3.2), indicating that the occupancy status of any given season depends on the previous one. Model 1.1 was chosen as the base structure of the modelling procedure because it considers all parameters (i.e. ψ, γ, ε, p) and is supported by AIC. Detection probability in models 2.1-2.7 (Table 3.2) was best explained by a positive relationship (β_1 0.343; S.E= 0.055) with understory vegetation cover. SU rotation within the season was not supported, meaning that the rotational design did not affect overall results. Indeed, none of the other predictors for p were substantiated by the model selection. Occupancy in the first season (ψ_1) was best explained by forest cover (models 3.0-3.6; Table 3.2). Initial occupancy was higher in sites with less forest cover but with a minor effect (β_1 =-0.0363; SE = 0.0138) and adding shrub cover only improved model fit marginally. Edge type fragmentation metrics and land subdivision were not supported as good predictors.

Table 3.2 Multi-season occupancy dynamics models for guiña (Leopardus guigna). Detection (p) and occupancy (ψ) probability were determined using a step-forward model selection procedure and Akaike's Information Criterion (AIC). ΔAIC is the difference in AIC benchmarked against the best model, wi is the model weight, K the number of parameters, and -2*loglike is the log likelihood. Selected models for each parameter are highlighted in bold and included when fitting the next parameter. Models ID 1.0-1.6 evaluate seasonal dynamics to define the base model structure for the subsequent model selection procedure. We assess whether changes in ψ do not occur (ID 1.6), occur at random (ID 1.5, 1.4), or follow a Markov Chain process (i.e. occupancy status of subsequent seasons is dependent on first season) (ID 1.0, 1.1, 1.2, 1.3). ψ_1 refers to ψ in the first of four seasons over which the guiña was surveyed.

ID	**Fitted parameter**	**ΔAIC**	**w_i**	**K**	**-2*loglike**
	Seasonal dynamics				
1.0	ψ(.), γ(.), {ε= γ (1- ψ)/ψ}, p(season)	0.00	0.443	6	3982.93
1.1	**ψ_1(.), ε(season), γ(season), p(season)**	**0.36**	**0.370**	**11**	**3973.29**
1.2	ψ_1(.), ε(.), γ(.), p(season)	1.88	0.173	7	3982.81
1.3	ψ_1(.), ε(.), γ(.), p(.)	6.83	0.015	4	3993.76
1.4	ψ_1(.), γ(.),{ε= 1- γ}, p(season)	41.78	0.000	6	4024.71
1.5	ψ_1(.), γ(season),{ε= 1- γ}, p(season)	42.78	0.000	8	4021.71
1.6	ψ(.), {γ= ε= 0}, p(season)	104.11	0.000	6	4087.04
	Detection/fitted with *ψ_1(.), ε(season), γ(season)*				
2.0	**p(season+Understory)**	**0.00**	**0.9999**	**12**	**3934.47**

2.1	p(season+Bamboo)	18.48	0.0001	12	3952.95
	Occupancy/fitted with *ε(season), γ(season),* p(season+Understory)				
3.0	**ψ_1(Forest)**	**0.00**	**0.5515**	**13**	**3927.46**
3.1	ψ_1(Forest+Shrub)	1.24	0.2967	14	3926.70
3.4	ψ_1(PatchNo)	4.00	0.0746	13	3931.46
3.5	ψ_1(.)	5.01	0.0450	12	3934.47
3.6	ψ_1(Subdivision)	5.69	0.0321	13	3933.15

Extinction and γ in models 4.0-4.18 and 5.0-5.12 (Table 3.3) reflected the same trends, irrespective of the order in which parameters were fitted. Extinction, rather than γ, yielded predictors that improved model fit compared to the null model. Where predictors of γ were fitted first (models 5.0-5.5), none of the plausible models (i.e. <2 AIC) improved fit compared to the null model, indicating that it was only explained by seasonal differences. Predictors for γ fitted second (models 4.7- 4.18) were better supported than the null model. However, this is an artefact of models 4.9-4.17 being a reduced fit of the best ε models (5.7 and 5.8). When ε was fitted second (models 5.6-5.13), it was best explained by the number of habitat patches in the landscape and land division (models 5.7 and 5.8). The goodness-of-fit test run on the final model (5.6) suggested some evidence of lack of fit when looking at the global metric (P-global<0.05), but inspection of survey-specific results show no evidence of lack of fit for any of the seasons ($p > 0.05$) except season 2 ($p = 0.032$). Inspecting the data from season 2, we find that the relatively large chi-square statistic value appears to be driven by just a few sites with unlikely capture histories according to the model (i.e. < 12). Given this, and the fact that data from the other seasons do not show lack of fit, we deem that the final model explains the data appropriately.

Table 3.3 Multi-season models of extinction (ε), and colonisation (γ) probability, using a step-forward model selection procedure and Akaike's Information Criterion (AIC), for guiña (Leopardus guigna). ΔAIC is the difference in AIC benchmarked against the best model, w_i is the model weight, K the number of parameters, and -2*loglike is the log likelihood. Selected models for each parameter are highlighted in bold. Order of parameter fitting was ε first and γ second, then vice versa. ψ_1 refers to ψ in the first of four seasons over which the guiña was surveyed, with changes in ψ following a Markov Chain process. The models selected for ψ and p are indicated in Table 3.2.

ID	**Order of fitted ε and γ parameters**	**ΔAIC**	**w_i**	**K**	**-2*loglike**
	Extinction first/ ψ_1(Forest), p(season+ Understory)				
4.0	**ε(season+PatchNo), γ(season)**	**0.00**	**0.4692**	**14**	**3920.10**
4.1	**ε(season+Subdivision), γ(season)**	**0.36**	**0.3919**	**14**	**3920.46**
4.2	ε(season+PatchShape), γ(season)	5.15	0.0357	14	3925.25
4.3	ε(season+Predation), γ(season)	5.24	0.0342	14	3925.34
4.4	ε(season), γ(season)	5.36	0.0322	13	3927.46
4.5	ε(season+FQencounter), γ(season)	5.92	0.0243	14	3926.02
4.6	ε(season+FQPredation), γ(season)	7.24	0.0126	14	3927.34
	Colonisation second/ψ_1(Forest), p(season+ Understory)				
4.7	**ε(season+PatchNo), γ(season)**	**0.00**	**0.1877**	**14**	**3920.10**
4.8	**ε(season+Subdivision), γ(season)**	**0.36**	**0.1568**	**14**	**3920.46**
4.9	ε(season+Subdivision), γ(season+PatchShape)	0.79	0.1265	15	3918.89
4.10	ε(season+PatchNo), γ(season+PatchShape)	1.29	0.0985	15	3919.39
4.11	ε(season+Subdivision), γ(season+PatchNo)	1.63	0.0831	15	3919.73
4.12	ε(season+PatchNo), γ(season+Edge)	1.84	0.0748	15	3919.94
4.13	ε(season+PatchNo), γ(season+Forest)	1.98	0.0698	15	3920.08
4.14	ε(season+Subdivision), γ(season+Edge)	2.16	0.0638	15	3920.26
4.15	ε(season+ Subdivision), γ(season+Forest)	2.20	0.0625	15	3920.30

4.16	ε(season+Subdivision), γ(season+Forest+Shrub)	3.50	0.0326	16	3919.60
4.17	ε(season+PatchNo), γ(season+Forest+Shrub)	3.60	0.0310	16	3919.70
4.18	ε(season), γ(season)	5.36	0.0129	13	3927.46
	Colonisation first/ψ_1(Forest), p(season+Understory)				
5.0	**ε(season), γ(season)**	**0.00**	**0.3303**	**13**	**3927.46**
5.1	ε(season), γ(season+PatchShape)	0.96	0.2044	14	3926.42
5.2	ε(season), γ(season+PatchNo)	1.55	0.1522	14	3927.01
5.3	ε(season), γ(season+Edge)	1.89	0.1284	14	3927.35
5.4	ε(season), γ(season+Forest)	1.95	0.1246	14	3927.41
5.5	ε(season), γ(season+Forest+Shrub)	3.41	0.06	15	3926.87
	Extinction second/ψ_1(Forest), p(season+Understory)				
5.6	**ε(season+PatchNo+Subdivision), γ(season)**	**0.00**	**0.8275**	**15**	**3913.45**
5.7	ε(season+PatchNo), γ(season)	4.65	0.0809	14	3920.10
5.8	ε(season+Subdivision), γ(season)	5.01	0.0676	14	3920.46
5.9	ε(season+PatchShape), γ(season)	9.80	0.0062	14	3925.25
5.10	ε(season+Predation), γ(season)	9.89	0.0059	14	3925.34
5.11	ε(season), γ(season)	10.01	0.0055	13	3927.46
5.12	ε(season+FQEncounters), γ(season)	10.57	0.0042	14	3926.02
5.13	ε(season+FQPredation), γ(season)	11.89	0.0022	14	3927.34

An increase in the number of habitat patches and reduction in land subdivision resulted in lower ε (β_1= -0.900; S.E.= 0.451 and β_1= 0.944; S.E. = 0.373 respectively; Fig. 3.2). Human encounters/attitudes predictors, such as livestock predation occurrence or intent to kill, were not supported as extinction drivers (Table 3.3). Occupancy estimates were high across seasons with derived seasonal estimates of 0.78 (SE =0.09), 0.64 (SE =0.06), 0.80 (SE =0.06) and 0.83 (SE =0.06).

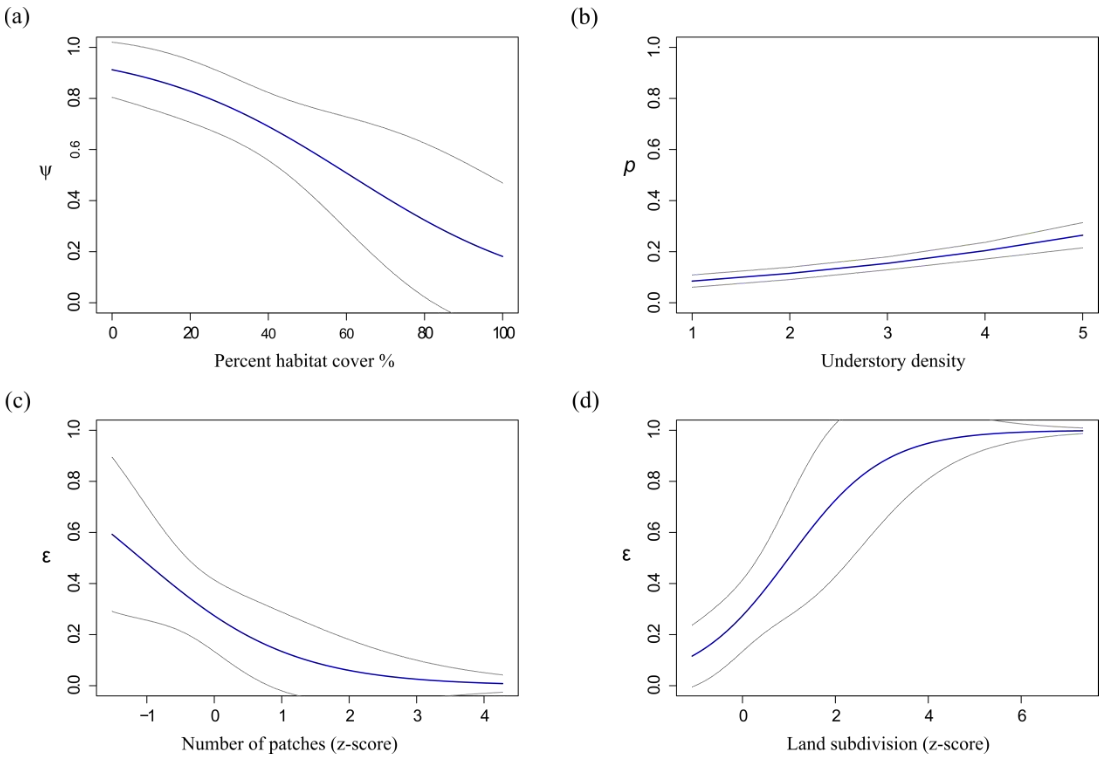

Figure 3.2 Predicted effects (blue lines) of forest cover, understory density, number of habitat patches and land subdivision on multi-season occupancy model parameters for guiña (Leopardus guigna). The grey lines indicate the 95% CI associated with the parameter values of the final selected model [ψ_1(Forest), p(season+Understory), ε(season+PatchNo+Subdivision), γ(season)] where: a) is the estimated occupancy probability (ψ) against forest cover; b) detection probability (p) against understory density; c) extinction probability (ε) against the number of patches; and, d) extinction probability (ε) against land subdivision.

3.5. Discussion

The guiña is an elusive forest specialist. As such, one might predict that the species would be highly susceptible to both habitat loss and fragmentation (Henle et al. 2004a; Ewers & Didham 2006). The uncertainty associated with occupancy at higher levels of forest cover (Fig. 3.2) suggests that the guiña is reliant on the spatial extent of available habitat. However, our results also indicate that the species can tolerate extensive habitat loss and can persist in areas with very low forest cover. Telemetry studies in the same study area confirm that the species uses permanent territories in agricultural landscapes and uses an array of patches of forest habitat (Schüttler E., unpublished data). Indeed, results highlight that intensive agricultural landscapes can be useful for conservation of the guiña and should not be dismissed as unsuitable. The dynamics of occupied and unoccupied sites across the study region are driven by fragmentation and human pressure through land subdivision. Ensuring that plenty of remnant habitat patches are retained in the landscape, and land subdivision is further prevented so that existing large farms are preserved, could ultimately safeguard the long-term survival of this threatened felid, rather than only focusing on the protection of large patches of habitat in agricultural landscapes or surrounding continuous forests in the Andes.

Retributive killing predominately occurs when the felid enters chicken coups (Gálvez et al. 2013). Although previous studies have suggested that human persecution may be a factor contributing to the decline of the guiña (Nowell & Jackson 1996; Sanderson, Sunquist & Iriarte 2002), retributive killing in the study region and our sample units in particular, seems low. Despite the fact that the species occupies a large proportion of the landscape across seasons, people rarely encounter the felid and rates of reported poultry predation are low. This elusive behaviour is reflected and reinforced by the low camera-trap detection probability we reported. However, twenty-one respondents (9%) admitted to killing a guiña over the last decade and we do not know the quantity of cats killed (i.e. not measured in this study). In addition, identification of individual cats from camera-trap images is unfeasible (F. Blair unpublished data), meaning that it is not currently possible to estimate changes in abundance through time or conduct population viability analyses. Consequently, we were unable to determine whether this low prevalence of retribution killing is having a detrimental impact on the population size of the species. However, there is evidence that guiña populations have suffered significant population reductions in the recent past (Napolitano et al. 2014). Where evidence suggests that retributive persecusions may be having an adverse impact on populations, conservation interventions to reduce persecution should be of benefit to carnivores, particularly measures which prevent females from being targeted (Chapron et al. 2008). Measures particularly aimed at deterrents near chicken coups or improvement of the closures should be cost effective. Understanding which human attributes might predict killing of a guiña would be valuable for informing social marketing campaigns (i.e. to target specific groups or behavioural attributes) aimed at altering human perceptions and behaviour towards the species and improvement of poultry management practices (Veríssimo 2013).

Following farming trends globally, larger properties in the agricultural areas of southern Chile are generally associated with high intensity production, whereas smaller farms are mainly subsistence-based systems (Carmona et al. 2010). It is therefore interesting, but perhaps counterintuitive, that we found occupancy to be higher where land subdivision is lower given the high intensity nature of large farms. However, native vegetation in non-productive areas, including ravines or undrainable soils with a high water table, is normally spared within agricultural areas (Miranda et al. 2015), and these patches of remnant forest can provide adequate refuge, food resources and suitable conditions for reproduction for a small carnivores (e.g. Schadt et al. 2002). It is likely that a greater number of small farms can increase human persecussion as a result of higher human density (e.g. Woodroffe 2000; Woodroffe & Ginsberg 2000) or drive higher pressure on natural resources from an increase in households (e.g. Liu et al. 2003). An increase in the number households has been shown to reduce the quality of remaining habitat patches as a result of frequent timber extraction, livestock grazing (Carmona et al. 2010) and could lead to an increase in competition/interference by domestic animals and pets (Silva-Rodriguez, Ortega-Solis & Jimenez 2010; Silva-Rodríguez & Sieving 2011, 2012; Sepúlveda et al. 2014). A current factor driving the subdivision of land and degradation of remnant forest patches across agricultural areas is the growing demand for residential properties (Petitpas 2010) facilitated by Chilean law which dictates that land subdivision can occur at a minimum plot size of 0.5 ha. Furthermore, it is common practice for sellers and buyers to completely eliminate all understory vegetation from such plots (Rios C., personal communication), which is a key component of habitat quality.

Our results therefore suggest that land subdivision, and the associated processes outlined above, are likely to be the main threat to the guiña in the region at a landscape scale. Conservationists should thus engage with householders, land-use planners and developers proactively to advocate actions such as lower intensity grazing or preservation of remnant habitat patches in the landscape, which will improve understory cover and quality. Regulatory guidelines and enforcement may also be required (e.g. Hansen et al. 2005). For example, government agencies may need to subsidise farmers to fence of some of forested areas on their land. Conservation measures such as these should prove to be more effective than investing limited conservation resources on retributive killing mitigation when this is deemed of low prevalence.

This case study highlights the value of using multi-season modelling techniques to evaluate and differentiate between the effects of habitat loss and fragmentation by contrasting factors that explain occupancy versus changes in status (i.e. extinction, colonisation), corrected for imperfect detection of an elusive species. Fragmentation, with a high number of forest patches retained in the landscape, is a more important predictor of occupancy than the real extent of habitat. Indeed, our findings imply that these remnant patches play a key role in supporting this territorial carnivore in areas where there has been substantial habitat loss and, perhaps, might even reduce the extinction threshold for the species (Fahrig 2002). However, future research should also evaluate if the occupancy dynamics shown by the guiña might be expressing potential maladaptive behaviour where these remnant patches in agricultural landscapes are attractive sinks but might be acting as ecological traps which negatively impact reproductive success (Robertson & Hutto 2006). Particularly, there is a need to further understand the mechanisms and processes by which human pressures increases as land is further subdivided so that detailed guidelines can be provided. Furthermore, studies of the effects of habitat loss and fragmentation could be confounded by time, and it is possible that we are not yet observing the impacts of habitat loss (Ewers & Didham 2006). However, this is unlikely to be the case in this study system as over 67% of the original forest cover was lost by 1970 and, since then, deforestation rates have been low (Miranda et al. 2015). An important future analytical step to support conservation action for the guiña will be to integrate our statistical models with spatial landcover data to predict how extinction probability is distributed in the landscape (Ewers, Marsh & Wearn 2010) which, in turn, can be used to identify habitat networks in need of protection.

The research presented here demonstrates the benefits of integrating ecological and social knowledge into a single modelling framework to gain a more systematic understanding of the drivers of species decline in a human-dominated landscape. It has allowed us to tease apart the relative importance of different threats to a carnivorous mammal and make informed recommendations as to where future conservation efforts should be prioritised over a large landscape.

3.6. Acknowledgements

We thank the Chilean Ministry of the Environment (FPA 9-I-009-12), Robertson Foundation, Recanati-Kaplan Foundation and Marie Curie Fellowship Program (POIF-GA-2009-252682) for financial support, L. Petracca from Panthera provided satellite imagery and landcover classification, and all the landowners for permission to work on their properties and for completing the questionnaire. Futhermore, we are grateful to B.J. Smith, A. Dittborn, J. Laker, C. Bonacic, G. Valdivieso, N. Follador, D. Bormpoudakis, T. Gálvez and C. Ríos for their support. NG received a postgraduate scholarship from the Chilean National Commission for Scientific and Technological Research (CONICYT-Becas Chile).

3.7. References

Acosta-Jamett, G. & Simonetti, J.A. (2004) Habitat use by Oncifelis guigna and Pseudalopex culpaeus in a fragmented forest landscape in central Chile. Biodiversity & Conservation, 13, 1135-1151.

Armesto, J., Rozzi, R., Smith-Ramírez, C. & Arroyo, M. (1998) Conservation targets in South American temperate forests. Science, 282, 1271-1272.

Bagchi, S. & Mishra, C. (2006) Living with large carnivores: predation on livestock by the snow leopard (Uncia uncia). Journal of zoology, 268, 217-224.

Bender, D.J., Contreras, T.A. & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology, 79, 517-533.

Braun-Blanquet, J. (1965) Plant sociology: the study of plant communities. Hafner, London.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J. (2008) Synergies among extinction drivers under global change. Trends in ecology & evolution, 23, 453-460.

Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media. London.

Carmona, A., Nahuelhual, L., Echeverría, C. & Báez, A. (2010) Linking farming systems to landscape change: an empirical and spatially explicit study in southern Chile. Agriculture, Ecosystems & Environment, 139, 40-50.

Ceballos, G., Ehrlich, P.R., Soberon, J., Salazar, I. & Fay, J.P. (2005) Global mammal conservation: what must we manage?. Science, 309, 603-607.

Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S. & Clobert, J. (2008) The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology, 45, 1667-1674.

Clark, T.W., Mattson, D.J., Reading, R.P. & Miller, B.J. (2001) Interdisciplinary problem solving in carnivore conservation: an introduction. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp.223-240. Cambridge University Press, Cambridge.

Congalton, R.G. (1991) A review of assessing the accuracy of classifications of remotely sensed data. Remote Sensing of Environment, 37, 35-46.

Delibes-Mateos, M., Díaz-Ruiz, F., Caro, J. & Ferreras, P. (2014) Activity patterns of the vulnerable guiña (Leopardus guigna) and its main prey in the Valdivian rainforest of southern Chile. Mammalian Biology, 79, 393-397.

Dickman, A.J. (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal conservation, 13, 458–466.

Di Minin, E., Slotow, R., Hunter, L.T.B., Pouzols, F.M., Toivonen, T., Verburg, P.H., Leader-Williams, N., Petracca, L. & Moilanen, A. (2016) Global priorities for national carnivore conservation under land use change. Scientific Reports, 6.

Dormann, C.F., M McPherson, J., B Araújo, M., Bivand, R., Bolliger, J., Carl, G., G Davies, R., Hirzel, A., Jetz, W. & Daniel Kissling, W. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography, 30, 609-628.

Dunstone, N., Durbin, L., Wyllie, I., Freer, R., Jamett, G.A., Mazzolli, M. & Rose, S. (2002) Spatial organization, ranging behaviour and habitat use of the kodkod (Oncifelis guigna) in southern Chile. Journal of zoology, 257, 1-11.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews, 81, 117-142.

Ewers, R.M., Marsh, C.J. & Wearn, O.R. (2010) Making statistics biologically relevant in fragmented landscapes. Trends in Ecology & Evolution, 25, 699-704.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics, 487-515.

Fahrig, L. (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications, 12, 346-353.

Fiske, I. & Chandler, R. (2011) unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software.

Gálvez, N., Hernández, F., Laker, J., Gilabert, H., Petitpas, R., Bonacic, C., Gimona, A., Hester, A. & Macdonald, D.W. (2013) Forest cover outside protected areas plays an important role in the conservation of the Vulnerable guiña Leopardus guigna. Oryx, 47, 251-258.

Guillera-Arroita, G., Ridout, M.S. & Morgan, B.J.T. (2010) Design of occupancy studies with imperfect detection. Methods in Ecology and Evolution, 1, 131-139.

Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H. & Jones, K. (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications, 15, 1893-1905.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004a) Predictors of Species Sensitivity to Fragmentation. Biodiversity and Conservation, 13, 207-251.

Henle, K., Lindenmayer, D.B., Margules, C.R., Saunders, D.A. & Wissel, C. (2004b) Species Survival in Fragmented Landscapes: Where are We Now?. Biodiversity and Conservation, 13, 1-8.

Hernandez, F., Galvez, N., Gimona, A., Laker, J. & Bonacic, C. (2015) Activity patterns by two colour morphs of the vulnerable guiña, Leopardus guigna (Molina 1782), in temperate forests of southern Chile. Gayana, 79, 102-105.

Hines, J.E. (2006) PRESENCE v.6.4 -Software to Estimate Patch Occupancy and Related Parameters.

Hughes, J. & Macdonald, D.W. (2013) A review of the interactions between free-roaming domestic dogs and wildlife. Biological Conservation, 157, 341-351.

Inskip, C., Fahad, Z., Tully, R., Roberts, T. & MacMillan, D. (2014) Understanding carnivore killing behaviour: Exploring the motivations for tiger killing in the Sundarbans, Bangladesh. Biological Conservation, 180, 42-50.

Inskip, C. & Zimmermann, A. (2009) Human-felid conflict: a review of patterns and priorities worldwide. Oryx, 43, 18-34.

Kery, M., Guillera-Arroita, G. & Lahoz-Monfort, J.J. (2013) Analysing and mapping species range dynamics using occupancy models. Journal of Biogeography, 40, 1463-1474.

Lahti, D. (2001) The “edge effect on nest predation” hypothesis after twenty years. Biological Conservation, 99, 365-374.

Landis, J.R. & Koch, G.G. (1977) The measurement of observer agreement for categorical data. Biometrics, 159-174.

Lindenmayer, D.B. & Fischer, J. (2007) Tackling the habitat fragmentation panchreston. Trends in Ecology and Evolution, 22, 127-132.

Luebert, F. & Pliscoff, P. (2006) Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, London.

Marvier, M., Kareiva, P. & Neubert, M.G. (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk analysis, 24, 869-878.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: spatial pattern analysis program for categorical maps.

Miranda, A., Altamirano, A., Cayuela, L., Pincheira, F. & Lara, A. (2015) Different times, same story: Native forest loss and landscape homogenization in three physiographical areas of south-central of Chile. Applied Geography, 60, 20-28.

Napolitano, C., Gálvez, N., Bennett, M., Acosta-Jamett, G. & Sanderson, J. (2015a) Leopardus guigna. The IUCN Red List of Threatened Species 2015. URL http://www.iucnredlist.org/details/15311/0. [accessed 11 September 2015].

Napolitano, C., Johnson, W.E., Sanderson, J., O'Brien, S.J., Hoelzel, A.R., Freer, R., Dunstone, N., Ritland, K., Ritland, C.E. & Poulin, E. (2014) Phylogeography and population history of Leopardus guigna, the smallest American felid. Conservation Genetics, 15, 631-653.

Napolitano, C., Diaz, D., Sanderson, J., Johnson, W.E., Ritland, K., Ritland, C.E. & Poulin, E. (2015b) Reduced Genetic Diversity and Increased Dispersal in Guigna (Leopardus guigna) in Chilean Fragmented Landscapes. The Journal of heredity, 106, 522-536.

Nowell, K. & Jackson, P. (1996) Wild cats: status survey and conservation action plan. IUCN Cat Spcialist group. Switzerland.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. Proceedings Biological sciences, 267, 1947-1952.

R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org [accessed 01 June 2015]

Rojas, I., Becerra, P., Gálvez, N., Laker, J., Bonacic, C. & Hester, A. (2011) Relationship between fragmentation, degradation and native and exotic species richness in an Andean temperate forest of Chile. Gayana.Botanica, 68, 163.

Sala, O.E., Stuart, C., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. &

Wall, D.H. (2000) Global Biodiversity Scenarios for the Year 2100. Science, 287, 1770-1774.

Sanderson, J., Sunquist, M.E. & W. Iriarte, A. (2002) Natural history and landscape-use of guignas (Oncifelis guigna) on Isla Grande de Chiloé, Chile. Journal of mammalogy, 83, 608-613.

Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T. & Trepl, L. (2002) Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecological Applications, 12, 1469-1483.

Sepúlveda, M.A., Singer, R.S., Silva-Rodríguez, E., Stowhas, P. & Pelican, K. (2014) Domestic dogs in rural communities around protected areas: conservation problem or conflict solution?. PLoS One, 9, e86152

Sillero-Zubiri, C. & Laurenson, M.K. (2001) Interactions between carnivores and local communities: Conflict or co-existence?. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 282-312. Cambridge University Press, Cambridge.

Silva-Rodríguez, E.A. & Sieving, K.E. (2012) Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. Biological Conservation, 150, 103-110.

Silva-Rodriguez, E., Ortega-Solis, G.R. & Jimenez, J.E. (2010) Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile. Austral Ecology, 35, 765-777.

St John, F.A., Keane, A.M. & Milner-Gulland, E.J. (2013) Effective conservation depends upon understanding human behaviour. Key Topics in Conservation Biology, 2nd ed (eds D. Macdonald & K.J.Willis), pp 344-361. Blackwell, Oxford.

St John, F.A.V., Edwards-Jones, G., Gibbons, J.M. & Jones, J.P.G. (2010) Testing novel methods for assessing rule breaking in conservation. Biological Conservation, 143, 1025.

St John, F.A.V., Keane, A.M., Edwards-Jones, G., Jones, L., Yarenell, R.W. & Jones, J.P.G. (2012) Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. Proceedings of the Royal Society: series B biological sciences, 279, 804-812.

Theobald, D.M., Miller, J.R. & Hobbs, N.T. (1997) Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning, 39, 25-36.

Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology, 17, 1491-1499.

Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A. & Wydeven, A.P. (2004) Predicting human-carnivore conflict: A spatial model derived from 25 years of data on wolf predation on livestock. Conservation Biology, 18, 114-125.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. (2006) Co-managing human–wildlife conflicts: a review. Human Dimensions of Wildlife, 11, 383-396.

Veríssimo, D. (2013) Influencing human behaviour: an underutilised tool for biodiversity management. Conservation Evidence, 10, 29-31.

Western, D., Groom, R. & Worden, J. (2009) The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. Biological Conservation, 142, 2538-2546.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005) People and wildlife, conflict or co-existence?. Cambridge University Press, Cambridge.

3.8. Supporting Information

3.8.1. Appendix 3.S1: Generation of the habitat loss/fragmentation predictors used to model multi-season occupancy dynamics of guiña (Leopardus guigna)

A total of ten habitat loss/fragmentation predictors were chosen for inclusion in the analyses, based on various hypothesis related to how habitat factors may influence guiña detectability, occupancy, colonisation and extinction probabilities. Landcover classification was carried out using a composite of four Aster images at 15 m resolution from between 2002 and 2007. Native forest cover within the study region did not change significantly between 1983 and 2007 (Petitpas 2010; Miranda et al. 2015). In addition, the current extent and configuration of forest across the sample units (SUs) has not altered perceptibly when compared visually with up-to-date Google Earth imagery from 2014. The study region was categorised into nine landcover classes (list them here…) using a supervised classification with maximum likelihood estimation, based on field data from 738 training points. A further 738 points were used to verify classification accuracy, which was ‘almost perfect’ (Kappa= 0.81 (SE= 0.017); (Landis & Koch 1977; Congalton 1991). Image processing and classification were conducted in ERDAS Imagine 2014 (Hexagon Geospatial, Norcross, GA, USA) and ArcMap v.10.1 (ESRI, Redlands, CA, USA).

We extracted forest extent, continuity and length of edge as habitat compositional metrics (Table 3.1 & Table 3.S1) using FRAGSTATS 4.1 (McGarigal et al. 2002). As shrub can be considered a marginal habitat for the guiña (Dunstone et al. 2002; Sanderson, Sunquist & W. Iriarte 2002; Acosta-Jamett & Simonetti 2004), we also measured the extent of shrub cover to evaluate possible additive effects with habitat cover (Table 3.1 & Table 3.S1). Habitat configuration was evaluated using metrics such as the landscape shape index (Table 3.1 & Table 3.S1).

We tested all predictors for collinearity. For correlated variables (Pearson's or Spearman's $|r| > 0.7$), we retained the covariate that conferred greater biological/social meaning and ease of interpretation (Table 3.1). Amount of habitat, rather than configuration, is highly relevant for species survival (Fahrig 2002) and previous research has indicated that this is likely to be true for the guiña specifically (Gálvez et al. 2013). We therefore prioritised extent of habitat against other compositional metrics (e.g. mean patch size area). All continuous variables were standardized to z-scores, except percentage values as they are already in a suitable scale.

3.8.2. Appendix 3.S2: Generation of the human encounter/pressure predictors used to model multi-season occupancy dynamics of guiña (Leopardus guigna)

A total of five human encounter/attitude predictors were chosen for inclusion in the analyses, based on various hypothesis related to how human factors may influence guiña detectability, occupancy, colonisation and extinction probabilities (Tables 3.1 & 3.S1). These were derived using a questionnaire (a translated version can be requested from the corresponding author).

The questionnaire consisted of six sections. The first part included socio-demographic/economic questions relating to age, amount of schooling, livelihood activities and income. The next section focussed on questions regarding killing wild animals, including species with protected (e.g. puma/ guiña) and non-protected status (e.g. introduced wild boar). To prevent any bias in responses, our questions included all native carnivores known to occur across the study region, as well as free-roaming domestic dogs. As killing of protected species is an illegal activity, we employed the randomized response technique (RRT) method described in St John et al. (2010; 2012). A dice was used a randomization tool; respondents were asked to provide a truthful answer if they rolled a one, two, three or four, must answer “yes” if they rolled a five (irrespective if it is true answer or not) and must answer “no” if the dice landed on six. The time period used to provide context to the question was ‘over the last ten years’, which was deemed most appropriate after the pilot exercise. Trial runs were conducted with non-sensitive questions to ensure rules were understood and being followed by the respondents. Special care was taken to ensure that the interviewer could not see the number on the rolled dice.

The third part of the questionnaire asked respondents to report livestock losses via predation over the past year, or an alternative time period they could quantify. In the fourth section, participants were probed about their knowledge of whether the hunting of each species was permitted or illegal, as well as asking how frequently the species were encountered during an alternative time period they could quantify. A fifth section aimed to evaluate scenarios of predation with a hypothetical livestock holding of 100 sheep and chickens. Respondents were asked what behaviour they would display towards the carnivores occurring in the study region after a specific level of predation (2, 10, 25, 50, >50 sheep or chickens) has been experienced. For sheep predation, we assessed the puma (Puma concolor) and domestic dogs (Canis familiaris), and for chicken predation we asked about guiña and Harris hawk (Parabuteo unicinctus). Respondents were offered a choice of possible actions that fell into the following categories: improvement of management through the use of enclosures, calling wildlife authorities to alert them to the presence of the species, non-lethal capture and handover to the authorities, use of predator deterrents and control via killing. The final section centred on the management of livestock, particularly sheep and chickens, in relation to behaviour such as enclosing livestock at night, the distance of the closure from household, the number of domestic dogs/cats associated with the property and how they are managed overnight (e.g. free-roaming, tethered), as well as how often they are fed and the type of food they are given.

3.8.3. Appendix 3.*S*3: Table 3.*S*1

Table 3.S1: Description of habitat loss/fragmentation, human encounter/attitude and microhabitat predictors used when modelling occupancy (ψ), colonisation (γ), extinction (ε) and detection (p) probability parameters of multi-season camera-trap surveys of guiña (Leopardus guigna). Further details can be found in Table 3.1.

Predictor	**Abbreviation in models**	**Description**
Habitat loss/fragmentation		
Percent forest cover	Forest	Area-edge metric that measures habitat loss as the extent of forest cover in a sample unit (0-100). Forest cover was obtained by pooling old-growth and secondary forest landcover classes, which are both considered to be suitable guiña habitat ((Nowell & Jackson 1996; Acosta-Jamett & Simonetti 2004).
Percent shrub cover	Shrub	Area-edge metric that measures the extent of shrub cover in a sample unit (0-100). The spatial configuration is not assessed because shrub is a marginal habitat.
Number of forest patches	PatchNo	Area-edge metric that measures the number of habitat patches (0-∞).
Shape index forest patches	PatchShape	Shape metric that measures the complexity of habitat patch shape compared to a square, weighted for the entire landscape. As the index value increases, that habitat patch shape is more irregular (1-∞).
Forest patch size area[†]	PatchAreaW	Area-edge metric that measures mean habitat patch area (0-∞) weighted for the entire landscape. It provides a landscape centric perspective of patch structure.
Forest patch continuity[†]	Gyration	Area-edge metric that measures habitat patch continuity (0-∞). It can be interpreted as the average distance an organism can move within the habitat before an edge is encountered (McGarigal et al. 2002). The value increases with greater habitat patch extent.

Predictor	Abbreviation in models	Description
Edge length of forest	Edge	Area-edge metric that measures the total length (0-∞) of habitat patch edge across a sample unit. This can be used instead of density because we are comparing sample units of the same size (McGarigal et al. 2002). The value rises with increasing edge.
Landscape shape index of forest‡	LSI	Aggregation metric that compares the landscape level edge of the habitat to one without internal edges or a square (0-100). This is a measure of the level of fragmentation in a sample unit.
Patch Cohesion†	COH	Aggregation metric that measures the physical connectedness (0-1) of habitat cover by measuring the aggregation of patches.
Land subdivision	Subdivision	Measures the number of land tenure divisions (i.e. owners) in a sample unit (0-∞). We expect higher subdivision to represent greater anthropogenic preassure from factors such as logging and presense of domestic dogs which were not measured directly in each sample unit (e.g. (Theobald, Miller & Hobbs 1997; Hansen et al. 2005; Western, Groom & Worden 2009).
Human encounters/attitudes		
Intent to kill	Intent	Intent to kill the guiña by households in a sample unit (categorical: yes= 1, no= 0). This measure describes a hypothetical response by the respondent to the predation of two chickens. It is a highly conservative indicative measure of tolerance to livestock predation before retribution killing is considered.
Predation	Predation	Occurrence of chicken predation by the guiña in a sample unit (categorical: yes= 1, no= 0).
Frequency of predation	FQPredation	Frequency of chicken predation by the guiña in a sample unit. Predation events were scaled to yearly frequency (0-∞).
Frequency of encounters§	FQEncounter	Numbers of encounters householders have had with the guiña, scaled to a yearly frequency (0-∞). Frequency of encounters is also used to fit detection probability as a proxy for the elusiveness of the species.
Number of dogs	Dogs	Maximum number of free-roaming dogs, owned by the household, at night in proximity to the camera-traps (0-∞). We assume this value to be a conservative proxy to dog activity and an index of interference/competition by dogs. We also fitted extinction probability with free roaming dogs as they have been documented to interfere and kill wildlife in Chile (Silva-Rodriguez, Ortega-Solis & Jimenez 2010; Silva-Rodríguez & Sieving 2012), therefore we included average number of free roaming domestic

Predictor	Abbreviation in models	Description
		dogs of nearby households (from our questionnaire Appendix S3) as a potential source of mortality. Because the guiña is mainly nocturnal (Delibes-Mateos et al. 2014; Hernandez et al. 2015) we excluded households that restrain dogs at night.
Microhabitat§		
Bamboo density (Chusquea spp.)	Bamboo	Bamboo density (Chusquea spp.) within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
Density of understory	Understory	Understory vegetation density within a 25 m radius of each camera-trap, recorded in five categorical percentage classes (Braun-Blanquet 1965).
SU rotation	Rotation	Each SU was included in one of four consecutively sampled rotations of camera-traps during each season.
Intensity of livestock activity	Livestock	Livestock activity was visually estimated next to each camera-trap, using three categories (high, medium or low intensity, based on signs such as presence of animals, grazed vegetation, trampled paths and manure).
Intensity of logging activity	Logging	Logging activity was visually estimated next to each camera-trap, using three categories (high, medium or low intensity, based on signs such as active firewood piles, clearings, logging paths, fresh stumps and fallen logs).
Water availability	Water	The availability of water was recorded as either present or absent at the patch level during each season (categorical: yes= 1, no= 0).

†Predictor excluded due to collinearity with percent of forest cover (Pearson's│r│>0.7)

‡Predictor excluded due to collinearity with number of forest patches (Pearson's│r│>0.7)

§Predictors fitted only with detection probability at the forest patch level

4. Predator killing in human-dominated landscapes: understanding the prevalence and drivers of human behaviour

Authors

Gálvez, N., St. John, F.S.V, Davies, Z.G. Submitted to Biological Conservation

4.1. Abstract

1. Human activities are driving the extinction of predators. Most species populations rely on habitats within human-dominated landscapes because protected areas are not sufficient to secure long-term survival. Predators that kill livestock in agricultural areas are often killed by farmers, which can have negative implications for the both the species and ecosystem integrity.
2. We assessed the prevalence of predator killing behaviour by farmers for a suite of native and introduced predators via a questionnaire. We did this using the randomised response technique (RRT), a method designed to pose sensitive questions to people, as the killing of carnivores often illegal. Furthermore, we evaluated a range of potential explanatory variables which might predict killing behaviour.
3. A total of 233 farmers completed the questionnaire which included sections on predator-killing behaviour, knowledge of hunting laws and whether it was permissible to kill a predator, encounter rates with predators, the number of livestock predated per year, reported behavioural responses to a hypothetical livestock predation event and various socio-demographic/economic characteristics.
4. The majority of respondents correctly stated the hunting laws of individual species, with the exception of the domestic dog. Reported encounter rates were low for felid species, high for canids and birds of prey. Farmers reported that the main predators of sheep were pumas and domestic dogs, whilst for poultry it was the guiña, foxes and hawks. The proportion of farmers admitting to killing predators

was highest for hawks (0.46, SE= 0.08), foxes (0.29, SE= 0.08) and dogs (0.30, SE= 0.08).

5. Knowledge of hunting laws did not explain killing behaviour by farmers, with legal protection not acting as a deterrent. Across the suite of predators, killing behaviour was predicted by the dependency of a farmer on his land parcel for their livelihood, frequency of predator encounters, levels of livestock predation and hypothetical behavioural response of killing a predator. However, the combination of these predictors that are significant for a species varied. Respondents who depend upon agricultural activities for their livelihood and report higher encounter frequency were more likely to kill the guiña, the only predator of conservation concern in the landscape.
6. Synthesis and application: Information campaigns focused on hunting laws are unlikely to make an important contribution to effective conservation strategies within the study region. For the guiña and foxes, interventions aiming to improve poultry management might reduce killing behaviour towards these species. For hawks, information campaigns highlighting the pest control benefits of the species are likely to be more successful. Domestic dogs are contentious predators and efforts to advocate responsible ownership should reduce sheep predation and thus dog lethal control. Studies such as this, which explicitly assess people's behaviour towards a range of predators across a large geographical area, are a necessary first step to developing informed and effective conservation interventions with local communities.

Key-words: agriculture, behavioural intent, carnivores, conservation, illegal behaviour, Leopardus guigna, livestock predation, predator control, random response technique, retribution killing.

4.2. Introduction

Human activities are driving the unprecedented levels of biodiversity loss we are currently experiencing globally (Barnosky et al. 2011). Predators inhabiting human-dominated landscapes, such as carnivorous mammals and birds of prey, are particularly prone to extinction because of their slow life histories (Purvis et al. 2000). The anthropogenic threats they face are diverse, arising from activities such as land-use change, habitat degradation, hunting for meat or trade, and retribution killing after livestock predation events or attacks on people (Ceballos & Ehrlich 2002; Treves & Karanth 2003; Cardillo et al. 2004; Woodroffe, Thirgood & Rabinowitz 2005; Inskip & Zimmermann 2009)).

Historically, human persecution of predators has been responsible for species population declines and contributed to extinction events (Woodroffe 2001). Killing individual mammals, particularly females, can have profound effects on the long-term local persistence of a species (Chapron et al. 2008). Furthermore, eliminating predators from landscapes may have knock-on impacts on ecosystem integrity and function (Sekercioglu 2006; Bruno & Cardinale 2008; Ripple et al. 2014). Human persecution is, therefore, often a focus of conservation interventions.

Understanding what drives a person to behave in a manner that is detrimental to conservation efforts, such as the killing of predators, is important if practitioners or policy-makers are to develop successful strategies to alter the behaviour or stop it occurring in the future. In recent years there has been a proliferation of studies examining people's attitudes towards specific environmental issues. However, these can be misleading because the attitudes people express rarely translate into a corresponding behaviour (Herberlein 2012). From a conservation perspective, behaviour is evaluated more frequently using social-psychology models that account for factors including subjective norms (the social pressures people perceive to engage or not in a behaviour) and the level of control people perceive they have over performing a particular act (in terms of the required skills or resources), in addition to personal beliefs and attitudes (Manfredo & Dayer 2004). Another layer of complexity comes from the fact that some conservation relevant human behaviours are also highly sensitive or illegal, making them hard to investigate as potential research participants may not wish to engage in a study for fear of punishment (St John, Keane & Milner-Gulland 2013).

In this paper we incorporate the randomised response technique (RRT), a method used explicitly to ask sensitive questions, into a questionnaire, with the aim of estimating the prevalence of predator killing by people living across an extensive agricultural landscape. While such assessments have been conducted in the past on carnivores, they have always been relatively localised in their scale (St John et al. 2012; St John, Mai & Pei 2014). We examined the proportion of our respondents who have killed nine legally protected predators, benchmarking these evaluations to those for three species the public is permitted to control via lethal means and free-roaming domestic dogs.

Additionally, we determined whether there are particular factors that can used to predict whether or not a person will exhibit persecution behaviour across the suite of predators. We selected our potential explanatory variables from six categories that represent different hypotheses, supported by existing literature, regarding what might drive a farmer to kill a predator: (i) socio-demographics/economics characteristic such as age, amount of schooling, livelihood activities and annual household income, as these can be associated with attitudes towards predators (Romanach, Lindsey & Woodroffe 2007) and behaviour (St John, Edwards-Jones & Jones 2010); (ii) economic loss as a result of livestock predation (Treves & Bruskotter 2014); (iii) the frequency of opportunistic encounters, which may facilitate the hunting of a predator (Sanderson, Sunquist & W. Iriarte 2002; Romanach, Lindsey & Woodroffe 2007); (iv) a lack of knowledge of the legal protection policies in place to preserve predators (Treves & Karanth 2003); (v) the perceived behavioural control the farmer has to kill a predator (i.e. if he/she has the skills and/or resources to carry out the behaviour) (Williams et al. 2012; Marchini & Macdonald 2012); and, (vi) behavioural intent, which has been used in the past as a proxy for estimating rates of large carnivore killing (Marchini & Macdonald 2012) and predation tolerance (Romanach, Lindsey & Woodroffe 2007).

The fate of most predators will ultimately depend on management and interventions within human-dominated landscapes (Sunquist & Sunquist 2001; Cardillo et al. 2004), meaning that an in-depth understanding of the prevalence and drivers of killing behaviour is necessary to provide a robust evidence-base for the development of effective conservation interventions. Here we examine how killing behaviour can vary between species, and the implications this has for mitigation strategies.

4.3. Methods

4.3.1. Study system and sampling

The study was conducted in the Tolten catchment of the Araucanía region in southern Chile, just at the northern limit of the South American temperate forest ecoregion (39º15´S, 71º48´W) (Armesto et al. 1998). The system comprises two distinct geographical sections common throughout southern Chile: the Andes mountain range and the central valley. Land- use in the latter is primarily intensive agriculture (e.g. cereals, livestock, fruit trees) and urban settlements, while in the Andes mountain agricultural lands become less intensively farmed (i.e. extensive livestock production and forestry) and are within narrow valleys surrounded by continuous forest tracks on high slopes which also include protected areas (Fig. 4.1). A grid of 4 km^2 potential sampling units (SUs) was laid across the study region, representing a gradient of forest habitat fragmentation due to agricultural use and human settlement below 600 m.a.s.l. A total of 145 SUs were selected at random from the 230 in the grid, with 73 and 72 located in the central valley and Andes mountain valley respectively (Fig. 4.1).

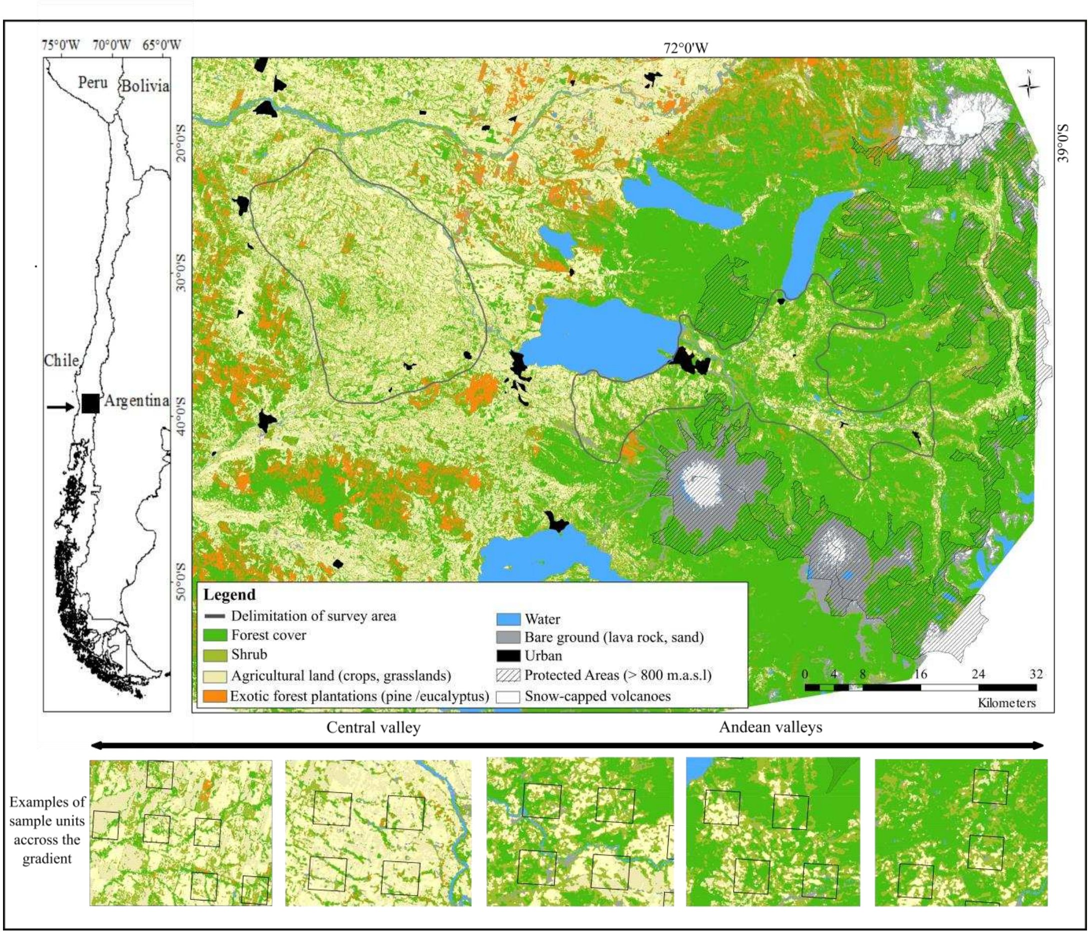

Figure 4.1 Landcover classes and protected areas of the study region (Araucanía Region of southern Chile). We have indicated the two zones within which the 145 sample units (SUs: 4 km^2 each) were located, with 73 SUs in the central valley (left polygon) and 72 in within the Andes (right polygon). The positions of each SU are not shown to comply with the ethical guidelines associated with studying illegal human behaviour. Illustrative examples of SUs across the gradient are shown (bottom of the figures). In each SU one or two households were surveyed.

The questionnaire (Appendix 4.S1 in supplementary information) was administered face-to-face with residents living in one or two households per SU during May to September 2013. N. Gálvez, who has lived in the study region for over 10 years, delivered all the questionnaires to ensure there were no discrepancies between SUs, or any cultural/language barriers with respondents.

4.3.2. Study species

Our questionnaire focussed on all native predators which occur across the study region and will hunt small domesticated ruminants and/or poultry: (i) puma (Puma concolor), the largest predator present in Chile and known to predate ruminants (Murphy & Macdonald 2010); (ii) guiña (Leopardus guigna) is the smallest wild felid in the neotropics with a distribution restricted primarily to Chile and known to predate poultry (Sanderson, Sunquist & W. Iriarte 2002; Gálvez et al. 2013); (iii) culpeo fox (Lycalopex culpaeus), a canid which will predate both small ruminants and poultry (Macdonald & Sillero-Zubiri 2004); (iv) chilla fox (Lycalopex griseus), another canid which will predate both small ruminants and poultry (Macdonald & Sillero-Zubiri 2004); (vi) Harris hawk (Parabuteo unicinctus); (vi) variable hawk (Geranoaetus polyosoma); and, (vii) chilean hawk (Accipiter bicolor). All the raptors are known to predate poultry (Jimenez 1986). To reduce the bias associated with respondents misidentifying species, we treated both canid species as ‘foxes’ and all diurnal birds of prey as ‘hawks’ in the analyses. Additionally, we included: (viii) the lesser grison (Galictis cuja), reported to predate on poultry (Silva-Rodríguez, Ortega-Solís & Jiménez 2007); and, (ix) Molina’s hog-nosed skunk (Conepatus chinga), which is considered a nuisance, rather than a predator of livestock. All nine of these native predators are protected by Chilean law, meaning that hunting them is prohibited. The only threatened species is the guiña (Table 4.2).

To examine whether the killing behaviour of respondents alters, dependent on if species is legally protected and or not, we also included three introduced species which people are allowed to hunt without restriction: (i) hare (Lepus capensis); (ii) rabbit (Oryctolagus cuniculus); and, (iii) wild boar (Sus scrofa). Once again, we group the hare and rabbit together for analyses and refer to them as ‘lagomorphs’. Free roaming domestic dogs (Canis familiaris) are an increasing problem in rural areas as they predate not only wildlife (Sepúlveda et al. 2014), but also livestock, especially small ruminants (Murphy & Macdonald 2010). Currently, dogs are not mentioned in the Chilean hunting law and, as such, they are not legally protected when roaming on private lands and ownership of the dog is unknown. We therefore included dogs in our survey to evaluate if people behave differently when it is a domestic species, closely associated with human activities, that predates on livestock.

4.3.3. Questionnaire development

The aim was to solicit information from the human inhabitants of the study region regarding their socio-demographic/economic background, predator encounters, the extent of livestock predation, tolerance of livestock predation, whether a retribution killing had ever been undertaken, and ownership of dogs on the land parcel. The questionnaire consisted of six sections. The first part included socio-demographic/economic questions relating to age (years), amount of schooling (years), livelihood activities (categorical) and annual household income (continuous). Before the data were analysed, the dependency of residents on their land parcel for their livelihood was converted into one of three categories: 1= did not depend on their land; 2= indirectly dependant on agricultural practices but received a salary from neighbouring farms; and, 3= income depended mainly on agricultural activities on their land such as growing crops and livestock.

The second part consisted of the questions regarding killing wild animals. Because of the sensitive nature of the questions, we employed the randomized response technique (RRT) method described in St John et al. (2010; 2012). A dice was used a randomization tool; respondents were asked to provide a truthful answer if they rolled a one, two, three or four, must answer “yes” if they rolled a five (irrespective if it is true answer or not) and must answer “no” if the dice landed on six. The time period used to provide context to the question was ‘over the last ten years’, which was determined after the pilot exercise. Respondents during pilots stated that these events were highly memorable and the time period was deemed most appropriate. During questionnaires, trial runs were conducted with non-sensitive questions to ensure rules were understood and being followed by the respondents. Special care was taken to ensure that the interviewer could not see the number on the rolled dice.

The third part of the questionnaire asked respondents to report livestock losses via predation over the past year, or an alternative time period they could quantify and we could then convert to an annual measure. The same alternative time period was asked for encounters with the predators. In the fourth section, participants were probed about their knowledge of whether the hunting of each species was permitted or illegal, as well as asking how frequently the species were encountered (number of encounters per unit of time). The hunting law in Chile (Number 19.473 of the Ministry of Agriculture) – the only official regulatory framework that dictates species under protection and sets quotas for species that are allowed to hunt - has been in effect since

1991 and there is constant dissemination of the rules via statutory agricultural agencies. Domestic dogs are not included in this law, and in practice, they are not protected from shooting when in private property. Responses to the questions on knowledge of hunting rules were categorised prior to data analysis as follows: 0= considered hunting of the species to be prohibited; 1= did not know; or, 2= considered hunting of the species to be permitted.

A fifth section aimed to evaluate scenarios of predation with a hypothetical livestock holding of 100 sheep and chickens. Respondents were asked what behaviour they would display towards the carnivores occurring in the study region after a specific level of predation (2, 10, 25, 50, >50 sheep or chickens) has been experienced. For sheep predation, we assessed the puma and domestic dogs, and for chicken predation we asked about guiña and 'hawks'. In order not to bias responses, respondents were offered a choice of possible actions that fell into the following categories: improvement of management through the use of enclosures, calling wildlife authorities to alert them to the presence of the species, non-lethal capture and handover to the authorities, use of predator deterrents and control via killing. Prior to analysis, we grouped scenario responses into three categories of increasing negative behaviour towards the predator species: 0= would remain passive and do nothing; 1= would carry out some sort of non-lethal or active management; or, 2= would carry out lethal control of the predator. To assess if farmers had access to the necessary skills and firearms required to hunt predators, we asked participants whether anyone in the household participates in sport hunting.

The final section centred on the current management of livestock, particularly sheep and chickens, in relation to behaviour such as enclosing livestock at night, the distance of the enclosure from the household, the number of domestic dogs/cats associated with the property and how they are managed overnight (e.g. free-roaming, tethered), as well as how often they are fed (meals per unit time) and the type of food they are given (categorical). A pilot was carried out with 10 local householders living outside the SUs, and feedback from this exercise helped to improve the wording and order of questions.

4.3.4. Data analysis

All data analyses were conducted in R version 3.2.0 (R Core Team 2015). For each species, the proportion of respondents who admitted to having killed at least one individual was estimated using the Hox and Lensvelt-Mulders model (Hox & Lensvelt-Mulders 2004), based on the following parameters:

$$\pi = \frac{\lambda - \theta}{s}$$

where π is the estimated proportion of people in the sample who have undertaken the behaviour, λ is the proportion of respondents who said “yes”, θ is the probability of the answer being a forced “yes”, s is the probability a respondent had to answer the question truthfully. A total of 10,000 bootstraps samples were run to calculate 95% confidence intervals, accounting for sample and RRT method uncertainty. All continuous predictors were z-transformed to standardise the scale of effects. Before exploring which of our explanatory variables may predict killing behaviour, we checked them for collinearity using a Spearman’s rank correlation coefficient matrix; where Spearman’s $|\text{rho}|>0.7$, one of the two variables was removed from the analysis. The RRlog function in the R package RRreg (version 0.5.0) was used to conduct the multivariate logistic regression with the forced response model. For each species, we fitted a logistic regression model with the potential predictors of killing behaviour and evaluate their significance with likelihood ratio tests (G^2).

4.4. Results

The questionnaire was completed in full by all 233 respondents, who were farmers, residing in households across the study region (Table 4.1). Most respondents were male (80%), had grown up in a rural area (80%), and live at their property full-time (97%). Only one farm was very large in size (1,200 ha), with the median being 29 ha. Respondents had 10 years of formal schooling on average, with 50% of people having received between 7 and 12 years of education. A high percentage of farmers (82%) reported that their dogs were left free to roam at night. The mean number of dogs per household was 3 (SE= 0.013; min= 1; max= 28).

Table 4.1 Socio-demographics/economic characteristics and livestock holdings of farmers, living within the agricultural landscapes of the Araucanía region in southern Chile, who completed our questionnaire (N= 233).

Socio-demographic/economic characteristics	Mean	SE	Median	Minimum	Maximum
Property size (ha)	98	0.85	29	1	1200
Time living at the property (years)	35	0.09	35	1	87
Age (years)	56	0.06	55	22	87
Amount of schooling (years)	10	0.01	10	0	18
Household income (USD per month)	558	2.81	341	59	5,934
No. of small ruminants	14	0.07	10	0	170
No. of chickens	23	0.09	18	0	120

Pumas, guiñas and the lesser grisson are rarely encountered by respondents, whereas hawks, foxes and lagomorphs are the most frequently observed species. Indeed, most of the farmers report seeing lagomorphs and hawks everyday (Table 4.2). The majority of respondents knew how the hunting law related to each species, with the exception of domestic dogs (Table 4.2).

The reported predators of sheep were puma (43% of farmers have experience livestock loss from the felid), domestic dogs (41%) and, to a much lesser extent, foxes (6%) (Fig. 4.2a). The number of sheep killed per year was similar across predators, with most respondents stating less than 10 are lost on average. However, there were some outliers, where dogs had killed substantial numbers of livestock. The main reported poultry predators were hawks (75%), foxes (50%) and guiña (16%) (Fig. 4.2b).

Table 4.2 Knowledge of how the Chilean hunting law relates to each of the predators in our study, and frequency of encounters with each species, as reported by our questionnaire respondents (N= 233) living within the agricultural landscapes of the Araucanía region in southern Chile. International Union for the Conservation of Nature (IUCN) Red List status is provided as an indication of conservation status. ‘Foxes’ refers to both culpeo and chilla foxes. ‘Hawks’ refers to all diurnal birds of prey. ‘Lagomorphs’ refers to rabbits and hares.

			Respondent knowledge of legal hunting status for each species (%)		Respondent encounters with species (per year)	
Species	IUCN Red List status	Hunting is legally permitted	Correct	Do not know	Mean (SE)	Median
Puma	LC	No	99	1	1.8 (0.02)	0.2

Guiña	V	No	79	17	0.2 (0.00)	0.0
Foxes	LC	No	94	3	41.2 (0.34)	12.0
Hawks	LC	No	78	15	204 (0.70)	360.0
M.H.N. Skunk	LC	No	70	20	23.7 (0.21)	12
Lesser grison	LC	No	62	30	2.8 (0.10)	0.0
Domestic dog	-	Yes	28	26	81.8 (0.57)	12.0
Lagomorphs	-	Yes	77	10	319.0 (0.45)	360.0
Wild boar	-	Yes	55	13	6.4 (0.11)	0.0

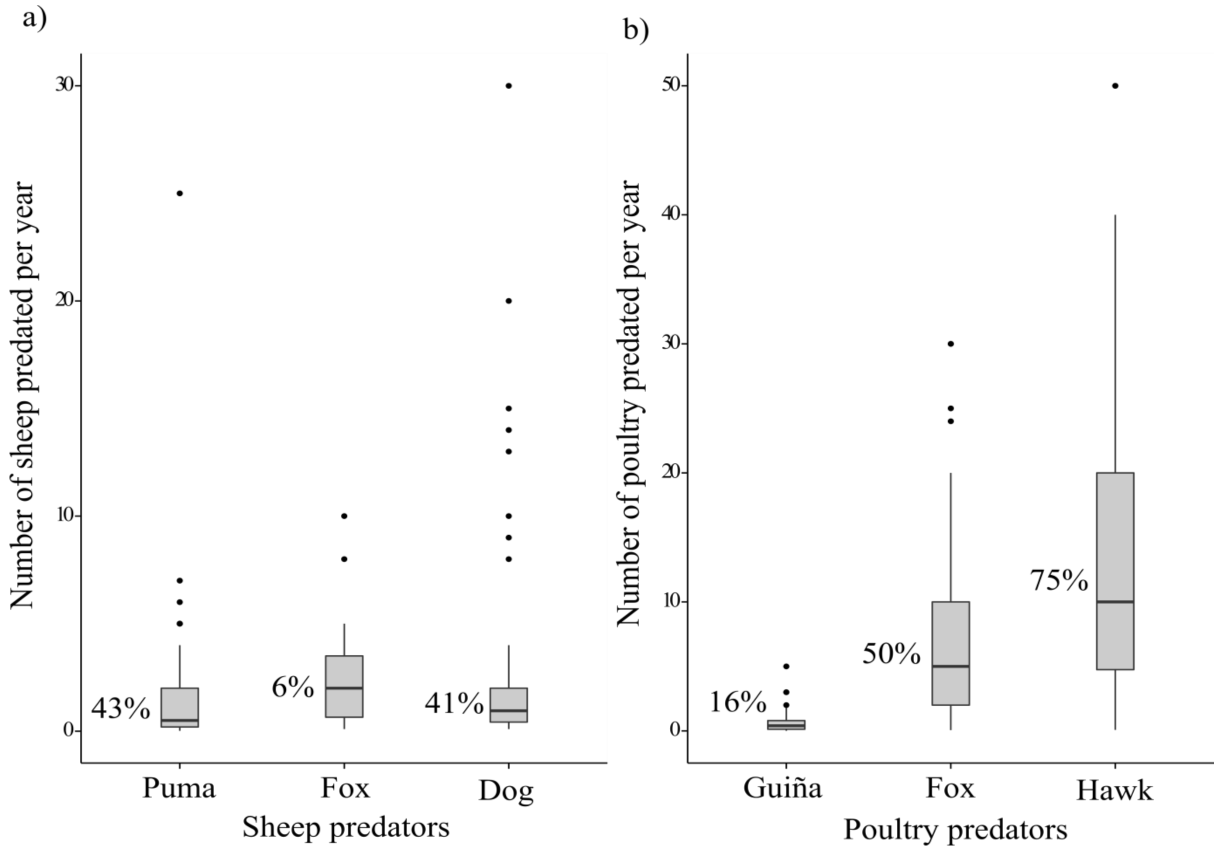

Figure 4.2 The number of reported attacks to (a) sheep and (b) poultry by predators per year, as stated by our questionnaire respondents (N= 233). The survey was conducted within the agricultural landscapes of the Araucanía region in southern Chile. The percentage of respondents reporting predation by each species is provided to left of each respective boxplot.

Across all our hypothetical predation scenarios, a significantly larger proportion of respondents said they would kill domestic dogs, compared to pumas (Fig. 4.3). Furthermore, the proportion of farmers stating that they would kill domestic dogs was relatively high (>0.6) across scenarios in contrast to the other predators, although rate of increase between low (two livestock loss) and high predation (>25 individuals killed) was greatest. For all predators, the proportion of respondents that would kill a predator remained constant after 25 animals had been predated.

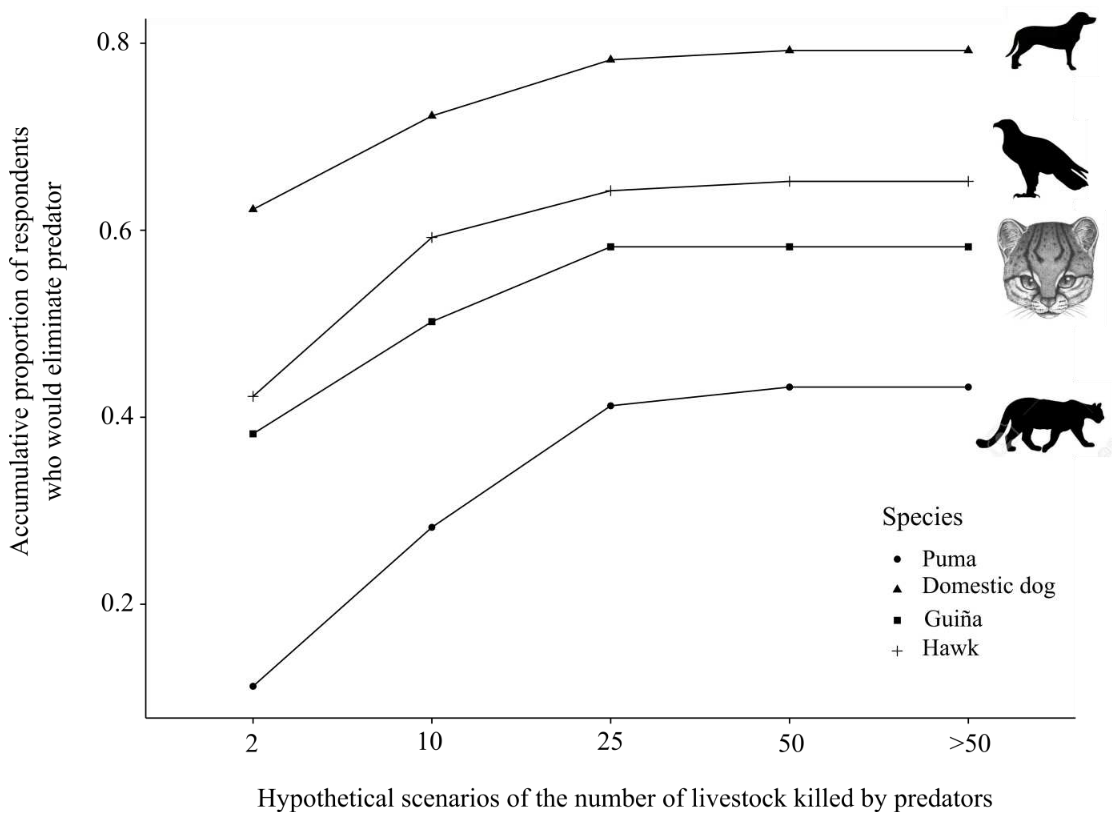

Figure 4.3 The proportion of questionnaire respondents (N= 233) who state they would kill a carnivore in response to the number of livestock predated in a hypothetical scenario. The survey was conducted within the agricultural landscapes of the Araucanía region in southern Chile. The baseline for each scenario was that a farmer had a total of 100 sheep or chickens, and experienced losses of 2, 10, 25, 50 and >50

individuals as a consequence of predation. The puma and domestic dog are assumed to be the sheep predators, whereas hawks and guiña are the poultry predators.

The proportion of respondents who have killed each species varied (Fig. 4.4). For the puma, the 95% confidence intervals overlap zero from very low number of “yes” responses, suggesting that the behaviour might be either insignificant, non-existent in the past decade within our sample. Only a small proportion of farmers report killing a guiña, while estimates for domestic dogs, foxes and hawks are greater. There are large differences in the proportion of respondents killing species that they are allowed to hunt legally; hunting of lagomorphs is widespread, but this is not the case for wild boar.

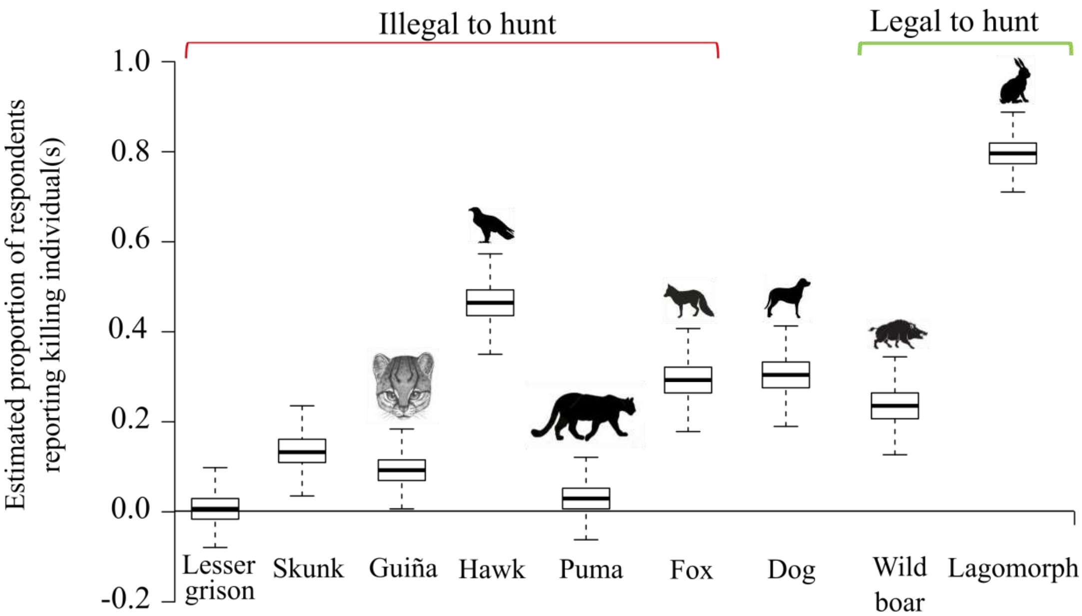

Figure 4.4 The proportion of questionnaire respondents (N= 233) who report they have killed at least one individual for each predator species in the past decade. The survey was conducted within the agricultural landscapes of the Araucanía region in

southern Chile. The species are grouped according to whether or not killing individuals is permissible under Chilean hunting law or not. Confidence intervals were obtained from 10,000 bootstraps.

A total of seven potential predictors of killing behaviour were retained after the collinear variables were excluded: (i) annual household income; (ii) the dependency of residents on their land parcel for their livelihood; (iii) number of chickens; (iv) correct knowledge of the Chilean hunting law; (v) predator encounter frequency; (vi) levels of livestock predation experience; and, (vii) hypothetical behavioural response towards predation of two livestock animals. The five most frequently reported predators were evaluated: puma, guiña, foxes, hawks, and domestic dogs (Fig. 4.2)

The predictors of killing behaviour varied depending on the species being examined (Table 4.3). For guiña, the probability of respondents having hunted an individual increased with dependency on their land parcel for their livelihood and more frequent encounters with the species. The former was also true for foxes. Hawk killing behaviour was positively related to encounter rate and the hypothetical behavioural response. In the case of domestic dogs, farmers were more likely to have hunted and killed them if livestock predation levels experienced were high and in line with their hypothetical behavioural response.

Table 4.3 Significant predictors ($p < 0.05$) of predator killing behaviour amongst questionnaire respondents (N= 233) within the agricultural landscape of the Araucanía region in southern Chile. The probability of a person exhibiting killing behaviour was estimated using an adapted multivariate logistic regression suitable for forced randomised response technique (RRT) data. For each predator species, a model was run with seven predictors: age (years), annual household income (USD), level of dependency on their land parcel for their livelihood (categorical), number of chickens kept as livestock, correct knowledge of how the Chilean hunting law relate to the predator (categorical), frequency of encounters with the predator (encounters/year), annual levels of livestock predation by the predator (animals lost/year) and the farmers hypothetical behavioural response to having two out of 100 livestock animals killed by the predator (categorical). Only significant predictors are shown.

Species	Predictors	Coefficient (SE)	ΔG^2 (p-value)
Guiña	Land parcel dependency	4.14 (3.35)	5.80 (0.01)
	Encounter frequency	5.37 (4.01)	8.57 (<0.00)
Foxes	Land parcel dependency	0.72 (0.34)	4.91 (0.02)
Hawks	Encounter frequency	0.61 (0.30)	4.22 (0.03)
	Hypothetical behavioural response	1.07 (0.41)	8.17 (<0.00)
Domestic dog	Predation level	3.60 (1.87)	6.67 (<0.00)
	Hypothetical behavioural response	2.93 (2.18)	12.58 (<0.00)

4.5. Discussion

In general, securing the long-term survival of predator populations in human-dominated landscapes requires effective conservation interventions (Linnell, Swenson & Anderson 2001). Before such measures can be implemented successfully, we must first understand what interactions are occurring between people and the species of interest, as well as quantifying the prevalence of potentially detrimental human behaviours and gaining an appreciation of what might be driving them.

Over three quarters of our questionnaire respondents knew how the hunting law in Chile related to each of the native predators occurring across the study region. The two exceptions, where people's knowledge was incorrect the majority of the time, were wild boar and domestic dogs. In both these cases, farmers believed that the species was illegal to hunt when, in fact, this is not the case. Our results demonstrate that knowledge of the hunting law and how it relates to a predator was not a significant predictor of killing behaviour. As such, people are not being compliant and the law may not be acting as a deterrent. This apparent disregard of the law is likely to be confounded by a lack of on-the-ground enforcement and low (perceived) risk of sanctions (Rowcliffe, de Merode & Cowlishaw 2004; Marchini & Macdonald 2012). Events where people get prosecuted for killing wildlife in Chile are scarce. While it may be impossible to eliminate all illegal human behaviours in a conservation context, improving tolerance and encouraging co-existence should be viable. For example, this could be mediated through information-based campaigns focused on promoting the positive benefits associated with the presence of predators in the landscape, rather than just dissemination of the legal situation (Slagle et al. 2013; Bruskotter & Wilson 2014).

Across the suite of predators, killing behaviour occurs where people are more dependent on their land parcel for their livelihood, encounters with the predator species are greater, predation levels are higher, and/or reflects their hypothetical behavioural response. However, the significant predictors did vary between species. Farmers who depend on income derived from their property were most likely to kill guiñas and foxes. Poultry production in these farming systems is mostly used as a subsistence source of protein, and is not directly related to income (which was not a significant predictor), and it appears that these rural households are more likely to defend their resources against these predators. For guiña and hawks, the frequency of encounters people have had with the species predict past killing acts. The guiña is the only threatened predator (Table 2) that is found within the agricultural landscape, and it is probable that their low encounter rate explains the relatively low prevalence of killing (Fig 4.4). In contrast, hawk encounters are reported as occurring very frequently (Table 4.2) and prevalence of killing hawks is substantially higher than for guiña (Fig. 4.4). Furthermore, the hypothetical response to predation is a good predictor of the killing of hawks and domestic dogs (Fig. 4.3).

Presented with the hypothetical scenario of a guiña predating on chickens, many farmers report that they would kill the offending animal, yet this was not a significant predictor of actual killing behaviour. This mismatch serves to highlight the negative attitudes people have towards the guiña in rural areas (Herrmann et al. 2013). If encounter rates were greater, our results suggest that the prevalence of guiña killing behaviour may be higher. People normally kill guiñas when caught inside the chicken coup (Sanderson, Sunquist & W. Iriarte 2002; Gálvez et al. 2013), so predator mitigation strategies should aim to reduce encounters with farmers through improving poultry management practices. Particularly night enclosures, for when the guiña is most active (Hernandez et al. 2015), are usually made from scrap pieces of wood that are easily trespassed by such a small cat (Gálvez & Bonacic 2008).

The only species for which reported livestock predation levels predict killings are domestic dogs. The hypothetical behaviour response of farmers to predation by dogs was the least tolerant across of the species, and was also a significant predictor of lethal control. Our findings, combined with anecdotal evidence from informal conversations with the respondents suggest attitudes towards domestic dogs in rural areas are very negative. Farmers continually mentioned domestic dogs as their main livestock predation "problem". Moreover, they described how people from urban settings, mainly from "animal rights groups", block potential solutions from statutory agencies, such as legislation in place which allows them to protect their livestock from domestic dogs by lethal control. This reflects the fact that more than two thirds of the questionnaire respondents are under the incorrect impression that domestic dogs are protected by Chilean hunting laws (Table 4.2). Based on the proportion of individuals who report having killed at least one dog in the previous 10 years, it appears that they believe or perceive that they have to take matters into their own hands. Policy-makers need to address this matter assertively. A comparable situation is found with tigers in Bangladesh, where the failure of the authorities to minimise livestock losses and human deaths has meant that killing predators has become a socially acceptable behaviour (Inskip et al. 2014). The difference here is that free roaming domestic dogs are not endangered predators, but are mostly uncontrolled pets from households. It is therefore a human-human conflict, given the vast majority of farmers do not tether or shut up their dogs overnight. As in other parts of Chile, farmers could become part of the solution by campaigning for more responsible ownership (Sepúlveda et al. 2014), which could reduce animal cruelty and improve dog welfare, as well as reducing livestock losses.

Predators will always come into contact with livestock in human-dominated landscapes, meaning that some level of predation is inevitable. Strategies need to focus on the mitigation of livestock losses by improved management but, most importantly, direct them to build tolerance in the farmers who are most likely to kill predators if the opportunity arises to do so (Treves & Bruskotter 2014). As shown here, tolerance to predation does not seem achievable as a result of disseminating information about legal protection. For example, it is likely that tolerance of hawks could only been increased through information campaigns which advocate the benefits and importance of birds of prey on the dynamics of rodents considered pest populations in agricultural land (e.g. Slagle et al. 2013). Involving local communities in the development of management strategies and solutions is crucial to fostering coexistence with predators (Treves et al. 2006) and a broader understanding of the social and environmental complexities of conflict, such as inequality, beliefs, values and land use and management amongst others, are needed to foster co-existence (Dickman 2010). Studies such as this, which explicitly assess people's behaviour towards a range of predators across a large geographical area, are a necessary first step to developing informed and effective conservation interventions with farmers residing in agricultural regions.

4.6. Acknowledgements

We thank the Chilean Ministry of the Environment (FPA 9-I-009-12), Robertson Foundation, Recanati-Kaplan Foundation and Marie Curie Fellowship Program (POIF-GA-2009-252682) for financial support, and all the respondents for participating in our questionnaire survey. Futhermore, we are grateful to A. Dittborn, J. Laker, C. Bonacic, G. Valdivieso, N. Follador, D. Bormpoudakis, T. Gálvez and C.

Ríos for their support. NG received a postgraduate scholarship from the Chilean National Commission for Scientific and Technological Research (CONICYT-Becas Chile).

4.7. References

Armesto, J., Rozzi, R., Smith-Ramírez, C. & Arroyo, M. (1998) Conservation targets in South American temperate forests. Science, 282, 1271-1272.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L. & Maguire, K.C. (2011) Has the Earth's sixth mass extinction already arrived?. Nature, 471, 51-57.

Bruno, J.F. & Cardinale, B.J. (2008) Cascading effects of predator richness. Frontiers in Ecology and the Environment, 6, 539-546.

Bruskotter, J.T. & Wilson, R.S. (2014) Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. Conservation Letters, 7, 158-165.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004) Human population density and extinction risk in the world’s carnivores. PLoS Biol, 2, e197.

Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. Science (New York, N.Y.), 296, 904-907.

Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S. & Clobert, J. (2008) The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology, 45, 1667-1674.

Gálvez, N., Hernández, F., Laker, J., Gilabert, H., Petitpas, R., Bonacic, C., Gimona, A., Hester, A. & Macdonald, D.W. (2013) Forest cover outside protected areas plays an important role in the conservation of the Vulnerable guiña Leopardus guigna. Oryx, 47, 251-258.

Herberlein, T.A. (2012) Navigationg Environmental Attitudes. Conservation Biology, 26, 583-586.

Hernandez, F., Galvez, N., Gimona, A., Laker, J. & Bonacic, C. (2015) Activity patterns by two colour morphs of the vulnerable guiña, Leopardus guigna (Molina 1782), in temperate forests of southern Chile. Gayana, 79, 102-105.

Herrmann, T.M., Schüttler, E., Benavides, P., Gálvez, N., Söhn, L. & Palomo, N. (2013) Values, animal symbolism, and human-animal relationships associated to two threatened felids in Mapuche and Chilean local narratives. J Ethnobiol Ethnomed, 9, 4269-4269.

Hox, J. & Lensvelt-Mulders, G. (2004) Randomized response analysis in Mplus. Structural equation modeling, 11, 615-620.

Inskip, C., Fahad, Z., Tully, R., Roberts, T. & MacMillan, D. (2014) Understanding carnivore killing behaviour: Exploring the motivations for tiger killing in the Sundarbans, Bangladesh. Biological Conservation, 180, 42-50.

Inskip, C. & Zimmermann, A. (2009) Human-felid conflict: a review of patterns and priorities worldwide. Oryx, 43, 18-34.

Jimenez, J.E. (1986) The conservation status of raptors in Chile. Birds of Prey Bulletin, 95-104.

Linnell, J.D., Swenson, J.E. & Anderson, R. (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation, 4, 345-349.

Macdonald, D.W. & Sillero-Zubiri, C. (2004) Wild canids-an introduction and dramatis personae. Biology and conservation of wild canids (eds D.W. Macdonald and C.Sillero-Zubiri.), pp 3-36.Oxford University Press, Oxford, United Kingdom.

Manfredo, M.J. & Dayer, A.A. (2004) Concepts for exploring the social aspects of human–wildlife conflict in a global context. Human Dimensions of Wildlife, 9, 1-20.

Marchini, S. & Macdonald, D.W. (2012) Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. Biological Conservation, 147, 213-221.

Murphy, T. & Macdonald, D.W. (2010) Pumas and people: lessons in the landscape of tolerance from a widely distributed felid. Biology and conservation of wild felids (eds A. Loveridge & D.W. Macdonald). pp 431-452, Oxford University Press. Oxford.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. Proceedings.Biological sciences / The Royal Society, 267, 1947-1952.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. Science (New York, N.Y.), 343, 1241484.

Romanach, S.S., Lindsey, P.A. & Woodroffe, R. (2007) Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. Oryx, 41, 185-195.

Rowcliffe, J.M., de Merode, E. & Cowlishaw, G. (2004) Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. Proceedings of the Royal Society, 271, 2631-2636.

Sanderson, J., Sunquist, M.E. & W. Iriarte, A. (2002) Natural history and landscape-use of guignas (Oncifelis guigna) on Isla Grande de Chiloé, Chile. Journal of mammalogy, 83, 608-613.

Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. Trends in ecology & evolution, 21, 464-471.

Sepúlveda, M.A., Singer, R.S., Silva-Rodríguez, E., Stowhas, P. & Pelican, K. (2014) Domestic dogs in rural communities around protected areas: conservation problem or conflict solution?. PLoS ONE 9, e86152.

Silva-Rodríguez, E.A., Ortega-Solís, G.R. & Jiménez, J.E. (2007) Human attitudes toward wild felids in a human-dominated landscape of southern Chile. Cat News, 46, 19-21.

Slagle, K., Zajac, R., Bruskotter, J., Wilson, R. & Prange, S. (2013) Building tolerance for bears: A communications experiment. The journal of wildlife management, 77, 863-869.

St John, F.A.V., Mai, C. & Pei, K.J. (2014) Evaluating deterrents of illegal behaviour in conservation: Carnivore killing in rural Taiwan. Biological Conservation.

St John, F.A., Keane, A.M. & Milner-Gulland, E.J. (2013) Effective conservation depends upon understanding human behaviour. Key Topics in Conservation Biology, 2nd ed (eds D. Macdonald & K.J.Willis), pp 344-361. Blackwell, Oxford

St John, F.A.V., Edwards-Jones, G., Gibbons, J.M. & Jones, J.P.G. (2010) Testing novel methods for assessing rule breaking in conservation. Biological Conservation, 143, 1025.

St John, F.A.V., Edwards-Jones, G. & Jones, J.P.G. (2010) Conservation and human behaviour: lessons from social psychology. Wildlife research, 37, 658.

St John, F.A.V., Keane, A.M., Edwards-Jones, G., Jones, L., Yarenell, R.W. & Jones, J.P.G. (2012) Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. Proceedings of the Royal Society, 279, 804-812.

Sunquist, M.E. & Sunquist, F. (2001) Changing landscapes: consequences for carnivores. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 399-418. Cambridge University Press, Cambridge.

Treves, A. & Bruskotter, J. (2014) Tolerance for predatory wildlife. Science, 344, 476-477.

Treves, A. & Karanth, K.U. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology, 17, 1491-1499.

Treves, A., Wallace, R.B., Naughton-Treves, L. & Morales, A. (2006) Co-managing human–wildlife conflicts: a review. Human Dimensions of Wildlife, 11, 383-396.

Williams, S.J., Jones, J.P., Clubbe, C. & Gibbons, J.M. (2012) Training programmes can change behaviour and encourage the cultivation of over-harvested plant species. PloS one, 7, e33012.

Woodroffe, R. (2001) Strategies for carnivore conservation: lessons from contemporary extinctions. Carnivore conservation (eds J.L. Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 61-92. Cambridge University Press, Cambridge.

Woodroffe, R. & Ginsberg, J. (2000) Ranging behaviour and vulnerability to extinction in carnivores. Behaviour and Conservation (eds L.M. Goslin &W.J. Sutherland), pp. 125-140. Press Syndicate of the University of Cambridge.

Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005) People and wildlife, conflict or co-existence?. Cambridge University Press.

4.8. Supplementary Information

4.8.1. Appendix 4.S1 Questionnaire

Respondent type Resident landowner where cameras were installed (1)_______ Non-resident landowner where cameras were installed (2)_______ Neiboring farm where cameras were set up (3)_______ Resident agricultural worker (4)_______ Other ______________________ (5)_______	**Questionnaire N°:**	
	DATE	
	GRID ID:	
	GENDER	

RRT	**YES**	**NO**		**YES**	**NO**		**YES**	**NO**		**YES**	**NO**		**YES**	**NO**
1			3			5			7			9		
2			4			6			8			10		
Have you killed species in the last 10 years?												11		

INFORMACIÓN DEL HOGAR		
12	What is the size of your property? há	
13	How long have you lived here? Where are you originally from?	
14	What is your age?	
15	What is your level of schooling?	
16	How many children do you have?	
17	Please classify in order of importance for your overall income, the following economic activities?	____Crops ___ Livestock ____Forestry ____Urban Services _____Agricultural services _____Tourism ____Subdivision of land for residential development _____ Other______

18	What is your average monthly income?	

4

Loss of domestic animals due to predation		Bovine	Ovine	Chickens	Otras Birds	Other
19	What are your ANIMAL holdings during the year					
20	In the last 10 years, how many animals have you lost because of the PUMA? If higher frequency, how frequent? and if further in the past, how many and when?					
21	Same for the Guiña.					
22	Same for the fox.					
23	Same for the Harris Hawk.					
24	Same for domestic dog.					
25	Same for skunk					
26	Same for weasel.					
27	Other?					

5

		Wildboar	Puma	Guiña	FOX	HARRIS HAWK	DOMESTIC DOG	SKUNK	WEASEL	RABBIT
28	From your knowledge, hunting the ANIMAL is prohibited (0) DON'T KNOW (1) NO (2) YES									
29	How frequently do you observe (or a sign or sound) of this ANIMAL on your property? MONTHLY, YEARLY									
30	**Let's suppose that you have 100 Sheep** **Let's suppose that you have 100 Chickens**	(1) Call authorities (2) Intent to hunt/kill it			(4) Scare off (5) Nothing			(6) Observe (7) Management (8) Nothing		

		(3) Capture and call authorities				
		2	**10**	**25**	**50**	**>50**
31	What do you think you would do if the **PUMA** kills **X/100** Sheep					
32	What do you think you would do if a **DOG or group of DOGS** kills **X/100** Sheep					
33	What do you think you would do if the **GUIÑA** kills **X/100** Chickens					
35	What do you think you would do if the **Harris hawk** kills **X/100** Chickens					

36	Does someone from your family hunt for sport?	Yes______	NO______
37	Do strangers enter the property to hunt, with or without permission?	Yes______	NO______
38	How frequent? MONTHLY, YEARLY		
39	Do you know what they hunt?		

			Ovine	**Chickens**	**Others**	**Dogs**	**Cats**
40	How do you keep your animals at night? (1) Closed housing (2) Open corral (3) Open field with dog (4) Open field without dog (5) Other, how?						
41	At what distance do you keep your animals at night? meters						
42	How many **DOGS/CATS** do you have?					A.	B.

43	What do you do with your DOGS/CATS at night? (1)Closure; (2) Tied (3) FREE ROAMING (0) OTHER	Size of dogs:				A.	B.
44	With what do you feed your pet? (1) Comercial pellet (2) Kitchen scraps (3) Mix of pellets/kitchen scarps (4) Grain (5) Nothing (6) Mix of grain/kitchen scraps (7) Other				Freq.	A.	B.

6

5. Discussion

The aim of this thesis was to contribute to our understanding of the impacts of human land-use and behaviour on threatened species. By focussing on a large agricultural landscape where land conversion, subdivision of land and further loss of forests are current and latent processes, we can inform much needed interventions based on evidence gathered at a pertinent scale for a carnivore of conservation concern (Ginsberg 2001). Many wild felids are currently declining as a result of anthropogenic pressures (Macdonald, Loveridge & Nowell 2010). The guiña (Leopardus guigna), listed as Vulnerable on the International Union for the Conservation of Nature (IUCN) Red List, has proved to be an interesting case study to evaluate how habitat loss, fragmentation and human behaviour can influence the dynamics of a territorial mammal.

It is clear that the interaction of these drivers offers complex lessons. The guiña case shows that species that can tolerate unexpected levels of habitat loss, can perhaps persist in the landscape if another set of conditions are met. Results of this thesis support the idea that there is wide variability in threshold values in terms of percentage of habitat cover – level at which a species will not persist or will non-linearly decline – and complexity regarding the responses of species at multiple scales and levels of human intervention (Lindenmayer & Luck 2005; Fischer & Lindenmayer 2007; Swift & Hannon 2010). In this case, it seems dynamics are largely driven by anthropogenic pressure from land subdivision and access to multiple patches, rather than by a habitat cover threshold value. There is a tendency for species to react negatively to habitat loss, but evidence of the effect of fragmentation has been shown to go both ways (Fahrig 2003). In addition, mammals do tend to respond significantly higher to landscape level variation than other taxa possibly due to higher mobility (Thornton, Branch & Sunquist 2011), which can also compensate for loss of habitat (Swift & Hannon 2010). The guiña study case supports the idea that if a species is not largely impacted by habitat loss, possibly due to its mobility, it is the configuration (i.e. fragmentation) and human pressure that impacts the dynamics in the landscape. Areas, where there is high subdivision of land and many small patches, could be acting as ecological traps if source-sink dynamics are operating in the landscape (Robertson & Hutto 2006). In other words, individuals may be attracted to highly subdivided areas that maintain a suitable habitat configuration, but are exposed to higher anthropogenic pressures and thus are more likely to migrate (i.e. leave area unoccupied), experience unsuccessful reproduction or are killed by farmers. The prevalence of guiña killing by farmers, althought lower than other predators, does show uncertainty as to the impact on the population. However, it does predict that encounters with the species are likely to result in death. Hence, we might expect that the likelihood of encounters might increase as land subdivision increases (e.g. higher density of households); however this should be explored in future work.

For conservation actions to be effective, research must be oriented to identify and prioritise where efforts should be targeted (Pullin et al. 2013). Occupancy models provided higher support for habitat loss/fragmentation variables rather than human pressure except for land subdivision. Thus human pressure measured at specific households possibly did not pick up specific signals of increased pressure, hence further research must focus on how different threats increase as land subdivision increases. Focus on these factors could contribute to further understanding the impact of landscape modification on biodiversity (Fischer & Lindenmayer 2007). Furthermore, the impact of landscape modification is often species-specific (Fahrig 2003), hence research of all native and domestic predators as a relevant guild for ecosystem processes (Sekercioglu 2006; Bruno & Cardinale 2008; Ripple et al. 2014), and how they are influenced by landscape modification, interspecifc interactions (e.g. competition) and human pressure, is warranted in order to guide integrated and effective conservation plans.

This thesis shows the complexities of conservation threats to a species in a human modified landscape. It does offer a view that data collected over time and integrating ecological and social data can provide perspective as to where conservation interventions may have a larger impact in the face of uncertainty and complexity that is intrinsic to biological and human systems. The conservation of many carnivores, particularly small wild felids, could greatly benefit from such research (Dickman 2010).

5.1. Cost-efficient occupancy surveys of territorial mammals

Carnivore populations are difficult to assess because of their cryptic nature (Macdonald 2001). **Chapter 2** shows that surveying elusive species (i.e. low detection probability) appropriately, in order to gain reliable data on occupancy status, is expensive**.** The cost function provided in the paper gives practitioners and researchers a tool with which they can assess trade-offs regarding how many sample units to survey, how long each unit should be surveyed for, and how many cameras should be installed to achieve statistical precision and minimum cost. Furthermore, it facilitates the analysis of a range of feasible and relatively cheap survey methodological scenarios that are available if a project is subject to specific constraints. For example, elusive species need to be surveyed for longer, irrespective if a species is common or rare, which can be difficult if there are logistical limitations such as a small budget, the need for short camera-trap rotations or if the sampling units are not easy to access. In circumstances like these, **Chapter 2** shows the value of deploying additional cameras per sample unit, particularly for species with larger home ranges, as this can compensate for the time spent surveying.

To date, research on carnivores has focused mainly on common and large species. Indeed, there is a paucity of studies on small to medium carnivores, particularly felids (Brooke et al. 2014). A total of 14 threatened felids have had less than 10 studies published on them, including the bay cat (Pardofelis badia), black-footed cat (Felis nigripes), guiña, andean cat (Leopardus jacobitus), flat-headed cat (Prionailurus planiceps) and fishing cat (Prionailurus viverrinus) (Brodie 2009). All these species require research to assess their conservation status and ascertain how human activities are causing their decline (Macdonald, Loveridge & Nowell 2010). It is my hope that the cost function in **Chapter 2** will be used in the future to support and develop cost-efficient surveys to monitor small elusive carnivorous species.

Moreover, the cost function has been developed in R, with the programming code being openly accessible, so that it can be adapted and advanced by other researchers.

For example, it could be modified to suit camera-trap surveys where the aim is to: (i) generate species abundance estimates as individuals can be recognised and mark-recapture methods applied (Royle et al. 2009); (ii) use random encounter models that can estimate abundance without individual recognition (Rowcliffe et al. 2008); or, (iii) estimate relative abundance (i.e. frequency) (Burton et al. 2015).

5.2. Drivers of guiña decline and the identification of future conservation priorities

As shown in **Chapter 3**, guiñas can occur in areas with a high degree of habitat loss, with their dynamics (i.e. changes in occupancy) being best explained by landscape level variables such as number of remnant forest fragments remaining and the extent of land subdivision into farming properties. Our results suggest, therefore, that guiñas can survive and move between forest fragments in agricultural areas. This is not to say that habitat extent is not important for the species, but rather that it might have a wider niche-breadth than has been assumed previously within the literature, where it has been presumed to be a native forest specialist (Sanderson, Sunquist & W. Iriarte 2002; Dunstone et al. 2002; Acosta-Jamett & Simonetti 2004).

Both **Chapters 3 & 4** shows that the prevalence of guiña killing by local human communities is relatively low compared to other predators, having less influence on the species than landscape modification. **Chapter 4** highlights that farmers are most likely to kill a guiña if they rely on their land for subsistence or have encountered the species more frequently. Nonetheless, the population level impact of this source of non-natural mortality could still have unwanted negative effects in the long-run, especially if female individuals are killed (see Chapron et al. 2008), so the situation does need to be monitored periodically.

Moving forwards, conservationists must no longer dismiss agricultural areas characterised by large farms as unsuitable for the guiña. The continued expansion of large-scale farming is a global phenomenon driven by food security, economic benefit and technology, from which Chile does not deviate (Deininger & Byerlee 2012). As a matter of fact, one of the Chilean government's principal aims is to become a major producer and exporter of agricultural products (Villalobos, Rojas & Leporati 2006). This undoubtedly means that the agricultural frontier will expand to the detriment of forest habitats (Lambin & Meyfroidt 2011). Conservationists thus need to preferentially focus their efforts on protecting remnant habitat fragments in such regions wherever possible. For instance, while deforestation rates are low and stable across the study region (Miranda et al. 2015), the small remaining patches of forests in the flat agricultural areas of southern Chile are continually threatened with conversion to pasture or crop land or are degraded/reduced due to logging activity (Echeverria et al. 2008). Currently, it is likely that the geophysical characteristics of the land, as well as abandonment of unproductive land, is providing the remnant patches of suitable vegetation required by the guiña for persistence within agricultural regions (Pan et al. 2001; Díaz et al. 2011). Characteristics that prevent economically viable land-use conversion include high clay content soil types, high water tables and ravines with steep slopes.

Conservation orientated land-use policy and planning in agricultural regions should promote and incentivise actions, such as lower intensity grazing within remaining native patches and the retention of forest fragments, through initiatives such as the protection of riparian buffer zones via legal means or payments for ecosystem services. Government agencies may need to subsidise farmers to fence off some forested areas on their land or to improve livestock management practices. For the guiña specifically, a “land sparing” approach where high yield agriculture protects remnant habitats from further expansion (Phalan et al. 2011), might be most effective conservation strategy. Furthermore, the demand for land subdivision needs to be reduced or mitigated, which would probably require the development of regulatory guidelines and enforcement (e.g. Hansen et al. 2005)

As demonstrated in **Chapter 4,** the killing of guiñas by humans can be explained by higher encounter rates with the felid. Areas in the landscape where subdivision is lower could also reduce the likelihood of people interacting with the species. Encouraging local communities to improve poultry enclosures, which are typically poorly constructed, could be advantageous and relatively easy to implement by holding workshops via farmers associations. These could focus on the benefits of predators as a good strategy for tolerance (e.g. Bruskotter & Wilson 2014), given that legal protection of most species does not seem to deter people from hunting and killing individuals. However, a solid understanding of which species is the most charismatic in the eye of the target audience is needed before any significant investment is made in such a campaign (Verissimo, MacMillan & Smith 2011).

Drivers of species population declines and extinction can act in synergistic, complex and sometimes unexpected ways (Brook, Sodhi & Bradshaw 2008). **Chapter 3** identifies the importance of low land subdivision for the survival of the guiña, but it is still unclear what factors make the matrix hospitable, or not, and how this might vary in response to the number of farm properties within the landscape. For example, the spraying of agrochemicals is common practice in large intensively managed farms, which could have potential toxic effects on species inhabiting the area (Berny 2007). Levels of interspecific competition may also alter as the resident carnivores change their patterns of resource-use in modified landscapes (Creel, Spong & Creel 2001). For the guiña specifically, assessing co-occurrence with domestic cats could be valuable, as the latter is known to transmit deadly or debilitating diseases to the already threatened felid (Mora-Cabello 2011). Additionally, an evaluation of the potential for hybridisation might be needed, as has been observed between Scottish wild cats and domestic cats (e.g. Macdonald et al. 2010), althought genetic distance (i.e. different genus between species) might be a providing a natural barrier.

All the conservation measures, research and policy discussed above, particularly for large farms which are concentrated along the central valley (Miranda et al. 2015), could support existing gene flow between three out of the five geographically and genetically distinct guiña management units (Napolitano et al. 2014). The migration rates from the Lake District group, which our study region sits within, are significantly higher than between other management units (Napolitano et al. 2014). Moreover, migration is directed from the Lake District group towards the central and northern groups, which are the most threatened by low genetic diversity (Napolitano et al. 2014) and climate change (Cuyckens, Morales & Tognelli 2014).

5.3. Final remarks

There is a paucity of empirical data on the effects of habitat loss and fragmentation on carnivores (Sunquist & Sunquist 2001). Furthermore, very few studies integrate data on both the social and ecological possible drivers of species population decline in a framework. In this thesis, I have done this within a robust and transparent modelling framework, allowing us to tease apart the relative importance of different threats at a local scale. In turn, this has permitted us to make informed recommendations as to where effective conservation efforts should be prioritised in the future. The ability of the guiña to survive in intensively farmed areas, and the fact that interactions with local communities are infrequent, is good news for the conservation of the species. However, there is genetic evidence of significant population reductions in the past (Napolitano et al. 2014). The guiña might have lost some of its nine lives as a result of anthropogenic pressures, but effective conservation informed by high quality research and monitoring should secure its persistence in the long-term.

5.4. References

Acosta-Jamett, G. & Simonetti, J.A. (2004) Habitat use by Oncifelis guigna and Pseudalopex culpaeus in a fragmented forest landscape in central Chile. Biodiversity & Conservation, 13, 1135-1151.

Berny, P. (2007) Pesticides and the intoxication of wild animals. Journal of veterinary pharmacology and therapeutics, 30, 93-100.

Brodie, J.F. (2009) Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodiversity and Conservation, 18, 2927-2939.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J. (2008) Synergies among extinction drivers under global change. Trends in ecology & evolution, 23, 453-460.

Brooke, Z.M., Bielby, J., Nambiar, K. & Carbone, C. (2014) Correlates of research effort in carnivores: body size, range size and diet matter. PloS one, 9, e93195.

Bruno, J.F. & Cardinale, B.J. (2008) Cascading effects of predator richness. Frontiers in Ecology and the Environment, 6, 539–546.

Bruskotter, J.T. & Wilson, R.S. (2014) Determining where the wild things will be: using psychological theory to find tolerance for large carnivores. Conservation Letters, 7, 158-165.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. (2015) Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology. DOI: 10.1111/1365-2664.12432. Available on-line.

Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S. & Clobert, J. (2008) The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology, 45, 1667-1674.

Creel, S., Spong, G. & Creel, N. (2001) Interspecific competition and the population biology of extinction-prone carnivores. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 35-60. Cambridge University Press, Cambridge.

Cuyckens, G.A., Morales, M.M. & Tognelli, M.F. (2014) Assessing the distribution of a Vulnerable felid species: threats from human land use and climate change to the kodkod Leopardus guigna. Oryx, 1-8.

Deininger, K. & Byerlee, D. (2012) The rise of large farms in land abundant countries: Do they have a future?. World Development, 40, 701-714.

Díaz, G.I., Nahuelhual, L., Echeverría, C. & Marín, S. (2011) Drivers of land abandonment in Southern Chile and implications for landscape planning. Landscape and Urban Planning, 99, 207-217.

Dickman, A.J. (2010) Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal conservation, 13, 458–466.

Dunstone, N., Durbin, L., Wyllie, I., Freer, R., Jamett, G.A., Mazzolli, M. & Rose, S. (2002) Spatial organization, ranging behaviour and habitat use of the kodkod (Oncifelis guigna) in southern Chile. Journal of zoology, 257, 1-11.

Echeverria, C., Coomes, D.A., Hall, M. & Newton, A.C. (2008) Spatially explicit models to analyze forest loss and fragmentation between 1976 and 2020 in southern Chile. Ecological Modelling, 212, 439-449.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics, 34, 487–515.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecology & Biogeography, 16, 265–280.

Ginsberg, J.R. (2001) Setting priorities for carnivore conservation: What makes carnivores different?. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 498-523. Cambridge University Press, Cambridge.

Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H. & Jones, K. (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications, 15, 1893-1905.

Lambin, E.F. & Meyfroidt, P. (2011) Global land use change, economic globalization, and the looming land scarcity. Proceedings of the National Academy of Sciences of the United States of America, 108, 3465-3472.

Lindenmayer, D.B. & Luck, G. (2005) Synthesis: Thresholds in conservation and management. Biological Conservation, 124, 351–354.

Macdonald, D.W., Loveridge, A.J. & Nowell, K. (2010) Dramatis personae: an introduction to the wild felids. Biology and conservation of wild felids, Biology and conservation of wild felids (eds A. Loveridge & D.W. Macdonald). pp 3-58, Oxford University Press. Oxford.

Macdonald, D.W., Yamaguchi, N., Kitchener, A.C., Daniels, M., Kilshaw, K. & Driscoll, C. (2010) Reversing cryptic extinction: the history, present and future of the

Scottish Wildcat. Biology and conservation of wild felids, Biology and conservation of wild felids (eds A. Loveridge & D.W. Macdonald). pp 471-492, Oxford University Press. Oxford.

Miranda, A., Altamirano, A., Cayuela, L., Pincheira, F. & Lara, A. (2015) Different times, same story: Native forest loss and landscape homogenization in three physiographical areas of south-central of Chile. Applied Geography, 60, 20-28.

Mora-Cabello, M.P. (2011) Pesquisa de infección con los virus inmunodeficiencia viral felina y leucemia viral felina en güiñas (Leopardus guigna) en la isla de Chiloé, Thesis, Universidad de Chile.

Napolitano, C., Johnson, W.E., Sanderson, J., O'Brien, S.J., Hoelzel, A.R., Freer, R., Dunstone, N., Ritland, K., Ritland, C.E. & Poulin, E. (2014) Phylogeography and population history of Leopardus guigna, the smallest American felid. Conservation Genetics, 15, 631-653.

Pan, D., Domon, G., Marceau, D. & Bouchard, A. (2001) Spatial pattern of coniferous and deciduous forest patches in an Eastern North America agricultural landscape: the influence of land use and physical attributes. Landscape Ecology, 16, 99-110.

Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science, 333, 1289-1291.

Pullin, A.S., Sutherland, W., Gardner, T., Kapos, V. & Fa, J.E. (2013) Conservation priorities: identifying need, taking action and evaluating success. Key Topics in Conservation Biology, pp. 3-22. Blackwell, Oxford.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. Science, 343, 1241484.

Robertson, B.A. & Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. Ecology, 87, 1075–1085.

Rowcliffe, J.M., Field, J., Turvey, S.T. & Carbone, C. (2008) Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology, 45, 1228-1236.

Royle, J.A., Nichols, J.D., Karanth, K.U. & Gopalaswamy, A.M. (2009) A hierarchical model for estimating density in camera-trap studies. Journal of Applied Ecology, 46, 118-127.

Sanderson, J., Sunquist, M.E. & W. Iriarte, A. (2002) Natural history and landscape-use of guignas (Oncifelis guigna) on Isla Grande de Chiloé, Chile. Journal of mammalogy, 83, 608-613.

Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. Trends in ecology & evolution, 21, 464–471.

Sunquist, M.E. & Sunquist, F. (2001) Changing landscapes: consequences for carnivores. Carnivore Conservation (eds J.L.Gittleman, S.M. Funk, D.W. Macdonald & R.K. Wayne), pp. 399-418, Cambridge University Press, Cambridge.

Swift, T.L. & Hannon, S.J. (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological Reviews, 85, 35–53.

Thornton, D.H., Branch, L.C. & Sunquist, M.E. (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology, 26, 7–18.

Verissimo, D., MacMillan, D.C. & Smith, R.J. (2011) Toward a systematic approach for identifying conservation flagships. Conservation Letters, 4, 1-8.

Villalobos, P., Rojas, A. & Leporati, M. (2006) Chile potencia alimentaria: compromiso con la nutrición y la salud de la población. Revista chilena de nutrición, 33, 232-237.