Integrating ecological and social approaches for promoting the conservation of carnivores in a human-dominated landscape of southern Chile

by

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ABSTRACT

Mammalian carnivores inhabiting human-dominated landscapes may face reduced and heterogeneous distributions of feeding resources while being more exposed to humans and introduced carnivores. Therefore, sustainable landscape planning intended to conserve carnivores in human-dominated landscapes requires the use of a multi-dimensional approach that integrates different conceptual and methodological components, such as: 1) habitat and prey selection patterns of carnivores at different spatio-temporal scales; 2) habitat selection models including fine-grain information of habitat structure; and 3) assessment of carnivore-human relationships from a sustainability perspective.

Here, I used an occupancy-modeling framework and Resource Selection Functions to evaluate how habitat transformation, human activity and introduced carnivores shaped the spatio-temporal patterns of habitat use and prey selection of seven native carnivores of Temperate Forest. The study was conducted in Nahuelbuta Mountain Range, Chile, a landscape now dominated by exotic commercial plantations. The study was conducted between 2011 and 2014 and the main findings were as follows:

i) Habitat use by carnivore species were significantly affected by native forest, road density and the presence of dogs (*Canis familiaris*). The magnitude of these effects were also influenced by the time of day and spatial scale. The positive effect of native forest on occupancy probability was stronger during the night for the Darwin's fox (*Pseudalopex fulvipes*) and cougar (*Puma concolor*), whereas roads reduced the occupancy probability of Darwin´s fox, being this effect stronger during day-time. Dogs reduced the occupancy probability of Darwin's foxes, but this effect was independent of the time of day. Conversely, cougars were negatively affected by dogs only during the day.

ii) Vegetation structure, derived from high-resolution LiDAR remote sensing systems, improved the performance of occupancy models for Darwin's fox and kodkod cat (*Leopardus guigna*), indicating that carnivore habitat use responds to fine-grain habitat heterogeneity rather than coarse habitat type.

iii) Carnivore prey selection differed between native forests and pine plantations. This foraging response was also associated with changes in habitat type and the variation in abundance of prey species.

iv) While people from rural communities across the Nahuelbuta Mountain Range were willing to conserve some carnivore species, they were unwilling to adopt husbandry practices such as leashing dogs or providing protection to poultry in order to avoid predation of domestic animals by carnivores.

Results of this research suggest that carnivore habitat use in this human-dominated landscape is affected by human activity, domestic dogs and fine-grain habitat structure. However, the magnitude of these effects may also vary in both time and space. Moreover, even though overall native prey availability decreases in plantations, some prey can reach similar or even higher abundance in these human-created habitats. In response to these changes, predators may modify their prey selection behavior between native forest and plantations. Thus, landscape planning for carnivore conservation should be based on: 1) sustainable forestry practices promoting the retention of native forest while restoring and improving habitat quality in forest plantations; and 2) sustainable practices by small farmers focused on the responsible management of dogs.

PREFACE

Throughout this thesis, I use the first person singular to maintain consistency. However, to that end, chapters in this thesis represented collaborative work with other researchers.

Chapter 2 has been published as Moreira-Arce, D., Vergara, P.M., Boutin, S. 2015 Diurnal Human Activity and Introduced Species Affect Occurrence of Carnivores in a Human-Dominated Landscape. PLoS ONE 10(9): e0137854. doi:10.1371/journal.pone.0137854. For this paper, I conceived the concept, designed the study, collected and analyzed the data and composed the manuscript. Data analyses were also assisted by Dr. Pablo M. Vergara from University of Santiago de Chile.

Chapter 3 represented a collaborative work with Dr. Raúl Briones and Mr. Gonzalo Carrasco. For this work, I conceived the research question and was responsible for data collection, study design, data analysis and manuscript composition. Mr. Gonzalo Carrasco provided LiDAR information and performed habitat suitability maps for carnivore species.

Chapter 4 is in press as 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, *in press*. doi: 10.1016/j.biocon.2015.09.015. For this paper, I conceived the concept, designed the study, collected and analyzed the data and composed the manuscript. Data analyses were also assisted by Dr. Pablo M. Vergara. Additional scats were provided by Dr. Gerardo Acosta-Jamett and DNA identification was conducted by Dr. Cristóbal Briceño.

Chapter 5 represents a collaborative work with Dr. Francisco Zorondo-Rodríguez. For this work, I conceived the research question and was responsible for study design, data analysis and manuscript composition. Dr. Zorondo-Rodríguez provided additional support for the design and conduction of questionnaires in field.

The research project, of which this thesis is a part, received research ethics approval from institutional animal care protocols (Chilean Agriculture and Livestock Bureau (SAG; resolution number 2201/2013) and University of Alberta animal use protocol # AUP00000039).

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Living in Canada is an enormous challenge for someone coming from a non English speaking country with a different culture. Meeting nice people therefore become crucial to have a good Canadian experience. My life in Edmonton would have not been possible without the kindly and lovely help and support of several Latin and Canadian people. I would like to thanks to Angelica and Duane and their kids Victor, Nelly and Karina who I lived with during the last period of my Ph.D. Thanks guys for sharing part of their life with me and for the wonderful Mexican-

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CHAPTER I

General Introduction

Overview of Thesis

This Ph.D. dissertation is largely motivated by two fundamental themes in conservation and ecology; the growing threat to wildlife by human activities, and the methodological uncertainty inherent in our understanding of ecological estimates of wildlife populations in human-dominated landscapes. Specifically, I aim to explore how mammalian carnivores respond to human-modified landscapes such as those dominated by commercial forest plantations, and how the understanding of carnivore-human relationships may successfully contribute to carnivore conservation on private lands. I investigate these themes by assessing the some aspects of the ecology and conservation of carnivores in a anthropized landscape in southern Chile by pursuing the following four goals: (i) to examine the extent to which anthropogenic and natural factors influence the habitat use of carnivores (ii) to evaluate the usefulness of recently developed predictive occupancy models and high-resolution information on habitat structure, for identifying suitable habitats for carnivores across large areas; (iii) to assess how carnivore foraging behavior responds to native forest replacement by commercial plantations; and (iv) to explore the potential for carnivore conservation by assessing the carnivore-human relationships in private lands around Nahuelbuta National Park. In this introductory chapter, I provide an overview of my motivating themes and the study context, and briefly introduce the four studies comprising the core of this dissertation.

Carnivores´ response to landscape heterogeneity and the challenge of uncertainty

Mammalian carnivores living in human-dominated landscapes are more likely to be exposed to human-caused habitat transformations, encounters with humans and introduced domestic carnivores causing death, injuries and behavioral changes, than those living in more undisturbed ecosystems (Crooks et al., 2011; Gittleman et al., 2001; Vanak and Gompper, 2009). Nonetheless, the ecology of many carnivore species in human-dominated landscapes is poorly understood. A better understanding of carnivore-habitat relationships is a necessary endeavor to address in order to determine the relative sensitivity of carnivores to land-use changes, and predict the consequences of anthropogenic activities on carnivore populations (Morrison et al., 2006). However, these relationships may become complex, involving species-specific responses to specific habitat attributes at different spatial and temporal scales (Manly et al., 2002).

Studies identifying the environmental factors affecting carnivore habitat use in human-dominated landscapes are needed to develop management actions to restore habitat conditions for these species, in these landscapes (Burton et al., 2012; Crooks, 2002; Morrison et al., 2006; Long et al., 2010; Virgós et al., 2002). Prey availability, refuges, breeding sites, human activity, and exotic species can fluctuate across space and time (Lindenmayer and Hobbs, 2004; Mortelliti et al., 2010; Vanak and Gompper, 2010, 2009). Carnivores may behaviorally respond to variation in human activities by modifying their space-use patterns, or adjust their activity patterns in order to avoid contact with humans or introduced domestic carnivores (George and Crooks, 2006; Knopff et al., 2014). In addition, carnivores may respond to the spatial variation of prey availability by becoming more efficient at searching for, pursuing, and capturing the more available prey species (Gorini et al., 2012). Landscape management for carnivore conservation, however, also requires an accurate description of habitat attributes and the species' response, over different spatial and temporal scales (Boyce, 2006; Guisan and Zimmermann, 2000). This can be achieved by combining large-scale survey methods such as camera trapping with a fine-grain description of habitat structure derived from high-resolution remote sensing information. Camera trapping is an efficient, cost-effective, and easily replicable tool to study and monitor carnivores over large areas (Rovero et al., 2014; Silveira et al., 2003). Camera trapping can be carried out over multiple occasions during a discrete season, which provides the information required to account for imperfect detection (hierarchical occupancy models as described by MacKenzie et al. (2002) and O'Connell and Bailey (2010)). Remote sensing such as LiDAR (Light Detection and Ranging) system offers a cost effective capacity to obtain high-resolution environmental information, providing a better characterization of habitat structure across large areas (Vierling et al., 2008).

Commercial forest plantations as human-created habitat

The 10th Conference of the Parties of the Convention on Biological Diversity (CBD) in 2010 established Aichi Targets to reduce pressures on biodiversity. These targets demand that by 2020 production-oriented lands have to increase wildlife-friendly practices that provide both goods and services, while contributing to ensure the conservation of biodiversity in these human-created habitats (CBD 2010). Commercial forest plantations are becoming dominant in many landscapes across the globe, as natural habitats are increasingly being replaced by these human-modified lands (FAO, 2001). The replacement of native forest to commercial forest plantations typically results in the modification of vegetation structure, with changes in the distribution and abundance of species (Brockerhoff et al., 2008; Lindenmayer and Hobbs, 2004). However, depending on forestry management, plantations may provide structural and functional habitat for many native species (Brockerhoff et al., 2008; Lindenmayer and Hobbs, 2004; Nájera and

Simonetti, 2010), including carnivores (Acosta-Jamett and Simonetti, 2004; Lantschner et al., 2012; Mazzolli, 2010; Simonetti et al., 2013). Thus, forest plantations may act as suitable habitat for biodiversity when compared to other human-modified lands such as crops, pasture, or urban areas (Lindenmayer and Hobbs, 2004). Assessing how commercial forest plantations modify the habitat conditions for carnivores, and how carnivores respond to these changes may be important for creating a bridge between timber activity and biodiversity conservation.

Carnivore conservation and conflict with humans

An understanding of carnivore-human relationships is pivotal to the success of carnivore conservation and recovery programs (Woodroffe et al., 2005). These relationships arise from the changing perceptions and attitudes towards carnivores across diverse cultural and socio-economic groups (Ceballos et al., 2005; Morrison et al., 2007; Schipper et al., 2008). Carnivore species inhabiting human-dominated landscapes are often perceived as "conflict" species (Zimmermann et al., 2005; Romanach et al., 2007; Soto-Shoender and Giuliano, 2011; Zorondo-Rodríguez et al., 2014). Large and small predators—such as bears, wolves, lions, leopards, jackals, or mongooses—have been aggressively persecuted throughout their distribution ranges due to their real, or perceived, negative impacts on human livelihood (Dickman, 2010; Woodroffe et al., 2005). Because protected areas are often not large enough to maintain long-term viable populations of carnivores (Hansen and DeFries, 2007; Simonetti and Mella, 1997), the main challenge becomes promoting carnivore-human coexistence in private lands surrounding protected areas (Soto-Shoender and Giuliano, 2011; Maroyi, 2012). Although many carnivore populations have declined worldwide due to increased carnivore-human conflicts, some species have exhibited population recovery when provided with adequate protection and social support in areas where carnivore co-occur with rural communities (Smith et al., 2003).

Loss and recovery of carnivore populations in these areas has highlighted their functional role within ecosystems, and focused attention on the significance of carnivore's protection for ecosystem stability (Morrison, 2009).

Carnivore ecology and conservation in South America

Anthropogenic disturbances preceding European colonization have contributed to shaping the current biodiversity of South America (Myers 2000, Erickson 2006). Land use transformations of natural ecosystems has involved selective culling of non-economic biodiversity, such as Neotropical mammalian carnivores (Cardillo et al., 2004; Crooks et al., 2011; Farias and Svensson, 2014). Regions with the highest concentration of carnivore species, such as tropical ecosystems, have been particularly exposed to accelerated habitat transformation by humans (Farias and Svensson, 2014; Menjeau et al., 2009). Consequently, attention to carnivore conservation has been focused most intensively on rainforests and other biodiversity hotspots in west-central South America. While such areas are deserving of funding and technical training for wildlife research and monitoring, little effort has been directed toward subtropical regions like the Temperate Forests and the Puna montane scrublands and grasslands. Although these non-tropical biomes exhibit reduced carnivore diversity in relation to rainforests, they usually harbour rare carnivore species for which ecological knowledge is scarce. Additionally, these areas also show higher threat levels derived from human activity including timber and mining (Loyola et al., 2008). As a cursory means of assessing the knowledge gap, I compared the number of publication records in the ISI Web of Knowledge database (http://apps.isiknowledge.com, accessed 10 June 2015) containing the topic keywords "carnivore" and "South America", and conducted either in "Rain/Wet forest", "Temperate Forest", "Puna montane", or "Patagonian steppe", with the results of these searches being limited to the subject area "Biodiversity &

Conservation." The results are shown in Fig. 1-1 and illustrate the relative paucity of scientific knowledge for carnivores in non rainforest regions.

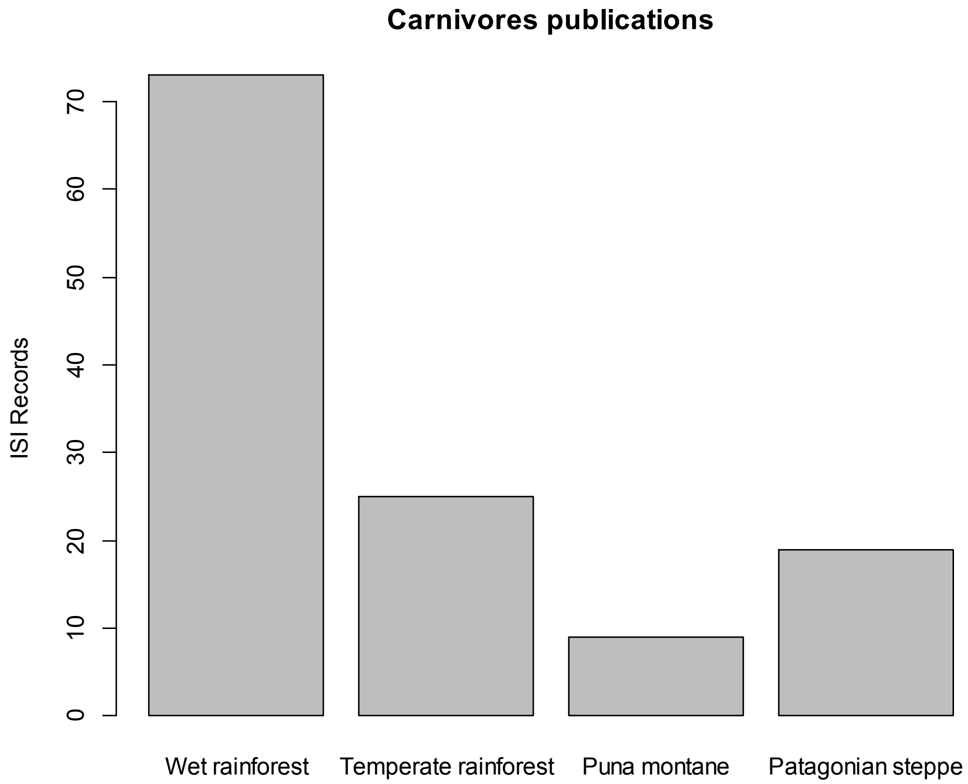

Figure 0-1. Number of publication records in the ISI Web of Knowledge database (accessed 10 June 2015) relative to carnivore ecology and conservation across four main biomes of South America.

Study area and species description

I considered the Nahuelbuta Mountain Range (hereafter MNR) of southern Chile (35°-40° S) as my focal study site. Nahuelbuta is located in the Temperate Forest Region of South America, which is characterized by intensive forestry, understudied and threatened biodiversity, as well as high carnivore-human conflict. Moreover, NMR represents a zone of faunistic transition between northern Mediterranean mammal species and southern Temperate Forest species (Armesto et al., 2005). A highly diverse carnivore community including species with different body sizes occur sympatrically in NMR (Zuñiga, 2014): kodkod cat (*Leopardus guigna*; ~2.5kg), lesser grison (*Galictis cuja*; ~2.0kg), Molina's hog-nosed skunk (*Conepatus chinga*; ~2.5kg), grey fox (*Pseudalopex griseus*; ~4.0kg), culpeo fox (*P. culpeo*;~7.5kg), puma (*Puma concolor*; ~40kg) and the endemic Darwin's fox (*P. fulvipes*; ~3.0kg), one of the world's most endangered canids (Jiménez et. al., 2008). Specifically, my study area (~150,000ha) encompassed a portion of NMR situated on the border of VIII and IX Districts (Fig.1-2). The predominant climate of this study area is temperate with mediterranean influence, with average temperatures between -1°C in winter and 9°C in summer, and an average annual precipitation of 1,500–2,500 mm. Snow is frequent during winter. The topography is rugged, with numerous ravines and ridges. The landscape of NMR consists of a mosaic of native forest habitats and human-created habitats, including large plantations of Monterrey pine (*Pinus radiata*) and various eucalyptus (*Eucalyptus* spp.) species, as well as open agricultural lands. Remnant native forest comprises a distinctive and relatively homogeneous association of native tree species. At the highest elevations, native forest comprises a mixed association between monkey-puzzle trees (*Araucaria araucana*), coigüe trees (*Nothofagus dombeyi*), and Antarctic beech (*Nothofagus antarctica*). At medium and high elevations a deciduous forest dominated by roble (*Nothofagus obliqua*) exists, whereas at lower elevations native forest is composed of secondary mixed broad-leaved evergreen tree species, including *Eucryphia cordifolia*, *Aextoxicon punctatum,* and *Laureliopsis philippiana* (Wolodarsky-Franke and Herrera, 2011).

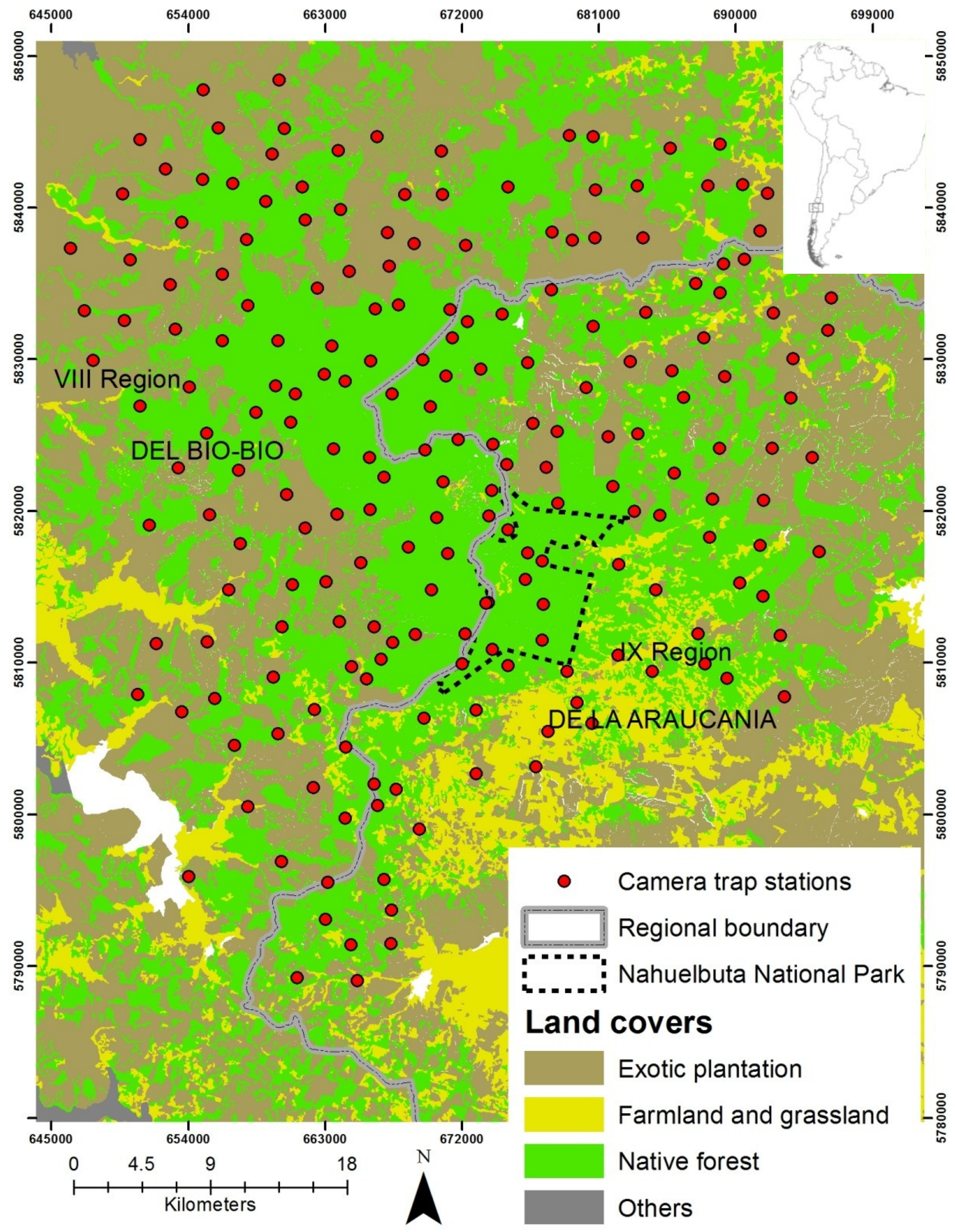

Figure 0-2. Study area in Nahuelbuta Mountain Range of southern Chile where I conducted this research on carnivore ecology and carnivore-human relationship from November of 2011 to July 2014.

Dissertation outline

In this dissertation, I used a multi-dimensional approach integrating various conceptual and methodological components to evaluate ecological hypotheses, and to explore the carnivore-human relationships in NMR.

In Chapter 2, I determined how landscape attributes, human activity, and domestic dogs affected carnivore habitat use at different spatial scales during my study period. Carnivores inhabiting this landscape have been exposed to land use changes from native forest to exotic plantations characterized by intense human activity. However, space-use of these species and their behavioral responses to this human-created habitat is poorly understood. I combined intense camera-trap surveys (conducted from November 2011 to December 2012) with an occupancy modeling framework to assess habitat use of carnivores as a function of the factors mentioned above. Because the intensity of human and dog activity may vary throughout the day in my study area, I assessed the effect of these factors on the habitat use of carnivores separately during day and night. Efficient monitoring and management of threatened species living in human-disturbed landscapes requires not only unbiased estimates of space use, but also an accurate description of habitat structure at different spatial scales. In Chapter 3, I assessed how fine-grain information of habitat structure arising from LiDAR remote sensing systems contributes to explaining habitat use of each carnivore species compared to coarse habitat types. For the purpose of analyses conducted in Chapter 2 and 3, I assumed that occupancy probability was correlated to the probability of site use (prob[used|occupied]) rather than true occupancy (prob[occupied]), given that my 'sites' were point locations of camera traps (Lele et al., 2013). Exotic plantations dominate landscapes in central-south Chile. Although their structural role as complementary or supplementary habitat for carnivores has been discussed, the functional role of exotic plantations as sources of food resources for predators is poorly understood. In Chapter 4, I assessed the variation in the abundance of prey between plantations and native forests and how this habitat-dependent change affects the prey-selection patterns of carnivores. In Chapter 5, given the ecological and cultural importance of carnivores, and their sensitivity to conflicts with local human communities, I assessed the willingness of rural community residents to conserve carnivores by adopting different management practices. Finally, in Chapter 6, I summarized the key findings and main conclusions of the dissertation and outline several important directions for future research in carnivore ecology and conservation in MNR and Temperate Forests.

CHAPTER II

Human activity and introduced species affect diurnal occupancy of carnivores in a human-dominated landscape.

Introduction

Habitat use by wildlife is a dynamic process involving species-specific responses at differing spatial and temporal scales (Battin, 2004; Thomas and Taylor, 2006; Gaillard et al., 2010). However, understanding habitat use by highly mobile species is complex, especially for elusive carnivores. These species exhibit marked diurnal fluctuations in a variety of activities such as movement, feeding, resting, hiding, vigilance, defending territory, and mating (Woodroffe and Ginsberg, 1999; Gittleman et al., 2001; Lodé, 2011).

Carnivores, and other terrestrial predators living in human-modified landscapes, face not only daily variation in prey availability (e.g., Ramesh et al., 2012), but also risk contact with humans or introduced carnivores, such as domestic/free-ranging dogs (hereafter referred to as "dogs") (*Canis familiaris*) (Forman, 1995; Murcia, 1995; Vanak and Gompper, 2009). However, most carnivore studies are usually based on the premise that anthropogenic landscape-scale processes that influence the persistence of carnivore populations are invariant over time, at least in the short-term (Kronfeld-Schor and Dayan, 2003). The replacement, loss, and fragmentation of native habitats tend to occur on relatively broad time scales, such as years, decades, or even centuries. However, the resulting land-use mosaics are characterized by daily heterogeneity in human activities across the landscape (Forman, 1995). Therefore, assessment of human disturbances at the landscape-scale requires consideration of the daily responses of carnivores to varying anthropogenic activity, including the presence of introduced species such as dogs that affect carnivore behavior (George and Crooks, 2006; Vanak and Gompper, 2009).

Carnivores might exhibit changes in diurnal habitat-use patterns emerging from multiple ecological processes. For example, the use of habitat by carnivores, such as small, but suitable forest patches, may be more intense when humans are less active, thus increasing the levels of intra- and interspecific interactions in these remnants (Beckmann and Berger, 2003; Ngoprasert, et al., 2007; Ordiz, 2013; Takahata, 2014). In addition, animals may explore distant habitat patches during some periods of the day or night due to human-induced habitat loss and transformation. For example, animals may use movement corridors more intensively during time when human activity is lower? to reduce dispersal costs in mosaic landscapes (Clarke and Schedvin, 1997; Hels and Buchwald, 2001; Marable, 2012) or avoid human-made structures such as roads during peak hours of traffic (e.g., Klar et al., 2009; Schwartz et al., 2010). Carnivores may also exhibit behavioral changes when approaching habitats influenced by human activities. For instance, during nocturnal forays in human-dominated areas, some carnivores are more cryptic and display opportunistic foraging behavior (Beckmann and Berger, 2003; Knopff et al., 2014). Furthermore, in landscapes containing conservation areas surrounded by human land uses (e.g., forest plantations, agricultural lands), the distance over which carnivores carry out excursions may increase as human activity decreases (Balme, 2010). Lastly, dogs can exclude native carnivores from using high-quality patches (Vanak and Gompper, 2009), and this effect may be more evident during the hours when dogs are more active (usually diurnally) within these habitats (e.g., Vanak and Gompper, 2010). However, native carnivores may reduce encounter rates with dogs by avoiding using landscape features in the hours dogs are more active (George and Crooks, 2006).

I assessed habitat use of carnivores separately during day and night as function of anthropogenic and natural factors in a human-dominated land-use mosaic of southern Chile. The mosaic landscape harbors a diverse carnivore guild, including the threatened Darwin's fox (*Pseudalopex fulvipes*) and kodkod cat (*Leopardus guigna*) (Jiménez and McMahon, 2004; Acosta and Lucherini, 2008). Carnivores living in southern Chile have been exposed to human pressure over the last century that has led to a dramatic replacement of native forest into monocultures of exotic trees (Echeverria, 2006; Aguayo, 2009). Previous studies suggest that some carnivores inhabiting land-use mosaics of southern Chile may be negatively affected by forest plantations, whereas other species may positively respond to these human-created habitats (e.g., Acosta-Jamett and Simonetti, 2004; Silva-Rodríguez, 2010). Interactions between carnivores and domestic dogs are frequent in agricultural and forestry land use areas (Silva-Rodríguez, 2010; Sepúlveda et al., 2014). Agriculture and forestry practices are predominantly carried out during daylight hours across the landscape. Therefore, native carnivores would have prolonged exposure to humans and dogs during these hours.

I used occupancy modeling corrected by detection probability under a spatial Bayesian approach to test the hypothesis that carnivores modify their habitat use patterns from day to night in order to reduce the probability of encountering or being detected by humans and dogs. For the purpose of this analysis, occupancy probability was assumed to be more likely representative of probability of site use (prob[used|occupied]) rather than true occupancy (prob[occupied]) (Lele et al., 2013), given that my ‘sites’ were point locations of camera traps. Similarly, detection was interpreted as the probability a species is detected, given the site is occupied and used during each occasion (prob[detected|site occupied and used]). Specifically, I predicted that i) a positive effect of patch size and native forest cover on the occupancy probability of native carnivores should be more pronounced during the daytime, when human activity is more intensive and animals move into undisturbed areas, ii) the occupancy of native carnivores should decrease as road density increases in the landscape, with this effect being stronger during the day, iii) a positive relationship between proximity to a conservation area and the occupancy of native carnivores should be more pronounced during the daytime when levels of human activity around conservation areas increase, and iv) the negative effect of dogs on the occupancy of native carnivores should be more intense during day, when dogs move along roads and explore habitats away from dwelling areas.

Methods

Study Area

See Chapter I for description.

Carnivore species and habitat preferences

A total of seven native carnivores were expected to occur in the study landscape (Zuñiga, 2014), including the lesser grison (*Galictis cuja*), Molina's hog-nosed skunks (*Conepatus chinga*), kodkod, and cougar (*Puma concolor*). A relic population of the endemic Darwin’s fox (*Pseudalopex fulvipes*) (Medel, 1990), a forest-specialist fox species that is one of the world’s most endangered canids (Jiménez and McMahon, 2004) also resides in the NMR. The chilla fox (*P. griseus*) and culpeo fox (*P. culpaeus*) occur in a variety of habitats, including native forest and shrub, exotic plantation, and grasslands (Acosta-Jamett and Simonetti, 2004; Silva-Rodríguez, 2010). The lesser grison has been described as using native forest (Redford and Eisenberg, 1992) and exotic plantations (Zuñiga, 2009). Studies conducted in Patagonia have shown Molina's hog-nosed skunks (*Conepatus chinga*) selecting open vegetation when active and shrub-forest when resting (Donadio et al., 2001). Cougars have been recorded using a variety of habitat types, including old-growth native forest, second-growth forest with low canopy cover, and grasslands (Muñoz-Pedreros et al., 1995; Franklin et al., 1999).

Camera-trap sampling

The presence of carnivores was monitored using intensive camera-trap surveys on a sampled area ca. 120,000ha, between November 2011 and December 2012. A total of 210 sites were sampled with passive infrared-triggered camera traps (Reconyx PC900 Holmen, Wisconsin and Bushnell Trophy Camera, Bushnell Corporation, Overland Park, Kansas, USA) mounted on trees ca. 50-60 cm above the ground, baited with a lure (commercial fox urine , Predator Pee, Maine, USA), and placed 3-4 m away from the camera. I estimated the percentage of sampled points where each species was recorded, which represents an uncorrected or ‘‘naïve’’ estimate of carnivore occupancy across the entire study area. At each sampling site, multiple photos of the same species taken during 24hr period were considered as the same detection event to avoid false counts emerging from temporal dependence. Although the study was conducted during almost one year, each sampling site was surveyed, on average, for 37±12 days during one season only (i.e., during either the breeding or no-breeding season). Once the survey period for a camera was completed, it was moved to a different site, completing a total of 9,450 camera-days for the whole study area. Daytime was defined as 1 h before sunrise until 1h after sunset. Conversely, nighttime was defined as 1h after sunset to 1h before sunrise. The daily sunlight and sunset times were obtained from a sun/moon calculator using the GPS coordinates of the center of the study landscape as reference.

Sampling sites were allocated randomly in the study area based on a habitat-stratified design. However, I maintained a minimum distance of 500m and maximum of 3,400m (average of 1,275m) between cameras to account for spatial independence among detections. I classified the dominant habitat types as being native forest, exotic forest plantations, or open farmlands-grasslands by using a 1:250,000 scale landcover GIS database developed by the Chilean Forestry Service and Environment Ministry of Chile (2007-2008) and satellite images available in Google Earth (earth.google.com).

Model covariates

To test the predictions described above, I quantified landscape and habitat covariates associated with each camera station that could affect carnivore detection and occupancy probabilities including: road density, native forest cover, patch size, and proximity to the conservation area (Nahuelbuta National Park), as well as the occupancy probability of dogs during day and night (Table 2-1). Landscape attributes were quantified at two spatial scales by creating 250m and 500m-buffer areas around each station in order to include scale-specific effects of landscape attributes on the occupancy of carnivores (e.g., Lyra-Jorge et al., 2009; Lantschner et al., 2012). Spatial data analyses were conducted using ArcMap10.1 (ESRI, CA, USA). For the posterior analyses described below, continuous covariates were normalized, when possible, with log transformation, as well as standardized to have a mean 0 and standard deviation 1 to improve model convergence and for estimates means to be comparable. Using Spearman correlation and the variance inflation factor of all covariates I did not find strong collinearity between non-categorical covariates. Indeed the absolute values of correlation coefficients between all covariates were < 0.62, while their variance inflation factors were < 3.2 (Table S2-1).

Table 2-1. Description of the covariates used in the hierarchical occupancy probability and detection probability models. Model covariates include landscape attributes that were measured at different spatial scales (plot, 250m and 500m).

Code	Variable description
Occupancy probability model	
Elv	Elevation (meter above level sea)
Prk	Distance between each camera station and Nahuelbuta National Park border
NF.plot	Binary variable indicating if camera-station was set in native forest or others vegetation type (mainly exotic plantation)
NF250	Native forest cover within 250m-radius buffer area around camera-station
NF500	Native forest cover within 500m-radius buffer area around camera-station
Rd250	Road density, measured as total m of road (paved and dirt road) within an area (km^2) of 250m-radius buffer area around camera-station
Rd500	Road density, measured as total m of road (paved and dirt road) within an area (km^2) of 500m-radius buffer area around camera-station
Pch250	Mean patch size (ha) of native forest within 250m-radius buffer area around camera-station
Pch500	Mean patch size (ha) of native forest within 500m-radius buffer area around camera-station
Dog	Dog occupancy probability (ψ_{Dij}) at camera-stations as estimated from model including the effect of landscape and habitat covariates on dogs' detection probability
Detection probability model	
Season	Proportion of camera-days sampled in the Austral spring-summer
Und	Percentage of understory vegetation within the detection range of each camera

I considered the carnivore detection probability as a variable being affected by the site-level factors that influenced the chance of, and time when, individuals entered the camera's detection zone. I estimated the cover of understory measured within 10 m in front of each camera station. Because the detection zone of cameras may be blocked by vegetation, I measured understory vegetation blocking the camera's field of view by using a 1x1 m checkerboard (modified from Nudds, 1977). I included the camera station as a random variable in models to control for the effects of other unobserved variables at the site-level. During their breeding season, density and movement of carnivores can increase, making individuals more detectable in some areas (Rowcliffe et al., 2008; Burton et al., 2015). To account for seasonal changes in detectability of carnivores I included the proportion of camera-days sampled during the Austral spring-summer, corresponding to the breeding season for most of these species.

Modeling framework

The statistical approach used to assess the habitat use patterns of the carnivores detected during camera trap surveys can be briefly described as follows: First, I specified a hierarchical single-species/single-season model for the occupancy probability of carnivores (ψ) detected during my camera trap surveys. I applied the model described by MacKenzie et al., (2006), and further used by Burton et al. (2012) for a multi-species assessment, but modified to evaluate the occupancy probability separately during day and night for each carnivore species. Second, to account for imperfect detection on uncorrected estimates of occupancy process, my modelling approach explicitly included the probability of detection (p) as a latent (unobserved) variable dependent on environmental covariates (MacKenzie et al., 2006; Burton et al., 2012; MacKenzie et al., 2002). Third, since species occupancy during day and night are not mutually exclusive events, I used predictions from the hierarchical occupancy model to obtain overall probability of occupancy.

I assumed that the presence or absence of a carnivore species at the site i=1,2, ..n=210, during the time period j (j= 1 if day and j=2 if night) is a Bernoulli distributed latent variable,$z_{ij} \sim Bern(\psi_{ij})$, where $z_{ij} = 1$ if the species is present and $z_{ij} = 0$ if the species is absent, whereas ψ_{ij} is the probability that the species occurs at site i during the time period j. I modeled observed detections, $y_{\mathrm{i,j,}}$ as $\mathrm{y}_{ij} \sim Bern(z_{ij} p_{ij})$ for k_{j} independent trials, where p_{ij} is the probability of detecting a species at site i during the time period j if it is present, and k_j is the number of trap days at site j as bivariate logit-normal random variables. Occupancy probability adjusted for imperfect detection was modelled as:

$$logit(\psi_{ij}) = (\psi_{ij}) = \alpha_{1j} + \beta_j X_i + \gamma_j \psi_{Dij} + U_i + d_j, \qquad \text{Eq.(1)}$$

where α_{1j} is an intercept parameter. The occupancy probability function given in Eq.(1) includes a vector of the time-dependent coefficients, β_j, for day and night periods (j=1 and j=2, respectively), associated with a vector of time-independent covariates at site i (X_i). These covariates were habitat and landscape attributes influenced by human disturbances at different spatial-scales (Table 2-1). I included elevation as an additional covariate because the pronounced altitudinal gradient in the study landscape could affect carnivore occupancy due to possible altitudinal gradients in prey abundance and human presence (Patterson, 1989). For each carnivore species, with the exception of dog, the time-dependent coefficient γ_j (Eq.1) represents the probability of a dog being present (ψ_{Dij}) at camera i during day and night. I estimated the occupancy probability of dogs, ψ_{Dij}, using a detection model including effects of environmental factors, as explained below in Eq.(2), but also by using an occupancy probability function without covariates for not including fixed-effects again in the function (Table S2-2). Parameter

d_j in Eq.(1) is a random effect for day and night, separately, because the assumption of temporal independence of errors was not supported by the observations. Parameter d_j was drawn from a bivariate normal distribution $d \sim \mathcal{N}(\mu, \Sigma)$ whose correlation matrix, Σ, provided the coefficient ρ representing the correlation between the probability of occupancy estimated during both day and night.

Detection probability, p_{ij}, at site i during the time period j was estimated by using the Equation:

$$logit(p_{ij}) = \alpha_{2j} + \delta_j X_i + S_i, \qquad \text{Eq.(2)}$$

which includes an intercept parameter, α_{2j}, as well as a time-dependent coefficient vector, δ_j, representing the effects of environmental factors at site i, X_i (Table 2-1), and a spatially unstructured random effect, S_i, for each site. I included the proportion of camera-days sampled in the Austral spring-summer to account for seasonal changes in detectability emerging from my sampling design (see Camera-trap sampling section for details).

A correlation between the occupancy and detection probabilities is probable, because an increase in animal activity (i.e., movement) within a particular area may be caused by more individuals being detectable by cameras set within that area (Rowcliffe et al., 2008; Burton et al., 2015). Thus, to account for the positive association between occupancy and detection probabilities, I modeled ψ and p as bivariate logit-normal random variables. The logit(ψ_{ij}) and logit(p_{ij}) values were combined into the two-dimensional vector G_j, such that $G_j \sim \mathcal{N}(\mu_j, \Sigma)$, where Σ is a covariance matrix and μ_j a mean vector that contains the occupancy, ψ_{ij} and detectability, p_{ij} probabilities.

To include temporal dependencies in occupancy and detection processes, I specified the same hyper-parameters (i.e., parameters of prior distributions of model parameters) for each time-dependent coefficient (β and δ) representing the effect of the same covariate, but at different time periods (day or night). My model assumed that the probability of daily and nightly occupancies at site i are correlated random variables. The occupancy probability during the overall 24-hour day was estimated as:

$$\psi_i = 1 - [(1 - \psi_{i1})(1 - \psi_{i2})] \qquad \text{Eq.(3)}$$

I controlled for spatial errors associated with the local neighborhood dependencies of camera stations in the occupancy probability function, Eq.(1), by including a spatial term for each site i, U_i, which was drawn from a Gaussian conditional autoregressive (CAR) distribution. The CAR approach assumes a set of area-specific spatially correlated Gaussian random effects (Besag and Kooperberg, 1995). Using Voronoi tessellation applied to the coordinates of camera stations, I subdivided the study landscape into non-overlapping areas (Voronoi polygons), each representing an "influence" area associated to each camera station. The elements of the adjacency matrix used for specifying the CAR function were defined as those Voronoi polygons that shared a boundary (e.g., Lawson, 2009).

I selected models using the posterior probability of all possible combinations of fixed-effects coefficient (β and δ), including a set of 2^{20} candidate models. Model ranking based on their posterior probabilities provides a suitable selection procedure for complex hierarchical models with latent variables, such as my hierarchical occupancy probability model (Royle and Dorazio, 2008). Models with posterior probabilities > 0.05 were considered to be the suitable supported models. Posterior probabilities were calculated by fitting inclusion parameters, w_c, to each fixed effect coefficient, where C is the complete set of fixed effects. The inclusion parameter gives the probability that a particular covariate is included in the "best" model. Inclusion parameters were assumed to be Bernoulli distributed and specified with uninformative prior probability parameter of 0.5. From Markov chain Monte Carlo (MCMC) samples I estimated the posterior probability of each model by calculating the proportion of times each combination of fixed effects appeared in the posterior sample (i.e., when w_c=1 for all model coefficients). I estimated model-averaged coefficients from posterior samples by averaging values where the corresponding w_c=1 (Lawson, 2009). The importance of each fixed effect was evaluated from the Bayesian credible intervals of the posterior distribution of coefficients. I only interpreted coefficients whose 95% credible intervals did not overlap zero.

Models were run using WinBUGSv. 1.4 (Spiegelhalter et al., 2003), which was remotely called from R v. 3.2.0 (R Development Core Team 2014) by using the R2WinBUGS package. Posterior distributions were based on five MCMC chains, each with 40,000 iterations, discarding the first 10,000 iterations and thinning by 5. I used vague non-informative prior distributions for all model parameters. I assessed convergence by visually examining trace and density plots of MCMC iterations, as well as by estimating the Potential Scale Reduction factor (Gelman et al., 2003).

Results

Occupancy patterns

Eight carnivore species were recorded during camera-trapping surveys, with *naïve* occupancy rates differing between day and night (Table 2-2 and Table S2-3). The culpeo fox, followed by the cougar, were the most frequently recorded species during day, present at >40% of the sampled sites (Table 2-2). During the night, the most frequently recorded species were the kodkod and chilla fox, with both species being detected at >30% of the sampled sites (Table 2-2). Diurnal variation in estimated mean occupancy, ψ, was more pronounced for the culpeo fox, for which estimated mean of ψ during day was three times larger than during night (Table 2-2).

The dog, cougar, and grison had higher estimated mean of ψ values during the day than night (7% - 20% higher), whereas the Darwin's fox, chilla fox, and kodkod had an estimated mean of ψ values higher during the night (6% -33% higher). The kodkod and skunk exhibited the largest correlation between day and night estimated mean of ψ ($\rho \leq$ 0.64 for all species), while the culpeo fox was the species with the lowest correlation between day and night estimated mean of ψ (Table 2). The culpeo fox, chilla fox, cougar, and kodkod exhibited the highest model estimates of overall occupancy probabilities $\psi_{overall} \geq 0.7$ (Table 2-2).

Table 2-2. Carnivore species recorded during the camera trap survey in Nahuelbuta Mountain Range in southern Chile. For both day and night, the following estimates are reported: The percentage of sampling sites where at least one detection occurred (Naïve occupancy), the model-averaged estimates (means and SDs from posterior probability distribution of estimates) of occupancy (ψ), detection probability (p), as well as the overall occupancy ($\psi_{overall}$) for day and night combined and the correlation (ρ) between day and night.

	Day			Night			Correlation	Overall occupancy
Species	Naïve occupancy	ψ (SD)	p (SD)	Naïve occupancy	ψ (SD)	p (SD)	ρ (SD)	$\psi_{overall}$ (SD)
Chilla fox	0.3	0.65 (0.09)	0.40 (0.05)	0.38	0.77 (0.06)	0.44 (0.04)	0.61 (0.14)	0.91 (0.13)
Cougar	0.4	0.55 (0.13)	0.58 (0.04)	0.32	0.51 (0.13)	0.58 (0.04)	0.47 (0.32)	0.78 (0.21)
Culpeo fox	0.71	0.80 (0.11)	0.80 (0.02)	0.18	0.24 (0.08)	0.60 (0.07)	0.08 (0.03)	0.83 (0.13)
Darwin's fox	0.09	0.14 (0.04)	0.54 (0.13)	0.11	0.21 (0.05)	0.48 (0.17)	0.63 (0.05)	0.32 (0.1)
Dog	0.34	0.46 (0.13)	0.54 (0.12)	0.21	0.38 (0.18)	0.43 (0.09)	0.58 (0.18)	0.66 (0.19)
Kodkod cat	0.33	0.49 (0.1)	0.43 (0.09)	0.37	0.52 (0.1)	0.67 (0.08)	0.64 (0.02)	0.75 (0.15)
Lesser grison	0.12	0.34 (0.13)	0.27 (0.03)	0.16	0.31 (0.17)	0.43 (0.03)	0.4 (0.03)	0.54 (0.18)
Skunk	0.17	0.25 (0.08)	0.30 (0.17)	0.13	0.25 (0.06)	0.47 (0.19)	0.64 (0.1)	0.43 (0.14)

Patch size and forest cover (prediction 1)

My results only weakly supported the prediction that patch size and native forest cover would positively influence occupancy of native carnivores especially during the daytime. As explained below, only the chilla fox, skunk, and Darwin's fox responded to forest cover as expected. However, for the rest of the species, this effect was scale-dependent and more accentuated during night. Similarly, the patch size effect was stronger during night for cougars whereas habitat generalists (culpeo foxes and skunks) responded negatively to patch size.

The cover of native forest measured at the camera-station (NF.plot) influenced the occupancy of all native carnivores (Table 2-3). However, for some species, such as the chilla fox, skunk, and Darwin's fox, this positive effect was only included in the best=supported models during the day (Table 2-3). In contrast, for the culpeo fox, the positive effect of native forest cover at the camera-station was stronger during the night than daytime, as shown by differences in nocturnal and diurnal coefficients of ψ (Table 2-4). Using data from the native forest plots with the 500m radius buffer revealed a temporal effect on the ψ of carnivores. Indeed, native forest at the 500m radius buffer had a positive and stronger effect on Darwin's fox and cougar occupancy probability during the night than during the day (Fig. 2-1), whereas a positive effect of this covariate was only included in the top-ranked occupancy models of chilla fox during the night (Table 2-3). In contrast, native forest at 500m radius buffer had a negative effect on the ψ of culpeo fox, but that effect was ca. 43% stronger during the night than the day (Table 2-4, Fig. 2-1). Occupancy probability was influenced by patch size for four of the eight carnivores, with this effect being mainly found at the 500m scale (Table 2-3). I detected a positive effect of patch size on the cougar occupancy probability only during night, whereas it negatively affected the ψ of culpeo foxes and skunks during day (Table 2-4).

Table 2-3. Posterior probabilities for the model set of best-supported candidate models (i.e., with posterior probability >0.05) for the occupancy probability (ψ) and detection probabilities (p) of carnivores in Nahuelbuta Mountain Range in southern Chile.

Species	Day	Night	Posterior probability
Kodkod cat	ψ(NF.plot) *p*(Season)	ψ (NF.plot) *p*(Season)	0.163
	ψ (Elv) *p*(.)	ψ (Elv) *p*(.)	0.10
	ψ (.) *p*(.)	ψ (NF.plot) *p*(.)	0.085
	ψ (.) *p*(Season)	ψ (.) *p*(Season)	0.061
	ψ (.) *p*(Season)	ψ(.) *p*(.)	0.061
Chilla fox	ψ (NF.plot) *p*(Season)	ψ (Dog) p(Season)	0.173
	ψ (NF.plot) *p*(Season)	ψ (NF500) *p*(Season)	0.055
	ψ (NF.plot+Dog) *p*(Season)	ψ (Pch500) *p*(Season)	0.052
	ψ (NF.plot) *p*(.)	ψ (.) p(Season)	0.051
Lesser grison	ψ (NF.plot+NF250) *p* (Season)	ψ (NF250) *p* (.)	0.148
	ψ (NF.plot+Prk) *p*(Season)	ψ (Prk) p (.)	0.111
	ψ (NF.plot+NF250+Dog) *p* (Season)	ψ (Elv+NF250+Dog) *p*(.)	0.074
	ψ (NF.plot+NF250) *p*(Season)	ψ (NF.plot+NF250) *p* (.)	0.074
	ψ (NF.plot) *p*(Season)	ψ (.) p (.)	0.073
Culpeo fox	ψ(NF.plot+Elv+NF500+Pch500+Dog) *p*(Season)	ψ(NF250+Rd250+Pch250) *p*(Season)	0.171
	ψ(Pch500+Dog) *p*(Season)	ψ(Elv+Rd250) *p*(Season)	0.072
	ψ(NF.plot+NF500+Dog) *p*(Season)	ψ(NF.plot+NF500) *p*(Season)	0.053
	ψ(Elv+Rd250+Pch500) *p*(Season)	ψ(Elv+Dog) *p*(.)	0.052
Darwin's fox	ψ(NF.plot+Rd250+Dog) *p*(.)	ψ(NF500+Dog) *p*(Und)	0.258
	ψ(NF.plot+Elv+NF500) *p*(.)	ψ(NF500) *p*(Season)	0.065
	ψ(NF.plot+Elv+Rd250+Rd500+Dog) *p*(Season)	ψ(NF500+Rd500+Dog) *p*(Season+Und)	0.055
Dog	ψ(Rd500) *p*(Season)	ψ(Rd250) *p*(Season)	0.229
	ψ(NF500) *p*(.)	ψ(NF500) *p*(.)	0.200
	ψ(.) *p*(.)	ψ(.) p(Season)	0.089
Cougar	ψ(NF.plot+NF500+Rd500+Dog) *p*(.)	ψ(NF.plot+NF500+Rd500) *p*(.)	0.112
	ψ(NF.plot+NF500+Dog) *p*(.)	ψ(NF.plot+NF250+NF500+Rd500) *p*(.)	0.106
	ψ(Elv+Dog)+*p*(Und)	ψ(NF.plot+NF250+Pch500) *p*(Und)	0.062
	ψ(NF.plot+NF500+Rd500) *p*(.)	ψ(NF250+NF500+Rd250+Rd500+Pch500) *p*(.)	0.057
	ψ(Elv) *p*(.)	ψ(NF.plot+Pch500) *p*(.)	0.057
	ψ(.) *p*(.)	ψ(NF.plot+NF250+NF500+Rd500+Pch500) *p*(.)	0.053
Skunk	ψ(Elv+NF250+Rd250) *p*(Und)	ψ(NF.plot+Elv+NF250) *p*(Season)	0.135
	ψ(Elv+NF250+Pch500+Rd250+Dog) *p*(Season + Und)	ψ(NF.plot+Elv+NF250+Rd250) *p*(.)	0.081
	ψ(.) *p*(Season)	ψ(.) *p*(.)	0.051

Variable acronyms: NF.plot= habitat type (native forest or exotic plantations) at camera-trap station; Prk= distance of camera-trap station to national park; Elv=elevation; NF250, 500= Native forest cover within 250m or 500m-radius buffers. Rd250, 500= Road density within 250m or 500m-radius buffers; Pch250, 500= Mean patch size of native forest within 250m or 500m-radius buffers; Dog=dog occupancy probability; Season= Proportion of camera-days in the Austral spring-summer; Und= understory vegetation cover within detection range of camera-trap.

Table 2-4. Posterior model-averaged coefficients, standard errors (SE), 95% credible interval (CI) and inclusion probability for covariates included in the best supported models (see Table 2-3), which are expected to influence diurnal and nocturnal occupancy (ψ) and detection (p) probabilities of carnivores in Nahuelbuta Mountain Range in southern Chile. (-) Covariate not included in the best-supported candidate models.

		Day			Night		
Species	Covariate	Mean (SE)	95% CI	Inclusion probability	Mean (SE)	95% CI	Inclusion probability
Kodkod	NF.plot	2.17 (0.01)	2.09, 2.16	0.64	1.98 (0.10)	2.17, 2.16	0.56
	Elv	-0.35 (0.02)	-0.39, -0.32	0.58	-0.34 (0.01)	-0.38, -0.31	0.52
	Season	-0.84 (0.12)	-0.86, -0.82	0.59	-0.83 (0.12)	-0.86, 0.81	0.41
Chilla fox	NF.plot	0.53 (0.02)	0.49, 0.57	0.6	-		
	Pch500	0.15 (0.014)	0.12, 0.18	0.69	0.10 (0.015)	0.07, 0.13	0.59
	NF500	-			0.19 (0.018)	0.15, 0.22	0.62
	Dog	0.79 (0.09)	0.61, 0.97	0.59	0.8 (0.08)	0.63, 0.98	0.82
	Season	1.14 (0.001)	1.14, 1.18	0.53	1.2 (0.001)	1.18. 1.22	0.58
Lesser grison	NF.plot	3.26 (0.20)	2.88, 3.63	0.87	3.24 (0.19)	2.86, 3.62	0.68
	NF250	0.90 (0.13)	0.64, 1.15	0.61	0.91 (0.13)	0.64, 1.16	0.7
	Prk	-0.04 (0.15)	-0.35, 0.26	0.12	-0.04 (0.15)	-0.34, 0.27	0.15
	Elv	-			-0.23 (0.17)	-0.57, 0.10	0.12
	Dog	0.31 (0.2)	-0.08, 0.70	0.34	0.35 (0.3)	-0.24, 0.94	0.37
	Season	1.76 (0.07)	1.62, 1.89	0.84	-		
Culpeo fox	NF.plot	2.53 (0.25)	2.02, 3.03	0.55	2.72 (0.26)	2.2, 3.20	0.72
	Elv	-0.14 (0.13)	-0.41, 0.12	0.32	-0.14 (0.13)	-0.41, 0.12	0.38
	NF500	-0.61 (0.14)	-0.89, -0.32	0.76	-0.87 (0.13)	-1.14, -0.60	0.61
	Pch500	-0.50 (0.15)	-0.81, -0.19	0.66	-		
	Rd250	-1.4 (0.19)	-1.77, -1.03	0.66	-1.9 (0.18)	-2.25, -1.54	0.75
	NF250	-			-1.43 (0.18)	-1.79, -1.07	0.63
	Dog	1.01 (0.17)	0.67, 1.36	0.63	0.90 (0.17)	0.64, 1.33	0.30
	Season	-1.26 (0.14)	-1.54, -0.97	0.82	-1.26 (0.14)	-1.53, -0.98	0.64
Darwin's fox	NF. Plot	2.44 (0.21)	2.02, 2.86	0.58	-		
	Elv	-0.73 (0.15)	-1.04, -0.42	0.54	-		
	NF500	0.18 (0.08)	0.02, 0.33	0.29	0.38 (0.10)	0.18, 0.57	0.40
	Rd250	-0.72 (0.15)	-1.02, -0.42	0.75	-		
	Rd500	-0.94 (0.13)	-1.04, -0.50	0.78	-0.49 (0.17)	-0.74, -0.23	0.65
	Dog	-0.27 (0.14)	-0.54, -0.003	0.74	-0.27 (0.13)	-0.54, -0.01	0.88
	Season	0.19 (0.15)	-0.12, 0.50	0.17	0.18 (0.16)	-0.13, 0.50	0.29
	Und	-0.61 (0.09)	-0.79, -0.43	0.76	-0.64 (0.09)	-0.83, -0.47	0.67

-

Dog	Rd500	0.29 (0.01)	0.26, 0.32	0.82			
	NF500	-0.26 (0.13)	-0.01, -0.51	0.66	-0.50 (0.20)	-0.11, -0.89	0.72
	Rd250	-			0.10 (0.02)	0.07, 0.12	0.55
	Season	-3.94 (0.05)	-4.05, -3.83	0.77	-3.99 (0.05)	-4.09, -3.89	0.78
Cougar	NF.plot	3.49 (0.24)	3.00, 3.97	0.7	3.50 (0.24)	3.02, 3.98	0.79
	Elv	-0.18 (0.15)	-0.48, 0.13	0.16	-		
	NF500	0.44 (0.15)	0.14, 0.74	0.72	0.74 (0.18)	0.38, 1.09	0.86
	Rd500	-1.90 (0.06)	-2.01, -1.78	0.72	-1.75 (0.11)	-1.96, -1.53	0.65
	NF250	-			2.03 (0.14)	1.74, 2.31	0.57
	Pch500	-			0.68 (0.16)	0.36, 1.00	0.72
	Rd250	-			0.02 (0.16)	-0.30, 0.34	0.24
	Dog	-1.11 (0.16)	-1.42, -0.80	0.78	-		
	Und	-0.21 (0.15)	-0.51, 0.09	0.22	-0.22 (0.16)	-0.52, 0.1	0.25
Skunk	NF.plot	1.89 (0.18)	1.52, 2.26	0.52	-		
	Elv	-0.22 (0.16)	-0.53, 0.09	0.38	-0.24 (0.16)	-0.55, 0.08	0.38
	NF250	0.27 (0.15)	-0.03, 0.57	0.29	0.26 (0.15)	-0.04, 0.56	0.27
	Rd250	-0.36 (0.14)	-0.63, -0.08	0.65	-0.59 (0.14)	-0.86, -0.30	0.67
	Pch500	-0.34 (0.17)	-0.67, -0.01	0.52	-		
	Dog	-0.08 (0.15)	-0.37, 0.21	0.49	-		
	Season	-2.45 (0.12)	-2.69, -2.21	0.67	-2.46 (0.12)	-2.70, -2.22	0.65
	Und	-0.35 (0.14)	-0.62, -0.07	0.58	-		

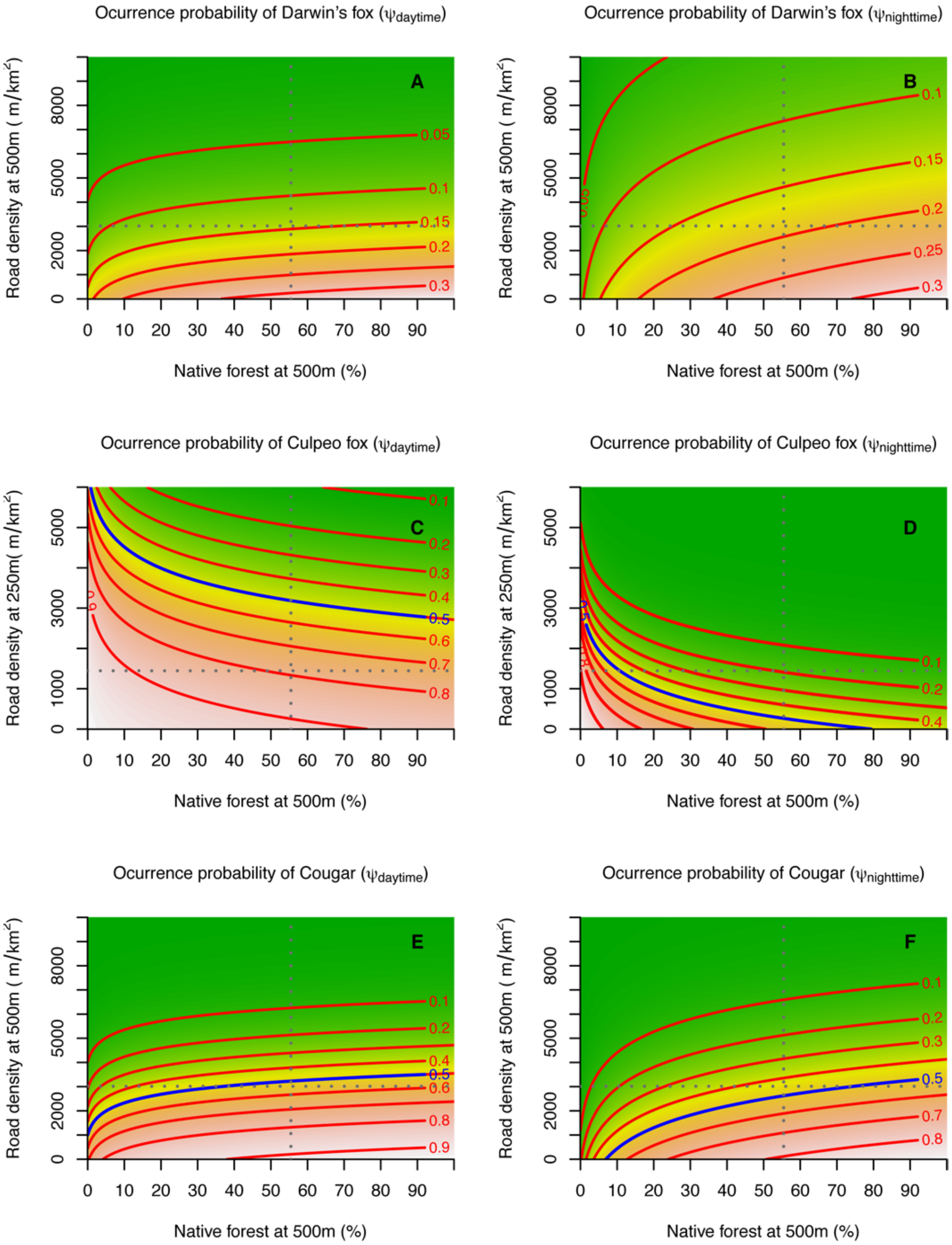

Figure 2-1. Contour plots showing model-predicted occupancy probabilities (ψ) of Darwin's fox (A and B), culpeo fox (C and D) and cougar (E and F) as function of two landscape-scale covariates: road density at two different scales (250m radius buffer and 500m radius buffer) and the amount (%) of native forest at 500m. Red isolines indicate combinations of the two covariates predicting a particular (ψ) level (with the blue isocline showing ψ =0.5). Vertical and horizontal dashed lines indicate the mean value of the covariate, as measured in the study landscape.

Road density (prediction 2)

The prediction that occupancy of native carnivores should decrease during the day as road density increases in the landscape was partially supported by the results. As explained in details below, only the cougar and the Darwin's fox responded more strongly, and negatively, to road density during day whereas the habitat generalists culpeo foxes and skunks were negatively affected by roads during night.

Road density influenced the nocturnal and diurnal occupancy probabilities of carnivores at multiple spatial-scales, as indicated by the best supported occupancy models (Table 2-3). Road density at 250m scale negatively affected the occupancy of Darwin's fox only during day (Table 2-4). Road density at 250m scale more strongly reduced the nocturnal occupancy of culpeo fox and skunk than the diurnal occupancy (Table 2-4, Fig. 2-1). Conversely, road density at 250m scale positively affected the nocturnal occupancy of dogs (Table 2-4). At the 500m scale, road density negatively affected both diurnal and nocturnal occupancies of Darwin's fox and cougar, with this effect being 31% and 27% stronger during day, respectively, as shown by differences between diurnal and nocturnal coefficients (β) (Table 2-4, Fig 2-1). Road density at 500m scale, however, showed a positive effect of dog occupancy probability during daytime only (Tables 2-4).

Proximity to a conservation area (prediction 3)

The prediction that the positive relationship between proximity to a conservation area and the occupancy of native carnivores should be more pronounced during the daytime was not supported by results. Only the best supported occupancy models for the lesser grison included the proximity to a conservation area as a covariate, but the effect was not significant (Table 2-3 and 2-4).

Dog occupancy (prediction 4)

The prediction that the negative effect of dogs on the occupancy of native carnivores should be more intense during day was only supported for cougars. Conversely, dogs affected habitat-specialist carnivores negatively, independently from the time throughout the day, whereas the habitat-generalist fox species were positively associated with dogs (see below and Table 2-3). Dog occupancy probability influenced the nocturnal and diurnal occupancy probabilities of native carnivores, as indicated by the best-supported occupancy models (Table 2-3). Dogs negatively affected the occupancy of Darwin's fox during daytime and nighttime whereas dogs' negative effect on the occupancy of cougar was evidenced only during daytime (Table 2-4). In contrast, dogs were positively associated to the occupancy probabilities of chilla fox and culpeo fox during day and night (Table 2-4).

Discussion

My results support the hypothesis that diurnal changes in habitat use were associated with human and dog activity, albeit weakly. These findings expand the understanding of the dynamics of the flexible habitat use by carnivores, which have been previously found to occur on a seasonal or annual basis rather than on diurnal scales, such as shown in this study (see Fig. 2-1). Although previous studies have addressed the temporal occupancy patterns of carnivores (e.g., Schuette et al., 2013), their diurnal occupancy patterns across human-modified landscapes have been poorly studied. Landscape ecology theory has contributed greatly to our understanding of ecological effects of land use changes, such as deforestation or land degradation, which typically occur at relatively broader temporal scales (Forman, 1995). However, human-dominated landscapes are short-term dynamic systems, with human activities being more intense at different times throughout the day. Thus, results of this study provide new insights for the conservation of threatened carnivore species within human-dominated landscapes.

All the study carnivore species, including the threatened Darwin's fox, had relatively high estimates of overall occupancy probability ($\psi_{overall}$ >0.3; Table 2-2). However, these carnivores neither exhibited similar occupancy probabilities between day and night nor responded consistently to changing human and dog activity. The occupancy probabilities of carnivores were higher during either the night or day, depending on both the species and the spatial scale. The best-supported models suggest that the variable effects of landscape attributes on the carnivores' occupancy depend on the time of day in which the species are more actively searching for prey, as well as, and are willing to move to, and use, the habitats where prey are available. I confirmed the positive and negative effects of native forest on forest-specialist and habitat-generalist carnivores, respectively, as previously documented (Jaksić et al., 1990; Acosta-Jamett and Simonetti, 2004). However, my results also indicate that the habitat effect is time- and spatial scale-dependent. Previous studies have documented that culpeo and chilla foxes exhibit a habitat-generalist behavior, using habitats with intensive land use and disturbance (e.g., forest plantations or agricultural lands; Acosta-Jamett and Simonetti, 2004; Silva-Rodriguez et al., 2010), unlike the Darwin's fox and kodkod cat that, are described as forest-specialist species. Moreover, dogs in semi-natural areas of southern Chile has been previously reported (Silva-Rodríguez et al., 2010; Silva-Rodríguez and Sieving, 2012). However, habitat specificity of the carnivore species included in this study changed between day and night. As supported by my findings, and discussed in details below, forest-specialized species, such as Darwin's foxes, showed stronger preferences for native forest during night. Conversely, habitat-generalist species, such as culpeo foxes and skunks, avoided using native forest during day. These findings provide new evidence by showing that habitat attributes (e.g., native forest cover, forest patch size) can affect the habitat use patterns of both habitat-generalists and forest-specialists, but that these effects can be time-dependent. Moreover, ecological information derived from this study can contribute significantly to the knowledge of these species in Nahuelbuta Mountain Range, by providing novel unknown evidence on the occupancy probabilities of carnivores in this ecosystem.

Patch size and forest cover (prediction 1)

I found that diurnal occupancies of native carnivores were affected by both native forest availability and patch size at different spatial scales. For Darwin's foxes and cougars, the stronger positive nocturnal effect of the amount of forest area and patch size of native forest at the 500m scale suggests that these species can concentrate their foraging effort in landscapes with more native forest during night. Native forest provides shelter and food resources such as small mammals, which are particularly abundant and constitute the major prey type for Darwin's fox (Jaksić et al., 1990). In these landscapes, Darwin's fox may also face reduced interference-competition from the habitat-generalist culpeo fox and dog which avoided landscapes with native forest during night (Table 2-4 and Fig. 2-1). On the other hand, cougars would benefit from large remnants of native forest where preying on southern Pudu (*Pudu puda*), one of their main native prey (Rau and Jiménez, 2010; Silva-Rodríguez and Sieving, 2012). The breadth of habitat use by carnivores, however, should be understood by considering their differential patterns of occupancy in landscapes during day and night. For example, culpeo foxes and skunks avoided landscapes with large native forest remnants only during day. Thus, the combination of time of the day and spatial scales at which the effects of landscape attributes become more intense may influence habitat use of carnivores. For example, the cover of native forest at camera stations increased the occupancy of most native carnivores in my study area. However, the positive effect of native forest at this scale was only detected during daytime for chilla fox, skunk and Darwin's fox, possibly suggesting that these small-sized carnivore species use native forest remnants as a daytime refuge, reducing the probability of encounters with humans or dogs (George and Crooks, 2006). In addition, although the occupancy of culpeo foxes decreased in areas covered by native forest, the less pronounced effect of this factor during the daytime (Fig. 2-1) suggests native forest would function as a habitat free of human activities for this predator.

Road density (prediction 2)

Native carnivores such as cougar and Darwin's fox were less likely to occur in areas with a high road density. This effect was more pronounced during day, probably as a response to increased traffic levels on the roads during the daytime (Fig. 2-1). Culpeo fox, however, had lower occupancy probabilities in landscapes with a high road density during night, probably to avoid encounters with dogs, which responded positively to roads during the night. Although areas with old and partially overgrown road cover may have a positive effect on carnivores activity by providing access to edge habitats where prey seems more abundant and vulnerable (Davis et al., 2011). Examples of carnivores responding negatively to dense road networks that act as movement barriers or mortality sources, prevail in the ecological literature (e.g. Whittington et al., 2004; Grilo et al., 2009). Diurnal variation in how strongly roads influence carnivores could reflect a changing risk perception, which, in turn, may be triggered by previous encounters with humans and dogs along roads during daytime. Short-term behavioral plasticity, resulting from changing habitat quality and availability or by variable human activity, could be critical for the survival of carnivores living in human-dominated, land-use mosaics (Boissy, 1995), as those species show in my study area (this chapter).

Proximity to a conservation area (prediction 3)

Contrary to the third prediction, carnivore occupancy did not respond to proximity of Nahuelbuta National Park. This finding suggests that there is no spatial gradient in habitat quality promoting increased spatial use near the national park. In addition, it is possible that the Nahuelbuta National Park is not large enough to support viable local populations (Simonetti and Mella, 1997). The role of protected areas on species conservation depends largely on the level of human activity that occurs in the matrix (e.g., agriculture, forestry or housing) surrounding protected lands (DeFries and Hansen, 2007). My results suggest that unprotected large native forest patches located northwest to Nahuelbuta National Park (see Fig. 2-1) play an important role in providing adequate habitat conditions for native carnivores, therefore favouring the animal movement within this landscape.

Dog occupancy (prediction 4)

The hypothesis that the diurnal occupancies of carnivores are influenced by landscape-scale human disturbances can be generalized by effects beyond habitat loss and degradation. Introduced species (e.g., dogs) that benefit from these environmental changes can increase the effects of human disturbance on biodiversity (Vanak and Gompper, 2010). In fact, the occupancy of dogs was largely influenced by road density (positive) and native forest (negative) at different spatial scales, supporting the notion that the detrimental effects of this introduced carnivore on local biodiversity is shaped by human land use. In southern Chile, dogs have also been suggested to move preferentially along roads and use human-created open areas (Silva-Rodríguez et al., 2010; Silva-Rodríguez and Sieving, 2012). In contrast, as shown in this study, cougars, chilla foxes, and Darwin's foxes tend to avoid areas with more roads while using large patches of native forest (Table 2-4 and Fig. 2-1). Therefore, native carnivores respond differentially during day or night not only to landscape attributes, but also to the diurnal use and movement of introduced carnivores across the landscape. However, dogs were positively associated with chilla fox and culpeo fox. Such a positive association should emerge from a similarity in habitat preferences rather than from a positive interaction between species (e.g., commensalism or mutualism). Thus, chilla fox and culpeo fox may become more prone to interact with dogs than the other carnivore species.

Concluding remarks

Results of this research suggest that native carnivores inhabiting this human-dominated landscape, and in particular the threatened Darwin´s fox, occur preferentially in areas covered by larger amounts of native forest and larger forest patches while displaying diurnal behaviors intended to reduce the encounters with human and introduced dogs. However, in landscapes experiencing increased forest loss or degradation, carnivores can concentrate into the few remaining patches, thus increasing the levels of spatial overlap among different carnivore species. Future studies addressing the hunting time activity of native carnivores are required to provide a conservation basis for reducing human effects on the foraging success of carnivores. Finally, I stress the need to 1) increase the patch size of native forest remnants; 2) develop an integrated management strategy taking into account large native-forest patches that belong to forestry companies and small native forest remnants that belong to smaller landowners; and 3) re-vegetate unused forestry roads and paths to connect habitat patches and implement dog-free zones to reduce the lethal and non-lethal effects of this exotic carnivore on native fauna.

Table S 2-1. Correlation coefficients (top) and variance inflation factors (down) for covariates used in models of carnivore occupancy and detection probability.

Correlation	Elevation	NF250	NF500	Prk	Rd250	Rd500	Ptch250	Ptch500
Elv	1							
NF250	-0.258	1						
NF500	-0.263	0.663	1					
Prk	-0.244	-0.233	-0.224	1				
Rd250	0.1	-0.452	-0.483	0.342	1			
Rd500	-0.004	-0.55	-0.585	0.391	0.611	1		
Ptch250	-0.48	0.06	0.06	-0.028	-0.076	-0.067	1	
Ptch500	0.206	-0.017	-0.04	-0.053	0.079	0.07	0.102	1

Covariate/species	Kd	Dog	Lg	Cf	Df	Gf	Co	Sk
NF.plot	1.751	1.320	1.46	1.16	1.71	2.01	1.67	1.9
Elv	1.675	1.190	1.750	1.673	1.555	1.305	1.119	2.525
NF250	1.559	1.260	1.422	1.253	1.135	1.041	1.56	2.74
NF500	1.358	1.900	1.230	1.280	1.120	1.550	1.620	1.660
Prk	1.121	1.760	1.010	1.110	1.540	1.760	1.900	1.220
Rd250	2.532	3.130	2.780	2.210	2.900	1.980	2.100	1.760
Rd500	3.149	2.980	3.030	2.790	2.880	3.120	3.220	3.120
Ptch250	1.458	1.870	1.210	1.400	1.560	1.870	2.012	1.320
Ptch500	1.258	1.430	1.110	1.090	1.800	1.470	1.346	2.112
Season	1.141	1.920	1.090	1.430	1.670	1.491	1.674	1.231
Und	1.041	1.100	1.113	1.556	1.359	1.517	1.845	1.765

Table S 2-2. Posterior model probabilities for the set of best-supported candidate models (i.e., with posterior probability >0.05) for the detection (p) probabilities of domestic dog in Nahuelbuta Mountain Range in central-south Chile. Dog's occupancy was estimated from a null model.

Species	Day	Night	Posterior probability
Dog	$\psi(.)\ p(\text{Season+Und})$	$\psi(.)\ p(\text{Season})$	0.37
	$\psi(.)\ p(\text{Und})$	$\psi(.)\ p(\text{Season+Und})$	0.18
	$\psi(.)\ p(\text{Und})$	$\psi(.)\ p(\text{Und})$	0.09
	$\psi(.)\ p(.)$	$\psi(.)\ p(.)$	0.06
	$\psi(.)\ p(\text{Season})$	$\psi(.)\ p(\text{Season})$	0.05

CHAPTER III

Using high-resolution LiDAR for predicting carnivore occupancy throughout a heterogeneous forest landscape in southern Chile.

Introduction

Effective habitat management of threatened species living in human-disturbed landscapes requires unbiased estimates of habitat use and selection at different spatial scales (Margules and Pressey, 2000). Reliable assessment of species-habitat relationships not only depends on providing accurate estimates of these species' parameters (Lele et al., 2013, MacKenzie et al., 2002), but also on how well habitat structure is described at different spatial scales (Boyce, 2006; Guisan and Zimmermann, 2000; Manly et al., 2002). Whereas accurate estimates of species habitat use require an appropriately design to record the species' individuals across sufficient sampling locations (Mackenzie and Royle, 2005), the description of habitat structure may be obscured by spatial constraints arising from field sampling methods. Field observations usually provide only a partial estimation of habitat attributes (e.g., vegetation height or cover), especially when animals have large home-ranges. High-resolution imagery, however, has improved our ability to characterize habitat heterogeneity over larger extents than field observations, allowing detailed characterization of habitat structure (Mason et al., 2003). Animal habitat use models including habitat variables derived from high-resolution imagery provide a basis for assessing the distribution of threatened animals in heterogeneous landscapes (Guisan and Thuiller, 2005).

Remote sensing Light Detection and Ranging (LiDAR) offers a cost-effective method to obtain high-resolution environmental information on forest structure including understory vegetation density, canopy height, canopy height profiles, canopy cover and biomass (Hernández et al., 2013; Hyde et al., 2006; Vierling et al., 2008). LiDAR uses laser light emitted from a source and reflected back to a sensor as it intercepts objects in its path (Dubayah and Drake, 2000; Lefsky et al., 2002). As the reflected light is detected at the sensor it is digitized, creating a record of returns that are a function of the distance between the sensor and the intercepted object. Although the usefulness of LiDAR for exploring species-habitat relationships has been discussed (e.g., Lefsky et al., 2002; Mason et al., 2003; Vierling et al., 2008), studies that directly relate wildlife data with LiDAR-derived data of habitat structure are comparatively scarce (Goetz et al., 2007; Müller and Brandl, 2009; see Vierling et al., 2008 for a review).

Carnivores living in central-south Chile have been exposed to human pressure over the last century from the accelerated replacement of native forest by exotic forest plantations (Aguayo et al., 2009; Echeverria et al., 2006). Although the perception of exotic plantations as "ecological deserts" has been widely accepted among wildlife managers, exotic plantations harboring a complex habitat structure may act as habitat for species whose native habitats have experienced accelerated declines (Brockerhoff et al., 2008; Carnus et al., 2003). Therefore, identifying structural variables that may help plantations become more biodiversity friendly is a challenge for conservationists and ecologists (Puettmann et al., 2008; Simonetti et al., 2013). Nonetheless, knowledge of the habitat-use patterns of Chilean carnivores inhabiting landscapes dominated by exotic monocultures is scarce (e.g., Acosta-Jamett and Simonetti, 2004; Silva-Rodríguez and Sieving, 2012; Simonetti et al., 2013). For instance, in central Chile, the habitat use of kodkod cat (*Leopardus guina*) has been largely associated with vegetation cover <1.5m, suggesting that exotic plantations containing dense understory cover may favor the movement of this native wild cat through fragmented landscapes (Acosta-Jamett and Simonetti, 2004). Considering that exotic plantations currently cover almost 17% of forested areas in central-south Chile (CONAF, 2011), carnivore conservation in these production-oriented lands requires identifying suitable habitat areas from a detailed, accurate, and unbiased habitat structure assessment (Marques et al., 2014). LiDAR offers detailed information about the structure of vegetation in native forests and exotic plantations with different age and management prescriptions (Hernández et al., 2013), thus improving accuracy and performance of habitat use models. I studied the habitat use of threatened carnivores in a landscape containing native forest and exotic-forest plantations in southern Chile by combining a camera-trapping dataset with fine-grained information of habitat structure derived from LiDAR. My study also aimed to determine how well LiDAR-derived habitat structure could be used to determine species' potential distribution across large spatial scale.

Methods

Study Area

The study area encompassed the Caramávida basin, a private conservation area of nearly 23,800 ha located north-west in the Nahuelbuta Mountain Range (37° 45'S, 73° 00' W), southern Chile. The topography of Canarávida is rugged, with numerous ravines and ridges. Elevation of Caramávida basin ranges from approximately 500 to 1,300 m. Vegetation includes native forest remnants with exotic plantations of Monterrey pine (*Pinus radiata*) and *Eucalyptus* spp. Native forest is comprised by two distinctive and relatively homogeneous native forest communities in different successional states: at higher elevations monkey-puzzle tree (*Araucaria araucana*), roble (*Nothofagus obliqua*), coigüe (*Nothofagus dombeyi*), and Antarctic beech (*Nothofagus antarctica*) forests dominate, whereas mixed broad-leaved evergreen forests are found at lower elevations (Wolodarsky-Franke and Herrera, 2011).

Carnivore presence/absence

I used camera-trapping to assess carnivores' presence/absence in Caramávida across Austral spring and summer seasons (from October 2011 to Feb 2012). Previous evidence showed increased activity of species during these seasons compared to the fall and winter (Jiménez et al., unpublished data). Moreover, both spring and summer are considered critical for replenishing energetic demands and for reproduction in native carnivores, increasing their movement rates and therefore their probability of being recorded (Burton et al., 2015; Jaksić et al., 1990; Jiménez et al., 1990; Muñoz-Pedreros et al., 1995). I sampled 85 stations using lured/baited passive infrared-triggered camera (Reconyx PC900 Holmen, Wisconsin and Busnell Trophy Camera, Bushnell Corporation, Overland Park, Kansas, USA) mounted on trees ca. 50-60 cm above the ground. I used a random design to place cameras throughout the landscape at a minimum distance ca 500m and maximum distance ca 1,630m between cameras (average distance 870m).

Model structure of habitat use and LiDAR variables

I used occupancy models accounting for imperfect detection to assess the habitat use of carnivores (MacKenzie et al., 2002). Similar to approach used in Chapter 2, I assumed habitat use being correlated to the probability of site use/occupy (prob[used|occupied]) rather than true occupancy (prob[occupied]), given that my 'sites' were point locations of camera traps (Lele et al., 2013). Similarly, detection was interpreted as the probability a species is detected, given the site is occupied and used during each occasion (prob[detected|site occupied and used]). Occupancy probability (ψ) and detection probability (p) of carnivores was assumed to vary across space and modeled with LiDAR-site covariates related with forest structure. Detection probability was modeled as a function of site-level factors that influenced the chance of, and time when, individuals entered the camera's detection zone. I estimated the cover of vegetation measured within 10m in front of each camera station. I used the checkerboard-type method (modified from Nudds, 1977) to measure vegetation cover, which was considered as being proportional to the degree of blockage of the detection zone of cameras.

Occupancy probability at point location (camera trap) was modeled by using three forest structure predictor variables derived from LiDAR data obtained from a Optech LiDAR sensor: (1) Understory cover (Und) as native dense shrub may provide refuge from human activity and introduced species such as free-raging dogs as well as represent better foraging conditions (e.g., Fuller et al., 2007; Lantschner et al., 2011), particularly in forest plantations (Simonetti et al., 2013). Understory cover was obtained by calculating the vegetation density at a camera-trap scale (50-m radius) and within 250-m radius buffer around each camera trap, considering the vertical stratum between 0-1.5m as follows:

$$\mathbf{Und} = \frac{\sum \mathbf{x}_{\mathbf{int\ veget}}}{\sum \mathbf{x}_{\mathbf{total}}}$$

Where $\sum x_{\text{int veget}}$ corresponds to the pulses intercepted by vegetation and $\sum x_{\text{total}}$ to the total amount of pulses in the determined height range (0-1.5m). (2) Complexity of forest structure was expressed as a structural diversity index (SDI) that incorporated vertical and horizontal variation in vegetation (e.g., tree size, canopy cover, shrub size, shrub cover, coarse woody debris, and snags (van Ewijk et al., 2011):

$$\mathbf{SDI} = \left(-\sum_{\mathbf{i=1}}^{\mathbf{HB}} [(\mathbf{p_i} * \mathbf{ln}(\mathbf{p_i}))]\right) / \mathbf{ln}(\mathbf{HB})$$

Where **HB** represents the total number of pulses for the total height classes and $\mathbf{p_i}$ is the proportion of pulses in the container at that height i. The SDI index was calculated at camera-trap station scale (within a 50m radius of the camera site.); (3) Canopy height was calculated as the max and modal canopy height (Canopy height [MOD] and Canopy height [MAX], respectively) within a 250m radius of the camera site by using a moving window. I also included habitat type, as well as the interaction between habitat type and understory cover. Finally, similar to Chapter II, I included elevation as an additional covariate because of the possible altitudinal gradients in native prey abundance and human presence (Patterson et al., 1989). Non-categorical covariates were standardized (e.g., $\mathrm{elev_t} = \mathrm{elev}/1000$) and if strong collinearity was detected ($|r| \geq 0.65$), they were not included in the same model.

Detection probability was modeled as a function of LiDAR covariates (understory cover within 250-m radius buffer and complexity of forest structure) but also the cover of vegetation measured within 10m in front of each camera-trap. Similar to Chapter II, I used the checkerboard-type method (modified from Nudds, 1977) to measure vegetation cover, which was considered as being proportional to the degree of blockage of the detection zone of cameras.

Species detection at increasing sampling effort

Previous to probability occupancy analyses, I used the cumulative camera-trapping days to determine if the carnivore occupancy survey was sufficiently long to detect the species of interest. Sample effort and detection events were included in an accumulation curve and randomized 1000 times to derive 95% confidence intervals around the mean. I also calculated the latency period (LP) for each species as the average number of camera days needed to obtain the first detection (not including cameras with no captures). Latency periods were then related to species' home-ranges available in Johnson and Franklin (1994), Donadio et al., (2001), Sanderson et al., (2002), Jiménez (2007), and Vidal and Sanderson (2012). Even though cumulative camera-trapping days and LP approaches ignore imperfect detection of individual species, they become baseline for future monitoring and provide useful information for comparison with other studies and techniques (Silveira et al., 2003).

Species model fitting

I fitted a single-season single-species occupancy model to model occupancy and detection probabilities at camera stations for each carnivore species (MacKenzie et al., 2002). The detection history for each camera station was constructed by dividing the 30 trap-days each camera was active, into six survey occasions comprised of five days each. I considered this survey period as short enough as to prevent violation of site closure assumption for occupancy models for some described species (e.g., Darwin's fox; Jiménez, 2007, but see Rota et al., 2009). I used a model selection approach and Akaike Information Criterion with small sample size correction (AICc) to rank candidate models and calculate their Akaike weights. Model selection was conducted by fitting a model that best explained probability of detection including LiDAR covariates mentioned above and vegetation cover in front of the camera-trap. Then, the best detection model was used to select the model that better explained occupancy (MacKenzie, 2006). I determined the level of support of each predictor variable by summing the Akaike weights (ω) across all models that contained the variable of interest (ω^+) (Burnham et al., 2010). I evaluated goodness of fit on the competing models by calculating a Pearson chi-square statistic and implemented a parametric bootstrapping to determine if the statistic was significantly large (MacKenzie and Bailey, 2004). Occupancy analysis was performed using the package ‘unmarked’ in R (Fiske and Chandler, 2011). The relative importance of the model parameters were calculated with the R package AICmodavg (Mazerolle, 2012).

Model testing and validation

For each species, I tested the assumption of spatial independence of the residuals on the best-ranked occupancy probability model using Moran's I correlograms (Fortin and Dale, 2005) implemented in SAM4.0 (Rangel et al., 2010).

In addition, I evaluated the accuracy of the final model for each carnivore species by calculating the area under the receiver operating characteristic (ROC) curve. The area under ROC curve indicates overall ability of the model to accurately predict the data used to create it (Fielding and Bell 1997; Pearce and Ferrier 2000). Values of this index range from 0.5 (i.e., no better than a null model) to 1.0 (i.e., perfect accuracy; Fielding and Bell, 1992; Pearce et al., 2000). However, low detection rates can contribute to inaccurate or misleading ROC values, as the failure to detect a species at a given location is assumed by ROC analysis to represent a true absence (Stafford et al., 2006). Thus, I calculated the accuracy of final models for Darwin´s fox, kodkod cat, chilla fox, and culpeo fox for whose detection probabilities ranged from 0.24 to 0.5. Web-based ROC analysis software (Eng, 2005) was used to generate ROC curves and to calculate area under ROC curve values for each carnivore. Finally, I used the coefficient estimates for each covariate of the final occupancy model, to derive a map of probability of occurrence for some carnivore species across the Caramávida conservation area on a spatial grid with a cell size of 20x20 m, as obtained from the output grain of data processing.

Results

Carnivore community

Camera traps recorded seven species of native carnivores during 2,550 camera days (Table 3-1). Other mammal species such as domestic dog (*Canis familiaris*) and the native Southern pudu (*Pudu puda*) were also captured. Culpeo fox and lesser grison were the most and the least recorded carnivores on 82 and nine different surveys occasions, respectively (ψ_{naive} = 0.41 and 0.08 for culpeo fox and lesser grison, respectively, Table 3-1).

Table 3-1. List of native carnivores recorded in Caramávida conservation area, central-south Chile and three main indices: number of detected survey occasions for each species (as the number of records of each species across the detection history of all camera-traps (N=85), *naïve* occupancy (number of sites that are positive to species' presence divided by the total number of sites sampled), and latency period (average number of camera days needed to obtain the first detection for each species).

Species	Detections (n)	$\psi_{naïve}$	Latency period (Days ± SD)
Darwin's fox (*Lycalopex fulvipes*)	41	0.22	15.18 ± 12.01
Kodkod cat (*Leopardus guigna*)	38	0.36	16.37 ± 11.27
Cougar (*Puma concolor*)	31	0.19	21.72 ± 16.53
Skunk (*Conepatus chinga*)	20	0.23	19.75 ± 19.32
Lesser grison (*Galictis cuja*)	9	0.08	35.05 ± 43.80
Culpeo fox (*Lycalopex culpaeus*)	82	0.41	16.54 ± 16.01
Chilla fox (*Lycalopex culpaeus*)	30	0.15	16.00 ± 16.94

Species accumulation curve reached an asymptote at approximately 2,000 camera days, when 100% of carnivore species of interest were recorded (eight species, Fig. 3-1). Latency to first detection did not differ among carnivores (ANOVA; F-value=0.41, p-value=0.83; Table 3-1), neither was positively correlated with species home-range size ($r_{Pearson}$=0.65; p=0.11).

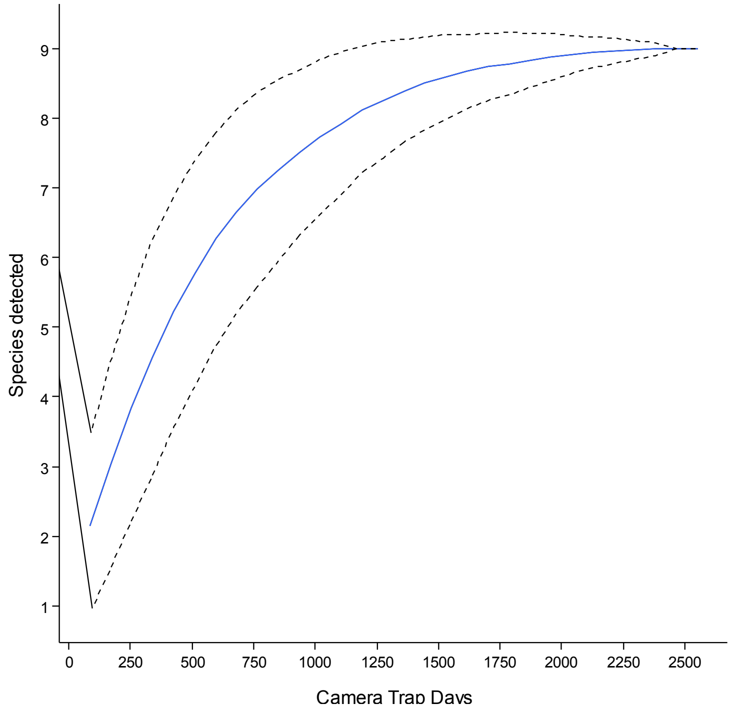

Figure 3-1. Species-detection accumulation curve (blue solid line) for carnivores detected by camera trapping in Caramávida conservation area, central-south Chile. Detection of species was randomized 1000 times to derive 95% confidence intervals (black dotted lines).

Carnivore occupancy probabilities and model fitting

Occupancy models were fitted for all recorded species except for the lesser grison whose naïve occupancy was <0.1. Occupancy models for the culpeo fox and chilla fox exhibited the highest and lowest occupancy estimates (ψ = 0.54±0.08 and 0.18±0.04, respectively; Table 3-2). Darwin's fox exhibiting the highest detection probability (p=0.5±0.05), while skunk showed the lowest detection probability (p=0.17±0.04; Table 3-2).

Models including LiDAR covariates were included in the top-ranked models (Δ AIC<3) for all species, with the exception of kodkod cat, for which the null model was also supported (Table 3-2). However, the effects of LiDAR covariates (i.e., model coefficients) and model goodness-of-fit were different among species (Table 3-2). Likewise, there was support for the fact that carnivores were less likely to be detected as vegetation cover in front of cameras increased (except for skunk; Table 3-2).

Table 3-2. Summary of predicted occupancy ± SE and detection probability (*p*) ± SE estimates for recorded carnivores in Caramávida conservation area. Outcomes of the effect of LiDAR covariates and their directionality (positive/negative) on ψ and *p* are indicated for species that had adequate detection for the analysis (except lesser grison showed with NA). Parentheses denote confidence interval of beta estimates did not overlap zero. For ψ (habitat) variable, [] indicates habitat type associated with the effect.

			LiDAR Covariates							
Species	ψ (SE)	*p*(SE)	ψ(Und250)	ψ(Undplot)	ψ(SDI)	ψ(Elv)	ψ(Canopy height(MOD))	ψ(Canopy height(MAX))	ψ(habitat)	*p*(Unders_camera)
Darwin's fox	0.24 (0.04)	0.5 (0.05)	(+)		(+)	+	-			(-)
Kodkod cat	0.47 (0.07)	0.25(0.04)	(+)		(+)	+		+	(-) [plantation]	(-)
Cougar	0.24 (0.05)	0.25 (0.05)	-	+	+	-	(+)			(-)
Skunk	0.37 (0.08)	0.17 (0.04)	(-)				(-)	(-)		(+)
Chilla fox	0.18 (0.04)	0.36 (0.06)	(+)		-	(+)	-	-		(-)
Culpeo fox	0.54 (0.08)	0.24 (0.03)	(-)	-	-	(-)	(-)	(-)	+ [plantation]	(-)
Lesser grison	0.1 (0.01)	0.01 (0.01)	NA	NA	NA	NA	NA	NA	NA	NA

Variable acronyms: Und250=understory forest cover within 250m-radius buffer; Undplot= understory forest cover within 50m-radius buffer (camera station scale); SDI: structural diversity index measured within 50m-radius buffer; Elev= elevation; Canopy height (MOD; MAX)= max and modal canopy height; Habitat=coarse habitat classification; Unders_camera=understory vegetation cover within detection range of camera-trap (10m).

Coefficients of the best-supported occupancy models strongly indicated: i) understory density at 250m scale increased the probability of occupancy of Darwin's fox (ω^+=0.87), but decreased the occupancy of skunk (ω^+=0.75); ii) elevation increased occupancy of chilla fox (ω^+=1); and iii) kodkod cat occupancy increased as structural diversity of forest also increased (ω^+=0.54). On the other hand, coefficients showed moderate evidence for: i) occupancy of culpeo fox decreased as understory density at 250m and elevation increased (ω^+=0.33 and 0.31, respectively); ii) occupancy of cougar and Darwin's fox increased as structural diversity of forest increased (ω^+=0.36 and 0.31, respectively). Finally, covariate coefficients indicated low support for: i) kodkod cat occupancy decreasing in exotic plantations (ω^+=0.14), as well as cougar occupancy decreasing as understory cover at 250m increased (ω^+=0.18); ii) the occupancy of chilla fox increased as structural diversity of forest increased (ω^+=0.19) and the occupancy of Darwin's fox increased as elevation also increased (ω^+=0.20); iii) the occupancy of culpeo fox decreased as elevation also increased (ω^+=0.24). Interaction between habitat type and understory was not included in the top ranked models. Details of model selection for each species are shown in Table S3-1. The relationships of ψ with the dominant LiDAR covariates and the main spatial patterns of predicted ψ for four species are shown in Fig. 3-2 and Fig. 3-3, respectively.

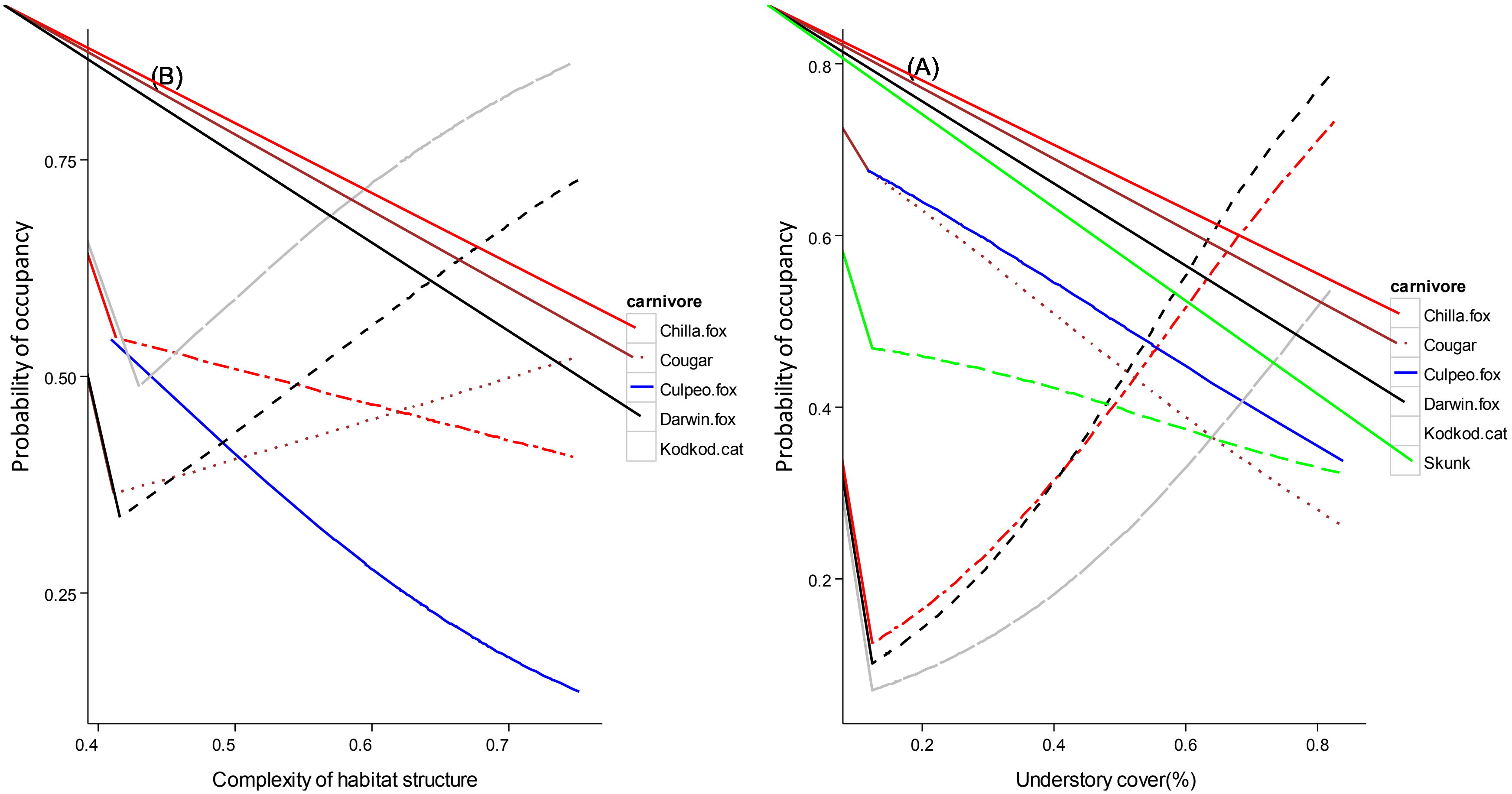

Figure 3-2. Predicted probabilities of carnivore occupancy relative to variation in understory cover within 250m-radius around each camera-trap (A) , and the complexity of habitat structure at camera-trap within 50m-radius (B). Species are given in the legend.

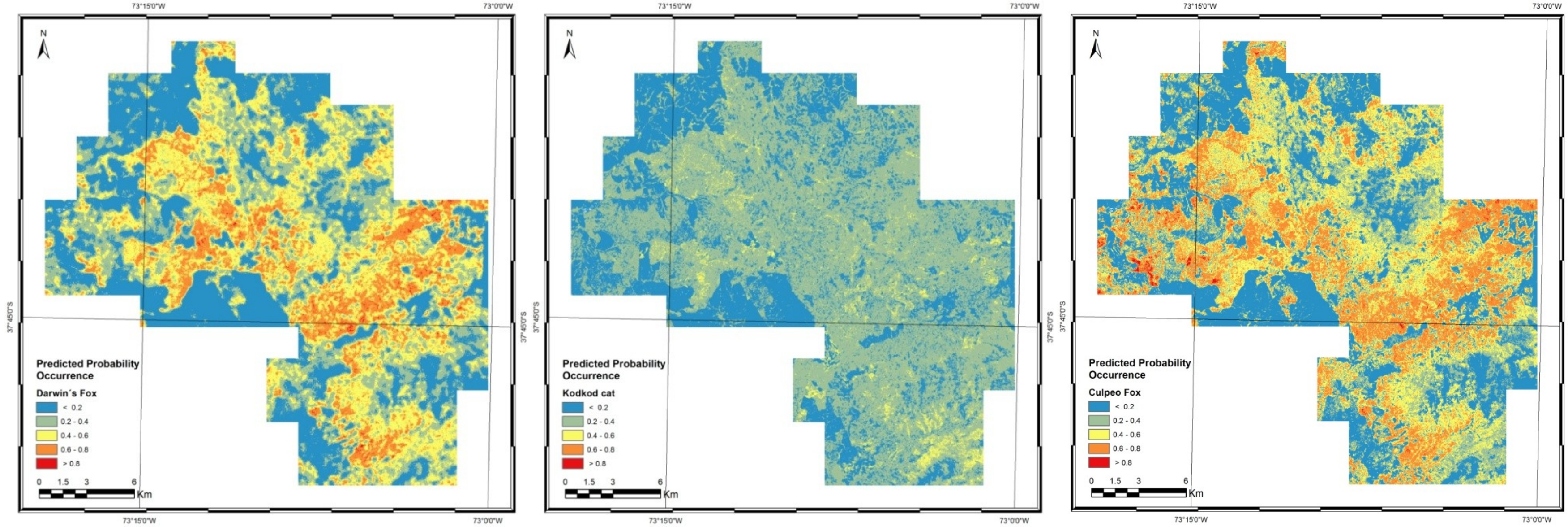

Figure 3-3. Predicted probability of occupancy based on model-averaging of the 95% model confidence set for three carnivore species occurring in Caramávida conservation area, southern Chile: Darwin's fox; kodkod cat; culpeo fox

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Model testing and validation

For all the candidate models, there was no evidence of lack of fit (all Bootstrapping p-values were >0.05, Table S3-1). Moran's-I correlograms indicated that model residuals were not spatially autocorrelated ($p<0.05$), with the exception of the cougar model for which a significant correlation at a lag distance of ca. 1000 m. The values for area under ROC curves were 0.90 and 0.83 for Darwin´s fox and kodkod cat models (based on the averaged 95% confidence set), respectively, whereas 0.85 for culpeo foxes, indicating considerable similarity between predicted and observed values (Fig. 3-4). Although less accurate than the Darwin´s fox and kodkod models, the averaged chilla fox model (area under ROC curve 0.68) performed substantially better than the null model (area under ROC curve = 0.5).

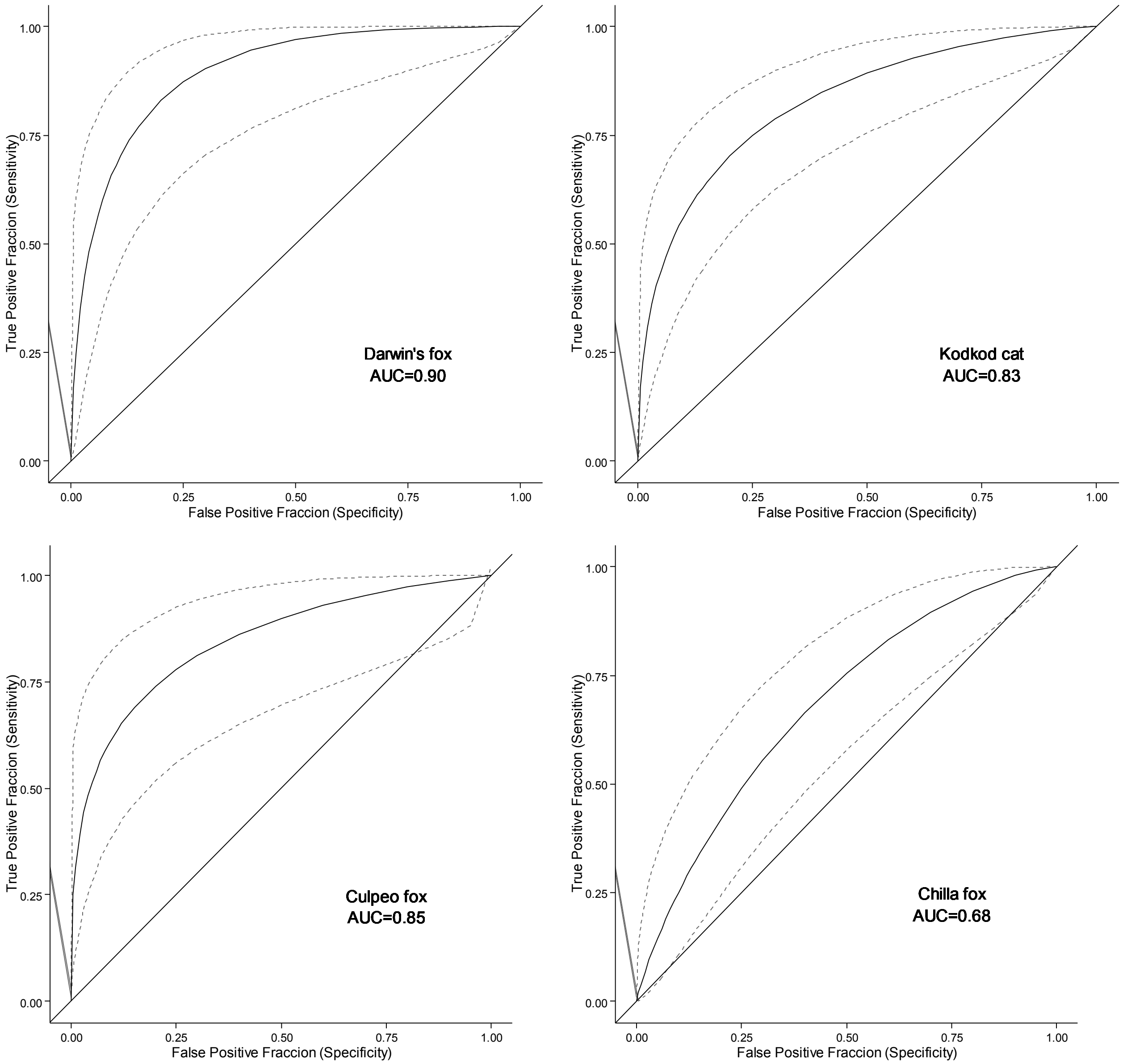


Figure 3-4. Area under Receiver–operator-characteristic (ROC) curves that resulted from averaging the 95% confidence sets of the best supported models for Darwin´s fox, kodkod cat, culpeo fox and chilla fox. Area under Receiver–operator-characteristic = 1.00 for a model that perfectly predicts occupancy at surveyed sites, and Area under Receiver–operator-characteristic = 0.5 for a model that predicts no better than a null model. Dotted lines represent upper and lower 95% confidence intervals.

Discussion

Predictive species occupancy models accounting for imperfect detection while based on accurate habitat description are useful for wildlife management in human-modified landscapes (Guisan and Zimmermann, 2000; MacKenzie et al., 2002). By combining non-invasive remote camera-trapping, occupancy modeling, and high resolution LiDAR habitat data, I derived carnivores' occupancy and detection probabilities. Such a mixed methodological approach provided us with reliable occupancy estimates for carnivores inhabiting a mosaic area comprising native forest and monoculture plantations in Nahuelbuta Mountain Range. Commercial plantations are becoming a dominant land-use type throughout temperate forest of South America (Simberloff et al., 2010), and if sustainably managed may have an important role as habitat for wildlife (Brockerhoff et al., 2008). However, this approach also may be extended to identify suitable habitat conditions for species living in heterogeneous landscapes comprising other production-oriented lands with different habitat structures.

The efficiency of camera-trapping for describing the ecology of wild carnivores has been widely shown by other multi-species studies in tropical ecosystems (e.g., Burton et al., 2012; Davis et al., 2011; Rovero et al., 2014; Tobler et al., 2008). Comparatively however, carnivore assemblages of South American temperate ecosystems, which contain several elusive species, remain poorly studied (e.g., Lantschner et al., 2012). In the Caramávida conservation area, a camera-trapping effort >2,000 camera/days was needed to detect all carnivores potentially described to occur in the study area. Moreover, cameras needed to be deployed for atleast 15 days for the first detection of all the species, with latency increasing as the home-range size of each species increased. Factors such as how elusive the species is, animal movement behaviour, and population density, have been suggested to strongly determine animal detection rates by cameras set in a particular area (Fig. 1 in Burton et al., 2015), so correlation between latency and home range size, as found in this study, confirm the importance of these factors when designing camera-trapping surveys.

The pool of the most-recorded species (Naïve ψ >0.2) included some carnivore species that are poorly known, and may have low detection rate using alternative methods such as track plates and scat collection (Acosta-Jamett and Simonetti, 2004; Jaksić et al., 1990; Zuñiga et al., 2009). For example, the kodkod cat, considered to be a rare species in coastal fragmented temperate forests (Acosta-Jamett and Simonetti, 2004), was the second most common species widely distributed in my study area (occupancy [ψ] = 0.47), agreeing with occupancy estimates from Gálvez et al., (2013) in temperate Andean forest. On the other hand, Darwin's fox, a low-density and elusive species in temperate forests, comprising only three known populations throughout Chile (Farias et al., 2014), was the fourth most common species in terms of occupied area in Caramávida conservation area (ψ = 0.24).

Among other commonly detected species, culpeo fox (ψ = 0.54) is expected to occur frequently in human modified landscapes given its flexible habitat behaviour (Acosta-Jamett and Simonetti, 2004; Lantschner et al., 2012). The difference between the naïve occupancy and model's occupancy for some species, such as kokdkod cat (from 0.36 to 0.47), culpeo fox (from 0.41 to 0.56), and skunk (from 0.23 to 0.37), highlights the need for: 1) accounting for imperfect detection (probability of animal detection < 1); and 2) modelling potential spatial variation in detection probability by using fine-scale habitat covariates (Burton et al., 2015).

I observed a low occupancy probability for cougar (ψ = 0.24) in Caramávida conservation area, which differed from previous studies conducted in undisturbed temperate forest landscapes, where the naïve occupancy of cougars was almost two fold higher (0.44; Muñoz-Pedreros et al., 1995). The low occupancy probability of cougars in this study landscape may be related to a smaller population size within this area, but also to a larger home-range in response to habitat transformation, low prey availability, and anthropogenic activity (Grigione et al., 2002; Knopff et al., 2014; Maletzke et al., 2014), which may reduce the chance for this species to be detected by fixed camera-traps (Burton et al., 2015). In addition to these non-documented observations, other carnivore species exhibited low detectability (i.e., lesser grison and skunk), with their natural history and conservation status remaining poorly understood for this region (Lantschner et al., 2012; Poo-Muñoz et al., 2014).

The occupancy probabilities of carnivores varied across the landscape, and were significantly affected by various LiDAR-derived estimates of habitat structure and elevation. Understory cover and habitat complexity were consistently included within the set of best-supported competing models across all carnivore species, having differential effects on the occupancy probability of these species. However, contrary to my expectations, habitat type (native forest or exotic plantation) did not improve models of habitat use patterns for most of the studied species. Both results confirm that fine-grained information of habitat structure, and not a coarse classification of habitat type, may be a better determinant for explaining the habitat use of native carnivores in mosaic landscapes.

The occupancy of Darwin's fox, kodkod cat and chilla fox increased with the increase of the understory cover. However, larger body-size cougars and culpeo foxes more often occurred in areas of low understory cover (Fig. 3-3). Moreover, the occupancy of kodkod cats, Darwin's foxes, and cougars increased as habitat structure became more complex, whereas occupancy probabilities of culpeo and chilla foxes decreased. An increased multi-strata vegetation and shrub cover are closely correlated with the abundance of food resources for small mammals and birds in southern temperate forests (Kelt, 2000; Saavedra and Simonetti, 2005; Vergara and Armesto, 2008), and may compel these small carnivores to intensively use areas with dense understory (Gorini et al., 2012; Jiménez et al., 1990; see also Chapter IV). In addition, the availability of arboreal small mammals is higher in areas with a more complex habitat structure (Fonturbel, 2009; 2010), facilitating the arboreal hunting behaviour of kodkod cat (Altamirano et al., 2013; Sanderson et al., 2002). Alternatively, as the cougar has been documented killing Darwin's fox (McMahon unpublished data), it is possible that dense vegetation might be used as an anti-predatory refuge by this smaller carnivore. Consequently, and as suggested from this study, cougars' hunting abilities for searching prey may be reduced by dense understory cover at larger scale (Gorini et al., 2012). However, concealment arising from habitat structural complexity at the site scale and presence of tall trees in undisturbed forest, would facilitate hunting behaviour of cougars, which can display a stalk approach and exhibit short pursuits for attacking prey (Husseman et al., 2003). Moreover, habitat type, and particularly, the presence of exotic plantations, did not affect negatively the cougar's occupancy probability. Previous studies have suggested that cougar occurrence may be enhanced by the presence of forest plantations (Lantschner et al., 2012; Lyra-Jorge et al., 2009; Mazzolli, 2010; Zuñiga et al., 2009). These human-created habitats may contain high abundance of introduced lagomorphs such as the European rabbit (*Oryctolagus cuniculus*) and hare (*Lepus capensis*), which may supplement cougars' natural diet based on native prey, such as Southern pudu (*Pudu puda*) (Rau and Jiménez, 2002).

The presence of exotic plantation did positively affect the presence of culpeo fox in the study area. Previous studies have documented culpeo foxes responding positively or negatively to exotic plantations, with such a response being influenced by the availability of native understory present within monocultures (Acosta-Jamett and Simonetti, 2004; Lantschner et al., 2012). Similar to native forest, the development of a understory vegetation in exotic plantations would support a larger prey availability such as small mammals, making exotic plantations with understory suitable habitats for this predator (Lantschner et al., 2011; Saavedra and Simonetti, 2005). Although a slightly positive effect of exotic plantations was found on this species, the negative effect of understory cover and habitat structural complexity did not support the prey availability prediction. Alternatively, I suggest that low levels of vegetation cover and simpler habitat structure could increase the hunting efficiency of culpeo foxes (Gorini et al., 2012), especially when hunting the introduced European rabbit and hare, and habitat generalist small mammals, such as long-haired field mice (*Abrothrix longipilis*) (Zuñiga et al., 2008).

My results showed a negative association between understory cover and skunk occupancy, which was consistent with previous studies showing this species using open areas (e.g., Donadio et al., 2001). Open habitats can provide skunks with food resources, including arthropods, earthworms, and vegetal matter for this diet generalist (Travaini et al., 1998; Castillo et al., 2011).

In undisturbed native forest at lower elevations may concentrate larger, abundance and diversity of prey for most of these carnivores (mainly small mammals) may be concentrated at lower elevations (Patterson et al., 1989). However, lower elevations in my study area contain numerous exotic plantations that are described as having lower diversity and abundance of native small mammals (Saavedra and Simonetti, 2005). Thus, I consider that the effect of elevation on carnivores species is mostly related to an anthropic gradient with human activity mostly concentrated at lower elevations (rural communities and timber activities). Thus, the positive response of Darwin's fox and kodkod cat to elevation might be explained by their sensitivity to this human presence. On the other hand, the negative association of elevation with occupancy of cougars and culpeo foxes would suggest these species may exploit areas close to intensive human land uses, as previously documented in Chile (e.g.,Vidal and Sanderson, 2012) and other regions (e.g., Knopff et al., 2014; Mazzolli, 2010). In my study area, cougars could use linear native forest remnants located along ravines to explore human-used lands. In turn, higher occupancy probability of culpeo fox in lower elevations may be explained by the active use of this carnivore on exotic plantations (mainly distributed close to human settlements) where they may prey on introduced lagomorphs. Based on these space use patterns, I note that the proximity of cougar and foxes to rural areas may trigger conflicts with local communities due to predation on domestic animals such as livestock and poultry.

Finally, due to their more generalist behaviour, chilla foxes may occur at lower elevations, and even, close to peri-urban areas (Silva-Rodríguez et al., 2010). However, the larger probability of occupancy of chilla foxes at higher elevations found in this study may be due to spatial segregation from the larger culpeo fox, rather than emerging as a positive response to suitable habitat conditions at higher elevations, which has been previously documented in northern Chile (Jiménez et al., 1996).

Management implications

The conservation of threatened carnivores occurring on human-modified landscapes dominated by exotic forest plantations requires identifying suitable habitats that can be integrated within sustainable landscape management strategies. Because most carnivore species occur at low densities and occupy large home ranges, assessment methods that reduce biases arising from imperfect detection, while incorporating high-resolution spatial information, are increasingly important to manage landscapes at larger scale. In this sense, I highlight the use of habitat covariates derived from LiDAR remote sensing implemented with occupancy modeling, which improve the description of vegetation structure at large spatial scales as continuous rather than categorical and coarse habitat classification, and thus better describing the animal–habitat relationships (Vierling et al., 2008). Based on that novel methodological approach, my results can be extended to sustainably manage forest plantations for carnivore conservation by increasing diversity of vertical strata and understory cover within these production-oriented lands. Therefore timber companies may be able to adopt management strategies which aim to maintain a mosaic of diverse habitat types, such as different plantation ages and structural classes. I also stress the need for protecting a full array of native forest patches, including those functioning as potential corridors as well as areas located at lower elevations and near densely populated settlements.

Table S 3-1. Ranking of candidate models (Δ AICc <3) for the six carnivores recorded in Caramavida conservation area, for which occupancy (ψ) (SE) and detection probability (*p*) (SE) were modeled with LiDAR covariates. K is the number of parameters in the model, AICc is Akaike's information criterion adjusted for small sample size, Δ AICc is the difference in AICc value of each model from the top model, and AICcWt is the Akaike weight. For each variable, beta coefficient and standard error (SE) are shown. For ψ habitat variable, [] indicates habitat type associated with the effect.

Carnivore	Model	K	AICc	Δ AICc	AICcWt	Intercept	ψ(Und_250)	ψ(Und_plot)	ψ(SDI)	ψ(Elev)	ψ(Canopy height(MOD))	ψ(Canopy height(MAX))	ψ(habitat)	ψ(habitat x Und250)	*p*(Unders_camera)	Chi-squared	p-value
Darwin's fox	psi(und_250),p(unders_camera)	4	227.89	0.00	0.36	0.57	5.70 (1.20)								-0.2 (0.06)	86.6	0.06
	psi(und_250,SDI),p(unders_camera)	5	228.24	0.34	0.31	9.71	8.07 (3.13)		0.89 (0.2)						-0.2 (0.06)	66.1	0.29
	psi(und_250, elev),p(unders_camera)	5	229.14	1.24	0.20	-3.45	7.89 (2.98)			0.55 (0.65)					-0.2 (0.06)	83.6	0.02
Kodkdod cat	psi(SDI,canopy_height [max]),p(unders_camera)	5	330.23	0.00	0.30	-5.94			6.36 (0.54)			0.11 (0.07)			-0.07 (0.1)	47.4	0.46
	psi(und_250, sid, habitat),p(unders_camera)	5	331.74	1.51	0.14	-6.52	4.22 (0.45)		0.25 (0.12)				-0.63 (0.1) [plantation]		-0.2 (0.11)	49.7	0.27
	psi(.),p(.)	2	332.38	2.15	0.10	-0.17										47.9	0.44
	psi(elev, SDI),p(p(unders_camera))	5	332.53	2.30	0.10	-6.17			0.15 (0.07)	2.70 (1.51)					-0.12 (0.4)	47.7	0.54
Cougar	psi(und_plot, SDI),p(unders_camera)	5	194.4	0.00	0.36	-7.13		15.30 (7.90)	1.98 (0.89)						-0.29 (0.1)	26.3	0.54
	psi(und_250),p(.)	4	197.12	2.72	0.09	0.004	-5.16 (2.8)								-0.37 (0.03)	27.8	0.44
	psi(und_250, elev),p(unders_camera)	5	197.16	2.76	0.09	2.46	-5.86 (2.96)			-2.40 (1.6)					-0.42 (0.03)	27.1	0.42
	psi(und_plot, canopy_height [mod]),p(unders_camera)	5	197.17	2.77	0.09	-10.38		9.8 (6.8)			0.04 (0.01)				-0.39 (0.03)	26.7	0.46
Skunk	psi(und_250, canopy_height [mod]),p(unders_camera)	5	204.97	0.00	0.32	6.78	-17.8 (8.71)				-0.291 (0.02)				0.61 (0.26)	26.5	0.54
	psi(und_250),p(unders_camera)	4	205.43	0.47	0.26	1.52	-8.15 (3.63)								0.58 (0.2)	26.3	0.63
	psi(und_250, canopy_height [max]),p(unders_camera)	5	207.59	2.62	0.09	2.35	-8.77 (4.16)					-0.03 (0.01)			0.57 (0.26)	26.4	0.64
	psi(und_250, elev),p(unders_camera)	5	207.65	2.68	0.08	1.89	-8.18 (3.60)			-0.39 (0.79)					0.56 (0.28)	26.2	0.82
Chilla fox	psi(elev, canopy_height [mod]),p(unders_camera)	5	165.67	0	0.35	-10.29				8.86 (2.86)	-0.1 (0.08)				-0.29 (0.14)	25.9	0.41
	psi(und_250, elev),p(unders_camera)	5	166.42	0.75	0.24	-11.43	2.15 (0.68)			8.78 (2.82)					-0.29 (0.24)	27.1	0.64
	psi(elev, canopy_height [max]),p(unders_camera)	5	166.59	0.92	0.22	-10.24				9.22 (2.92)		-0.05 (0.08)			-0.31 (0.22)	25.5	0.45
	psi(SDI, elev),p(unders_camera)	5	166.93	1.26	0.19	-10.04			-1.90 (1.01)	9.24 (2.91)					-0.30(0.24)	26.2	0.36
Culpeo fox	psi(und_plot, SDI),p(unders_camera)	5	347.85	0	0.15	14.53		-19.11 (8.34)	-4.94 (8.33)						-0.46 (0.15)	50.1	0.45
	psi(und_250, elev),p(unders_camera)	5	347.92	0.07	0.14	-5.39	-7.39 (3.8)			-4.24 (2.15)			0.74 (0.4) [plantation]		-0.46 (0.16)	50.1	0.27
	psi(und_plot, canopy_height[mod], habitat),p(unders_camera)	5	348.13	0.28	0.13	15.66		-16.33 (10.35)			-0.041 (0.012)				-0.46 (0.15)	50.4	0.54
	psi(elev, canopy_height[mod]),p(unders_camera)	5	348.58	0.73	0.1	-0.76				-2.88 (1.3)	-0.19 (0.1)				-0.38 (0.16)	51.7	0.45
	psi(und_250),p(unders_camera)	4	348.64	0.79	0.1	-1.33	-8.52 (4.40)								-0.47 (0.15)	50.9	0.27
	psi(und_250, canopy_height [max]),p(unders_camera)	5	348.77	0.92	0.09	2.53	-5.61 (2.37)					-0.15 (0.10)			-0.46 (0.15)	50.5	0.54
	psi(elev, canopy_height [max]),p(unders_camera)	5	349.46	1.6	0.07	1.91				-2.06 (1.6)		-0.16 (0.08)			-0.398 (0.16)	51.1	0.27

Variable acronyms: Und250=understory forest cover within 250m-radius buffer; Undplot= understory forest cover within 50m-radius buffer (camera station scale); SDI: structural diversity index measured within 50m-radius buffer; Elev= elevation; Canopy height (MOD; MAX)= max and modal canopy height; Habitat=coarse habitat classification; Unders_camera=understory vegetation cover within detection range of camera-trap (ca.10m).

CHAPTER IV

Native forest replacement by exotic plantations triggers switching in prey selection of mesocarnivores

Introduction

Exotic forestry plantations are becoming increasingly widespread as natural ecosystems are replaced by productive forestry lands (FAO, 2001), thus changing the distribution and abundance of species throughout different trophic levels (Lindenmayer and Hobbs, 2004; Brockerhoff et al., 2008). Carnivores can respond positively, or negatively, to plantations depending on their ecological requirements and management prescriptions within these anthropic habitats (Acosta-Jamett and Simonetti, 2004, Di Bitetti et al., 2006, Pita et al., 2009, Mazzolli, 2010, Lantschner et al., 2012, Simonetti et al., 2013; Coelho et al., 2014). The decline in carnivore populations arising from the replacement, or loss, of natural habitats may result in cascading effects affecting biodiversity at lower trophic levels (Jaksić et al., 1992; Thompson and Gese, 2007; Byrom et al., 2014). Assessing how exotic plantations alter prey populations and how carnivores respond to these habitat-mediated changes in prey abundance,could provide a bridge between sustainable forestry management and the trophic ecology of carnivores.

Small mammal species represent a significant amount of animal biomass available for mesocarnivores in natural forest ecosystems (Carey and Johnson, 1995; Hanski et al., 2001; Dupuy et al., 2009). Although some small mammal species are abundant in forest plantations (e.g., Muñoz-Pedredros et al., 1990; Lindenmayer and Hobbs, 2004, Saavedra and Simonetti, 2005; Lantschner et al., 2011), the overall density of small mammals tends to decrease as native habitat is disturbed. Indeed, habitat quality for small mammals decreases with the loss of habitat elements contributing to habitat complexity, such as understory cover, logs, snags and large decayed trees (Lindenmayer et al., 1994; Carey and Johnson, 1995; Lindenmayer and Hobbs, 2004; Saavedra and Simonetti, 2005; Robitaille and Linley, 2006; Fontúrbel et al., 2012). Small mammals living in plantations may not only be limited by food, but also by reduced availability of natural refuges against predators (e.g., burrows, tree holes, and cavities; Balme et al., 2007; Gorini et al., 2012).

Mesocarnivores inhabiting landscapes dominated by plantations can respond to changes in small mammal composition and abundance by modifying their prey selection patterns. Predators can become more efficient at searching for, pursuing, and capturing the more abundant prey species (Emlen, 1966; Murdoch, 1969; Charnov et al., 1976; Chesson, 1983; Jaksic et al., 1992; Joly and Patterson, 2003; Prugh, 2005; Dell'Arte et al., 2007). However, prey may become more alert to the presence of nearby predators because of poorly developed vegetation, reducing the carnivores' ability to search and find prey (Mills et al., 2004; Gorini et al., 2012). The sensitivity of carnivores to habitat modifications resulting from forest plantations may depend on their species-specific habitat specialization, which influences their capacity to adjust foraging behavior in response to changing habitat conditions (Gorini et al., 2012). Therefore, depending on their ability to respond to habitat-dependent changes in prey catchability and abundance, carnivores may modify their prey selection behavior when native habitats are replaced by exotic plantations.

Mesocarnivores occurring in temperate forests of central-south Chile face considerable structural and compositional habitat change resulting from intensive forestry land use (Aguayo et al., 2009). However, recent studies have shown that exotic plantations are not "biological deserts" for these species, because they can provide suitable habitats when they maintain native understory and they can contribute to landscape heterogeneity (Acosta-Jamett and Simonetti, 2004; Lidenmayer and Hobbs, 2004; Simonetti et al., 2013). Exotic plantations in this region seem to support fewer small-mammal species compared to native forests. In some cases however, plantations might harbor a high abundance of sigmodontines species, such as long-haired field mouse (*Abrotix longipilis*), olivaceus field mouse (*A. olivaceus*) and long-tail colilargo (*Oligoryzomys longicaudatus*) (e.g., Muñoz-Pedreros, 1992; Saavedra and Simonetti, 2005; Garcia et al., 2013). Thus, even though the structural role of exotic plantations as habitat for carnivores has been documented, the functional role of these human-created lands as feeding grounds for mesocarnivoes, is poorly understood.

Mesocarnivores living in temperate forests have been shown to prey on a wide range of small mammals species (e.g., Jiménez et al., 1990; Roa and Correa, 2005; Sade et al., 2012). However, carnivores prey selection in relation to changes in prey availability arising from the replacement of native forest by plantations is unknown. Addressing this knowledge gap is essential because exotic plantations currently cover almost 17 percent of forested areas in Chile (CONAF, 2011). In this study, I investigated the role of exotic plantations as feeding grounds for four sympatric native mesocarnivores inhabiting a mosaic landscape dominated by exotic plantations in south-central Chile: kodkod cat (*Leopardus guigna*), Darwin's fox (*Pseudalopex fulvipes*), culpeo fox (*P. culpaeus*), and chilla fox (*P. griseus*). The Vulnerable kodkod cat and the Critically endangered Darwin's fox (Napolitano et al., 2015; Jiménez et al., 2008, respectively) have been documented to be negatively affected by exotic plantations (Acosta-Jamett and Simonetti, 2004), yet mechanisms underlying their responses are unknown. Specifically, I assessed variation in the abundance of small mammals between plantations and native forest and I asked if this prey variation triggered changes in prey-selection patterns of these carnivores. First, I predicted that in exotic plantations compared to native forest the abundance of small mammals would be lower as previously documented in other studies (e.g., Saavedra and Simonetti, 2005; Garcia et al., 2013). Second, I predicted that mesocarnivores respond to changes in small mammal abundances by switching their prey selection patterns towards the prey species that are more abundant at each habitat type. However, I predicted that prey selection behavior of forest-specialist kodkod cat and Darwin's fox may be also affected by the change of habitat structure derived from the replacement of native forest into exotic plantations.

Methods

Study area

The study area encompassed ca. 16,000 ha and is located in Nahuelbuta Mountain Area (NMA) (Fig. 4-1). The description of the study area is found in Chapter I.

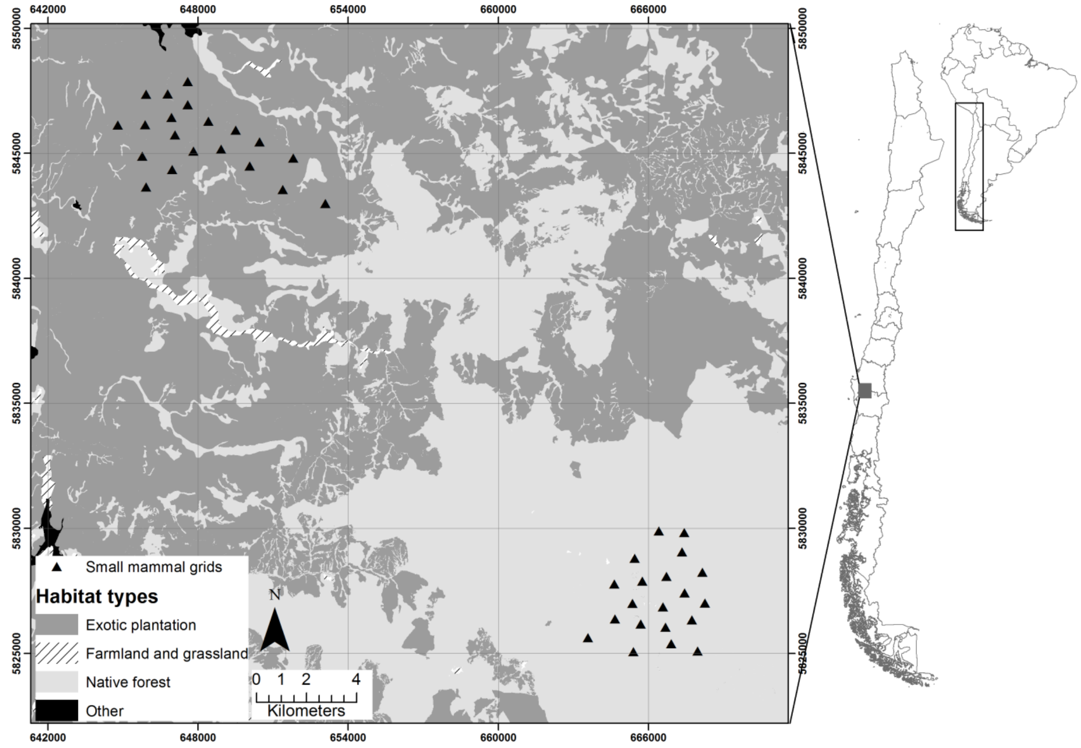


Figure 4-1. Map of the study area in Nahuelbuta Mountain Area, central-south Chile, showing the dominant habitat types. Black triangles represent 6x6 small mammal trapping grids surveyed.

Prey abundance

Prey abundance was obtained from small mammal trapping conducted during spring 2012. I used a combination of wire-mesh (Tomahawk-style) and Sherman (7.6 × 8.9 × 22.8 cm) traps in 40 grids of 6 × 6 live traps each. Grids were at least 700 m apart from each other and distributed across two habitat types, with 20 grids located in mixed forest dominated by southern beech (*Nothofagus* spp.), and 20 in monoculture of exotic plantations of Monterrey pine (Fig. 4-1). At each grid, traps were placed on and above ground level (~ 2m height) in order to improve the capture of both ground-level and arboreal small mammals (Fontúrbel et al., 2010). Trapping at each grid was conducted for five consecutive nights (totaling 7,200 trap-nights), using rolled oats as bait. Captured individuals were identified to species, marked with unique patterns in their fur, and released at the capture site. Differences in small mammal abundance between native forests and plantations may change seasonally (Murúa et al., 1986; Meserve et al., 1991; Meserve et al., 1999) so surveys were repeated during autumn of 2013 and I included season as a covariate in the analyses.

I used the minimum number of individuals known alive (MNA) to obtain estimates of absolute and relative small mammal abundances in different seasons and habitats. This method has been previously used to assess population estimation of Chilean small mammals (e.g., Meserve, 1981; Simonetti, 1983; Iriarte et al., 1989). All animals were captured and handled in accordance with approved governmental and institutional animal care protocols (Chilean Agriculture and Livestock Bureau (SAG; resolution number 2201/2013); University of Alberta animal use protocol # AUP00000039).

Prey consumption

The prey consumption by the four studied mesocarnivores was assessed by analyzing diet composition from their scats collected through systematic and intensive searches (35 day/grid) around each trapping grid (Fig. 4-1). I identified carnivore scats through DNA analysis, which overcomes difficulties in identifying species on the basis of morphology and size in areas where similar body-size species co-occur. DNA was isolated from each scat using a QIAGEN Stool Mini Kit (QIAGEN, CA, USA), amplified a fragment of the mitochondrial cytochrome *b* gene, and the resulting sequences compared to those of reference samples. Analyses were conducted at the Primate Immunogenetics and Molecular Ecology (PRIME) Laboratory at University of Cambridge, UK. To identify the prey items of carnivores, I dried and washed scats, and examined their contents. I identified small-mammals in carnivores scat to species by using available keys for comparing teeth and hair patterns of the species occurring in the study area (Reise, 1973; Pearson, 1995). I expressed the use of each prey species by each carnivore as the proportion of that food item in their diet, i.e. the number of occurrences of one food item divided by the total number of occurrences of all food items (Klare et al., 2011).

Prey abundance analysis

Differences in the mean abundance of small mammals between plantations and native forests across seasons were assessed using Bayesian Mixed Effects Zero-Inflated Poisson (ZIP) models. These models were appropriate for analyzing my abundance data because they included excess zeros and overdispersion (Zuur et al., 2009). ZIP models provide a mixed likelihood function that combines: 1) a binomial logistic regression that models an excess of zeros (also known as inflation), thus, dealing with false zero counts that emerge from low detectability at the grid; and 2) a log-Poisson regression that models abundance data (Zuur et al., 2009). I specified the fixed-effects of season (spring vs. autumn), habitat type (pine plantation vs. native forest) and their interaction (season × habitat type) on the abundance of small mammals at each grid. I included grids as a random variable to account for the effects of other unobserved variables at the grid-level. The importance of each fixed effect (habitat, season, and season × habitat type) was evaluated from the Bayesian Credible Intervals of the posterior distribution of coefficients. Models with different combinations of fixed effects were assessed using Deviance Information Criteria (DIC; Spiegelhalter et al., 2002). Models were run using WinBUGSv. 1.4 (Spiegelhalter et al., 2003), which was remotely called from R v. 3.2.0 (R Development Core Team 2014) by using the R2WinBUGS package. Posterior distributions were based on three MCMC iterations, each with 20,000 iterations, discarding the first 10,000 iterations and thinning by two. I used vague non-informative prior distributions for all model parameters. I assessed convergence by visually examining trace and density plots of MCMC iterations as well as by estimating the Potential Scale Reduction factor (Gelman et al., 2003).

Prey selection analysis

I assessed prey selection of carnivore species across seasons and habitat types based on prey use, as obtained from prey consumption (dietary analysis), and prey availability, measured from small mammal abundance. I considered prey availability being representative of small mammal abundances rather than true availability (a combination of abundance and the vulnerability of prey). I used Aebischer (1993)'s Resources Selection Function model, which assumes that the use of prey *j,* U_j, by a predator is proportional to availability of that prey, a_j, times its selection S_j, such that:

$$U_j = \frac{s_j a_j}{\sum_{j=1}^{D} s_j a_j},$$

where the denominator of eq(1) is the sum of the product of availability times selection over all prey ($j = 1,2 \ldots D$). I assumed that observed prey-count data, c_j, from each scat recollected in a grid, during a season, followed a multinomial distribution with parameters U_j and N, the total count of used prey ($N = \sum_1^D c_j$). I used the relative abundance of each prey species in the grid k as an estimate of its availability (a_j). The effect of habitat type and season on selection of a particular prey species, S_j, by a carnivore species was modeled for each grid as:

$$S_{jk} = \frac{\exp(\phi_{jk})}{\sum_{j=1}^{D} \exp(\phi_{jk})},$$

with

$$\phi_{jk} = Season_j + Habitat_j + Season_j \times Habitat_j + G_k + D_k \ ,$$

where the fixed-effect coefficients $Season_j$, $Habitat_{jk}$ and $Season_j \times Habitat_{jk}$ are estimated for each prey species, whereas G_k is a random factor for controlling dependence of data from each grid. The term D_k is a multivariate Gaussian term whose covariance matrix was expressed as an exponential decay function of the Euclidean distance between grid center coordinates, therefore controlling for spatial autocorrelation. Bayesian model specifications were similar to those described above for the ZIP models. To compare differences in the strength of selection of prey *j* between native forests and exotic plantations, I computed Bayesian estimates of log-ratios for each habitat type as $d_j = \log(U_j / a_j)$. Values of $d_j > 0$ and $d_j < 0$ imply that prey *j* is preferred and not preferred for that habitat, respectively (Aebischer et al., 1993). All model coefficients and log-ratios (d_j) were assessed by examining their Bayesian Credible Intervals (BCI). The 95% BCIs that did not overlap zero were interpreted as being significant.

Results

Small mammal abundance

A total of 778 individuals were captured, including individuals from six rodent species as well as the marsupial monito del monte (*Dromiciops gliroides*: Microbiotheria) (Fig. 4-2). Total abundance of small mammal species differed significantly among habitat types (Repeated measures ANOVA: F=25.89, df=1, p<0.01) and seasons (F=9.17, df=1, p<0.01), with larger small mammal abundances recorded in native forest and during autumn (Fig. 4-2).

Models fitted to individual species that included habitat, season, and their interactions (season×habitat) were the best-supported candidate logistic and count ZIP models (ΔDIC < 2) based on DIC values (Table S4-1). The abundances of colilargo, monito del monte, and Chilean climbing mouse (*Irenomys tarsalis*) were significantly greater in native forest than in plantations. Conversely, the abundance of long-haired field mouse was higher in plantations (Table 4-1 and Fig. 4-2). The interaction between season and habitat was retained in the best-supported count models of six small mammal species (Table S4-1), but this interaction was strongly supported for only two small mammals (Table 4-1). During spring, long-haired field mouse was more abundant in exotic plantations, while Darwin's leaf-eared (*Phyllotis dawini*) mouse was more abundant in native forests (Fig. 4-2). Season was important to only three species; the abundance of colilargo and olivaceus field mouse increased from spring to autumn, while the abundance of monito del monte was higher in autumn than spring (Table 4-1 and Fig. 4-2).

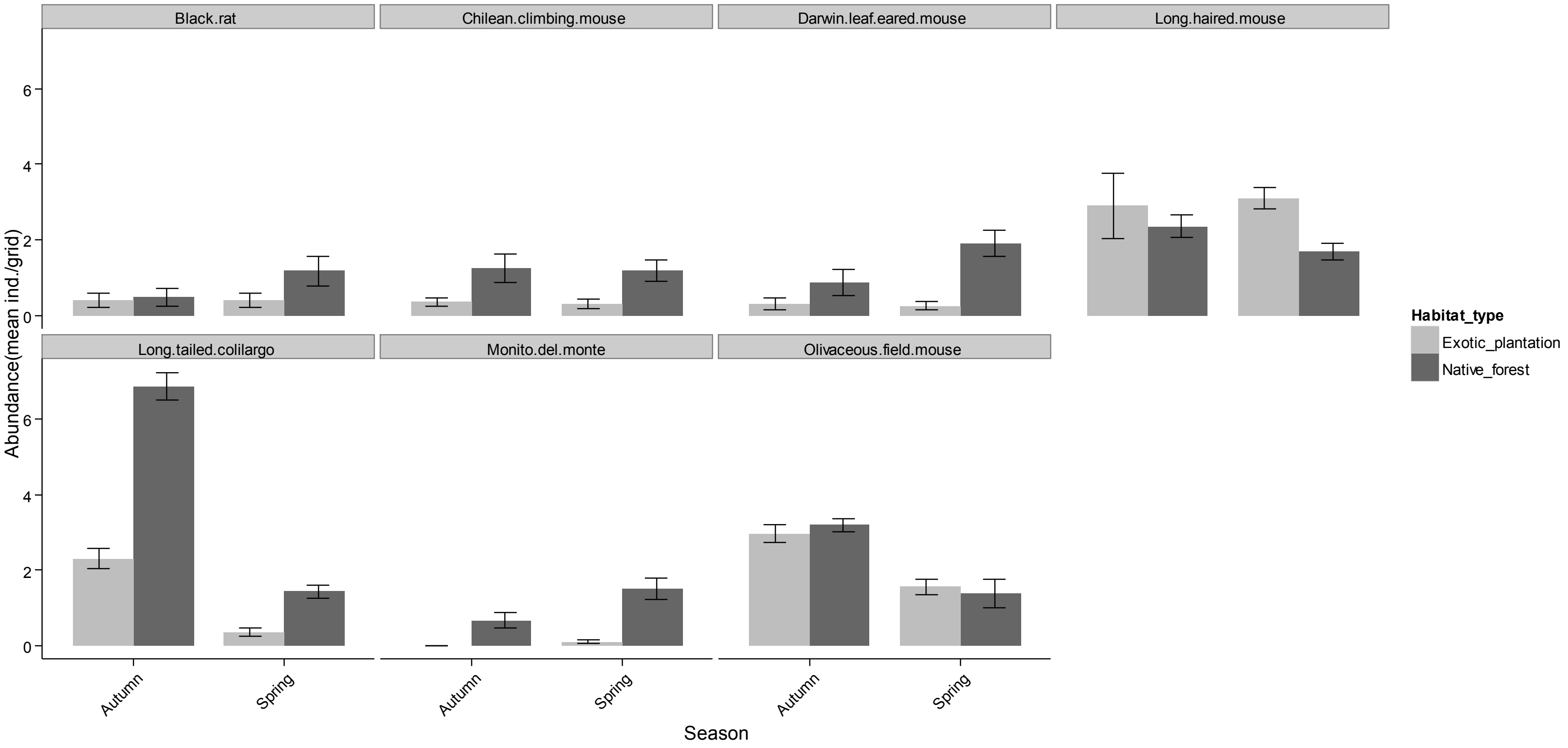


Figure 4-2. Mean number of individuals of each small-mammal species captured per survey grid (means ± standard error) out of 20 grids in native forest and 20 grids in exotic plantation during two seasons.

Table 4-1. Bayesian Zero-Inflated Poisson models predicting the abundance of small mammals in the study area. The means, standard deviations (SD), and 95% Lower and Upper Bayesian Credible Intervals (CI) of the most parsimonious model are presented. For comparison reasons, coefficients for exotic plantation and spring levels are set at zero.

Species	Variable	Coefficient	SD	Lower BCI	Upper BCI
Long-haired field mouse (Lf)	Season	0.96	0.63	-0.28	1.68
	Habitat	-2.00	1.17	-4.43	-0.11
	Season × Habitat	-1.47	0.7	-3.02	-1.04
Monito del monte (Mm)	Season	-1.81	0.87	-3.88	-0.26
	Habitat	0.62	1.61	0.39	4.02
Olivaceous field mouse (Of)	Season	1.06	0.44	0.20	1.92
	Habitat	-0.56	0.39	-1.92	0.34
	Season × Habitat	-1.08	0.4	-1.7	0.1
Long-tailed colilargo (Lc)	Season	5.98	1.36	3.70	8.96
	Season × Habitat	-2.7	1.76	-5.14	1.0
	Habitat	1.21	0.52	0.24	1.89
Darwin's leaf-eared mouse (Dm)	Season	2.57	2.22	-1.78	6.92
	Season × Habitat	2.18	1.99	0.14	4.86
Black rat (Br)	Season	-1.37	1.02	-3.52	0.57
	Season × Habitat	2.67	1.37	-0.06	5.68
	Habitat	0.86	1.1	-1.57	4.01
Chilean climbing Mouse (Cc)	Habitat	2.24	1.76	0.05	4.87
	Season × Habitat	2.88	0.78	1.35	4.40

When comparing among small mammal species, I found that the relative abundance (fraction of the total abundance) of most species varied between habitat types (Fig. 4-3). The abundance of Darwin's leaf-eared mouse, monito del monte, and Chilean climbing mouse were 3.1, 2.4, and 2.3 times higher in native forest than in pine plantation, respectively (Fig. 4-3). In contrast, the relative abundance of long-haired field mouse was 2.5 times higher in pine plantation than in native forest (Fig. 4-3). Seasonal changes in the relative abundances of prey were detected for long-tailed colilargo (ca. 3.5 times higher in autumn compared to spring) and monito del monte (ca. 3.4 times higher in spring compared to autumn; Fig. 4-3).

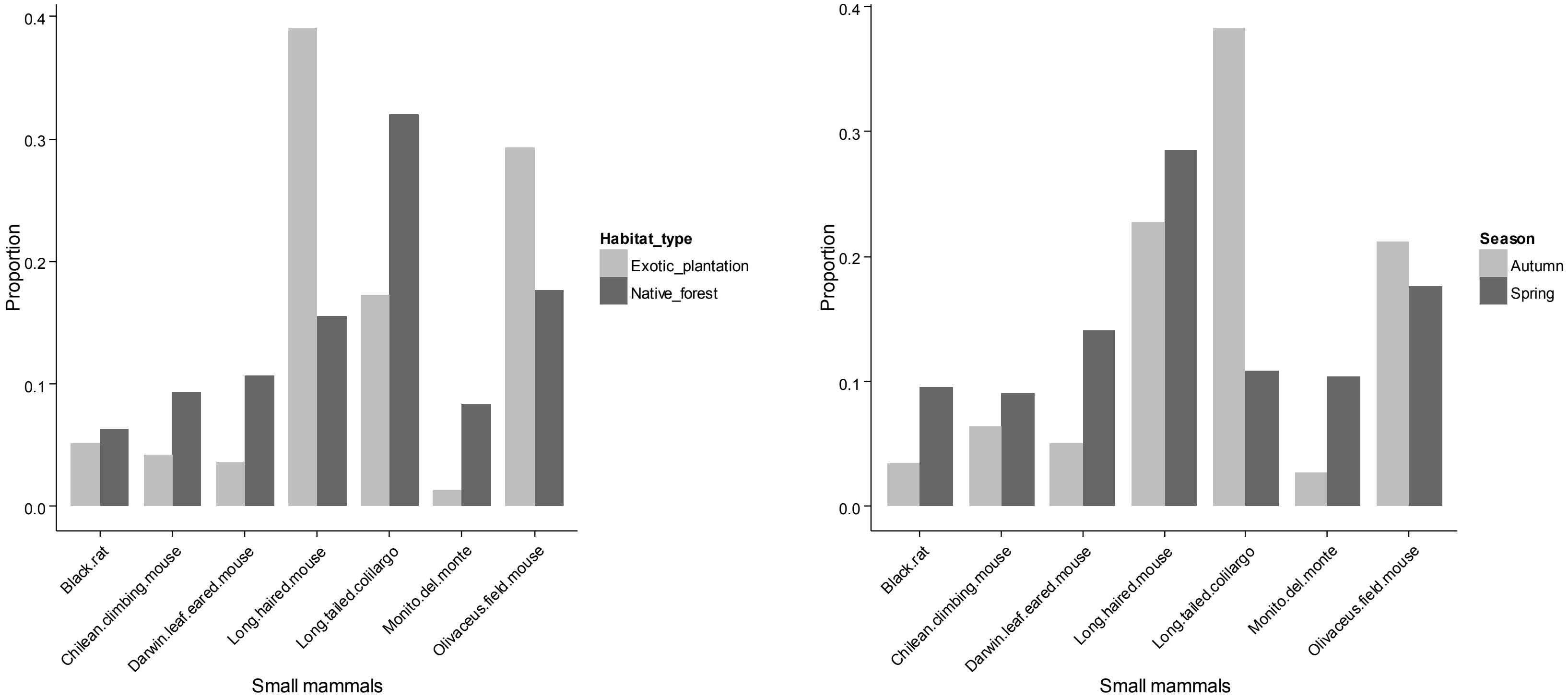


Figure 4-3. Relative abundance (fraction of the total abundance) of each small-mammal species in native forest and exotic plantation (left) as well as during two seasons (right).

Prey consumption and selection by mesocarnivores

I analyzed a total of 156 scat samples from chilla fox (n=30), kodkod cat (n=52), Darwin's fox (n=18), and culpeo fox (n=58). These scats were spatially distributed as followed: for kodkod cats, 37 and 15 scats were collected in native forests and plantations, respectively. For Darwin's fox, 12 and six scats were collected in native forests and plantations, respectively, whereas for chilla fox, scats were found more frequently in plantations (n=20) than in native forest (n=10). For culpeo fox, 21 and 37 scats were collected in native forests and plantations, respectively. Scats contained the same species captured during small mammal trapping, as well as Bridges's degu (*Octodon bridgesi*).

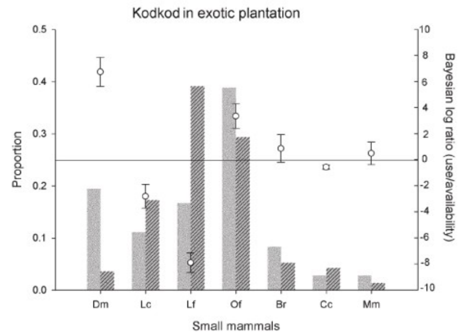
The most abundant small mammals species; long-tailed colilargo, long-haired field mouse, and olivaceus field mouse, were also consumed most often by the four mesocarnivores; comprising over the 50% of total prey consumed by each carnivore. Less common arboreal small mammals, such as Chilean climbing mouse and monito del monte were, however, important in the diet of kodkod cats, accounting for ca. 50% of kodkod prey consumed in native forests. Black rat (*Rattus rattus*) and Darwin's leaf-eared mouse were mainly found in the scats of Darwin's fox and chilla fox.

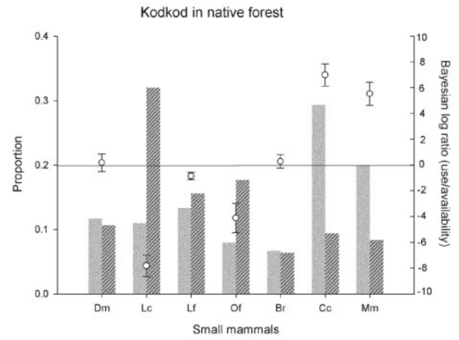
Resources Selection Functions fitted to diet composition indicated that, although prey selection was influenced by habitat type and season, these effects differed among carnivores and involved different prey species (Table 4-2). Kodkod cat selection of both monito del monte and Chilean climbing mouse, was significantly and positively affected by the presence of native forests, whereas selection for black rat was positively related to the presence of exotic plantations (Table 4-2). Similarly, kodkod cat’s selected olivaceus field mouse, long-haired field mouse, and Chilean climbing mouse more in spring than autumn (Table 4-2). The selection of culpeo fox on long-tailed colilargo and Chilean climbing mouse was positively influenced by the presence of exotic plantations and by the seasonal change from spring to autumn (Table 4-2). The selection of long-tailed colilargo by chilla fox was significantly higher in native forest and in autumn, whereas selection for black rat was higher in exotic plantations (Table 4-2). Similarly, the selection of Darwin's fox on Darwin leaf-eared and long-tailed colilargo was positively related to the presence of native forest (Table 4-2).

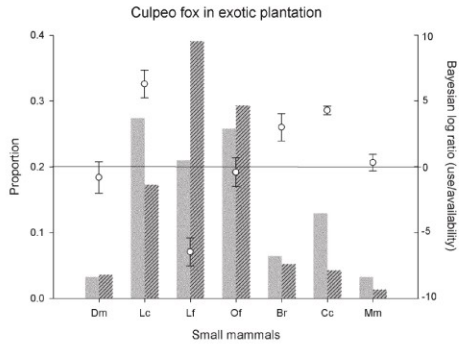
Table 4-2. Significant environmental variables affecting the prey selection of small- mammals by native carnivores in Nahuelbuta Mountain Area, south-central Chile, based on the Resources Selection Function combined with multinomial response distributions in a Bayesian framework. For season and habitat categories, spring and exotic plantation were set at zero and their significances are measured against autumn and native forest.

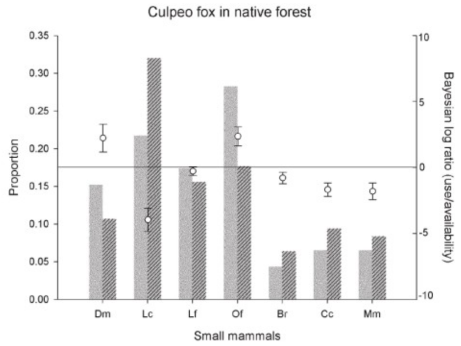
Carnivore	Prey species	Variable	Mean	Lower CI	Upper CI
Kodkod cat	Chilean climbing mouse	Habitat	6.687	2.147	9.822
	Monito del monte	Habitat	4.889	0.086	8.864
	Black rat	Habitat	-6.909	-9.895	-2.056
	Long-haired field mouse	Season	-5.449	-9.709	-0.315
	Olivaceus field mouse	Season	-7.853	-9.861	-4.577
	Chilean climbing mouse	Season	-8.412	-9.937	-5.315
Culpeo fox	Chilean climbing mouse	Habitat	-7.256	-9.87	-2.682
	Long-tailed colilargo	Habitat	-6.147	-9.543	-1.818
	Long-tailed colilargo	Season	5.722	1.42	9.388
Chilla fox	Long-tailed colilargo	Habitat	5.02	0.011	8.215
	Black rat	Habitat	-5.782	-9.803	-0.188
	Long-tailed colilargo	Season	6.54	2.398	9.788
Darwin's fox	Darwin's leaf-eared mouse	Habitat	7.372	2.798	9.891
	Long-tailed colilargo	Habitat	4.087	0.713	6.204

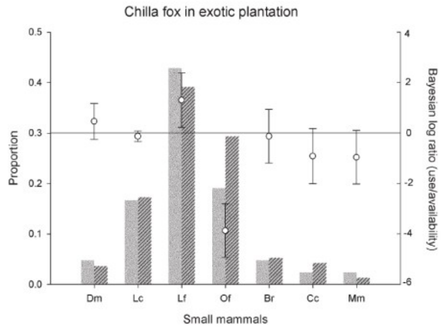
Carnivores switched their prey selection between native forests and exotic plantations, as exhibited by Bayesian log-ratio changes between habitats from negative to positive values (and vice versa; see Fig. 4-4). Kodkod cats strongly selected Chilean climbing mouse and monito del monte in native forests, whereas negative log ratios indicated that kodkod cats avoided Chilean climbing mouse in exotic plantations (Fig. 4-4). Conversely, kodkod cats’ selection of olivaceus field mouse and Darwin's leaf-eared mouse occurred in plantations only, whereas the consumption (use) of both species in native forest was less than or equal to available in native forest (Fig. 4-4). Culpeo fox strongly selected long-tailed colilargo, black rat, and, Chilean climbing mouse in pine plantations, but selected Darwin's leaf-eared mouse and olivaceus field mouse in native forests (Fig. 4-4). In spite of a high availability of long-tailed colilargo in native forests, consumption of this prey species was lower than its availability (Fig. 4-4). Chilla foxes exhibited positive log-ratios (i.e., prey selection) for long-haired field mouse in native forests and plantations, whereas in native forest only, chillas selected black rat (Fig. 4-4). In exotic plantations, chilla foxes also consumed long-tailed colilargo and olivaceus field mouse equally to, or less than, their availability (i.e., prey avoidance; Fig. 4-4). Darwin's foxes strongly selected long-tailed colilargo in both habitats (Fig. 4-4), but switched selection of Darwin's leaf-eared mouse; from a positive log ratio in native forest to a negative log ratio in exotic plantations (Fig. 4-4). Darwin's foxes also selected olivaceus field mouse in native forests, but not in plantations. There was no evidence of consumption of arboreal small mammals (monito del monte and Chilean climbing mouse) by Darwin's fox in native forests or in exotic plantations. Similar to chilla fox and kodkod cat, Darwin's foxes consumed black rats equally to their availability in exotic plantations. However, black rats were not observed in the diet of this carnivore in native forests (Fig. 4-4).

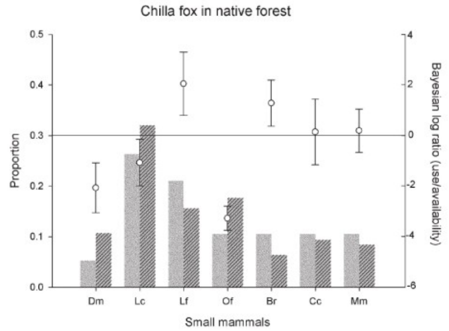

Kodkod in exotic plantation

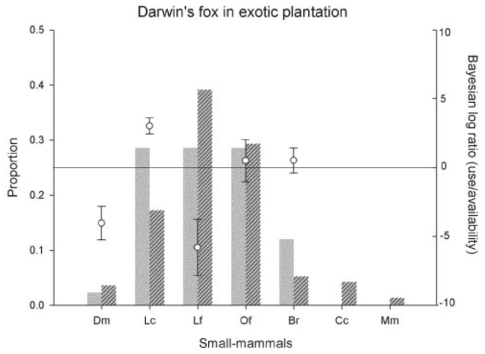

Kodkod in native forest


Culpeo fox in exotic plantation


Culpeo fox in native forest


Chilla fox in exotic plantation


Chilla fox in native forest


Darwin's fox in exotic plantation

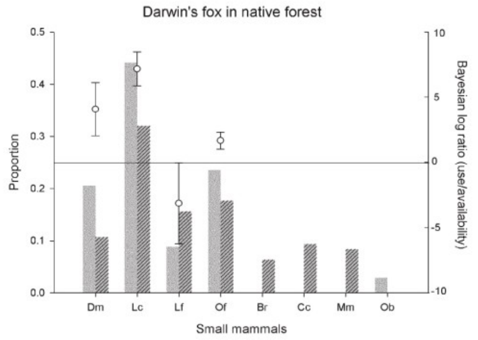

Darwin's fox in native forest

Figure 4-4. The observed prey use (grey-clear bars) and prey availability (grey-shaded) as well as the Bayesian estimates of log ratios of use and availability of prey (mean: unfilled dots, bars: 95% credible intervals) of four mesocarnivore species are shown for two habitat types, native forest on the right and forest plantations on the left. Bayesian log ratios whose credible intervals overlap the zero value (isoline) indicate that the use of this prey equal its availability, whereas negative and positive ratio values represent prey preference and avoidance, respectively. For prey use and prey availability, error bars correspond to bootstrapped 95% (percentile) confidence-intervals. Codes for small mammal species are: (Dm) Darwin's leaf-eared mouse, (Lc) Long-tailed colilargo, (Lf) Long-haired field mouse, (Of) Olivaceus field mouse, (Br) Black rat, (Cc) Chilean climbing mouse, (Mm) monito del monte and (Ob) Bridges's degu.

Discussion

In my study area native forests and exotic plantations harboured a similar composition of small mammals. However, the abundance of some species differed between habitats, which may have promoted changes in the prey selection behaviour of mesocarnivores. Both findings, suggest that plantations in my study area may function as a valuable source of food for native carnivores. Variation in prey abundance was also affected by seasonality, indicating that in the absence of habitat perturbations (e.g., forestry), prey selection by mesocarnivores may be also affected by natural fluctuations in some small mammals (Murúa et al., 1986; Meserve et al., 1991; Meserve et al., 1999).

Prey selection of studied mesocarnivores for some small mammals was also significantly influenced by habitat type (native forest or exotic plantation), and did not result from changes in relative or absolute prey abundance. These results provide strong support for habitat-dependent prey selection patterns of carnivores, suggesting that differences in prey selection emerge not only from different prey abundances between habitats, but also from the species-specific ability of mesocarnivores to search, pursue, and capture prey under different habitat conditions.

Habitat-variation in small mammals abundance

Although I observed no differences in small-mammal composition, the absolute abundances of prey species differed significantly between habitat types. Zero-inflated Poisson models supported the importance of native forests for arboreal species, such as monito del monte and Chilean climbing mouse, whose abundances were higher in native forests than in plantations in both seasons. Previous studies suggest that these small mammal species are habitat specialists using the understory and canopy vegetation of old and second-growth native forests (Fonturbel, 2009; Fonturbel, et al. 2010). I found monito del monte and Chilean climbing mouse in exotic plantations; contrary to previous studies carried out in other landscapes of south-central Chile dominated by exotic plantations (Saavedra and Simonetti, 2005). The presence of aged plantations containing higher herbaceous-shrub cover across some grids could explain the presence of these forest-specialist species considering understory cover is recognized as an ecologically important habitat component for small mammals (Carey and Johnson, 1995; Kelt, 2000; Bellows et al., 2001; Lindenmayer and Franklin, 2002; Hayes et al., 2005; Amacher et al., 2008).

The native olivaceus field mouse and long-haired field mouse were frequently captured in both habitats; with abundances that were equal to, or higher, in exotic plantations than in native forests. This is consistent with previous studies conducted in the region, which show that both species exhibit low habitat specificity (Saavedra and Simonetti, 2005; Garcia et al., 2011), have a broad diet (Pearson, 1983; Muñoz-Pedreros et al., 1990), and are associated with abundant herbaceous and shrub understory cover in exotic plantations (Muñoz-Pedreros et al., 1990, Saavedra and Simonetti, 2001; see also Lantschner et al. 2011). Colilargo was more abundant in native forest than plantations, and these differences were even more important in autumn than spring. Colilargo shows strong intra-annual cycles in response to seasonal primary productivity of temperate forests, disappearing entirely during summer (Murúa et al., 1986). As documeted by Meserve et al., (1999), colilargo have even been found to irrupt from a few individuals (< 0.1 per ha) in Austral spring to ca. 10-20/ ha in Austral winter. Given the response of native small mammals to plantations, as well as the presence of understory vegetation in the studied exotic plantations, it is possible that small mammal assemblages in this landscape can tolerate disturbances caused by forestry land-uses. This supports the idea that commercial plantations containing ground structures similar to that found in native forest, such as shrubs, do fulfill at least partial habitat requirements for these species inhabiting NMA, mitigating the negative impacts on native species (Lindenmayer et al., 2006).

Black rats were similarly abundant in native forest and plantations during autumn, but during spring, their abundance was slightly higher in native forest. The habitat generalist behavior of this introduced species makes black rat an alternative prey for native mesocarnivores inhabiting landscapes dominated by plantations.

Mesocarnivore prey use and selection

Results of this study provide support that mesocarnivores occurring in my study area use exotic plantations as feeding grounds. Also, carnivore species did not show strict diet specialization, and instead consumed almost all species recorded by small mammal trapping. However, I found mesocarnivores frequently preyed on the three most abundant small mammals (colilargo, long-haired field mouse, and olivaceus field mouse). Even for kodkod cat, which showed a slight specialization for arboreal species in native forests, the most abundant prey became important alternative prey in plantations. These findings agree with diet patterns found in studies conducted in Temperate Forest and Mediterranean shrubland for these mesocarnivores (e.g., Iriarte et al., 1989, Jiménez et al., 1990, Roa and Correa, 2005; Sade et al., 2012), and imply that the studied carnivores may display flexible hunting behavior when occurring in native forest or exotic plantations.

Mesocarnivores, however, differed in their prey selection and modified their prey selection patterns between habitats, supporting habitat-dependent changes in prey selection. Studied carnivores intensified or weakened their selection of some small mammal species between native forests and plantations, and these changes did not always reflect changes in prey abundance. For example, the kodkod cat consumed monito del monte and Chilean climbing mouse more than their availability in native forest, which reflected their specialization on this species when abundances of these small mammals were higher in exotic plantation. Interestingly, selection for these arboreal species occurred even when other terrestrial species (e.g. the colilargo) were extremely abundant in native forest. Kodkod cats are naturally good at climbing trees (Sanderson et al., 2002), which would make them more successful when hunting prey that move within overstory or large-trees (e.g., Altamirano et al., 2013). The simplification of arboreal-vegetation structure arising from the replacement of native forests by exotic plantations could negatively impact kokdkod cats by reducing the abundance of their preferred prey (e.g., arboreal small mammals), as well as reducing their effectiveness for capturing prey using arboreal strata. Consequently, forest plantation management intended to increase habitat complexity can be important for conserving populations of kodkod cats (Brockerhoff et al., 2008).

Darwin's foxes selected colilargo independently from habitat type, whereas culpeo foxes showed strong prey selection for colilargos at exotic plantations only. The consistent selection of Darwin's fox on colilargo in both habitats suggests the importance of this native rodent in the diet of this mesocarnivore, and the efficiency of Darwin´s fox at capturing colilargo throughout. Conversely, the lack of a positive association between colilargo's abundance and culpeo fox selection for this small mammal may be influenced by the ability of this carnivore to cope with anti-predatory behaviors, such as escape responses, reduced mobility or refuge use by prey (Simonetti, 1989; Norrdahl and Korpimäki, 1998).

The biological and environmental factors influencing prey catchability and accessibility are therefore important for controlling the "realized availability" of prey (Balme et al., 2007). Although my analyses did not account for the effect of these factors, I suggest that kodkod cat selection for Chilean climbing mouse and monito del monte, even when colilargo were extremely abundant during autumn, supports the existence of a degree of forest-specialist behavior of this felid. Likewise, I hypothesize that density-dependent prey-selection behavior, as shown by culpeo foxes, may explain its flexible habitat-selection patterns. The flexibility of culpeo fox prey selection in different habitat conditions is consistent with the fact that culpeo foxes consume prey that are not only abundant (e.g., long-haired field mouse), but also that are easier to capture due to low vegetation cover found in monoculture plantations that facilitate searching (Saavedra and Simonetti, 2005, Balme et al., 2007, Andruskiw et al., 2008; Keim et al., 2011). Similarly, culpeo fox and kodkdod cat selected black rats in exotic plantations even when black rat abundance was low, indicating that the carnivores' ability to capture black rats did not decrease when exotic plantations replaced native forest. Therefore, introduced black rats may become an important source of biomass in exotic plantations for these carnivores, because introduced rats are up to four fold the body mass of native rodents (Muñoz-Pedreros and Yañez, 2008).

A potential confounding factor emerging from this study is that the scats could have contained prey captured from outside my study boundaries. Home ranges of mesocarnivores living in disturbed landscapes of southern Chile range from 180-230 ha, with maximum movement distance varying between 2.4 and 3.7 km (Sanderson et al., 2002; Silva-Rodriguez et al., 2010). These home range sizes, as well as high carnivore activity recorded in my study area during camera-trap surveys (see Chapter II), indicates that individuals most likely remained within the boundaries of my study area.

Concluding remarks

The findings of this study not only provide insights into prey selection of culpeo fox, chilla fox, Darwin's fox, and kodkod cat, but also expand the knowledge about how the replacement of native forest by exotic plantations affects the abundance of small mammals as well as carnivores' prey selection. The methodological approach combining prey availability and consumption rates computed by a Resources Selection Function provided evidence of prey-switching behavior across habitat types, once seasonal fluctuations of prey availability are accounted for. Reduced abundance of selected prey species resulting from habitat transformations may negatively affect carnivore populations with narrow diet and habitat requirements. Forest managers may conserve small mammal populations by maintaining some areas of unaltered habitat conditions needed for species persistence in human-altered landscapes, thus increasing the suitability of remnants patches for carnivores (Mortelli and Boitani, 2008). Alternatively, the maintenance of a mosaic of plantations with different ages and management regimes would favor the coexistence of carnivores with different predation strategies. In heterogeneous mosaics of plantations some carnivores would consume the more abundant prey, independent from the habitat type, while other carnivores may use particular habitats that make them more efficient in searching and capturing specific prey items.

Table S 4-1. Best supported Bayesian Zero-Inflated Poisson models used to predict the abundance of small mammals prey species in the study area. Covariates including in the Logistic and Count model are shown separately. The number of fixed-effects in the model (*K*), Deviance's Information Criterion (DIC), DIC difference with the lowest DIC model (ΔDIC) and model weights (ω) are shown. Null refers to models without covariates.

Species	Logistic model	Count model	k	DIC	ΔDIC	ω
Long-haired field mouse (LH)	Season + Habitat	Season + Habitat	4	238.63	0.00	0.25
	Season + Habitat	Season × Habitat	4	238.82	0.19	0.22
	Season + Habitat	Null	2	239.19	0.56	0.19
Monito del monte (Mm)	Season + Habitat	Season + Habitat	3	53.89	0.00	0.44
Olivaceous field mouse (OF)	Season + Habitat	Season + Habitat	4	189.28	0.00	0.37
	Season	Season + Season × Habitat	2	190.61	1.33	0.19
	Season + Habitat	Season + Habitat + Season × Habitat	5	191.01	1.73	0.15
Long-tailed colilargo (LT)	Null	Season + Season × Habitat	2	212.31	0.00	0.21
	Season	Season + Season × Habitat	3	212.49	0.18	0.19
	Null	Season + Habitat + Season × Habitat	3	212.99	0.68	0.15
	Season	Season + Habitat + Season × Habitat	3	213.45	1.14	0.12
	Season + Habitat	Season + Season × Habitat	4	213.61	1.30	0.11
Darwin's leaf-eared mouse (DL)	Null	Season + Season × Habitat	2	81.10	0.00	0.53
	Season + Habitat	Null	2	84.17	3.08	0.11
Black rat (BR)	Null	Season + Season × Habitat	2	74.85	0	0.14
	Null	Habitat + Season × Habitat	3	75.11	0.26	0.13
	Season	Season + Season × Habitat	3	75.11	0.26	0.13
	Season + Habitat	Null	2	75.23	0.38	0.12
	Season + Habitat	Season + Season × Habitat	4	75.32	0.47	0.11
	Season + Habitat	Season × Habitat	3	76.25	1.4	0.07
	Null	Null	1	76.33	1.48	0.07
Chilean Climbing Mouse (CC)	Season + Habitat	Habitat	3	53.89	0.00	0.37
	Season + Habitat	Season × Habitat	2	54.68	0.78	0.25
	Season + Habitat	Null	2	55.73	1.84	0.15

CHAPTER V

Perceptions and attitudes towards carnivore conservation in human-dominated landscapes: a case study from southern Chile

Introduction

An understanding of human-carnivore relationships is pivotal for the success of carnivore conservation and recovery programs of (Hagvar, 1994; Beedell and Rehman, 2000; Romanach et al., 2007; Schumann et al., 2012). Human-carnivore relationships are frequently determined by perceptions and attitudes toward carnivores, and as such, have been highly emphasized in the Aichi targets of the Strategic plan (2011-2020) of the Convention on Biological Diversity (CBD).

Carnivores living in human-dominated landscapes are often perceived as conflict species (Zimmermann et al., 2005; Romanach et al., 2007; Soto-Shoender and Giuliano, 2011; Zorondo-Rodríguez et al., 2014). Carnivores are frequently killed by people due to supposed predation on domestic animals and the associated negative impact carnivores have on people's well-being (Woodroffe and Ginsberg, 2005; Dickman et al., 2011). As protected areas are often not large enough to maintain viable populations of carnivores in the long term (Hansen and DeFries, 2007; Simonetti and Mella, 1997), carnivores in such landscapes require social support to persist (Soto-Shoender and Giuliano, 2011; Maroyi, 2012). Thus, the main challenge in their conservation is to promote coexistence between carnivores and humans, rather than to reduce spatial overlap among them (for instance, using protected areas only).

In Chile, carnivores require urgent conservation efforts for three main reasons. First, lack of control of rural free-ranging dogs (*Canis familiaris*) and the transformation of native forest to agricultural lands or commercial tree plantations facilitate the spill-over of diseases and cause further habitat reduction, respectively (Simonetti, 1994; Acosta-Jamett et al., 2003; Acosta-Jamett and Simonetti, 2004; Silva-Rodriguez et al., 2009; Galvez et al., 2013; Sepúlveda et al., 2014; Zorondo-Rodríguez et al., 2014). Second, protected area networks still lack the extent, distribution, and –in many cases– management, to maintain viable carnivore populations (Simonetti and Mella, 1997; Pauchard and Villarroel, 2002; Tognelli et al., 2008; Squeo et al., 2012). Third, and as a consequence of this lack a of protected areas system, many populations of carnivores still occur in non-protected and human-dominated lands (e.g., Acosta-Jamett et al., 2003; Silva-Rodriguez et al., 2010), where the willingness of people to accept these species is largely unknown. Accordingly, the establishment and success of carnivore conservation programs in these human-dominated landscapes will ultimately depend upon understanding the interactions between people and carnivores.

I evaluated the social acceptability of carnivores in Nahuelbuta Mountain Area (hereafter, NMA), a coastal region of southern Chile (35°-40° S) that has been dramatically transformed into agricultural lands and exotic plantations (Smith-Ramirez, 2004; Echeverria et al., 2006; Aguayo et al., 2009), but still contains a diverse carnivore community. I specifically assessed (i) perceptions of carnivores by rural people living in this landscape, and (ii) the willingness of people to conserve these species by adopting husbandry practices for domestic animals (i.e. livestock, poultry, and dogs) that promote conservation of native carnivores.

Methods

Perceptions and attitudes towards carnivores were obtained from semi-structured questionnaire surveys conducted in three rural communities located around Nahuelbuta National Park in the NMA from December 2013 to January 2014: Alto los Ríos, Vegas Blancas, and Elicura (Figure 5-1). Questionnaires were distributed during meetings held by local neighbourhood councils as I found a higher willingness by people (mainly landowners) to address issues related to land management in local meetings, and therefore, I was able to obtain adequate representation of landowners concerning the potential for the conservation of carnivores in NMA. Questionnaires were conducted on nine groups (three groups per community) and included 57 participants. Although working in groups may generate some biases in responses (e.g., degree of complacency), perception and attitude responses towards carnivores can be enriched by the discussion among people within each group, bringing out contrasting views, encouraging reflection, and producing in-depth explanations of the reasoning behind the answers that were expressed (Newing et al., 2011). This strategy might even decrease some plausible complacency biases by some individuals expressed (Newing et al., 2011). Before being administered, the questionnaire was previously tested in a subsample of 15 individuals to assess whether questions were easily understood. Informed consent was obtained from the participants included in the study, and I communicated to participants that gathered data would be used for research only.

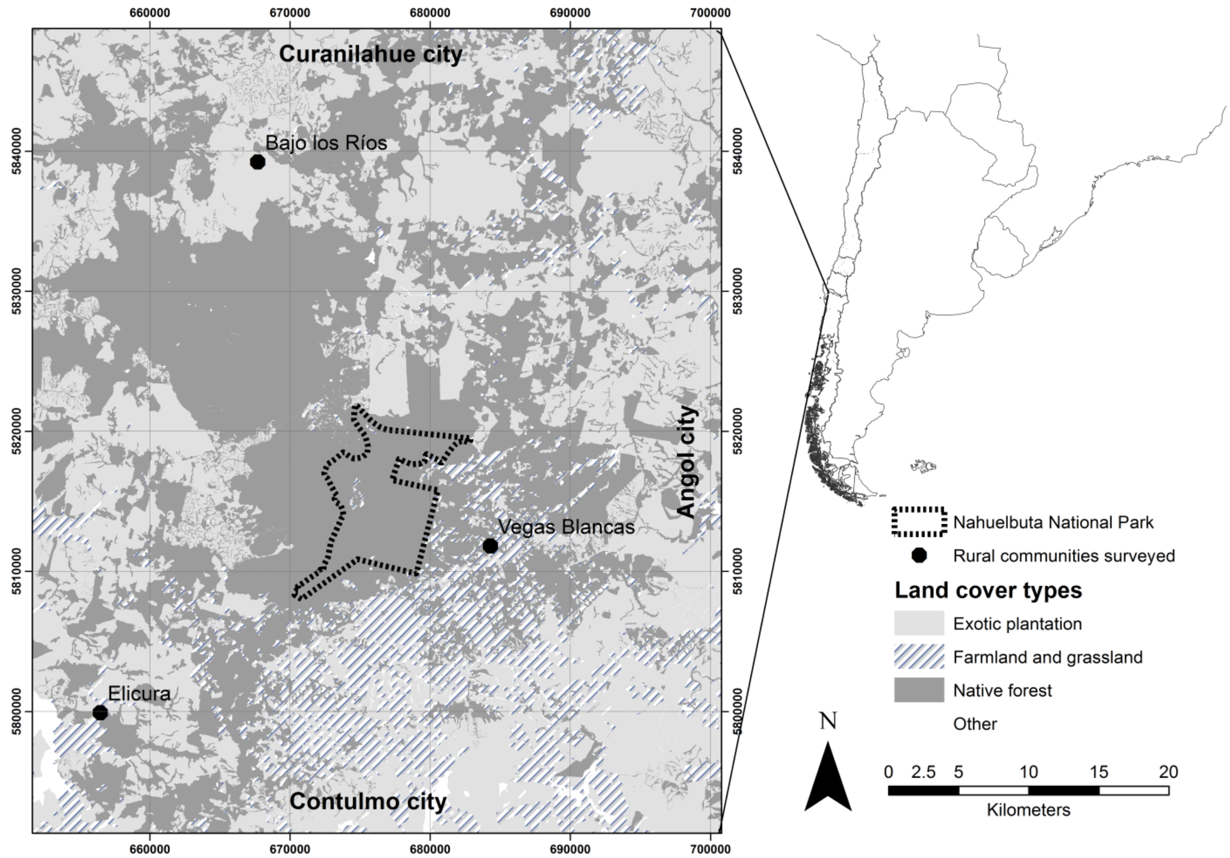


Figure 5-1. Rural communities surveyed (filled circles) in Nahuelbuta Mountain Area, Southern Chile.

Target carnivores assessed

Threatened carnivores, based on IUCN red list, included cougar (*Puma concolor*; Least Concern), kodkod cat (*Leopardus guigna;* Vulnerable), culpeo fox (*Pseudalopex culpaeus*; Least Concern), chilla fox (*P. griseus*; Least Concern) and Darwin's fox (*P. fulvipes*; Critically Endangered). I was particularly interested in the perception towards the endemic Darwin's fox because NMA includes an isolated and relict population of this species (Medel et al., 1990).

Perceptions and attitudes towards native carnivores and their threats

I assessed public perception of how frequently the following threats towards carnivores occurred in NMA: deforestation and native forest replacement by exotic plantations, forest fire, domestic dog attacks, hunting of carnivores' prey, and lethal control of carnivores. I asked individuals to rank the frequency of occurrence of each threat on a scale of 1-6, where values close to 1 and close to 6 referred lower and higher frequency of occurrence, respectively. Second, I assessed the perceptions of frequency of attacks on poultry or livestock by carnivores. People were asked to value the predation frequency using the same scale of 6-values where values close to 1 and close to 6 referred lower and higher frequency of predation on domestic animals, respectively. I prompted people to give an explanation for each evaluation.

Willingness to conserve carnivores by adopting husbandry practices of domestic animals that promote conservation of native carnivores

Firstly, I assessed the willingness to conserve native carnivores from 1 (low willingness) to 6 (high willingness) on the basis of the Likert scale (Liker, 1932). Because of my interest in the conservation of Darwin's fox, I tested if people were able to distinguish three fox species occurring in the study area. I then assessed the willingness to adopt a set of management practices that might reduce human-carnivore conflicts: i) the maintenance of poultry and livestock enclosures during day or night, ii) investment in infrastructure of henhouses and cowsheds, iii) shepherding poultry and livestock during feeding times in opened spaces, iv) reducing the use of pasturages in summer, v) the use of pasturages in places with lower risk of attacks by native carnivores (as perceived by people), and vi) partial or total dog confinement at houses. All practices were emphasized as plausible strategies for reduction of human-carnivores conflicts for the Chilean case (e.g. Silva-Rodriguez et al., 2009; Silva-Rodriguez and Sieving, 2011; Sepúlveda et al., 2014; Zorondo-Rodríguez et al., 2014). Similar to previous questions, I asked people to use the 6-values scale, where values closer to 1 referred to highly disagree and values closer to 6 referred to highly agree.

Results

Perceptions and attitudes towards native carnivores and their threats

Listed threats were perceived to occur with moderate frequency by people in the NMA. Forest fires were perceived by people as the least frequent threat to carnivores in the study area. Conversely, people perceived the deforestation and replacement of native forest by exotic plantation (*Pinus* spp. and *Eucalyptus* spp.) to be the most frequent threat to carnivores (median =3.0) (Table 5-1). The risk of human hunting of carnivore prey and domestic dog attacks on carnivores were perceived as a threat to carnivores with moderate frequency (median=2.5, Table 5-1). Participants mentioned that lethal control of native carnivores occurs with low frequency in the study area, although they also recognized that culpeo foxes and cougars are sometimes killed in response to predation of domestic animals (Table 5-2). There was a local consensus that lethal control of Darwin's foxes and kodkod cats occurs rarely, or not at all.

Table 5-1. Perceptions on the frequency of occurrence of threats towards native carnivores around Nahuelbuta National Park (December 2013 to January 2014).

Threat	Perceived frequency of occurrence*	
	Median	Min-Max
Deforestation/Replacement of native forest by exotic plantations	3	2-6
Forest fires	1	1-2
Hunting carnivores' prey	2.5	1-6
Attacks by domestic dogs	2.5	1-6

* Answers about the perceived occurrence of the threats were on the base of a 6-value scale: 1= never / almost never; 2=low-middle frequency; 3= middle frequency; 4= middle-high frequency; 5= high frequency; 6=always.

The perception of people towards the predation of domestic animals varied across carnivores. People reported that attacks by culpeo fox, chilla fox, and cougar, are more frequent than attacks by other carnivores (Table 5-2, column b). Although people showed high willingness to support actions towards carnivore conservation, there were differences among species. For instance, conservation efforts for Darwin’s fox and kodkod cat received high support by people, with a value over 5; whereas, conservation efforts for culpeo fox, chilla fox, and cougar received lower social support (Table 5-2, column c).

Table 5-2. Occurrence of lethal carnivore control by rural people (a), local perceptions about frequency of predation over domestic animals by native carnivores (b) and willingness to conserve carnivores among rural communities (c) around Nahuelbuta National Park, South of Chile (December 2013 to January 2014).

Carnivores	Frequency of lethal control by local people* (a)	Frequency of attacks on domestic animals* (b)	Willingness to conserve** (c)
Darwin's fox	1.0	1.0	6 (4-6)
Culpeo fox	1.0 (1-2)	3.5 (2-5)	4.0 (3-6)
Chilla fox	1.0	2.0 (1-5)	4.5 (3-5)
Cougar	1.0 (1-2)	3.0 (1-6)	3.5 (2-6)
Kodkod cat	1.0	1.1 (1-2)	5.5 (5-6)

*Answers on the base of scale of 6 values. For the case of columns a and b, scale values refer to 1=never/almost never, 2=low-medium frequency, 3=medium frequency, 4=medium-high frequency, 5=high frequency, and 6=always. **For the case of column c, scale values refer to: 1=totally reject, 2=medium reject, 3=low reject, 4=low support, 5=medium support, and 6=totally support. Cells show medians and, in parentheses, minimum and maximum scores, of values reported by people to each variable on the base of scale used for answers.

Carnivore conservation by adopting husbandry practices of domestic animals

Participants showed a diverse willingness to adopt husbandry practices of domestic animals. People were highly accepting of overnight confinement of poultry (median=6) and livestock (median=6), as well as investment in infrastructure of henhouses (median=5.5) and cowsheds (median=5.5). People were also willing to keep livestock and poultry in feeding places with lower perceived risk of predation (median=5.5). People reported a medium-high level of willingness to reduce the access to summer pasturages (median=5, Table 5-3). However, people were less willing to care for livestock during feeding periods either with sheepdogs or by themselves (median=3.5). Finally, people were reluctant to leash domestic dogs on their property as a responsible ownership practice (median=1). On the contrary, people preferred to keep free domestic dogs (median=6; Table 5-3).

Table 5-3. Willingness to adopt husbandry practices of domestic animals that promote conservation of native carnivores among people from communities around Nahuelbuta National Park (December 2013 to January 2014).

Responsible practice	Willingness to adopt*	
	Median	Min-max
Overnight protection of poultries with henhouses	6	5-6
Investment on henhouse infrastructure	5.5	3-6
Overnight protection of livestock	6	4-6
Investment on cowshed infrastructure	5.5	5-6
Pasturage in places with a low risk of predation	5.5	2-6
Restriction on the use of summer pasturages	5.0	2-6
Taking care of livestock with sheepdogs or by owners	3.5	1-6
Dogs tied in the property	1.0	1-4
Dogs free in the property	6.0	3-6

* Answers were recorded in a 6-value scale: 1=never/almost never, 2=low-medium frequency, 3=medium frequency, 4=medium-high frequency, 5=high frequency, and 6=always.

Discussion

Carnivore management constitutes a central concern to conservation biologists. Human-carnivore conflicts, such as carnivore-related threats to human life, local economy and security, or recreation, pose an urgent challenge world-wide because these conflicts often pit human communities against carnivores (Treves and Karanth, 2003). This study provides a critical step to promote positive human-carnivores relationships, by evaluating perceptions and attitudes toward threatened carnivores in a landscape dominated by anthropic activities (Romanach et al., 2007; Dickman et al., 2011)

My results show the perception and attitudes towards carnivores in NMA are species dependent, suggesting that a favorable scenario to successfully implement conservation actions may vary among species. Darwin's fox and kodkod cat were not perceived as a conflict species, whereas culpeo and chilla foxes, and as cougars were reported as important livestock predators. Previous studies have documented that people from rural areas of Chile disliked culpeo fox, grey fox, and cougars (Franklin et al., 1999; Silva-Rodriguez et al., 2009; Zorondo-Rodríguez et al., 2014). However, kodkod cat was not perceived as a predator of domestic animals in my study area. This is surprising as other areas where this species occurs have shown the people perceive kodkod cats as important predators of poultry (Dunstone et al., 2002; Sanderson et al., 2002; Herrmann et al., 2013; Zorondo-Rodríguez et al., 2014). Differences between results of this study area and other regions in Chile suggest that perceptions and attitudes towards these carnivores (or at least for kodkod cat) may be also dependent on other factors not accounted for by this study; such as income and education.

My results also indicate the willingness to conserve carnivores for this landscape depends on differential perceptions towards these species, which agrees with previous research in Chile (Silva-Rodriguez et al., 2009; Zorondo-Rodríguez et al., 2014) and other regions (Dickman et al., 2011). People were more willing to conserve species perceived as non-conflictive, such as Darwin's fox and kodkod cat, than species perceived as conflictive (culpeo fox, chilla fox, and cougar). The perception of domestic animal predation appears to be a determinant factor on the social willingness to conserve Chilean native carnivores. Nevertheless, usually people´s perceptions do not match with the frequency of attacks on domestic animals reported to public agencies (Rasmussen, 1999; Holmern, 2007), and so, it is expected that people overestimate the predation upon domestic animals by native carnivores. In this sense, strategies for encouraging human-carnivores coexistence based on direct compensation to those people negatively affected by carnivores may have a low long-term viability if there is a lack of verification of livestock depredation incidents (Dickman et al., 2011)

Adopting husbandry practices of domestic animals that promote conservation of native carnivores is pivotal to reducing persecution and killing of carnivores by local people, one of the major threats to carnivore conservation (Silva-Rodriguez et al., 2010; Acosta-Jamett et al., 2011; González et al., 2012; Sepulveda et al., 2014). Results of this study highlight that people from NMA are willing to adopt some management practices to reduce predation risk by carnivores. The willingness to protect poultry and livestock through enclosures could also be used to prevent theft of domestic animals, which is frequent at NMA. However, people were unwilling to keep dogs tied into their property and preferred to keep them free. People argued that dogs contribute to the security of households and therefore would play a keystone role for the livelihood of local people. The unwillingness to adopt measures to reduce the threats towards carnivores such as dog confinement not only contrasts with high willingness to conserve some species such as Darwin's fox and kodkod by the rural communities in my study area, but also with the negative association between dogs and some of these carnivores found in temperate forest (e.g., Silva-Rodríguez et al., 2009 and this study). These findings suggest both species might face a conservation paradox where conservation actions, especially for the critical conservation status of Darwin's fox, may not promise a positive result across the NMA unless some actions such as dog population management can be adopted by the rural communities. Management of domestic dogs can become crucial for native carnivore conservation because of lethal and non-lethal effects on these species and their prey (Vanak and Gompper, 2009; Silva-Rodriguez and Sieving 2012, see Chapter II). Since security of households, including maintenance of food sources for family and home safety, appears to be a fundamental dimension of human well-being in my study area (see for details in Costanza et al., 2007), the willingness to adopt practices of responsible dog ownership in NMA as a strategy for carnivore conservation would be also associated with plausible impacts on well-being (e.g., security of households and livestock).

Thus, I argue that practices that promote the conservation of carnivores and strengthen the fulfillment of well-being will be supported by local people.

Conclusions

I emphasize two main conclusions. First, perceptions and attitudes toward carnivores are species dependent. Therefore, I state that the design of strategies addressing human dimensions of conservation of conflictive species such as carnivores should take into account the relationships of each species with rural communities. Second, husbandry practices to promote carnivore conservation related to protection of domestic animals (e.g., poultry and livestock) were acceptable to people. However, domestic dog management requires urgent attention because their documented negative effect on native carnivores (Vanak and Gompper, 2009). Findings of this study give relevant insights for the design of conservation strategies focused on relationships between humans and biodiversity in human-dominated lands, contributing to the efforts to fulfill the Aichi targets of CDB.

CHAPTER VI

Conclusions & Directions for Future Research

My results provide valuable insight for carnivore conservation and ecology in Nahuelbuta Mountain Area (NMA) of southern Chile, with emphasis on human-wildlife dynamics in increasingly human-dominated landscapes. In this concluding chapter, I summarize and discuss the key findings of my four research studies, and highlight several important directions for future research.

Summary of key findings

In my first study (Chapter 2), I used presence/absence data of carnivores from intensive camera-trapping surveys to derive occupancy models representing separately the space use during day and night. Then, I focused on anthropogenic and natural factors potentially impacting the occupancy patterns of seven native carnivore species. Occupancy models included the effects of habitat variables at different spatial scales on site-specific carnivore occupancy and detection probabilities. Spatial autocorrelation terms were included within models and Deviance Information Criterion was used to compare the support of competing hypotheses. There was variation across species in their estimated occupancy probabilities during day and. best supported models showed native carnivores responded differently to landscape attributes and domestic dogs depending on both the time of day and the spatial scale of landscape attributes. During night, native forest and patch size had either positive or negative effects on the occupancy probabilities of carnivore species. By contrast, during day, road density had a stronger negative effect on the occupancy probabilities of several species, and domestic dog's occupancy negatively affected some carnivores during the same period of time. Camera trap deployment (vegetation cover) and species-specific activity influenced carnivore detectability, thus contributing to explain the occupancy of the rarest and elusive carnivore species in the study area. However, carnivore occupancy may be biased by assuming that processes that influence the persistence of carnivore populations are invariant over short-term scales. Therefore, I argued that assessing long term carnivore occupancy at the landscape-scale requires consideration of their diurnal responses to varying anthropogenic activity, including the presence of introduced species such as dogs that affect carnivore behavior.

In Chapter 3 I showed the importance of using an advanced analytical tools to model animal occupancy with estimates of habitat complexity derived from high-resolution LiDAR remote sensing systems. This novel analytical approach provides unbiased ecological information to identify suitable habitat conditions for carnivores needed to implement long-term ecological management programs for these species. The occupancy probabilities of threatened species such as Darwin's fox (*Pseudalopex fulvipes*) and kodkod cat (*Leopardus guigna*) increased as understory cover and habitat structure complexity also increased. In contrast, the occupancy probabilities of the habitat-generalists culpeo (*Pseudalopex culpaeus*) fox and chilla fox (*Pseudalopex griseus*) responded negatively to these variables. Receiver operating characteristic analyses indicated that performance of carnivore occupancy models was improved with the addition of high-resolution LiDAR remote sensing data. While the results of Chapter 2 indicate that the carnivore community has been impacted by the transformation of native forest into exotic plantations over recent decades, Chapter 3 highlights how fine-grained heterogeneity in vegetation affects space use by carnivores within forest stands. Consequently, a mechanistic approach is required to understand how carnivores use human-created lands.

In Chapter 4, I more closely examined the effects of exotic plantations on the foraging behavior of carnivores by comparing their prey selection patterns in native forest and exotic plantations. While exotic plantations and native forest comprise similar small mammal prey composition, the abundance of most prey species decreased in exotic plantations. Moreover, whereas habitat transformations are expected to reduce the ability of carnivores to capture prey species, the low understory cover in plantations could make the search for prey easier by some carnivores. My results provide support that carnivores occurring in the study area use exotic plantations as feeding grounds, as previously described, and that these habitat transformations trigger pronounced changes in the prey selection behavior of these medium-size predators.

Carnivores usually require social support to persist in human-dominated landscapes, especially when protected areas are small and isolated. In this scenario, private and productive surrounding lands become key to maintaining viable populations of species with large-area requirements. In Chapter 5, I assessed the social acceptability of carnivore conservation by rural communities around Nahuelbuta National Park. I found that carnivore conservation received partial support by people, with perceptions and attitudes varying across species. The main husbandry practice of domestic animals acceptable by people was to provide overnight protection of poultry but maintain free-ranging poultry during day. In contrast, leashing dogs within the property was a highly rejected practice. Particularly, this latter practice becomes a conservation paradox that can be critical to promoting conservation of some threatened carnivores, such as Darwin's fox. Even though rural communities strongly agree with the conservation of Darwin's foxes, urgent management practices of constraining the free ranging domestic dogs may not be accepted by people. This represents a conservation conundrum that is not easily resolved.

In conclusion, my findings support previous suggestions that carnivores populations in the Temperate Forest are subject to significant anthropogenic pressure, particularly from forestry activities and the presence of the introduced domestic dogs. Nevertheless, I showed that these relationships are complex exhibiting dynamic behavioral responses to anthropogenic factors over varying temporal scales. In addition, understanding how native forest transformation into exotic plantations modify prey resources for carnivores provides a basis for sustainable forestry practices. My study strengthened the fact that monitoring data are sensitive to measurement biases that confound interpretation of wildlife populations over time and space, and I showed that future carnivore monitoring conducted in heterogeneous landscapes should incorporate advanced analytical tools and high-resolution spatial information. In this sense, my results, when compared to previous carnivore research in Chile, demonstrated the utility of camera trapping as an useful survey methodology yielding important insights for carnivores when surveying large areas. Camera data are particularly valuable when combined with robust analytical tools (such as hierarchical occupancy modeling) that explicitly address common sources of bias like temporal heterogeneity in detection probability. I highlighted the functional role of forest plantations as feeding habitat for carnivores while determining that the replacement of native forest modifies prey selection patterns and habitat use by predators. Finally, because humans have caused most of the population decline of carnivore populations worldwide, I suggest that successful conservation of carnivore species in NMR, and elsewhere, should involve multidisciplinary collaboration between ecologists and social scientists in order to develop public policies intended for inclusion in carnivore conservation policies.

Directions for future research

From the results and themes of this research arise scientific questions for which further work is needed. Wildlife conservation in human-dominated landscapes should be based on long-term monitoring data, which provides species' population trends and identifies threats (e.g., population increase of introduced species). For instance, results of my research can be seen as a baseline for carnivore occupancy and I have demonstrated that domestic dogs are expanding their distribution across NMR. One important avenue for further research is to set a reliable and feasible long-term monitoring strategy for native and introduced carnivores (Danielsen et al., 2003). In this sense, multi-season occupancy modeling and CMR modeling would provide some insights about carnivores' occupancies are expanding or contracting. This is particularly important for the critically endangered Darwin's fox, whose relic population in NMR is thought to be one of the smallest ones (Farias et al., 2014; Jiménez and McMahon, 2004). In this sense, recently developed analytical approaches that explicitly model detection data arising from latent ecological processes may provide robust inference regarding changes in local carnivore populations (Cressie et al., 2009; Kéry et al. 2010).

In spite of the regional importance of Nahuelbuta National Park for carnivore conservation, the viability of carnivore populations present in this region has not been assessed. Indeed, basic information on demographic parameters is lacking (i.e., population size, rates of reproduction and survival), and, as noted, available population size data have been estimated with considerable uncertainty due to measurement error (Acosta-jamett et al., 2003; Jiménez and McMahon, 2004). Further, powerful tools for assessing wildlife populations, such as radio telemetry, has been rarely used in carnivores inhabiting Chilean temperate forests (but see Jiménez, 2007; Silva-Rodríguez et al., 2010), with some studies making unsuccessful attempts to record demographical parameters for carnivores inhabiting NMR (McMahon, unpublished data). Telemetry data can provide estimates of survival rates, sources of mortality, species interactions, and patterns of movement and habitat selection (Manly et al., 2002; Millspaugh and Marzluff, 2001). Individuals of wide-ranging species, like cougars and culpeo foxes, are likely to move across park boundaries (Nahuelbuta National Park) and interact with adjacent human communities. Thus, remote monitoring of such interactions through telemetry could be of enormous benefit for addressing human-wildlife conflict (Balme et al., 2010). Cross-boundary management will be critical to the long-term viability of most carnivore populations inhabiting landscapes where protected areas are not large enough to maintain viable populations (Baeza and Estades, 2010; DeFries et al., 2007; Woodroffe and Ginsberg, 1998), and telemetry studies could help identify important unprotected habitats and wildlife corridors (Chetkiewicz and Boyce, 2009). Furthermore, demographic data obtained from telemetry could be used to parameterize population viability models, are useful when performing extinction risk analyses and evaluating alternative management scenarios (Carroll et al. 2003; Linkie et al. 2006; Beissinger et al. 2008). In this sense, the Conservation, Management and Restoration Plans (RECOGE in Spanish) of some threatened species including carnivores inhabiting NMR, has been addressed by the Environmental Ministry of Chile throughout collaborative management programs directed toward identifying critical wildlife information.

Successful carnivore conservation in the Temperate Forest landscape will ultimately depend on our understanding of complex socio-ecological interactions (Dickman, 2010; Woodroffe et al., 2005). Most of temperate forest landscapes in central-south Chile are dominated by anthropogenic activity (Echeverria et al., 2006), while interactions between carnivores and local people typically occur as antagonistic encounters (Silva-Rodríguez et al., 2009; Zorondo-Rodríguez et al., 2014). While ecological data are critical to achieve conservation and management endeavors, relevant sociological data are of utmost importance. I collected data on human-carnivore relations during this study, some of which were described in Chapter 5, but further work is required. A better understanding of perceptions of carnivores and wildlife, and attitudes toward their conservation is vital when planning and supporting collaborative management (Treves and Karanth, 2003; Woodroffe et al., 2005). More knowledge of the dynamics of carnivores and rural communities around protected areas such as Nahuelbuta National Park is urgently needed. Furthermore, there are many outstanding questions related to the role of these private lands in the conservation of wide-ranging species, such as carnivores. For instance, Are surrounding private lands seasonally used by these species? Do surrounding private lands support lower prey availability for carnivores when compared to protected areas? What attributes of surrounding private lands do increase the predation risk on domestic animals by native carnivores?

Finally, considering future scenarios where remnant native forest is increasingly replaced by human land uses different from forest plantation (e.g., urban areas), I suggest that further studies will be needed to assess the generality of the results of this study and make comparative analyses with carnivores living in different regions dominated by temperate forest.

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