More Than Habitat Loss and Fragmentation: The Effect of Human-Modified Landscapes on the Spatiotemporal Use and Interactions of Mesocarnivores

by

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Abstract

Anthropogenic habitat destruction is one of the major causes of biodiversity loss, driving species declines across the planet. The resultant human-modified landscapes are not detrimental for all species. Some species such as small to medium-sized habitat generalist carnivores (hereafter referred to as 'mesocarnivores') are able to thrive because of the exclusion of natural enemies and anthropogenic sources of food. With the benefits of human-modified landscapes come novel threats, such as increased exposure to hunting and introduced antagonists. Mesocarnivores may respond to these threats with changes in space and time use, with potential consequences for species interactions. In this dissertation, I examine how drivers of mesocarnivore space and time use align with physical characteristics of the human-modified landscape and associated factors, and what implications these results have for interactions between native species. I do this using empirical work across two temperate systems (Chapters II, III, and IV), and a simulation model (Chapter V).

Chapter II is based in the state of Michigan, USA, across four sites that represent an urban-rural gradient. Across this urban-rural gradient, I assessed the temporal use of coyotes (*Canis latrans*) and raccoons (*Procyon lotor*). Coyotes and raccoons are both species which are commonly found in human-modified landscapes in North America. As the larger species coyotes may pose a threat to raccoons as a predator, though there is little evidence of raccoons avoiding coyotes spatially. I tested whether raccoons were instead avoiding coyotes by altering their use of time, and if the amount of temporal overlap between the two species varied based on the amount of human pressure across the urban-rural gradient. I found that raccoons' time use was

more diurnal (using the daytime) in areas of high coyote use across the entire gradient except at the urban site, where their time use did not shift. However, it was unclear whether this result arose because raccoons are shifting time use to avoid coyotes, or whether coyotes are more nocturnal in areas of higher use. Raccoon time use in general was most unique and most diurnal at the other end of the gradient, at the most rural site. While the evidence for raccoons avoiding coyotes temporally was mixed, it was clear that the amount of temporal overlap between the species varied depending on the amount of human pressure.

Chapters III and IV are based in an agricultural landscape in Los Lagos, Chile. I explored the human landscape associated spatial drivers of three mesocarnivores in the landscape. The chilla fox (*Lycalopex griseus*) is a species that is commonly associated with open landscapes (such as deforested areas in Los Lagos), but that may be dependent on forest patches as refuges. The culpeo fox (*Lycalopex culpaeus*) is a habitat generalist species that is also present in the landscape, and is larger and more carnivorous than the chilla. Lastly, the guina (*Leopardus guigna*) is a small wildcat that was found across the site and is considered a forest specialist. In Chapter III, I examined if habitat amount, habitat configuration, and domestic dogs (*Canis familiaris*) described the spatial use of these three study species. I found that the occupancy of the chilla fox increased with isolation of habitat patches. In contrast, culpeo and guina did not respond to habitat drivers. Instead, the occupancy of the culpeo was negatively correlated with the occupancy of domestic dogs. Since dog occupancy had a negative correlation with habitat amount, this was evidence for an indirect effect of habitat loss on culpeos via an introduced antagonist. Guinas were distributed widely across the site, resulting in occupancy that was not described by any of the covariates we measured. To determine if the weak habitat associations in Chapter III were due to a time-lagged response, I tested whether past landscapes better described

the current occupancy of culpeos and chillas than the current landscape in Chapter IV. Habitat configuration from past years did describe the current occupancy for culpeos and chillas, though the scale at which patch isolation was important varied, as did the amount of time lag. Chilla occupancy was best described by habitat configuration at a broader scale than culpeos, and from metrics from a landscape further in the past.

In Chapter V, I tested whether the heterogeneity in human-modified landscapes (such as the study sites in Chapters II, III, and IV) could change the frequency of an interaction between native species based on the movement of each species being altered. While this chapter did not focus on mesocarnivores, the simulated predator-prey system is applicable to intraguild predation among mesocarnivores. I used an agent-based model to determine how different combinations of movement responses to changes in habitat amount and configuration for a species pair affected the interaction between them. Specifically, I examined the predator-prey interaction between two mobile species, which is relevant to both classic and intraguild predation for mesocarnivores. I highlighted that for both habitat loss and fragmentation, the time until predation increases drastically under nearly every scenario (favoring the prey, or subordinate guild member) except when predator and prey choose the same habitat type. In even this single scenario favoring the predator, the lower time until predation was lost under higher fragmentation. Overall, I demonstrated that changing the amount and configuration of habitat (as is common in landscapes undergoing human-modification) altered the encounter rate for interacting species. The direction of the change however, was dependent on how similar the movement response of the species was to the change in the landscape.

My dissertation highlights two main points when considering the space and time use of mesocarnivores in human-modified landscapes. Firstly, that for species that are resistant to or

thrive in human-modified landscapes, the importance of remnant habitat may mediate or be masked by other factors. In Chapters III and IV, I demonstrated that the importance of the remnant habitat may be hidden by a time lag, or because it mediates domestic dog occupancy. Secondly, that even if native species are widespread in human-modified landscapes, the interactions between these species may be altered. In Chapter II, I demonstrated that the amount of temporal overlap between two native species varies depending on where along the urban-rural gradient they co-occur, and in Chapter IV, I show through simulations that the encounter rate changes based on the landscape. Understanding the spatial and temporal drivers of mesocarnivores and how those drivers translate into interactions is especially important in the landscapes that we most commonly share with wildlife. These dynamics are integral to the health of human and human associates (livestock, pets), and to pursuing mutually beneficial outcomes for humans and wildlife.

Chapter I

Introduction

We are currently in an era of great global change, marked in part by a sixth mass extinction event (Kolbert 2014) with current extinction rates considerably higher than background rates (De Vos et al. 2015). Human pressures on wildlife are widespread and varied, impacting wildlife through overexploitation, the introduction of non-native species, extinction cascades, habitat destruction and climate change (Turvey and Crees 2019). Habitat destruction in particular is considered the greatest threat for terrestrial vertebrates and mammals, and to survive in the resultant human-modified landscapes species must be plastic in their habitat requirements (Ducatez and Shine 2017; Ducatez et al. 2018). In this dissertation I explore spatial and temporal responses of wildlife to different dimensions of the human-modified landscape, and the consequences those responses have for interactions. I focus on generalist mesocarnivores, which are found across a range of human-modified landscapes.

Human-modified landscapes

The goal of conservation is to prevent species declines and extinction, and to balance the needs of people and wildlife. To consider favorable outcomes for wildlife following alterations to the landscape, we must first understand how the landscape has been changed. While habitat loss and fragmentation are important drivers of biodiversity loss (Foley 2005; Newbold et al.

2015), what we replace the native vegetation with has important consequences for biodiversity loss and community functioning (Ricketts 2001; Watling et al. 2011; Ruffell et al. 2017). Human-modified landscapes range widely, from agroecosystems with various degrees of native vegetation integrated amongst crops, to urban systems where native vegetation is replaced by human-built structures and impermeable surface. Additionally, the dynamics of a landscape may be just as important for community functioning as the current state of the landscape (Kuussaari et al. 2009; Wearn et al. 2012a; Lira et al. 2019). While habitat destruction continues unabated in areas such as the Amazon and the Atlantic forests of South America, the modification of landscapes is not a new phenomenon. Humans have used large portions of terrestrial surface of the earth for food production for thousands of years (Ellis et al. 2021), but recent agricultural intensification leaves landscapes with less complexity, refugia, and connectivity (Tscharntke et al. 2005). While landscapes do change naturally, the speed, intensity, and longer persistence of anthropogenic modifications have greater negative impacts and can lead to maladaptive evolutionary outcomes compared to natural processes (Hylander and Ehrlén 2013; Cheptou et al. 2017). Additionally, habitat destruction does not act in isolation; there are synergies with other major drivers of species declines such as the spread of introduced species, overexploitation, and climate change (Peres 2001; Brook et al. 2008). Since species have considerable variation in their physiological limits, lifespans, home range requirements, and reproductive capacities, they respond to habitat destruction at different rates with consequences for interactions among species (Keinath et al. 2017; Figueiredo et al. 2019; Liu et al. 2021). Thus, while habitat destruction and land use change are often marked by biodiversity losses, some species increase in abundance and geographic range in human-modified landscapes.

The human-tolerant mesocarnivore

Human-tolerant mesocarnivores are common examples of species which are successful in human-modified landscapes. In North America, coyotes have expanded their range across the continent (Hody and Kays 2018). In addition to coyotes (*Canis latrans*), raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*) and skunk (*Mephitis mephitis*) are found throughout even heavily built urban systems (Gehrt 2010; Lesmeister et al. 2015; Gámez and Harris 2021). Golden jackals (*Canis aureus*) are commonly found in many human-modified landscapes, and have expanded their range considerably in the last 50 years across Eastern Europe and Asia (Fenton et al. 2021). In Central and South America, several species of carnivores are found throughout human-modified agricultural landscapes (Farias and Kittlein 2007; Hody et al. 2019; Malhotra et al. 2021). While the large carnivores that normally suppress mesocarnivore populations are excluded by humans or at least limited in their activity and movement, many mesocarnivores are more resistant to human impacts and are able to exploit human food subsidies (Prugh et al. 2009). Their higher reproductive rates, broader dietary niche, behavioral plasticity, and habitat generality make them better suited to human-modified environments, where they are 'released' from the high mortality caused by larger carnivores (Devictor et al. 2008; Ducatez et al. 2018; Stanton et al. 2021). Consequently, human-tolerant mesocarnivore species are abundant, widespread, and not typically considered conservation targets. While synanthropic mesocarnivores are often considered nuisance species rather than conservation priorities, understanding their space and time use is of particular importance because by definition they are among the wildlife that most interact with and are directly impacted by humans. For example, mesocarnivores are predators of domesticated animals such as livestock and pets (Crooks and Soulé 1999; Berger 2006; Gallardo et al. 2020), and are important

reservoirs of pathogens (e.g. rabies (Dyer et al. 2014), giardia (Mateo et al. 2017), baylisascaris (Wise et al. 2005)). Mesocarnivores have positive impacts on humans as well, such as reducing animal waste and controlling pest species (Ćirović et al. 2016). Furthermore, mesocarnivores have the potential to be a charismatic first point of contact with the natural world for many people, especially in cities; they are an integral part of considering human-modified landscapes as unique and novel ecosystems with conservation value (Gámez and Harris 2021; Harris 2022). To manage the impacts that mesocarnivores have on humans (or translate to more sensitive wildlife), we must first understand mesocarnivore spatiotemporal use within human-modified landscapes, beyond just their ability to persist in an environment that is inhospitable for many other species. Rather than simply testing for landscape metrics as a direct predictor of mesocarnivore space and time use, the major theme of my research is to incorporate the landscape as a factor that mediates other drivers.

Overarching research themes

The impacts of habitat loss and fragmentation on biodiversity and in regard to species declines are well studied (Fischer and Lindenmayer 2007; Fahrig et al. 2019; Powers and Jetz 2019). Instead, I focused on factors that were associated with the current human-modified landscape, including the possibility of remnant habitat as an indirect or delayed driver of spatiotemporal use. My aim was to use several case studies to build an understanding of habitat generalist mesocarnivore space and time use in the context of human-modified landscapes, as a foundation for understanding the consequences of anthropogenic landscape change for species interactions. Towards this goal, in Chapter II, I examined overlap in coyote and raccoon temporal activity, and whether the amount of temporal overlap is mediated by a broad gradient of human-altered landscapes in Michigan, from pristine primary forest to a built up urban system. Chapters III and

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IV are situated in an agricultural landscape in southern Chile, where I assessed drivers of

mesocarnivore spatial use that are tied to a history of habitat loss and fragmentation. Finally, in

Chapter V, I used simulations to examine how anthropogenic habitat loss and fragmentation can

alter the movement of a predator-prey pair, with resultant consequences for the frequency of the

interaction.

Chapter II

Temporal Refuges Differ Between Human and Natural Top-Down Pressures in a Subordinate Carnivore

Preamble: This chapter was accepted with minor revisions in the journal *Ecology and Evolution*. The citation for this chapter is: Malhotra, R. Lima, S., Harris, N. C. (2022) Temporal refuges differ between human and natural top-down pressures in a subordinate carnivore

Abstract

*Background***:** Animals exhibit variation in their space and time use across an urban-rural gradient. As the top-down influences of apex predators wane due to human-driven declines, landscape level anthropogenic pressures are rising. Human impacts can be analogous to apex predators in that humans can drive increased mortality in both prey species and carnivores, and impact communities through indirect fear effects and food subsidies. Here, we evaluated the time use of a common mesocarnivore across an urban rural gradient, and test whether it is influenced by the intensity of use of a larger carnivore. *Methods:* Using multiple camera-trap surveys, we compared the temporal response of a small carnivore, the raccoon (*Procyon lotor)*, to the larger coyote (*Canis latrans)* at four sites across Michigan that represented a gradient of pressure from humans. *Results:* We found that raccoon time use varied by site and was most unique at the rural

extreme. Raccoons consistently did not shift their activity pattern in response to coyotes at the site with the highest anthropogenic pressures despite considerable interannual variation, and instead showed the stronger responses to coyotes at more rural sites. Temporal shifts were characterized by raccoons being more diurnal in areas of high coyote activity. *Conclusions:* We conclude that raccoons do partition time to avoid coyotes. Our results highlight that the variation in raccoon time use across the entirety of the urban-rural gradient needed to be considered, as anthropogenic pressures may dominate and obscure the dynamics of this interaction. In an increasingly anthropocentric world, to understand species interactions, it is imperative that we consider the entire spectrum of human pressures that it may occur within.

Introduction

Cities are a rapidly growing, emergent habitat type with projected increases to 120 million ha globally by 2030 (McDonald et al. 2018). Human pressures such as urbanization increasingly drive the decline of apex predators at a global scale (Ripple et al. 2014; Young et al. 2016). Similar to apex predators, humans can induce non-consumptive consequences on subordinate species through changes in space and time use (Ciuti et al. 2012; Clinchy et al. 2016). However, humans are unique in their top-down pressures in that they can exert fear effects across trophic levels, superseding hierarchies in natural systems (Smith et al. 2017; Suraci et al. 2019). The resultant heterogeneity of apex predator distribution from human pressures can induce differences in community structure as well as coexistence mechanisms within the carnivore guild (Berger 2007; Muhly et al. 2011; Moll et al. 2018). In urban areas, where spatial overlap among

species are inevitable due to the limited amount of habitat available, temporal partitioning may be particularly important for species' persistence (Adams and Thibault 2006; Santos et al. 2019; Stark et al. 2020).

Urban-rural gradients provide comparisons of ecosystem function between natural (e.g. top down predation) and anthropogenic forces (e.g. fear of humans) (McDonnell and Pickett 1990; Ellington and Gehrt 2019). Thus far, urban-rural gradients have predominantly highlighted changes in physical characteristics (e.g., body size) that can affect ecological interactions, or changes in biodiversity and species composition across taxa (Marzluff 2001; Urban et al. 2006). Although not specifically casted in an urban-rural framework, there are further evidence that humans and built structures can alter animal behavior (Van Donselaar et al. 2018; Avilés-Rodríguez and Kolbe 2019). For example, global meta-analyses found that intensity of human pressure can drive increased nocturnality and reduce movement (Gaynor et al. 2018; Tucker et al. 2018). Altered time use due to humans can further translate into altered interspecific interactions (Lewis et al. 2015; Gallo et al. 2019). We can recast the implications of urban expansion to consider cities as novel ecosystems that have conservation value by shifting the focus from degradation instead to evolutionary potential (Kowarik 2011; Seto et al. 2011; Alberti 2015). We leverage and expand upon the urban-rural gradient formed by human pressure to examine spatiotemporal dynamics between a widely distributed carnivore and a smaller sympatric competitor.

As a highly adaptive mesocarnivore, coyotes *(Canis latrans)* exploit a wide range of habitats and exhibit tolerance to disturbance (Flores-Morales et al. 2019; Bekoff and Gese 2003. Coyotes exemplify mesopredator release through range expansion that aligns with human caused extirpation of gray wolves (*Canis lupus*). Though coyotes are subordinate to gray wolves where

they are sympatric, they are an aggressor species for several smaller carnivores and account for high rates of mortality for some species (e.g., *Vulpes velox*, *Vulpes macrotis*) (Bekoff and Gese 2003; Berger 2007). As a result, coyotes are commonly cited as a species that can act as both a mesopredator or an apex predator in their community, depending on the presence of the gray wolf (Prugh et al. 2009; Roemer et al. 2009; Colborn et al. 2020). Similarly, raccoons (Procyon lotor) exhibit tolerance to human pressures and spatially overlap through much of the coyotes North American range (Timm et al. 2017; Kays 2018). Coyote-raccoon interactions are interesting because of how widespread both species are, the size difference that should typify intraguild aggression or predation, and yet lack evidence for any sort of spatial or temporal partitioning (Gehrt and Clark 2003; Donadio and Buskirk 2006; Shedden et al. 2020). There has yet to be a study that examines the temporal dynamics of these two species across the urban-rural gradient.

Raccoons exhibit spatiotemporal variation in behavioral attributes, leading us to expect that the response of raccoons to coyotes may vary by differences in habitat and other characteristics across sites (Beasley et al. 2011). Gehrt and Prange (2007) put forth a convincing argument that raccoons and coyotes do not fit into the mesopredator release hypothesis, and there little evidence that coyotes act as a control on the abundance or spatial use of raccoons (Lesmeister et al. 2015). Telemetry studies of raccoons have found some evidence of mortality due to coyotes, but only as a rare occurrence (Gehrt and Clark 2003; Prange et al. 2003). In North Carolina, the temporal use of coyotes and raccoons largely overlapped and that raccoons overall exhibited low levels of vigilance, indicating low levels of fear from coyotes (Chitwood et al. 2020).

Given that coyotes pose some risk to raccoons based on size and sympatry, but that overall risk is low, we tested whether raccoons showed any finer scale shifts in time based on heterogeneity in coyote risk within a site. Employing a camera survey across an urban-rural gradient, we tested whether raccoon time differed between intensities of coyote spatial use. For context, we tested the variation in raccoon time use across two scales: between sites (across the urban-rural gradient) and within site, between years (interannual variation) (Fig. 1-1), with hypotheses that: a) there raccoon time use at the most urban site would be significantly different than at the other three sites, and b) interannual variation would be more least pronounced at the urban site. Based on the strong fear effects that humans can exert on wildlife, we hypothesized that raccoon time use would not shift on the urban end of the gradient, due to activity patterns of both species avoiding peak hours of human activity. Conversely, we hypothesized that raccoons would shift in areas of intense coyote use on the rural end of the spectrum. As anthropogenic pressures increase, our knowledge of contemporary baseline ecological interactions becomes dated. Thus, it becomes essential to understand how these competitive interactions compare across landscapes with varying human pressures.

Methods

Study area

We investigated raccoon temporal dynamics across differing levels of coyote activity at four sites across the state of Michigan, USA (Fig. 1-2) which represent an urban-rural gradient.

1) The Huron Mountain Club (HMC) is a privately-owned property along the southern shore of Lake Superior, encompassing around 6,900 hectares in Marquette County, Michigan, USA. This site has a wide variety of habitats including beech-sugar maple hardwood forests,

aspen dominated stands, and coniferous boreal forests. Sympatric large predators include: gray wolves, black bears (*Ursus americanus*), and coyotes. Anthropogenic pressures are limited to a small, seasonally occupied area of human habitation near the north central part of the property. Hunting and fishing occur on the property, and the intensity is presumably low due to restrictive public access.

2) The University of Michigan Biological Station (UMBS), a ~4,000 hectare research station and forest in Pellston County, Michigan, USA served as one of our intermediate disturbance sites. With repeated logging and fire disturbance until 1923, the secondary forest is a mix of transitional hardwood and boreal forests. Douglas and Burt lakes along the north and south, and the town of Pellston and a major highway along west and east, respectively border this study area. Large co-occurring predators include: black bears, coyotes, and coyote-wolf hybrids. We were able to distinguish the few known coyote-wolf hybrids in the area due to them having collars from a different study, which were visible in the camera trap images (Wheeldon et al. 2012). Human pressures resulted from regulated research infrastructures for climate monitoring and housing facilities with low levels concentrated seasonally during the summer.

3) The Shiawassee National Wildlife Refuge (SNWR) is a 9,870 hectare wildlife refuge managed by the US Fish and Wildlife Service. The refuge is comprised of forested hardwood wetlands and lakeplain prairie. The city of Saginaw abuts the northern edge of the refuge and is surrounded by agricultural land for crop farming. The only large native predator present is the coyote. Anthropogenic pressures, in addition to the urban and ex-urban nature of the boundaries, are in the form of recreational visitors. Public hunting for deer and waterfowl, and furbearer trapping are permissible on the refuge in accordance with lawful seasons.

4) The Detroit Metro Parks (DMP) is a collection of greenspaces interspersed throughout southeast Michigan that is managed by the Detroit Parks and Recreation Department. We chose twenty-five of these parks that varied in size from ~1.6-480 hectares, tree cover, human visitation, and degree of disturbance. Roads, buildings, or a riverine edge bound all parks. The only large native predator present is the coyote. Strong anthropogenic pressures are present in the form of the surrounding urban matrix, as well as the associated presence of humans and domestic pets across parks

Camera trap survey

We deployed remotely-triggered camera traps (Reconyx© PC 850, 850C, 900, 900C) throughout each site with camera placement and sampling design proportional to study area size (Table 1). Our study uses data from three surveys at DMP (2017, 2018, 2020), three surveys at SNWR (2016, 2017, 2018), two surveys at UMBS (2015, 2016), and four surveys at HMC (2016, 2017, 2018, and 2019). We captured the heterogeneity of habitat and other environmental features to ensure ecological representation in the micro-site selection of camera traps. Camera traps were affixed to trees > 0.5m diameter and placed 0.5-1.0 m off the ground. Site-specific placement of camera traps was determined by signs of animal activity such as game trails and scat. Camera trap settings included: high sensitivity, one-second lapse between three pictures in a trigger, and a 15-second quiet period between triggers. Camera traps were not baited.

Image identifications were initially crowd-sourced and filtered for carnivores using a public-science program called *Michigan ZoomIN* in combination with a consensus algorithm and

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expert validation (Gadsden et al. 2021). Carnivore species identifications were later sorted and confirmed by at least two independent researchers in the Applied Wildlife Ecology Lab.

Temporal activity

Time stamps associated with the camera trap images were used to conduct temporal analyses. Prior to all analyses, a 30-minute quiet period was introduced for every species to account for pseudoreplication, given the tendency of some animals to remain in front of the camera trap and trigger it multiple times. Since surveys were conducted across different times of the year, we scaled times to sunrise and sunset times using the *sunTimes* function in the 'circular' package in R (Ridout and Linkie 2009).

Variation between sites

We first compiled all raccoon triggers from each survey within a site to have an aggregate across years of overall raccoon temporal activity at each site. We then compared raccoon temporal activity between sites using the Mardia-Watson-Wheeler (MWW) test, which is a nonparametric test of differences in the angular means between samples of circular data using the 'circular' package in R (version 4.1.0). When the W value is high it results in a significant *p* value ($p <$ 0.05), which we conclude to mean that the compared temporal activities are unique.

Seasonal and yearly variation

Our multi-site camera study allowed us to compare differences in raccoon temporal activity based on landscape level differences along an urban-rural gradient. Comparing between seasons can confound inferences from the analyses, due to different seasons potentially resulting in different detection rates (Marcus Rowcliffe et al. 2011). While we did not have identical seasonal

coverage for every site, the multiple surveys at every site resulted in coverage for the entire year at every site with the exception of UMBS (Fig. S1.1). To determine if there was consistency at sites regardless of season and year, we compared raccoon activity between each survey within each site, and then looked for broader patterns across sites.

Coyotes on raccoon temporal activity

For each survey, we used a kernel density estimation for the independent coyote triggers and designated the cameras that fell within the top quantile of as 'HIGH' coyote intensity of use zones in ArcGIS Pro (version 2.3.1). We used this rather than a fixed cutoff value of expected detection rate because our sites spanned the entirety of the urban-rural gradient and expected detection rates for coyote vary depending on the composition of a site (Magle et al. 2014). Coyote triggers were checked for spatial independence using Moran's I prior to kernel density estimation. We compared raccoon temporal activity between the high coyote cameras and the rest of the site using the MWW test. For additional evidence that temporal shifts by raccoons were due to avoidance of coyotes, we then compared the overlap between coyote and raccoon time use in the two raccoon test groups from the MWW test. To do this, we calculated an overlap (Δ) coefficient of temporal activity for coyotes and raccoons within each group ('HIGH' and 'LOW' coyote intensity of use) along with 95% confidence intervals generated from 10,000 parametric bootstraps of the temporal distribution models. Δ values range from 0 to 1, with 0 indicating completely distinct and non-overlapping temporal activity between comparison groups, and 1 indicating complete overlap. Δ_1 was used for comparisons when one of the sample groups had less than 50 triggers; otherwise Δ_4 was used to estimate temporal overlap (Ridout and Linkie 2009). Finally, the activity distributions were visually assessed to determine qualitative

characteristics of shifts (e.g. raccoons shifting towards increased nocturnality in high coyote zones).

Results

We obtained 1,378 coyote and 11,136 raccoon triggers with a 30-minute quiet period across 12 surveys in 82,595 trap nights (HMC- 36,868; UMBS- 12,953; SNWR- 12,477; DMP- 20,297) from 2015-2020. Raccoons and coyotes were the most common carnivores in almost every survey, comprising 57-98% of all the carnivore triggers. In Detroit, where domestic dogs and cats comprised 35% of the triggers, coyotes were the fourth most common carnivore species after raccoons, cats, and dogs.

Coyote relative activity

 Kernel density estimates indicated coyotes were distributed non-randomly in space (Fig 1-2). At DMP with heavy anthropogenic pressure (average 77 coyote triggers per camera in "HIGH" coyote zones), coyote activity was concentrated in two heavily forested parks and had few human triggers compared to the rest of the surveyed parks in Detroit. In contrast, at HMC with heavy natural apex pressure, the highest coyote activity occurred in a recreation area that contained several buildings and homes but had few overall triggers (average 3 coyote triggers per camera in "HIGH" coyote zones). Coyote activity formed distinct zones in SNWR and UMBS as well, and the location of hotspots varied by survey. Hotspots at these two sites were not associated with any discernible landscape level measures of anthropogenic pressures. Raccoon triggers were recorded within both the low and high zones of coyote activity across all sites, establishing spatial overlap between the two species

Variation in racoon activity between sites (Fig 1-1a)

Raccoon activity at each site was unique, showing significant differences in every pairwise comparison of sites from MWW tests (Table 1). We expected raccoon activity to be the most distinct at DMP, our most urban site. Instead, we found that raccoon activity was most unique at HMC, showing considerably more use of the diurnal period (Figure 5) and significantly less overlap with the other three sites (combined confidence intervals showing 76-87% overlap) than comparisons between UMBS, SNWR, and DMP (combined confidence intervals showing 87-96% overlap) (Figure 4).

Seasonal/annual variation in raccoon activity (Fig. 1-1c)

Raccoon activity varied significantly by survey and year for every site with the exception of UMBS (Table 2). At the most urban end of the urban-rural gradient, , raccoon activity was significantly different between every year surveyed at DMP and SNWR. At UMBS, the comparison between the two years approached significance (W = 5.53, p = 0.063). While at HMC the results varied, depending on the years compared. For example, 2016/2017 and 2017/2018 comparisons showed that raccoon time use varied significantly between these years, while raccoon time use between 2018 and 2019 was similar (W = 3.03, p = 0.220).These results refuted our hypothesis that interannual variation would be weakest at DMP, instead showing that there is considerable variation across years at all sites.

Coyote use on raccoon temporal activity (Fig. 1-1b,c)

Overall, our hypothesis for raccoon-coyote temporal interactions was largely correct, with

raccoons at DMP consistently exhibiting no shift in time use relative to coyote intensity of use

zones. However, there was reduced overlap between coyotes and raccoons within the high

coyote zone. Results for the other sites varied by survey year (Fig. 1-3). Below, we first present

for each site the results for the comparison of raccoon activity between the high and low coyote

zone. Then we provide the comparison of raccoon and coyote temporal activity within the high

coyote zone (relative to the same comparison in the low coyote zone), to determine if there is

evidence that a shift in raccoon activity between zones is due to temporal avoidance of coyotes.

HMC: At the most rural site, we found results for the effects of coyotes varied by survey. The

2016 and 2017 surveys exhibited no shifts, while surveys in 2018 and 2019 showed significant

shifts in raccoon activity between coyote low and high zones (W $= 15.12, 10.02, p < 0.00$

respectively) (Table 1). Results were consistent even when the 2017 survey was broken up into

summer and winter survey seasons since it covered an entire year, indicating no shifts in raccoon

activity between coyote zones. When comparing coyote and raccoon temporal activity within

each zone the 2018 survey showed some evidence of decreased temporal overlap between coyote

and raccoons in the high coyote zone, while for 2019 the confidence intervals were too wide to

be meaningful (Fig. 1-3).

UMBS: For both surveys, we found there were significant shifts in raccoon activity between

coyote zones (W $= 9.63, p < 0.00$ for 2016, and W $= 7.39, p = 0.025$ for 2015). Both surveys

showed evidence of reduced temporal overlap between coyote and raccoons in the high coyote

zone.

SNWR: We found that again, results varied by survey, with two out of three surveys showing significant shifts in raccoon activity between coyote zones; 2016 ($W = 6.08$, $p = 0.047$) and 2018 ($W = 10.46$, $p < 0.00$) showed shifts, while in 2017 ($W = 3.65$, $p = 0.162$) raccoons did not shift activity. Only the 2018 survey showed evidence of reduced temporal overlap between coyotes and raccoons in the high coyote zone.

DMP: We found that raccoons exhibited no shifts in activity between coyote zones consistently across for all four years surveyed in our study. Curiously, two out of the three surveys (2018, 2020) showed evidence of reduced overlap between raccoons and coyotes in the high coyote zone, with the difference reaching significance in the 2020 survey (Δ_4 CI in the high coyote zone: 0.46-0.58 vs. low coyote zone: 0.61-0.80).

Discussion

Behavioral adjustments in diet, spatial, and temporal use can reduce competition for resources to promote coexistence (Inouye 1978). We tested for spatial and interannual variation in the time use of raccoons across an urban-rural gradient and measured the use of temporal refuges by raccoons in the presence of coyotes across that same gradient. As expected, we found that raccoon time use varied both across the gradient and between years. More importantly, we highlight that there were consistent patterns across the urban-rural gradient in raccoon temporal response to coyotes. We found that at the most urban site (DMP), raccoons consistently did not shift their temporal activity in response to coyotes, despite significant interannual variation in raccoon activity. In contrast, all other sites showed some evidence of behavioral plasticity in raccoon time use with the intensity of coyote spatial use. These results complement other

findings that: a) non-consumptive effects impact the spatial use within the carnivore guild (Newsome and Ripple 2015); and b) that non-consumptive effects (fear effects) are present within the hierarchy of the carnivore guild (Gordon et al. 2015).

Urban systems represent an extreme of human pressures, and the continuing increase in urban habitat makes understanding the unique behaviors and ecologies of wildlife in urban spaces such as Detroit, Michigan particularly important. Breck et al. (2019) found that coyotes at urban sites are bolder in comparison to their rural counterparts, which would support their role as a fear source in cities. In absence of shifts in raccoon activity at our DMP site, it seems that this fear effect does not extend to raccoons. Given that we did find some evidence of temporal avoidance at our other sites, a more plausible explanation is that fear of coyotes is not strong enough to elicit a shift in raccoon time use in the face of a stronger force; the most obvious in an urban system being humans and domestic dogs, as reflected by raccoons at DMP having the least diurnal activity (Fig. 1-5) (Gaynor et al. 2018; Nix et al. 2018; Sévêque et al. 2021). Despite raccoon activity consistently being similar between zones of coyote intensity of use, raccoon activity did seem to show somewhat reduced overlap with coyote activity in the high coyote intensity of use areas. This implies that coyotes were potentially using time differently depending on how heavily used an area was by conspecifics. A plausible explanation would be intraspecific competition (Cunningham et al. 2019), or this result could more generally suggest coyotes are more plastic in their time use than raccoons in urban systems (McClennen et al. 2001). The latter would make sense; although both species are cosmopolitan, raccoons are more human tolerant than coyotes (Crooks 2002; Randa and Yunger 2006).

Surprisingly, it was not the human-dominated urban system that was the most unique in raccoon temporal use amongst the sites, but instead the more pristine HMC in northern

Michigan. The overall raccoon activity pattern showed considerable use of the diurnal period during which humans tend to be most active (Fig. 1-5), resulting in low overlap with other sites. HMC also showed the greatest interannual variation in raccoon response to coyotes out of the four sites, once again perhaps reflecting a lack of human impact in the form of food subsidies (Manlick and Pauli 2020). The availability of resources can modulate the strength of competition, and so annual variation in food resources could drive the avoidance response of raccoons to coyotes (Newsome et al. 2015). At the other three sites, human food waste and other human-derived subsidies likely offset years that may otherwise be relatively resource-poor for raccoons (Oro et al. 2013). Unlike UMBS and SNWR, which have nearby towns, HMC is isolated, surrounded by forest and with the few cabins on the property only seasonally occupied.

Our results highlight broad patterns in raccoon temporal use between zones of high and low coyote activity. The mechanisms that underlie these patterns require further study and a temporal shift could very likely have more nuance than simple avoidance by a subordinate carnivore. A shift in temporal use by a subordinate (as shown in our SNWR and DMP sites) might instead reflect indirect avoidance of competition with a larger competitor rather than direct avoidance of antagonistic interactions (Newsome et al. 2015). While our results indicate the response of the raccoon to be driven by a larger predator, it does not preclude an interaction between top-down and bottom-up forces, which may be important to understanding what raccoons are directly responding to across sites and survey seasons (Elmhagen and Rushton 2007). For example, resource availability, such as the abundance of small mammal prey, fluctuates with season and could be a driver of varying levels of competition between coyotes and raccoons (Batzli 1992; Fedriani et al. 2000; Neale and Sacks 2001). At an urban site (e.g., DMP), food subsidies in the form of trash could reduce seasonal variation in resource

competition (Oro et al. 2013; Newsome et al. 2015). Thus, we would expect patterns of temporal use, particularly in the presence of a competitor, to vary seasonally (Sovie et al. 2019). Seasonal variation in temporal response may explain the divergent result for the 2017 SNWR survey, which occurred during the summer months. The other two surveys at the site occurred during the fall and the spring, periods which are associated with heightened resource gathering for the imminent winter, and heightened coyote aggression because of the coyote breeding season (Way 2001). Pairing dietary studies that explore the seasonal variation in coyote and raccoon diets across all sites with spatiotemporal analyses would elucidate if seasonal variation in resource availability drives resource partitioning between these species.

Though the two sites at the opposite ends of the gradient (i.e., HMC and DMP) best highlight the variation in raccoon temporal activity and temporal response to coyotes, there were site specific patterns for the entire gradient. We intended for our sampling sites to represent opposing gradients of humans and native apex predator presence, which were reflected in the amount of built structures and which carnivores were captured on camera at each site. However, given that we did not test for the effect of the relative activity of apex predators and humans , we cannot discount the possibility that factors other than top-down forces drove the urban-rural gradient we observed in our results. Sites varied in vegetative cover, topography, latitude, and distribution of resources. Though, differences in the sources of top-down forces are the most obvious and likely ecological factor that differs between the sites for generalist species such as raccoons and coyotes. Similar outcomes have been reported for other coyote-subordinate predator systems when compared across sites that vary in the presence of an apex predator (Shores et al. 2019).

Conclusion

We conclude that there is evidence of temporal partitioning being used by raccoons in the presence of coyotes. On the surface, our results seemingly contradict recent works that suggest that coyotes are not an important intraguild predator for raccoons, and that raccoons thus do not partition time to avoid coyotes (Gehrt and Clark 2003; Chitwood et al. 2020). Instead, we suggest that time use shifts may be at a fine scale, and whether they are present depends on a suite of factors. Therefore for a behaviorally plastic species such as the raccoon, it is difficult to make broad conclusions about time use without considering the considerable variation across the urban-rural gradient they inhabit. Similarly for the coyote, their role as an intraguild aggressor for raccoons is not static across the urban-rural gradient. Instead, the competitive dominance of coyotes is likely dependent on the amount of human pressure and the presence of other larger competitors. Ultimately, as the human footprint on the planet continues to deepen, we need to continue reevaluating interactions across the gradient that it creates. The paradigm in conservation is also shifting to include *in situ* conservation of species in urban habitats, rather than considering these areas solely as suboptimal sink habitats (Magle et al. 2012; Athreya et al. 2013; Mormile and Hill 2017). Studies comparing the ecological roles of species within a community between urban and natural systems are timely. Such work will prove invaluable in understanding how wildlife communities in these novel habitats differ not just in composition, but also in their function.

Acknowledgements

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Table 1-1. Temporal overlap (Δ) coefficients and 95% confidence intervals for raccoon and coyote activity in low and high coyote zones within each camera survey in Michigan. Trap nights equals the total number of cameras multiplied by the number of nights each camera was active. Mardia-Watson-Wheeler test results comparing raccoon activity between the top quantile and the bottom three quantiles of raccoon activity for each survey are contained in the last two columns, where W is the test statistic (approximately Chi-sq distributed), and p value are included.

Survey period	Site/Year	Trapnights (n)	# Cameras	Δ (CI) High	Δ (CI) Low	W	*pvalue*
May-Aug	HMC'19	3445	96	0.32-0.72	0.28-0.85	10.024	**0.000**
Jun-Aug	HMC'18	8338	43	0.49-0.76	0.68-0.91	15.122	**0.007**
Jul-Jun	HMC'17	10874	43	0.65-0.83	0.56-0.80	3.841	0.147
Jun-Oct	HMC'16	14211	101	0.59-0.85	0.45-0.83	0.918	0.632
Jul-Nov	UMBS'16	8586	61	0.65-0.85	0.71-0.87	9.631	**0.008**
Oct-Dec	UMBS'15	4367	59	0.42-0.73	0.66-0.86	7.392	**0.025**
Sep-Dec	SNWR'18	3862	41	0.59-0.78	0.66-0.89	10.458	**0.005**
May-Aug	SNWR'17	3076	49	0.60-0.84	0.54-0.88	3.647	0.162
Feb-May	SNWR'16	5539	56	0.63-0.79	0.61-0.81	6.086	**0.048**
Jan-Sep	DMP'20	11713	39	0.46-0.58	0.61-0.80	3.302	0.192
Oct-Feb	DMP'18	4487	41	0.52-0.75	0.61-0.85	0.376	0.829
Nov-Mar	DMP'17	4097	39	0.59-0.83	0.57-0.84	0.692	0.708

Table 1-2. Mardia-Watson-Wheeler test results comparing raccoon activity at each site between each survey year. W is the test statistic (approximately Chi-sq distributed), and associated degrees of freedom and *p* value are included.

Years	Site	W	*df*	*pvalue*
19 vs 18	HMC	3.030	2	0.220
18 vs 17	HMC	22.99	2	**0.000**
17 vs 16	HMC	6.77	2	**0.034**
16 vs 15	UMBS	5.533	2	0.063
18 vs 17	SNWR	35.319	2	**0.000**
17 vs 16	SNWR	26.202	2	**0.000**
20 vs 18	DMP	7.948	2	**0.018**
18 vs 17	DMP	9.884	2	**0.007**

Between sites
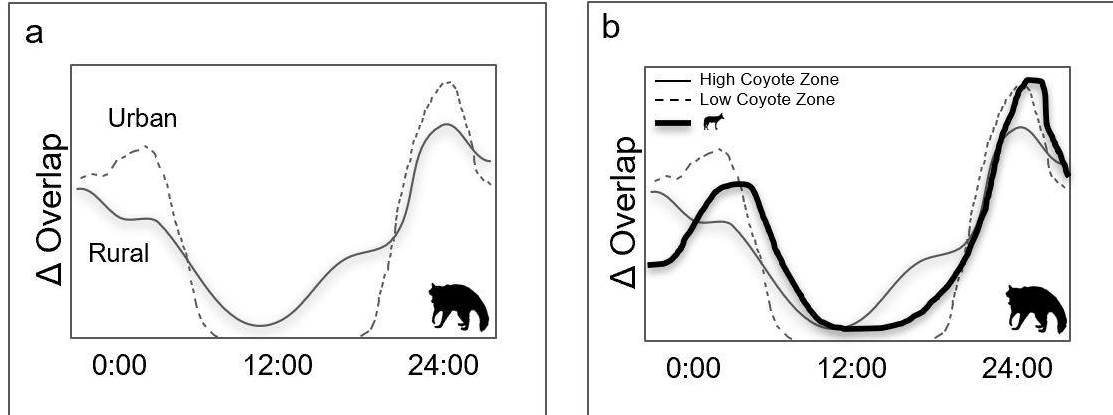
Within site
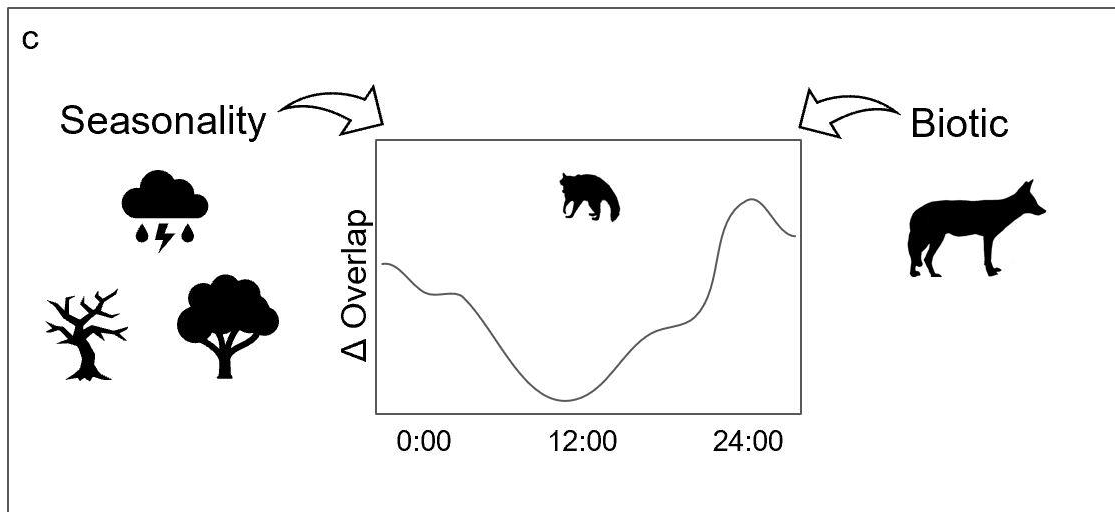
Fig. 1-1. The three comparisons considered within our study: a) Raccoon temporal activity was compared between sites; b) raccoon activity was compared between years, and across zones of coyote intensity of use within each site; c) the results from the within site comparisons of raccoon time use in response to coyotes were compared across sites.
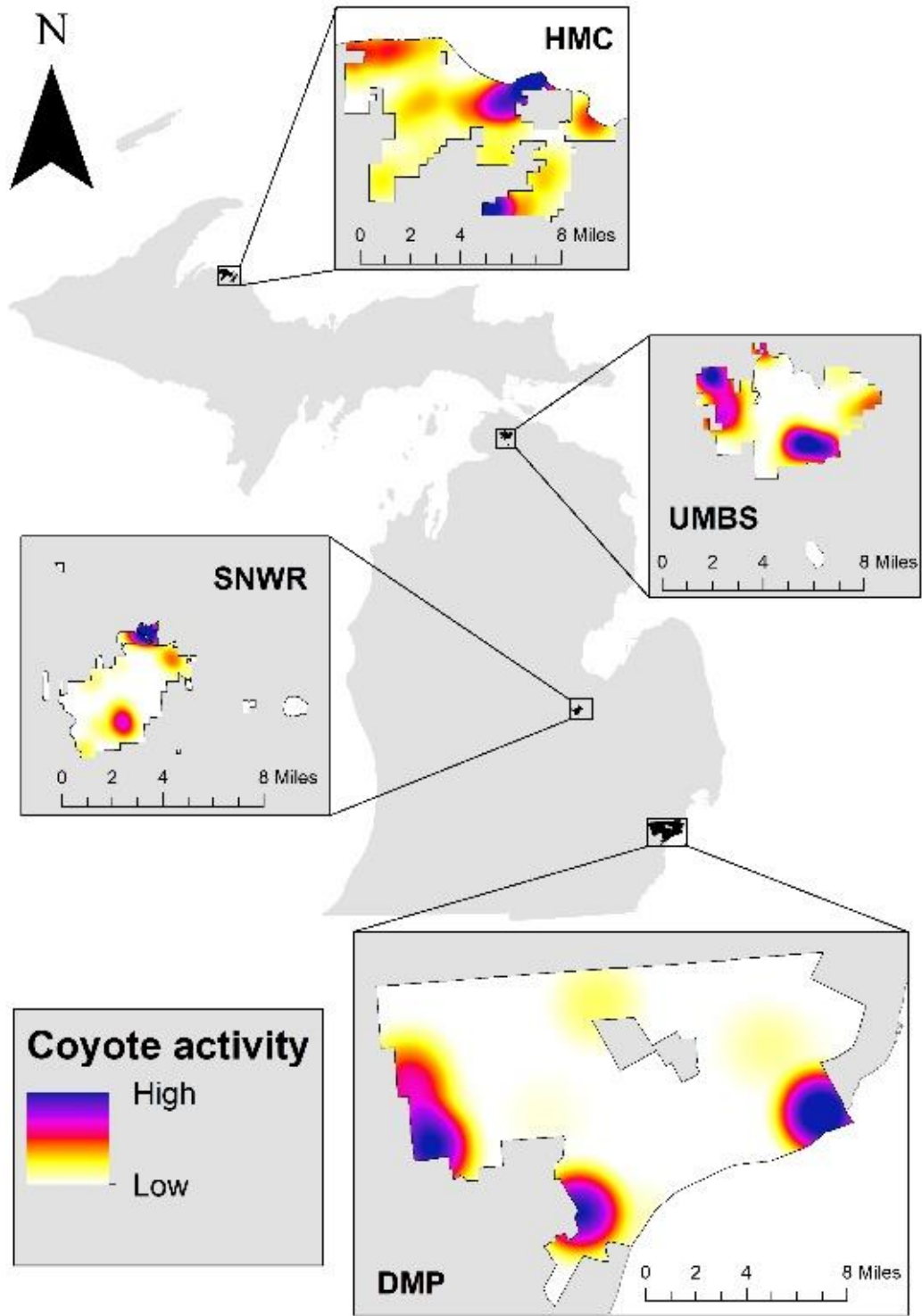
Fig. 1-2. Kernel density (KD) heatmaps of coyote spatial use at the four study sites based on the number of independent coyote detections at each camera. From north to south, the Huron Mountain Club (HMC), the University of Michigan Biological Station (UMBS), the Shiawassee National Wildlife Refuge (SNWR), and the Detroit Metroparks (DMP). These represent a single year at each of the sites; hotspots in coyote detections varied by year, and KD maps were generated for each survey.

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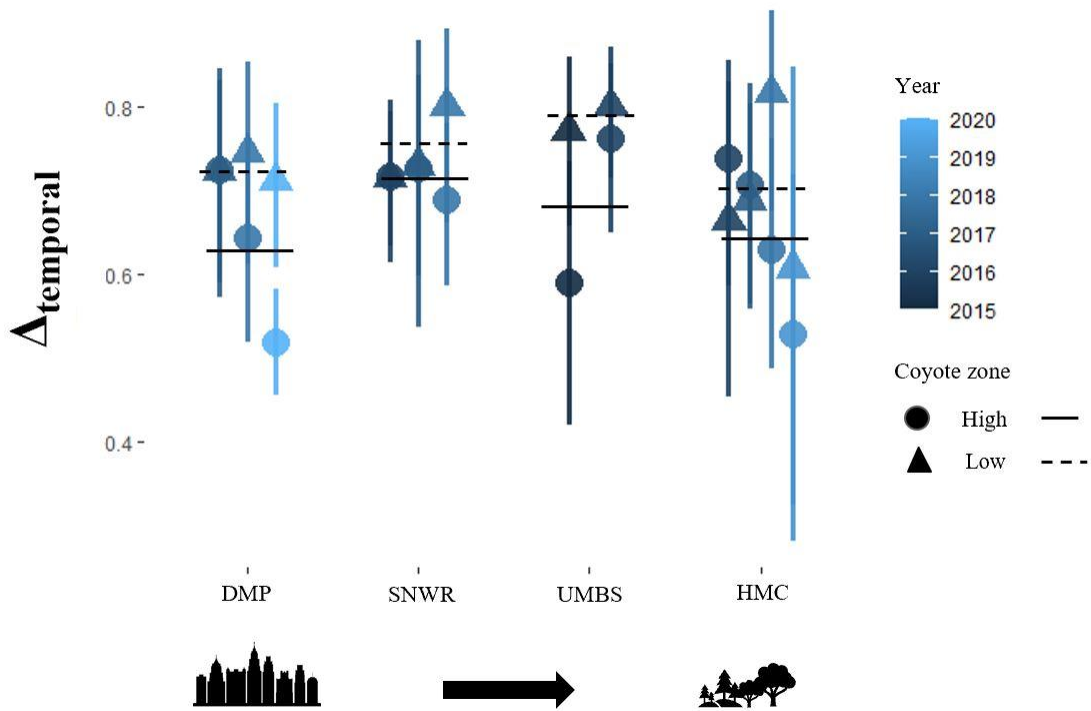
Fig. 1-3. Mean temporal overlap ($\Delta_{temporal}$) between raccoons and coyotes in high and low spatial zones of coyote activity with 95% confidence intervals.
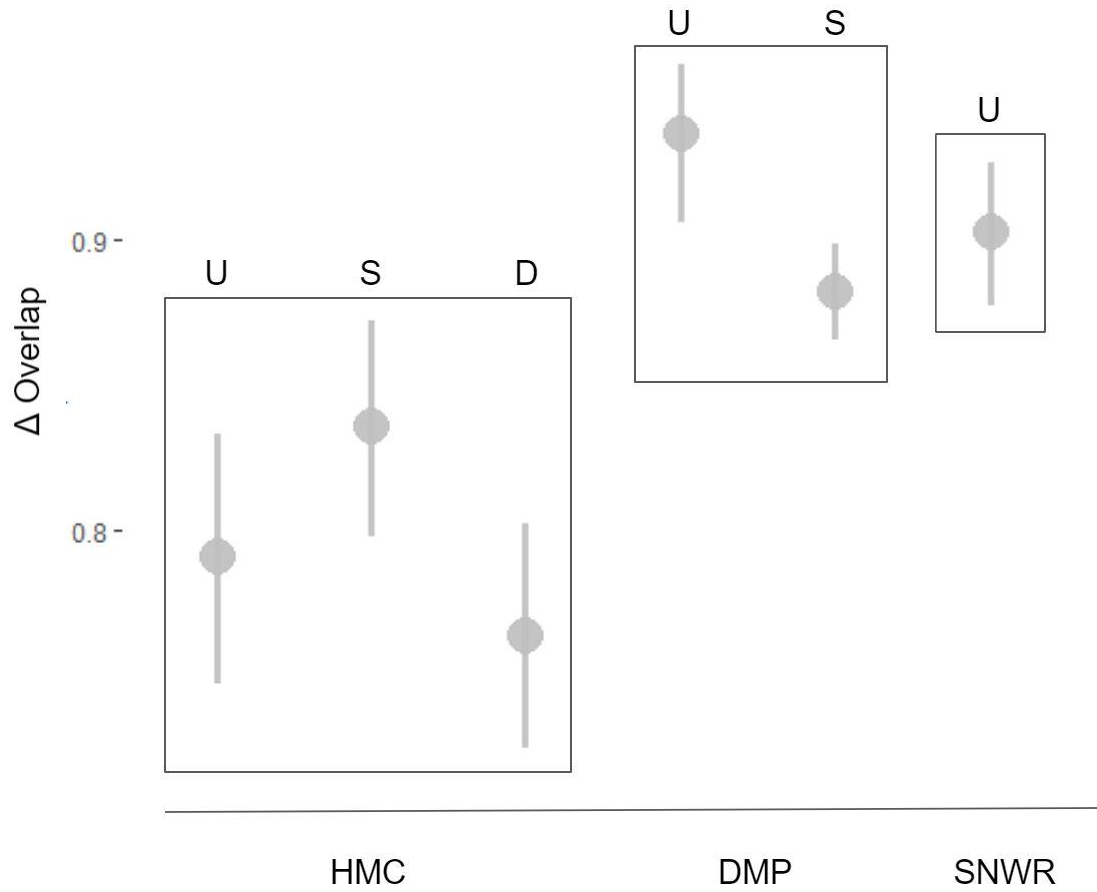
Fig. 1-4. Mean temporal overlap (Δ Overlap) in raccoon activity conducted pairwise between sites with 95% confidence intervals. The letters correspond with each site (H=HMC, U=UMBS, S=SNWR, D=DMP), with the site it was compared to on the axis below. The differences between sites in each pairwise comparison were significant (using the MWW test).
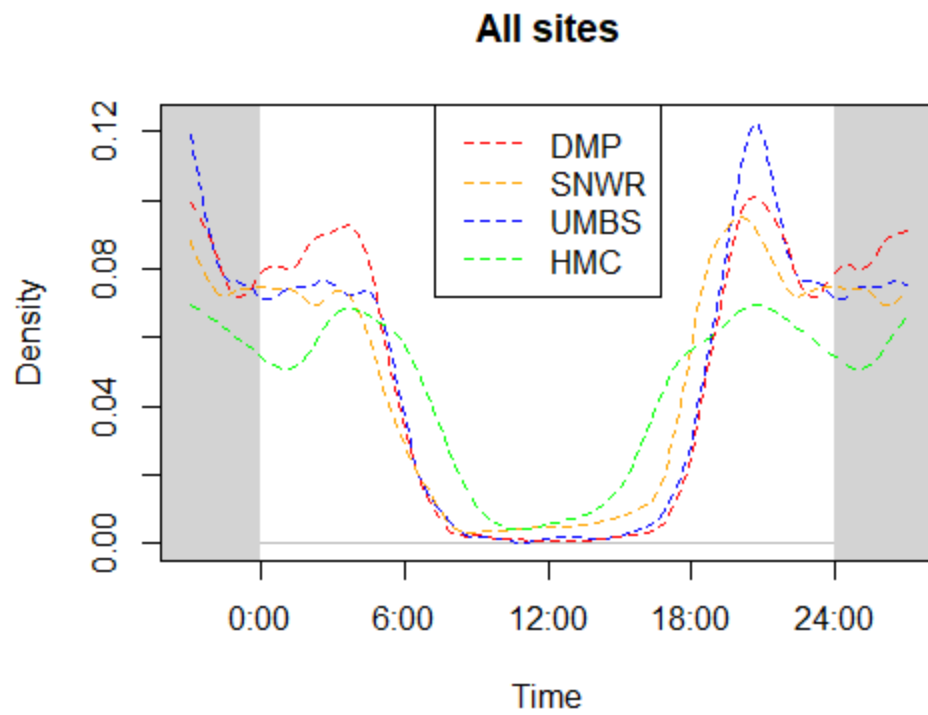
Fig. 1-5. Raccoon activity across all four sites. Time use of raccoons was summed for all surveys within a site.

Chapter III

Patch Characteristics and Domestic Dogs Differentially Affect Carnivore Space Use in Fragmented Landscapes in Southern Chile

Abstract

Aim

In an increasingly anthropogenic world, species face multiple interacting threats. Habitat fragmentation and domestic dogs are two perturbations threatening terrestrial mammals globally. Our aim was to determine if (1) the spatial use of domestic dogs increases with habitat destruction and (2) whether domestic dogs and habitat destruction drive the spatial use of native carnivores in a heavily degraded agricultural landscape.

Location

Central valley/Andean foothills transition of Los Lagos, Chile.

Methods

We implemented a camera trap survey in a fragmented landscape comprised of native forest patches amidst a matrix of pastureland. We used single-species occupancy models to assess the impact of domestic dogs and habitat destruction on three mesocarnivores – the foxes, culpeo (*Lycalopex culpaeus*) and chilla (*Lycalopex griseus*) and the wild cat güiña (*Leopardus guigna*). Additionally, we compared temporal overlap of all study species (including domestic dogs).

Results

Detection rates for both the foxes increased with domestic dog occupancy, while factors driving occupancy differed for each of the native species. We found that a 12% projected increase in domestic dog occupancy negatively impacted the spatial use of the culpeo. Habitat loss and fragmentation were positive drivers for chilla and domestic dog occupancy. The güiña did not respond to fragmentation and other habitat covariates or domestic dog occupancy. All native carnivore species were primarily nocturnal, while the domestic dog was almost entirely diurnal.

Main Conclusions

We highlight that domestic dog occupancy was positively correlated with habitat loss. Native species showed varied tolerance to domestic dog occupancy, and no negative response to habitat destruction. Future conditions of increased fragmentation and habitat loss will likely increase the potential contact between domestic dogs and native carnivores.

Introduction

Fragmentation and habitat loss remain a global threat to biodiversity, increasing isolation between habitat patches, with emergent consequences from edge effects (Haddad et al. 2015; Pfeifer et al. 2017). Globally, 70% of forests are within 1 kilometer of an edge and are becoming increasingly fragmented, which has resulted in abundances for over 85% of vertebrates being impacted by edge effects (Haddad et al. 2015; Pfeifer et al. 2017; Montibeller et al. 2020). The negative effects of fragmentation remain highly debated given inconsistent impacts across species and ecological interactions (Fahrig 2013; Rielly-Carroll and Freestone 2017; Fletcher et al. 2018; Fahrig et al. 2019; Harrison and Banks-Leite 2020). While species may be able to inhabit edge habitats, they may be excluded via biotic factors such as competition or predation (Michel et al. 2016). Additionally, fragmentation may interact with other factors such as habitat loss, fire prevalence, and hunting, challenging ascertain of individual drivers that alter species or interactions (Cochrane 2001; Peres 2001; Bennett & Saunders 2010; Bartlett et al. 2016).

Domestic dogs (*Canis lupus familiaris*, hereafter referred to as 'dogs') represent another global threat to biodiversity as the most abundant carnivore worldwide with a global population estimated at 700 million (Gompper 2013; Hughes and Macdonald 2013). Therefore, dogs are a widespread invasive species that can commonly exploit fragmented landscapes as they more easily permeate from areas of human residence (Oehler and Litvaitis 1996; Broadbent et al. 2008; Paschoal et al. 2018). Dogs commonly harass and kill native carnivores, compete for prey species, and transmit pathogens to wild populations (Laurenson et al. 1998; Vanak and Gompper 2009; Doherty et al. 2017). These disturbances can alter activity patterns and reduce relative abundance of native carnivores. For example, carnivores in Madagascar exhibited spatial avoidance when dogs were present, and were more likely to be replaced by dogs in degraded

forests near human settlement (Farris et al. 2016, 2017). Similarly, chilla fox (*Lycalopex griseus*) visits to scent stations in Southern Chile were negatively correlated with dog presence, and telemetry data showed that foxes rested in a habitat type that was not preferred by dogs (Silva-Rodríguez et al. 2010b). In general, how dog-wildlife interactions are facilitated by habitat fragmentation and concurrent loss (hereafter referred to as habitat 'destruction') is largely unstudied. Furthermore it is also unknown whether habitat destruction and dogs have similar, opposing, or synergistic impacts on carnivores. Given the pervasiveness of both dogs and habitat destruction as major disturbances, it is surprising that few studies have measured and compared their simultaneous effects on native species.

Predicting the effects of habitat destruction on native carnivores, especially in conjunction with dogs, is difficult because our expectations for mesocarnivore response to these two threats (destruction and dogs) may not align. Based on intraguild predation theory, we would expect smaller carnivores such as mesocarnivores to be particularly susceptible to harassment by dogs modulated by body size (Donadio and Buskirk 2006). In contrast, for fragmentation and edge effects, a component of habitat destruction, large-bodied mammalian carnivores are particularly susceptible due to their relatively small population sizes, slow growth rates and extended habitat requirements and corresponding home ranges (Schipper et al. 2008). In general, the impacts of habitat destruction on carnivores are harder to predict because many aspects of their ecology such as prey availability and habitat quality are also impacted. Mammals vary in their sensitivity to fragmentation and in their adaptive responses to fragmentation (Crooks 2002; Janecka et al. 2016; Smith et al. 2019; Palmeirim et al. 2020). For example, a disturbance from fragmentation may shuffle species distributions and facilitate the invasion of nonnative competitors or other species (Crooks 2002; Echeverría et al. 2007; Jessen et al. 2018). Overall,

the impacts of fragmentation are even less clear for mesocarnivores, many of which are generalists and have smaller home ranges than their larger counterparts, and thus, may be more resistant to or even benefit from fragmentation (but see Crooks et al. 2017; Rocha et al. 2020). Similar to fragmentation, our expectations for the effect of habitat loss on carnivores are not straightforward, and the importance of habitat type may be superseded by intraguild dynamics (Randa and Yunger 2006). For example, Massara et al. (2016) found that the occupancy of generalist mesocarnivores was negatively correlated to reserve size throughout the remnant patches of the Atlantic Forest in Brazil, while in an urban-rural gradient in the US, Randa & Yunger (2006) found that raccoon occupancy increased with residential/urban habitat rather than forest.

In the Valdivian temperate forests biodiversity hotspot of Chile, both habitat destruction and the presence of dogs are widespread and potentially devastating endemic species (Myers et al. 2000). These forests are being rapidly lost and converted to exotic plantations and pasturelands (Echeverría et al. 2008; 2012). Protected areas are insufficient for meeting goals to maintain the biodiversity value of these forests because protected areas are restricted to the inland Andes rather than to the endemic-rich coastal areas (Smith-Ramírez 2004). The central valley, which formerly connected the coastal and montane sections as contiguous forest, has been heavily deforested and is now dominated by cow pastures and exotic plantations (Smith-Ramirez et al. 2010). Today, only small patches of native forests remain as available wildlife habitat that are interspersed throughout this landscape that are privately-owned and managed (Fig. 2-1). Free-ranging dogs pose a major threat to the persistence of at least two mammal species of conservation concern, pudu (*Pudu puda*, IUCN status of Vulnerable) and Darwin's fox (*Lycalopex fulvipes*, IUCN status of Endangered) (Silva-Rodríguez et al. 2010a, 2016).

Here, we model the effects of habitat destruction, the presence of dogs, and their interactions on the spatial use of carnivores. Specifically, we surveyed privately-owned forest patches that were outside of protected areas or forestry company ownership using remotely-triggered cameras. We expected habitat destruction metrics to be more important than dog space use in explaining the occupancy of forest specialists (e.g., güiña, *Leopardus guigna*). In contrast, we also expected that in these largely altered landscapes dog occupancy would be the major driver of native canid spatial use, due to the immediate threat they present, and induced fear effects (Palomares and Caro 1999; Vanak et al. 2009; Vanak and Gompper 2010). We hypothesized that increasing patch isolation and reducing the proportion of forest would be important drivers of dog occupancy, providing evidence that their presence is facilitated by fragmentation (Fig. 2-2). Our work will enhance our understanding of native carnivore occurrence in the later stages of human-altered landscapes and reconcile the relative contributions of interacting threats from fragmentation and dog presence.

Methods

2.1 Study area

From mid-May 2019 through the end of August 2019, we surveyed the carnivore community in the Los Lagos region of Chile, near the city of Osorno, between Lago Rupanco and Lago Llanquihue (40° 76′ to 41° 21′ S, 72° 54′ to 72° 97′ W, Fig. 2-1). This area is characterized by Valdivian temperate rain forest (mean daily temperature ranging from 3-23°C for the year) with a cold, rainy winter season between May and September (1346 mm annual rainfall) and warm temperate summers (en.climate-data.org). The landscape, formerly dominated by native forest, was at the time of the study dominated by pastures that were used primarily for cattle as well as plantations of pine (*Pinus radiata*) and eucalyptus (*Eucalyptus* sp.) with small remnant stands of

native forest. The study area was relatively flat and sandwiched between a large protected area (Parque Nacional Vicente Rosales) on the eastern edge and the Osorno metropolitan area on the western edge. Native forest patches were mostly made up of degraded strips along the edges of pastures comprised of a mix of *Lophozonia obliqua*, *Nothofagus dombeyi*, *Persea lingue*, and *Laurelia sempervirens* with a bamboo understory (*Chusquea quila*).

2.2 Camera trap survey

We deployed 50 remotely-triggered cameras (Reconyx© PC 850, 850C, 900, 900C) in forest patches throughout the study area from June to August 2019 (the austral winter), aiming for maximum coverage of areas where we obtained permission. We affixed cameras to trees (minimum diameter 0.25 m) with cable locks and placed 0.5 m off the ground. We used signs of animal activity such as game trails and scat to determine the specific micro-site location of camera placement, to maximize detections. Cameras were placed at least 0.5 km apart from each other, and efforts were made to place within the core of each patch if minimum spacing allowed. Each camera was baited with canned mackerel placed inside a bottle with a perforated cap, wired down to keep animals from accessing or removing the bait. Camera settings included: high sensitivity, one-second lapse between three pictures in a trigger, rapidfire (no quiet period between triggers).

At the end of the survey period, we retrieved images from the cameras and identified them by a single observer to the species level. After image identification, we applied a 30-minute quiet period to ensure independence of species detections (Wang et al. 2015; Suraci et al. 2016). These images and the associated site-level environmental variables (explained below) were used to estimate individual species occupancy. We used Moran's I in ArcPro (vers. 2.3.1) and did not

find evidence of spatial autocorrelation. The 'camtrapR' package was used to organize camera trap images and extract data for modeling (Niedballa et al. 2016), implemented in Program R vers. 3.6.2 (R Core Team 2019).

2.3 Occupancy modeling

Using single-species single-season occupancy models (MacKenzie et al. 2003), we evaluated the impacts of habitat degradation on the occupancy (Ψ) and detectability (*p*) of dogs, and evaluated the impacts of habitat degradation and dog occupancy (*dogo*) on the occupancy and detectability of three focal native species: the chilla (*Lycalopex griseus),* culpeo (*Lycalopex fulvipes*), and güiña (Fig. 2-3). Covariates for habitat degradation included proportion of native forest (*forest*) and patch isolation (*iso*), as well as a measure of understory (*10uds*). We also included small mammal trap success (*sm*) as a coarse measure of prey availability. We first separated species detections into 7-day observation periods (Wang et al. 2015). We then modeled detection probabilities for each species holding occupancy constant, to account for non-detection. Finally, we used the best detection models to model the occupancy for each species.

2.3.1 Detection covariates

We modeled detection probabilities with covariates that could increase or decrease the likelihood of an animal being captured on camera if it occupied the vicinity. We measured understory cover using a point-intercept method, with the understory height measured every meter for 10m in the four cardinal directions surrounding each camera (Karl et al. 2017). We then aggregated values for the understory cover into three categories: 0m (no understory), 0.25m, and 0.5m. Understory at 10m (*10uds*) is an average of all understory measurements taken every meter within a 10-meter radius of the camera tree (40 measurements per camera site). Understory was not included in the detection model for the culpeo, as inclusion prevented convergence of the global model.

We first modeled occupancy of dogs using habitat covariates (*10uds*, *forest*, *iso*, *sm*), and then included the resulting site level estimates as the *dogo* covariate for native species models (Fig. 2-3). Patches were digitized in ArcPro (vers. 2.3.1) using high resolution satellite imagery from 2018 (Maxar Vivid, 0.5m resolution, 5m accuracy) to obtain *forest*, *iso*, and *edge* estimates. The *iso* covariate was measured as the mean border-to-border distance to the nearest patch within a 1-km radius of each camera. The *edge* covariate was measured as the mean ratio of patch perimeter size to patch area for all patches within a 1-km radius of each camera. However, *edge* was excluded from the final global model, as it was highly correlated with both *forest* and *iso* covariates ($p < 0.01$). We estimated *sm* as a metric of prey availability, using the total number of all independent lagomorph, rodent, and shrew opossum triggers per camera standardized by the number of trap nights. Camera type (*cam*) was included to distinguish between white-flash cameras and infrared cameras. Lastly, trap nights (*trap*), the number of nights an individual camera was operational to collect species detections, were included to determine if sampling effort affected detection rates. Covariates were compared using Pearson's R, with a cutoff threshold of R > 0.5 or $p < 0.05$.

2.3.2 Occupancy covariates

Occupancy for each species was modeled with *dogo* and habitat covariates (*10uds*, *forest*, *iso, sm); edge* was highly correlated with *forest* and omitted from the model. To test whether the impact of dogs on carnivores was facilitated by lack of understory, we included an interaction term between *dogo* and *10uds*.

2.3.3 Model evaluation

The dog global model included mean understory height within 10m (*10uds*), camera type, and trap night (*cam*, *trap*) covariates for detection, while occupancy covariates included understory (*10uds*), prey (*sm*), proportion forest (*forest*) and patch isolation (*iso*). Native species global models used the same covariates as the dog model, with the addition of dog occupancy (*dogo*) for detection, and an interaction term for dog occupancy and understory (*dogo*10uds*) for occupancy. All detection and occupancy covariates were tested for correlation by site using Pearson's R. Model ranking was carried out using Akaike Information Criterion, corrected for small sample sizes (AICc), or quasi-AICc (QAICc) if the global model was overdispersed (c-hat > 1.2), with the top model being defined as the one with the lowest AICc or QAICc score. Goodness of fit was tested for all top models (<2 ΔAICc units or ΔQAICc units of the highest rank model) using a Chi-square statistic. All occupancy modeling was completed in the 'unmarked' package (Fiske and Chandler 2011) in Program R vers. 3.6.2 (R Core Team 2019).

2.3.4. Threshold response to dogs

We interpreted the β coefficient of *dogo* and confidence intervals not overlapping zero when occurring in top models to conclude significant effects of dogs on carnivore occupancy. When the top models included *dogo* as a covariate with a non-significant negative coefficient, we determined the threshold level of dog occupancy required for *dogo* to become a significant negative driver on carnivore occupancy. We incrementally increased the value of the *dogo* to the maximum occupancy value (1), a single camera at a time. The order was determined by ranking cameras from highest to lowest *dogo* value.

2.4 Temporal use

As sympatric carnivores may be more likely exhibit temporal instead of spatial partitioning to promote coexistence (Santos et al. 2019), we estimated pairwise temporal overlaps for all species, and compared the overlap of native carnivore pairs with the overlap of native carnivores-dog pairs. We plotted the temporal activity distributions of each species and determined the degree of overlap between pairs (Δ) with 95% confidence intervals generated by 10,000 parametric bootstrap iterations. Δ values range from 0 indicating completely distinct and non-overlapping temporal activity to 1 indicating complete overlap between the comparison groups. Δ_1 was used for comparisons when one of the sample groups had less than 50 triggers; otherwise Δ_4 was used to estimate temporal overlap between species pairs (Ridout & Linkie 2009). We then used the Mardia-Watson-Wheeler test to determine if the temporal patterns varied significantly between individual species, which compares two sets of circular data and determines if there is homogeneity in the means or variances. We implemented the temporal analyses using the 'overlap' and 'circular' packages in Program R (Ridout & Linkie 2009, Agostinelli & Lund 2017).

Results

We detected all three carnivore species over a total effort of 3500 trap-nights. Naïve occupancy estimates for the güiña (n=56 independent triggers), chilla (n = 225), and culpeo (n=39) were 0.51, 0.59, and 0.16 respectively. Dogs were fairly common (n=64) found at 20/49 camera sites (naïve $\psi = 0.41$). Additional native carnivores that were detected, although rare, included the chingue (*Conepatus chinga*, n=13) and the puma (*Puma concolor*, n=4). We also detected two additional introduced species: the mink (*Neovison vison*, n=20) and domestic cat (*Felis catus*, n=21). Darwin's fox (*Lycalopex fulvipes*) was not detected during our camera survey in the area,

though it has been found in the area previously (personal communication J. E. Jiménez).

3.1 Detection of carnivores

Our study area was comprised of an understory that ranged from completely open to thickets of dense vegetation with specific camera sites comprising no understory to over two meters in height. As such, we expected detection to vary by understory, depending on species preference on microsite selection for dense vegetation, and the ability of the understory to reduce the visibility range for a camera trap. For the chilla (β = -6.16, SE = 1.38) and dog (β = -7.44, SE = 1.84), understory was a strong driver of detection probability, decreasing the detectability for both species (Table S2.1, see Appendix B). For both chilla (β = 1.77, SE = 0.37) and culpeo (β = 3.23, SE = 0.834), dog occupancy increased detectability. The null model best described güiña detection; that is, no effect of covariates improved model fit.

3.2 Occupancy of carnivores

Overall, modeling occupancy with covariates and accounting for imperfect detection improved our understanding of carnivore space use. Chillas had the highest overall occupancy (ψ = 0.67), while culpeos had the overall lowest occupancy, but nearly doubled from the naïve estimate (ψ = 0.36). Güiña was the only species for which the null model was the best model, and the occupancy estimate was thus the same as the naïve estimate (ψ = 0.51). In comparison to the native carnivores, dog occupancy was higher than the culpeo and güiña, but lower than that of the chilla (ψ = 0.58).

Factors driving occupancy of carnivores varied by species (Fig. 2-4, Table 1). Despite the importance of understory for species detection, it did not appear in the best model for any species. It was however a negative driver of chilla occupancy in 4/10 top models which had

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comparable weight to the best model (Table 1). Given the reliance of mammalian carnivores on prey, unexpectedly, small mammal trap success was important only for the occupancy of the culpeo ($\beta = 1.05$, SE = 0.53).

Our work contrasted the ecological consequences of habitat destruction (loss and fragmentation), and dog occurrence on the space use of carnivores (Table 1, 2). Habitat metrics were important drivers of chilla and dog occupancy but did not appear in the model sets for culpeo or güiña. For example, patch isolation was in the top two models for the chilla ($\beta = 0.09$, SE = 0.04), and was positively correlated with occupancy. Proportion of forest did not appear to be important for occupancy of any native species. It was however important for dogs ($\beta = -26.06$, SE = 12.1), with increasing proportion of forest decreasing dog occupancy. Dog occupancy appeared in 4/5 top models for culpeo (including the best model) and was important for model fit for the culpeo but was not a significant driver of culpeo occupancy ($\beta = -4.19$, SE = 2.74).

Similarly, results varied in quantifying responses of native carnivore occupancy to dog presence. For chilla, dog occupancy was not in the best chilla model but appeared as a positive driver in 6/10 top models, which had comparable weight to the best model (Table 1, see Appendix B). The dog occupancy covariate was not influential, positive or negative, on occupancy for güiña. Culpeo was the only species with dog occupancy in the top model with a negative (non-significant) β coefficient. The dog landscape level occupancy from the top model was 0.58. Increasing dog occupancy to 0.65 (an increase of 12.1%) resulted in dog occupancy becoming a significant negative driver of culpeo occupancy (Fig. S2.1, see Appendix B).

We found no evidence for the interaction of dog occupancy and understory affecting occupancy for native mesocarnivore species occupancy. Overall, we conclude that landscape

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characteristics via metrics of increasing fragmentation have similar positive effects for both generalist native carnivores and for dogs (Fig. 2-4).

3.4 Temporal activity

We evaluated temporal activity patterns of all of our study species to determine if there was evidence for temporal avoidance with dogs (Fig. S2.2, see Appendix B). Activity patterns for the three native carnivores was largely restricted to the nocturnal and crepuscular hours. Overlap among the native carnivores was high (Δ ranging $0.78 - 0.89$) and did not vary significantly among pairs (Table 3: *p values*: 0.08-0.79). In contrast, dog activity was almost entirely diurnal, resulting in significantly different activity patterns from native species (Δ ranging 0.35-0.43; $p <$ 0.001). Furthermore, 95% confidence intervals for Δ dog-native species pairs and for Δ native-native species pairs did not overlap in a single case, indicating that native species overlapped significantly more with other native species than they did with dogs.

Discussion

The threats that mammals face from habitat loss and fragmentation are especially relevant in the context of the temperate rainforests of central Chile, which have included rapid deforestation and fragmentation in the past 50 years (Echeverría et al. 2006; Nahuelhual et al. 2012; Uribe et al. 2020). An additional human-related threat is the presence of dogs, which antagonize native species and preferentially use the matrix that separates the remaining patches (Silva-Rodríguez et al. 2010b). Using single species models, we investigated the impacts of these two phenomena (habitat destruction and dogs) on the occupancy of three native carnivores (foxes – chilla and culpeo; cat – güiña), in remnant forest patches within an agricultural matrix. Our results varied by species, indicating that components of habitat destruction have opposing effects for the two

foxes, as do dogs. For dogs, we found evidence that occupancy increases with habitat loss. Time use of all native species was concentrated during the nocturnal period, in stark contrast to the diurnal time use of the dog. Our results provide the necessary baseline to understand dogs and habitat destruction metrics as drivers of native species occupancy and could be further expanded to multispecies models to examine species interactions.

For the species included in this study, at first glance our results suggest that landscape degradation does not pose an immediate concern. For the chilla, the positive correlation between patch isolation and occupancy is likely a reflection of the ecology of the fox, which primarily forages in the open fields that comprise the matrix between patches (Silva-Rodríguez et al. 2010b). However, this species also utilizes interior habitat of these patches as a refuge and thus, would likely have negative consequences if patches fell below a threshold size(Silva-Rodríguez et al. 2010b). Our results for culpeos and güiñas, which did not show any response to either habitat loss or patch isolation could indicate that: a) these species are plastic in their habitat requirements; b) fragmentation and habitat loss have not reached a sufficient threshold to elicit a response; c) there is a time lagged 'extinction debt', or d) these species are tracking spatial patterns of prey, predator, or competitor species instead (Hanski and Ovaskainen 2002; Ryall and Fahrig 2006; Swift and Hannon 2010; Halley et al. 2016). The model results for the culpeo suggested this latter mechanism, as they were positively driven by prey availability and dog occupancy was consistent in the top models having a negative coefficient (though note that neither covariate was significant using a significance level of $\alpha=0.05$) While landscape characteristics did not appear as a negative driver in any native species models, the inverse relationship between dog occupancy and proportion of forest indicates as habitat loss increases in

this region native species will have less refuge habitat to avoid exposure to domestic dogs (Torres and Prado 2010; Paschoal et al. 2018).

We expected dogs to influence native carnivore occupancy because of their documented impact on small carnivores through interference and exploitation competition, and the increased mortality risk they pose as disease reservoirs (Laurenson et al. 1998; Rhodes et al. 1998; Sillero-Zubiri et al. 2004; Vanak and Gompper 2009, 2010). Dogs have been linked to the decline of the pudu, a potential prey item for the two fox species in this study (Silva-Rodríguez and Sieving 2012). Despite the threat that a dog encounter presents, dog occupancy did not clearly present a negative driver of native species occupancy, and only featured as a non-significant negative covariate for culpeo top models. While this partially fit our expectation that native canids would more likely have antagonistic interactions with dogs and exhibit avoidance, we expected the smaller chilla fox to have greater sensitivity to dog presence (Donadio and Buskirk 2006; Vanak and Gompper 2009). Previous studies corroborate this expectation as dogs enforce interference competition to alter space use and have been observed harassing and killing chilla (Silva-Rodríguez et al. 2010b). A lack of a negative response from chillas to dogs using our occupancy framework could indicate that foxes were avoiding dogs at finer spatial or temporal scales, or that dog density was not sufficiently high to elicit a spatial avoidance (Zapata-Ríos and Branch 2018; Qi et al. 2020). Indeed, our analysis of activity patterns suggests temporal partitioning as a mechanism for avoidance of dogs (Kronfeld-Schor and Dayan 2003; Schuette et al. 2013). In contrast to chillas, culpeos did indicate a potential response to dogs at a landscape level, and showed no response to habitat loss and fragmentation. Our result for culpeo occupancy was consistent with that of Zapata-Ríos & Branch (2018), despite differences in the landscape histories between our formerly contiguously forested site, and their historically patchy Andes

site. Congruent with the dog occupancy estimates ($\overline{\Psi}$ =0.66, range: 0.53 - 0.73) from Zapata-Ríos & Branch (2018), it took a projected 12% increase in dog occupancy in our study site for it to have a significant negative effect on culpeo occupancy.

While dogs had opposite effects on the occupancies of the fox species, they increased detection for both the culpeo and the chilla. Movement data for canids highlight quicker speeds through riskier areas, which would likely impact detection rates (Péron et al. 2017; Broadley et al. 2019). Thus, increased detection for the fox species may reflect a finer scale response to the risk posed by dogs, rather than a broader change in spatial use (Broekhuis et al. 2013). This interpretation, along with mismatched time use, would reconcile the open habitat preferences of the chilla fox with its increased susceptibility to dog antagonism based on size (Donadio and Buskirk 2006).

Fragmentation can facilitate the spread of invasive species through numerous pathways, such as roads increasing the occurrence of dogs (Loss et al. 2013; Moreira-Arce et al. 2015). Yet, few occupancy studies have looked at the impacts of both dogs and habitat loss and fragmentation on native carnivores. Dogs are typically considered human associated, though they may travel considerable distances and thus, can impact the larger landscape (Young et al. 2011, Gompper 2014). Furthermore, their space use, while tied to human impacts on the landscape, are more nuanced than simply being a result of nearby human habitation. In a North American system for example, dog occupancy has been found to increase with proportion forest (Morin et al. 2018), in contrast with our results that dog occupancy decreased marginally with proportion of forest. However, Morin et al. (2018) also found that pastures and grasslands were an even stronger positive predictor of dog occupancy; the land type that was the inverse of our measured metric for proportion forest. Whether the interaction between dogs and proportion forest impacts

native carnivores can be intuitively answered when we see that dog occupancy can be a negative driver of culpeo occupancy if it surpasses a threshold. In 'working' landscapes this is particularly relevant as habitat loss and dog occupancy will likely continue to increase over time. Our occupancy results suggest that the spatial use of both fox species (indirectly in the case of the culpeo, through dog occupancy) is tied to fragmentation and habitat loss. Furthermore, habitat destruction in the landscape increases the exposure of both foxes to the threat of a dog encounter (Farris et al. 2017, 2020). In the currently remaining forest stands that we surveyed, the largely nocturnal temporal use of native species provides a likely avoidance mechanism (Gerber et al. 2012; Shores et al. 2019).

Our study gives us insight into the drivers of native carnivore space use in 'working' landscapes rather than the protected areas that represent ideal and untouched habitats. By situating our study on privately-owned smallholder lands, we also have the unique opportunity to inform the conservation of species in these increasingly anthropogenic landscapes through local education efforts (Gramza et al. 2016). The remnant patches in these private lands may be particularly important for the persistence of native carnivores in the landscape, and in general agricultural landscapes may hold considerable biodiversity and conservation value (Kremen and Merenlender 2018; Lindenmayer 2019; Wintle et al. 2019). Many landowners do not have access to camera traps, and thus are unlikely to encounter elusive carnivores that are present even in small patches of forest along the edges of their pasturelands. While voluntary strategies for conservation have greater social acceptance than prescribed management action, they are not possible without landowners first having the knowledge of what species are on their land (Kamal et al. 2015). By partnering with landowners, scientists and managers can facilitate species conservation in these important landscapes, which are not typically considered conservation

targets (Naugle et al. 2020). This partnership may yield dividends in collaboratively designing management solutions for dogs (Ford-Thompson et al. 2012). The management of domestic animals can be a source of intense debate, especially in regards to animals typically considered as pets (Wald et al. 2013). The impacts of dogs on wildlife is underestimated; conservation practitioners can learn from the intense controversy generated by the management of feral cats by involving local stakeholders, and by bringing a strong understanding of what factors drive the impacts of dogs (Loyd and Miller 2010; Doherty et al. 2017).

Table 2-1. Top occupancy (Ψ) and detection (p) models for native carnivore and dogs ranked by AICc, with model weights (**w**) provided. *QAICc was used instead of AICc in model ranking for güiña occupancy to account for overdispersion of the global model. *dogo*: dog occupancy; *cam*: camera type; *10uds*: average understory height within 10m; *iso*: average distance between patches; *forest*: proportion native forest; *sm*: small mammal trap success.

Species	Top models	AICc	ΔAICc*	w
Chilla	Ψ(iso) p(dogo, 10uds)	429.809	0	0.175
	Ψ(iso) p(dogo, 10uds, cam)	430.289	0.480	0.138
	Ψ(dogo) p(dogo, 10uds)	430.613	0.804	0.117
	Ψ(dogo, 10uds) p(dogo, 10uds)	430.782	0.974	0.108
	Ψ(dogo) p(dogo, 10uds, cam)	430.948	1.139	0.099
	Ψ(iso, dogo) p(dogo, 10uds)	431.139	1.331	0.090
	Ψ(dogo, 10uds) p(dogo, 10uds, cam)	431.511	1.702	0.075
	Ψ(iso, 10uds) p(dogo, 10uds)	431.736	1.927	0.067
	Ψ(~1) p(dogo, 10uds)	431.738	1.929	0.067
	Ψ(iso, dogo,10uds) p(dogo, 10uds)	431.792	1.982	0.065
Culpeo	Ψ(dogo, sm) p(dogo, cam, 10uds)	124.932	0	0.273
	Ψ(dogo, sm) p(dogo, 10uds)	126.238	1.306	0.142
	Ψ(sm) p(dogo, cam, 10uds)	126.280	1.348	0.139
	Ψ(dogo, sm) p(dogo, cam)	126.598	1.666	0.119
	Ψ(sm) p(dogo, trap, 10uds)	126.734	1.802	0.111
	Ψ(sm) p(dogo, 10uds)	126.753	1.821	0.110
	Ψ(dogo, sm) p(dogo, cam, trap)	126.802	1.870	0.107
Dog	Ψ(forest) p(10uds, trap)	272.000	0	0.370
	Ψ(forest) p(10uds, trap, cam)	272.306	0.306	0.318
	Ψ(forest, 10uds) p(10uds, trap)	273.704	1.704	0.158
	Ψ(forest, 10uds) p(10uds, trap, cam)	273.757	1.757	0.154
Güiña	Ψ(~1) p(~1)	6.830	0	0.101

Table 2-2. Untransformed β coefficients with 95% confidence intervals for the top model for each species.

Species	Ψ covariates					p covariates			
	Forest	Patch isolation	Understory	Small mammal	Dog occupancy	Trapnights	Camera type	Understory	Dog occupancy
Chilla	-	0.09 (0.00 – 0.17)	-	-	-	-	-	**-6.16 (-8.85 – -3.46)**	**1.77 (1.05 – 2.49)**
Culpeo	-	-	-	1.00 (-0.11 – 2.11)	-4.32 (-9.65 – 1.01)	-	**1.60 (.48 – 2.73)**	-	**3.18 (1.50 – 4.85)**
Dog	-23.06 (-46.83 – 0.71)	-	-	-	-	**-0.12 (-0.23 – -0.01)**	-	**-7.45 (-11.05 – -3.84)**	-
Güiña	-	-	-	-	-	-	-	-	-

Table 2-3. Overlap coefficients (Δ) and Mardia-Watson-Wheeler test for homogeneity of means for every pairwise combination of the study species. Δ_4 was used for every comparison except for those pairs containing the culpeo, where Δ_1 was used to account for lower number of triggers.

Comparison	Δ Overlap (95% CI)	W statistic	*p-value*
Chilla-Dog	0.40 (0.25-0.44)	83.62	<0.001
Culpeo-Dog	0.35 (0.22-0.48)	42.96	<0.001
Guigna-Dog	0.43 (0.30-0.56)	47.84	0.001
Chilla-Culpeo	0.78 (0.66-0.89)	5.02	0.08
Chilla-Guina	0.89 (0.80-0.97)	0.47	0.79
Guina-Culpeo	0.78 (0.75-1.03)	4.79	0.09

Fig. 2-1. (a) Study area located in the Los Lagos Region of south-eastern Chile. (b) Landscape level distribution of camera deployment throughout patches of native forest straddling the Osorno Volcano. The borders of the box for (b) roughly delineate a ~6km dairy farm, with the cameras placed within the patches of native forest that are interspersed throughout cow pastures.
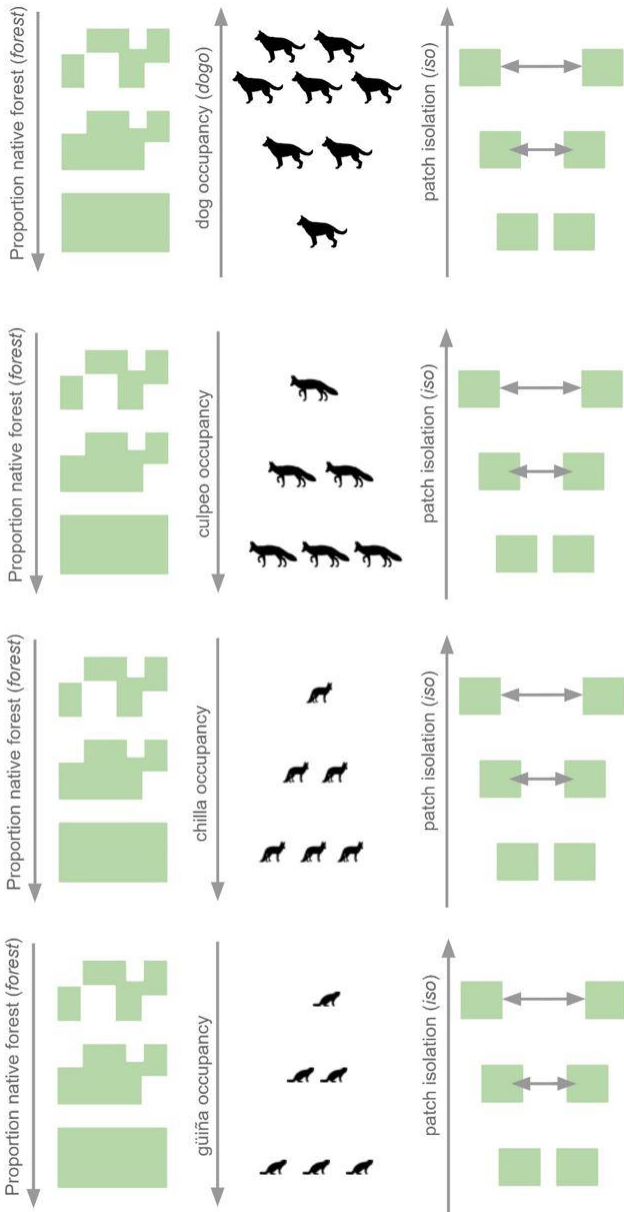
Fig. 2-2. Projected facilitation of dog occupancy by habitat loss and fragmentation with expectation that decreasing proportion of native forest and increasing patch isolation would promote higher dog occupancy. Expectations for native carnivore response to fragmentation were opposite those of dogs, with native carnivore occupancy expected to decrease with decreasing forest and increasing patch isolation.

Fig. 2-3. Focal carnivores in this study for size comparison of the three native species relative to and dogs: the güiña (1.5-3kg), chilla (2.5-5.5kg), dog (10-25kg), and culpeo (5-13.5kg) from top left clockwise. Note that the upper weight range of the culpeo likely represents more southern parts of the range than the study area; they are relatively bigger than chillas, and smaller than dogs. Photo credit: R. Malhotra and NC Harris, Applied Wildlife Ecology Lab.
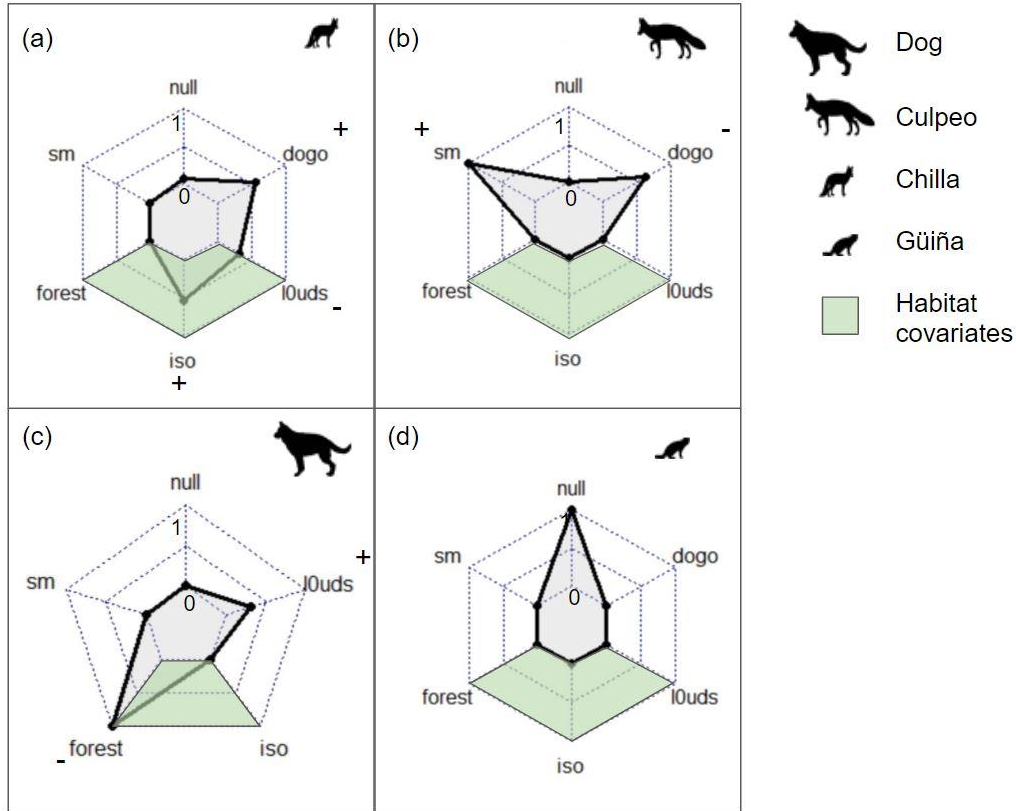
Fig. 2-4. Relative importance of each covariate on species occupancy based on summed model weights for top model sets (< 2 ΔAICc/QAICc). *dogo*: dog occupancy; *cam*: camera type; *10uds*: average understory height within 10m; *iso*: average distance between patches; *forest*: proportion native forest; *sm*: small mammal trap success. Beta coefficients for each covariate were averaged across the top model set. (a) dog occupancy and patch isolation were positively correlated with chilla occupancy, while understory was negatively correlated; (b) small mammal trap success was positively correlated with culpeo occupancy, while dog occupancy was negatively correlated; (c) proportion of native forest was negatively correlated with dog occupancy, while understory was positively correlated; (d) güiña occupancy was best described by the null model.

Chapter IV

Past Landscapes Best Predict Current Distribution of South American Foxes

Preamble: This chapter has been submitted to the journal *Landscape Ecology*. The citation for this chapter is: Malhotra, R., Jiménez, J. E., Harris, N. C. (2022) Temporal refuges differ between human and natural top-down pressures in a subordinate carnivore

Abstract

Aim

Species distributions are expectedly sensitive to landscape changes at different spatial and temporal scales. While time-lagged responses have been found across multiple taxa, these studies examine mostly species richness and are geographically restricted. Biodiversity aggregates such as species richness are useful for assessing and mitigating future losses, but ignore the variation in species-specific responses. Instead, we test for time-lagged responses in occupancy of two mammal species that are ecologically similar but differ in geographic range and body size.

Location

Agriculture dominated landscape, Central valley/Andean foothills transition of Los Lagos, southern Chile.

Methods

We built single-species occupancy models from detections obtained through a systematic camera trap survey in 2019 to determine if present-day landscapes or past landscapes better explained

current occupancy of two generalist mesocarnivores, the chilla (*Lycalopex griseus*) and the culpeo fox (*L. culpaeus*). Specifically, we extracted habitat amount and configuration metrics at three scales (250m, 500m, 1000m) from satellite imagery spanning a 33-year time-series to incorporate into models.

Results

Across 3500 trap nights, we obtained 39 culpeo and 225 chilla detections. Culpeo and chilla occupancy both exhibited a time-lagged response to habitat configuration, with models with covariates from past years outperforming models with covariates from the same year the presence-absence data was collected. The scale and magnitude of the time lag varied by species; patch isolation (+) and edge/area (-) from 2015 at the 500m scale best described culpeo occupancy, while patch isolation (+) from 2011 best described chilla occupancy.

Main Conclusions

We demonstrated that past landscapes better explained the present-day occupancy of two generalist carnivores, and that the scale at which past habitat metrics were measured resulted in opposite effects expected from range size. Past landscape configuration may be an important hidden driver of occupancy even for generalist species residing in regions with extensive forest loss and fragmentation. Therefore, given the wide use of occupancy modeling in conservation efforts, we encourage incorporating metrics to test for time lags in single-species models.

Introduction

Landscapes change rapidly under the influence of humans, degrading rapidly under agricultural intensification, the spread of urban systems, and the production of livestock (Carr 2004;

Laurance et al. 2014; Armenteras et al. 2017). The resultant loss and fragmentation of native habitats is considered one of the major threats to biodiversity globally (Foley 2005; Haddad et al. 2015; Pfeifer et al. 2017). There is considerable variation in how alterations to the landscape affect species based on species life history traits as well as the magnitude and type of disturbance to the landscape (Ovaskainen and Hanski 2002; Cousins and Vanhoenacker 2011). Part of this variation lies in the amount of time required for species or communities to respond: the time-lag between the disturbance and the response (Kuussaari et al. 2009; Figueiredo et al. 2019)

The presence of time lagged responses to changes in physical factors is well documented in ecological literature. For example, there is considerable evidence that past climates in deeper time (paleoclimates) may better explain patterns of biodiversity in some regions than the present day climate (Rowan et al. 2020). In the context of changes to the physical landscape, the time lag literature is centered around 'extinction debt', and more recently 'extinction credit'. These ideas posit that a loss or change of habitat amount or configuration may result in a decline in species richness or the extirpation of populations ('debt') or increase in species richness ('credit') that are not immediately realized, but instead take some amount of relaxation time that varies based on life history traits and the magnitude of the habitat change (Diamond 1972; Tilman et al. 1994; Watts et al. 2020). Typical response variables are broad metrics such as species richness (Metzger et al. 2009; Wearn et al. 2012; Chen and Peng 2017), measured in unpaid debt (e.g. Montgomery et al. 2020) or extinction half-life of communities (time until half the resident species are lost) (Gibson et al. 2013; Halley et al. 2016). These metrics predict the biodiversity trajectory following loss and determine a time frame for future losses or gains but ignore the varying levels of sensitivity to landscape change that individual species may exhibit (Hylander and Ehrlén 2013). These broader metrics are essentially the sum of time-lagged population

dynamics of each species, which can be decomposed further at a finer scale to the time-lagged effects of landscape change on the space-use of each species. This is similar to the two approaches that Fischer and Lindenmayer (2007) identify in broader body of research on the impacts of fragmentation: pattern-oriented and species-oriented. In the case of the time-lagged effects of habitat destruction, the literature largely skews towards pattern-oriented research. Few studies examine time lags in individual species responses, though doing so can yield important conservation insights for the target species. For example, Jiménez-Franco and colleagues (2022) demonstrated that land-use change in Spain had a negative 20 year time-lagged effect on the reproductive rates of the endangered spur-thighed tortoise (*Testudo graeca*), and simulated the size of the extinction debt for different future landscape trajectories.

Whether measured in terms of broad biodiversity metrics or by individual species response, there are geographic and taxonomic biases that hinder our understanding of time-lagged responses, although these research gaps have been shrinking over the past 10 years (Table 1). Even within biomes that seem well represented there remain geographic biases, as the numerous studies of time-lagged responses to habitat change in temperate systems are almost entirely restricted to the northern hemisphere. For example, Löeffler and colleagues (2020) found evidence of time-lags for butterflies and plants, representing one of many studies in European calcareous grasslands. Plants remain by far the best represented group for which time-lagged responses have been established (Vellend et al. 2006; Cousins and Vanhoenacker 2011; Jamin et al. 2020), while vertebrates remain understudied (Lira et al. 2019). Amongst vertebrates, mammalian carnivores are particularly interesting because their susceptibility to habitat destruction is based largely in edge effects and increased human caused mortality and persecution in human-modified landscapes rather than in just habitat dependencies (Cardillo et

al. 2005). Larger body size and area requirements result in higher encounter rates with humans, and thus heightened extinction risk in human-modified landscapes (Woodroffe 2000; Cardillo et al. 2005; Crooks et al. 2011, 2017). Sensitivity to fragmentation, a major feature of habitat destruction, varies amongst carnivores (Crooks 2002). Species with large geographic ranges are at lower extinction risk from fragmentation because they tend to be habitat generalists (Brown 1984; Crooks et al. 2017). Many medium sized carnivores ('mesocarnivores') typify this profile (large ranges, habitat generalists, listed as Least Concern) and are resilient to edge effects because of higher reproductive rates, greater dietary flexibility, and because they are perceived as less threatening and persecuted to a lesser degree than larger carnivores (Palomares et al. 1995; Prugh et al. 2009). Mesocarnivores are highly successful in human-altered areas in part because humans suppress mesocarnivores less effectively than larger carnivores (Prugh et al. 2009). However, this does not entirely free mesocarnivores from habitat sensitivities; in areas where human pressures are high and the landscape is highly modified, mesocarnivores are dependent on patches of habitat as refuges (Sushinsky et al. 2013; Poessel et al. 2016; Wurth et al. 2020). Our aim in this study was to determine if habitat generalist mesocarnivores show sensitivity to changing spatial distribution of these refuges, and if that sensitivity is masked by a time lag.

Here we investigated time lags in an agricultural landscape for two widespread mammalian mesocarnivores in Chile. Our study is situated in winter-rainfall Valdivian temperate rainforest, a system that is almost entirely absent from the time lag literature (see Noh et al. 2019 for the lone exception in plants). Our study species (*Lycalopex culpaeus* and *L. griseus*) are closely related and both exhibit a broad latitudinal range through South America along the Andes and are able to use a variety of habitats but have recorded habitat associations that may indicate

varied sensitivity to changes in the landscape (Jiménez 1993; Lucherini 2016a; b; Tchaicka et al. 2016). Culpeo foxes (*L. culpaeus*) are generally larger and are commonly found in a range of habitats including agricultural lands (Jiménez et al. 1995, 1996). They generally thought to use rougher or higher altitude terrain, though they are also found in some lowland areas and are sympatric with chillas in the southern part of both species' ranges (Fuentes and Jaksić 1979; Johnson and Franklin 1994). Home ranges for this species are poorly studied, but estimates range from 2-10 km^2 in south and central Chile (Johnson and Franklin 1994; Guntiñas et al. 2021). Chilla foxes (*L. griseus*) preferentially use open habitats such as agricultural lands and thus, may have a competitive advantage where humans convert landscapes to more open habitats and also exclude their larger native competitors. However, chillas may have some dependence on forests as refuges, as their smaller size make them more susceptible to predation and harassment by introduced domestic dogs which also use open habitats (Silva-Rodríguez et al. 2010b). Chilla home ranges are smaller than culpeo home ranges, approximately 2 km^2 (Wilson and Mittermeier 2009). Based on the natural history of these species and the few studies available on time-lag in mammals, we present two hypotheses:

A. If there is a time-lagged response in species occupancy to habitat metrics, they will be detected at larger spatial scales. We expect this because finer scale spatial use (closer to microhabitat selection) is likely driven by immediate stimuli that are tied to the present-day landscape (e.g. cover to escape detection from predators, or habitat that with high prey abundance).

B. Chillas will either show no habitat dependence or exhibit a greater time lag than culpeos. The open human-modified agricultural habitat that surrounds the remnant forest patches we surveyed within are the preferred habitat type for chillas. Thus we expect them to be

more resilient to changes in the landscape, with changes in the amount and configuration of remnant forest taking longer to manifest as changes in occupancy.

Methods

Study area

We deployed 50 remotely triggered cameras (Reconyx© PC 850, 900) in remnant forest during the austral winter (June to August 2019) on privately owned land following Malhotra et al. 2021 in Los Lagos region of Chile. The study area falls between Lago Rupanco and Lago Llanquihue in the Valdivian temperate rain forest ecoregion (40° 76′ to 41° 21′ S, 72° 54′ to 72° 97′ W, Fig. 3-1). The study area was situated in the lowlands, but was located adjacent to the large protected area (Parque Nacional Vicente Rosales) in the Andean foothills on the eastern edge and the Osorno metropolitan area on the northwestern edge. This region is characterized by annual temperature ranging from 3-23°C and 1346 mm (mean) of rainfall with a cold, rainy winter season between May and September (en.climate-data.org). During our survey period, the study area was dominated by pastures used for cattle grazing as well as scattered plantations of pine (*Pinus radiata*) and eucalyptus (*Eucalyptus* sp.) with only small remnant stands of native forest. Native forest comprised of a mix of *Lophozonia obliqua*, *Nothofagus dombeyi*, *Persea lingue*, and *Laurelia sempervirens* trees, and were mostly limited to degraded strips between pastures or along waterways. Bamboo (*Chusquea quila*) was the primary understory, and dominated forest edges. Other parts of Los Lagos are covered by extensive pine plantations (such as north of the site, along the Coihueco river), but plantations were largely absent from our camera sites and the surrounding buffer 1km buffer.

Image classification and covariate extraction

We obtained Landsat imagery from Landsat 5 TM for 1986, 2005, 2011, and 2015 as well as

Landsat 8 OLI for 2019 to determine landscape characteristics. From the year of data collection

(2019), we chose the interval between imagery years of approximately 5 years in the past based

on the lifespans of the study species with the addition of 1986 as the earliest comparable imagery

for the site. However, the actual interval varied by up to a year depending on the availability of

cloud-free imagery. Images were clipped to the extent of the camera placements within the study

area. Spectral bands 1-7 were used for unsupervised classification of the clipped images from

both Landsat 5 and 8 at a 30-m resolution (the highest available resolution the Landsat imagery)

into the most basic landcover types that would allow us to distinguish forest from all other types

of terrestrial landcover (primarily pasture), which we referred to collectively as 'matrix'. Our

final classified images contained 'core forest', 'suboptimal forest' (see below for explanation of

why we used two forest classes), 'matrix', and 'water' classes. Since fixed points for ground-

truthing the classifications were not available for past years at this site, we used very general

classes (forested cover vs cleared land i.e. 'matrix') that were high contrast and were easily

visually verifiable in this landscape, without attempting to distinguish finer classification, such as

identifying forest types. Furthermore, from our 2019 field survey, we determined that some areas

that are forested, particularly along forest edges, have few trees but are heavily vegetated with

dense stands of the native understory bamboo . These areas are distinct and visually identifiable

from satellite imagery (appearing similar to other forest, but lighter color). However, boundaries

between these areas and denser forest are difficult to define, particularly since the bamboo is

present in the understory of higher quality forest as well. Thus, we used two different

designations in building models to represent a liberal definition of forests versus a more

conservative definition of forests. The 'suboptimal forest' classification includes all forested cover without attempting to distinguish between forests and bamboo stands. The 'core forest' is a more conservative classification, and only includes forest cover within a narrower spectral subset. The images that were generated by unsupervised classification were compared against the satellite imagery at five randomly chosen camera placement to visually check that the classification followed the boundaries of the forested cover within the 1km buffer accurately for different parameter combinations in ArcGIS Pro (vers. 2.7.26828). The same parameters for classification were applied across all years. For 2019, we also compared the classification designations against field notes for each camera and the surrounding habitat.

Occupancy modeling

We used single-species single-season occupancy models to evaluate the impacts of landscape changes on the occupancy (Ψ) of two native carnivores: chillas and culpeos (MacKenzie et al. 2003). For the 'core habitat' set of models, only the 'core forest' class was considered as habitat to generate environmental covariates, while the 'suboptimal forest' class was combined with the 'matrix' class. For the 'broad habitat' set of models, the 'core forest' and 'suboptimal forest' classes were aggregated as habitat to generate environmental covariates. The scale at which covariates are collected can be important in determining species response (Presley et al. 2019; Moll et al. 2020). Thus, for both model sets, covariates were collected within multiple buffer sizes surrounding each camera: 1km (following Malhotra et al. 2021), and two smaller scales (500m, 250m) for finer scale space use.

Covariates for habitat degradation included: proportion native forest (*forest*), patch isolation (*iso*), and edge/area ratio (*edge*), generated at each scale (250m, 500m, 1km) for each year (see detailed descriptions below).

Detection covariates

We modeled detectability of each species with covariates that were previously found to affect the likelihood of capturing the species on camera in this area. Following Malhotra et al. (2021), we binned species detections into 7-day periods, and modeled the detectability (p) of both species using the understory height (*10uds*) and dog occupancy (*dogo*) in 2019. Additionally, we included metrics specific to the study design and sampling effort; namely camera type (*cam*) to distinguish between white-flash cameras and infrared cameras as well as trap nights (*trap*), the number of nights an individual camera was operational to collect species detections.

Occupancy covariates

Occupancy for each species was modeled with habitat covariates (*forest*, *iso*, *edge*) at the three spatial scales for every year. We measured *forest* as the total amount of forest cover within the buffer of the camera. For *iso*, we used the average nearest distance measurements from patches that intersected the buffer in all directions. For *edge,* for all patches of forest that intersected the buffer we totaled the perimeter distance of the patches and divided it by the total area of those patches. All covariates were plotted over a time series to determine whether there were landscape-level changes over time. We also plotted by camera to determine if the distribution and configuration of habitat changed over time. All covariates were scaled and centered (standardized) for modeling.

Model evaluation

For each scale and year, the global models included mean understory height within 10m (*10uds*) and camera type and trap night (*cam*, *trap*) covariates for detection, and proportion forest (*forest*) patch isolation (*iso*) and edge/area ratio (*edge*) for occupancy. All detection and occupancy

covariates were tested for correlation using Pearson's R. Global models were tested for

overdispersion, and model ranking was carried out using Akaike Information Criterion, corrected

for small sample sizes (AICc). To account for spatial autocorrelation, models were fit with and

without a spatial random effect with a threshold size of 1km, and compared using Pareto-

Smoothed Importance Sampling Leave-One-Out cross validation (PSIS-LOO) as a measure of

predictive accuracy. If the model with the spatial random effect did not show better predictive

performance (Δ'elpd_diff' > 2*SE of 'elpd_diff') than the model without the spatial random

effect according to PSIS-LOO cross validation (Vehtari et al. 2017), we concluded the absence

of spatial autocorrelation at 1km. At each scale (250m, 500m, 1km), model sets for each year

were compared, with the top model being defined as the one with the lowest AICc. We tested for

goodness-of-fit for all top models (<2 ΔAICc units of the highest rank model) using a Chi-square

statistic. Top models from all years were aggregated, and model weights were calculated used

just the aggregated top model set. We concluded that the presence of a time-lagged response to

the landscape existed if models using covariates from past years outperformed models using

covariates from 2019. All occupancy modeling was completed in the 'unmarked' and 'ubms'

packages (Fiske and Chandler 2011; Kellner et al. 2022) in Program R vers. 3.6.2 (R Core Team

2019).

Results

Landscape change over the time series

While the distribution of forest changed over the 33-year time series (Fig. S3.1, Appendix C) ,

there was not a consistently increasing or declining trend over time in the amount of forest cover

regardless of the scale (Fig. 3-2). Overall, covariates collected within the camera buffers matched

trends in the landscape over time regardless of scale. The sole exception was patch isolation at

the 1km scale, for which 2011 and 2015 showed higher patch isolation and a general increasing

trend in patch isolation from 2005-2019. In contrast, at the smaller scales and in the whole

landscape, 2011 and 2015 represented a period of decreased patch isolation.

Carnivore detection

We detected both carnivore species over a total effort of 3500 trap-nights. Naïve occupancy

estimates for chillas (n = 225), and culpeos (n=39) were 0.59, and 0.16 respectively. We used the

same detection covariates as in Malhotra et al. (2021), and that similarly outperformed the null

detection model. For chillas (β = -0.81, SE = 0.16) and culpeos (β = -1.83, SE = 0.61) *10uds* was

a strong negative driver of detection probability. Additionally, *dogo* increased detectability for

both chillas (β = 0.81, SE = 0.16) and culpeos (β = 0.87, SE = 0.35).

Carnivore occupancy

Modeling carnivore occupancy with covariates and accounting for imperfect detection improved

our understanding of carnivore space use. The covariates driving occupancy varied for each

species (Tables 1) and with the presence of a time lag. The spatial random effect did not improve

fit for any models, and so modeling results were obtained from the models excluding the spatial

random effect (Table S2.1). We present the results from the 'core habitat' set of models, since

none of the top model set included models from the 'broad habitat' set. Occupancy estimates

from our best supported models showed an increase in occupancy from naïve estimates for both

chillas (ψ = 0.75, CI: 0.645-0.875) and culpeos (ψ = 0.25, CI: 0.188-0.5).

For both species, occupancy was better described by metrics derived from past years,

with chilla occupancy exhibiting a longer time lag than culpeo. However, the best models for

culpeos and chillas incorporated habitat metrics from the past (Table 2). For both species, models

containing metrics from the present-day landscape measured within the broadest scale (1km) outperformed the null model.

Spatial scale

The consistency of the scale at which habitat metrics were important revealed a scale dependency in habitat drivers of space use for both species (Table 2). Metrics at the smallest scale (250m) did not describe culpeo or chilla occupancy well with no models in the top model set for either species. Metrics at the 500m scale best described culpeo occupancy, comprising 5/6 models in the top model set (> 2 ΔAICc better than the null occupancy model). In contrast, no model at this scale outperformed the null model for chillas. Metrics at the 1km scale best described chilla occupancy, comprising 6/6 models in the top model set while only a single model at this scale was in the top model set for culpeos.

Habitat amount and configuration

Overall, past habitat configuration metrics (*iso*, *edge*) were more important than past habitat amount (*forest*) as drivers of culpeo and chilla occupancy (Table 3). In contrast for culpeos, *forest* was an important positive driver in present day (2019) model set. Best models from past years (primarily 2015 and 2005) significantly outperformed models from 2019. For culpeos, occupancy was best described by the distance between patches (*iso*) in 2015, at a scale of 500m (Fig. 3-3). At this scale, *iso* was a significant positive driver of culpeo occupancy (β= 1.77, SE = 0.833), while *edge* approached significance as a negative driver (β= -2.08, SE = 1.232). Culpeo occupancy increased with *iso* (β= 1.12, SE = 0.612) and decreased with *edge* (β= -1.73, SE =0.939) at the 500m and 1km scales.

In contrast with the results for culpeos, the top model set for chillas was entirely driven by habitat metrics at the broadest scale. Chilla occupancy consistently increased with patch isolation and exhibited a larger time lag than culpeos, with all top models of comparable weight in the top model set including *iso* from 2011 as a significant positive driver of occupancy (β= 2.84, SE = 1.17) (Fig. 3-3).

Discussion

Habitat loss continues to drive the decline of species globally, while the negative effects of fragmentation remain debated (Foley 2005; Fahrig et al. 2019). Many studies have shown that species responses to habitat loss may be time-lagged dependent on various traits, though vertebrates are relatively understudied (Lira et al. 2019). Our study adds to the limited literature exploring the presence of time lags in mammals in response to a changing landscape, including metrics of both habitat amount and configuration. To our knowledge, this is the first study exploring the scale dependency of past habitat amount and fragmentation on present-day spatial use of mammals, and the first study exploring time-lagged responses in mammals in this biodiversity hotspot. Focusing on two medium-sized mammalian carnivores in a system that is highly disturbed, we provide evidence that past habitat configuration can drive contemporary occupancy.

The response to similar habitat covariates in both of our species likely reflects their similar habitat tolerances. The habitat metrics explaining culpeo and chilla occupancy align well with the natural history of the species and previous findings (Lucherini 2016a; b; Malhotra et al. 2021). The association of culpeos with more 'rugged' terrain (Jiménez and Novaro 2004) was reflected in percentage of forest in the current landscape being positively correlated with culpeo occupancy at a large scale. The distance between patches and edge to area ratio from 2015 better

described culpeo occupancy, indicating that past landscape configuration is more important than current habitat amount. Our results for culpeos are similar to the findings of Semper-Pascual et al (2021), who showed that mammals and bird occupancy was best described by current habitat amount, but past fragmentation. Similarly, chilla occupancy was driven by the configuration of the habitat regardless of which year the metrics were collected from, although the time lag was stronger for this smaller species. Our result is easy to reconcile with the natural history of chillas, which preferentially forage in open areas which typify the matrix in our study site, but need forests as refuges (Silva-Rodríguez et al. 2010b). Increasing patch isolation as a positive driver of occupancy without forest cover as a negative driver indicates that both species may be using areas that historically had patches of forest spread out evenly within the agricultural matrix . Furthermore, given that 2011 and 2015 had the highest overall amount of habitat and relatively low patch isolation and edge habitat, the occupancy of both species may be reflecting the most forested landscape in the recent history. While chillas and culpeos generally matched in which metrics drove occupancy, they differed in the scale and year at which the covariates were collected.

The scale at which the habitat metrics were important differed by species, but the length of the time lag was not scale dependent. At the finest scale (250m), the null model seemed to be the best model regardless of time lag, or species. Likely this scale is representative of microhabitat selection for medium-sized mammals such as our study species, and were better described by other factors or would require higher temporal resolution than was captured in a presence-absence camera trap framework (Bai et al. 2020). Measuring habitat metrics at the appropriate scale is particularly important to capture the effect of habitat amount and configuration on mammals occupancy (Prugh et al. 2008; Presley et al. 2019). Therefore, it was

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surprising that culpeo occupancy was best described by metrics derived at the 500m scale, while

occupancy of the smaller chilla was driven by broader scale habitat configuration at 1km. Based

on expectations from home range size (Jiménez 1993; Guntiñas et al. 2021), chillas should be

sensitive to habitat configuration at a smaller scale than culpeos. A potential explanation for this

unexpected result is that the time lag that chilla occupancy is tied to habitat preferences while the

time-lagged response of culpeo occupancy is tied to other factors that are also habitat dependent,

such as prey.

Of the traits that differentiate these ecologically similar species, the increased carnivory

and thus prey limitation of culpeos (Jiménez 1993; Johnson and Franklin 1994; Novaro et al.

2004) provides the most plausible explanation for the differences in time-lags for our study

species. Culpeo range expansions towards lowlands east of the Andes have been driven by

increasing availability of introduced prey (Jaksic 1998; Novaro et al. 2000; Lucherini 2016a).

The time-lagged response we found could reflect the underlying landscape, or the resultant

spatial distribution and availability of prey the latter of which represents a future direction for

this study (see Malhotra et al. 2021, where trap success of small mammals was a consistent

positive but nonsignificant driver of culpeo occupancy). While latitudinally, the culpeo range

extends to the southern tip of South America, they are considered a recent invader into the

lowland area that comprises our study area (pers. obs., unpublished data). The most recent IUCN

(International Union for Conservation of Nature) range maps do not show culpeos in the central

valley and lowlands of the Los Lagos region (Lucherini 2016a); although, there are recent

photographic records of them in the area (Gbif.org 2022) and our study confirms their presence

in this region. Differences in other traits for our study species lead to conflicting expectations;

for example, for mammals extinction risk increases with body size and is inversely related to

geographic range (Ripple et al. 2017). Since culpeos have a larger geographic range than chillas (Jiménez 1993; Guntiñas et al. 2021), they should be more robust to short term changes in the landscape (Krauss et al. 2010) and exhibit a more time-lagged response (Devictor et al. 2008), which is the opposite of what we would expect for the larger body size.

More broadly, landscape configuration may be the ultimate or proximate cause of species distribution depending on how it may mediate interspecific interactions. Chillas for example, can be spatially excluded from optimal habitats where they are sympatric with culpeos (Johnson and Franklin 1994; Jiménez et al. 1996). Both species may be impacted by domestic dogs mediated by the amount of open habitat (Silva-Rodríguez et al. 2010b; Zapata-Ríos and Branch 2018; Malhotra et al. 2021). One of the limitations of this study is the lack of inclusion of other important factors such as the distribution of invasive species and prey abundance (e.g. culpeos predating European rabbits, Rubio et al. 2013) that are likely to be landscape dependent and may be driving the observed time lags. Monitoring prey abundance both as a response variable for habitat metrics as well as a driver of carnivore occupancy would be a fruitful future direction. Lastly, collecting additional presence-absence data for chillas and culpeos at a future time point would lend perspective to our results. This is crucial because we did not find an obvious trajectory for the amount and configuration of habitat in the landscape. Although the broader pattern within temperate forests in Chile is one of loss, fragmentation, and replacement by exotic plantations (Echeverria et al. 2006; Nahuelhual et al. 2012), dynamics within smaller subsets of the landscape such as our site may differ. This is likely because the landscape in this area is nearing (if it is not already at) a point where there is little habitat left to lose (Ridding et al. 2020), where the degraded remnant forest is confined to areas that have low value for commercial uses such as agriculture or dairy farming. Repeating this study over future years will

determine whether culpeo and chilla occupancy is consistently time-lagged or if reflects the most recent forested maximum.

Occupancy modeling can inform competition interactions and other dimensions of ecology and conservation and with the availability of remotely sensed data. It is straightforward to test for the presence of time lags, and accounts for imperfect detection (Fuller et al. 2016; Hagen et al. 2016; Chen et al. 2021). We suggest that past landscapes should be more regularly incorporated into occupancy modeling, especially when current habitat covariates do not provide explanatory power. Doing so can reveal important insights for conservation, such species being more threatened and meeting the criteria for a higher threat listing when accounting for the effects of time lags (Broekman et al. 2022). Additionally, we recommend examining individual species for time-lagged responses and comparing them to the broader expectations found time lag literature. Ultimately, in an era of rapid environmental change incorporating metrics from past landscapes may reveal important drivers that would otherwise remain hidden (even if the time lag is small) and used in conjunction with repeated monitoring it can provide insight into future trajectories.

Fig. 3-1. (a) Study area located in the Los Lagos Region of south-eastern Chile. (b) Landscape level distribution of camera deployment throughout patches of native forest straddling the Volcano Osorno.
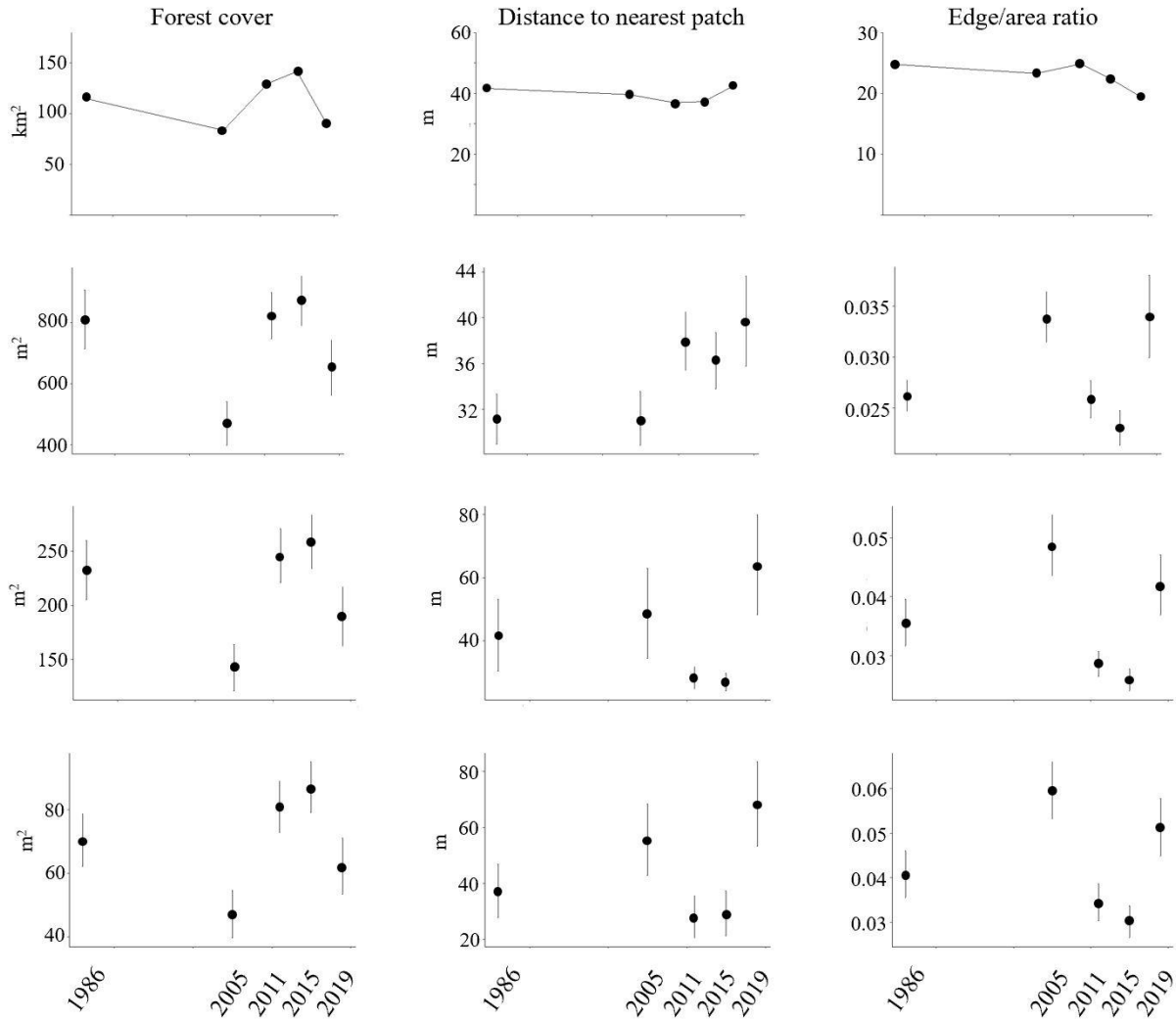
Fig. 3-2. The three landscape covariates (*forest*, *iso*, *edge*) at different scales. Cameras were placed in remnant patches of forest, and while the habitat amount (*forest*) collected at each scale (1km, 500m, 250m) around the cameras generally reflected the broader landscape over the time series, there were some differences in the habitat configuration metrics depending on the scale (*iso*, *edge*). *forest*: total forest cover within the buffer; *iso*: average distance to nearest patch for all patches intersecting the buffer; *edge*: total edge to area ratio for all patches intersecting the buffer.
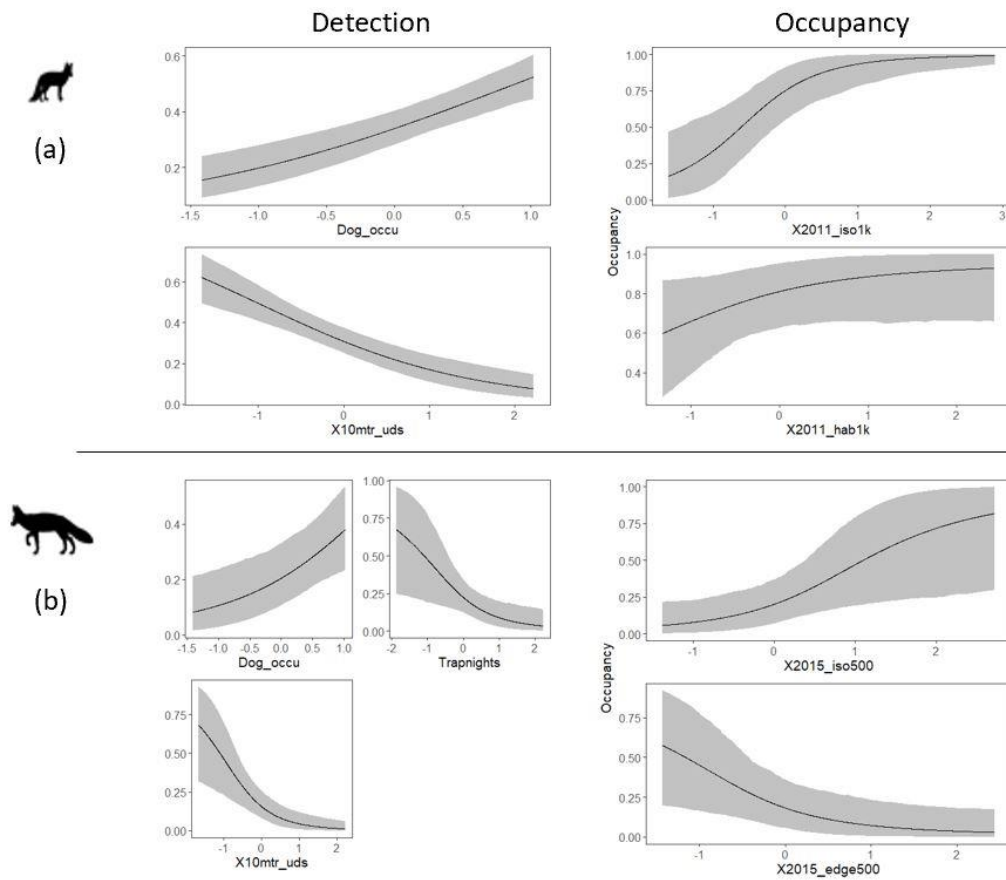
Fig. 3-3. Marginal covariate effects on detection (p) and occupancy (Ψ) of (a) chilla and (b) culpeo for the overall top model across years and scales derived from Bayesian estimation (*ubms*). The direction and significance of the covariate effects were checked for congruency with results from maximum likelihood estimation (*unmarked*).

Table 3-1. Examples of studies exploring time lags across different taxa and biomes. *Kuussaari et al. 2009 is a review of the time lag literature, and Lira et al. 2019 is a follow-up review 10 years later, assessing the state of the initial gaps in the literature. For a more comprehensive list of time lag studies, see these two reviews.

Authors; Year	Biome	Taxa
Brooks et al; 1999	Tropical forests	Birds
Cousins et al; 2007	Temperate grasslands	Plants
Kuussaari et al*; 2009	Review	Review
Vellend et al; 2011	Temperate forest	Plants
Niisalo et al; 2017	Tropical forest	Plants
Chen & Peng; 2017	Global forest	Reptiles, amphibians, mammals
Noh et al; 2019	Temperate forest	Plants
Lira et al*; 2019	Review	Review
Montgomery et al; 2020	Temperate wetlands	Fish
Löeffler et al; 2020	Temperate grasslands	Plants, insects
Semper-Pascual et al; 2021	Tropical forest	Birds, mammals

Table 3-2. All models that outranked the null occupancy model by more than 2 ΔAICc for each species. The scale indicates the buffer size around each camera within which covariates were collected. (occupancy(Ψ), detection(p)). *dogo*: dog occupancy; *cam*: camera type; *10uds*: average understory height within 10m; *iso*: average distance between patches; *forest*: proportion native forest; edge: edge/area for patches intersecting buffer

Species	Top models	Scale	Year	AICc	ΔAICc	w$_i$
Chilla	Ψ(iso, hab) p(dogo, 10uds)	1000m	2011	425.2895	0	0.318
	Ψ(iso, hab) p(dogo, 10uds, cam)	1000m1	2011	425.986	0.697	0.224
	Ψ(iso) p(dogo, 10uds)	000m	2011	426.1903	0.901	0.204
	Ψ(iso, edge) p(dogo, 10uds)	1000m	2011	426.3627	1.073	0.186
	Ψ(iso) p(dogo, 10uds)	1000m	2015	429.7181	4.429	0.035
	Ψ(iso) p(dogo, 10uds)	1000m	2019	429.7724	4.483	0.034
Culpeo	Ψ(iso, edge) p(dogo, 10uds, trap)	500m	2015	123.5158	0	0.291
	Ψ(iso, edge) p(dogo, 10uds, cam)	500m	2015	124.3247	0.809	0.194
	Ψ(iso, edge) p(dogo, cam)	500m	2015	124.418	0.902	0.185
	Ψ(iso) p(dogo, 10uds, trap)	500m	2005	125.3452	1.829	0.116
	Ψ(iso, edge) p(dogo, 10uds, trap)	1000m	2015	125.4433	1.928	0.111
	Ψ(iso) p(dogo, 10uds)	500m	2005	125.5893	2.074	0.103

Table 3-3. β coefficients with standard error for the top model for each species at each scale. No model at the 500m scale outperformed the null occupancy model for chillas. Significant covariates (95% CI not overlapping 0) are **bolded**.

Culpeo	Ψ covariates			p covariates			
Scale	Forest	Patch isolation	Edge/area	Trap nights	Dog occupancy	Understory	**Year**
1000m	-	1.12 (0.61)	-1.73 (0.94)	**-1.56 (0.545)**	**0.73 (0.31)**	**-2.08 (0.61)**	2015
500m	-	**1.77 (0.83)**	-2.08 (1.23)	**-1.38 (0.55)**	**0.87 (0.35)**	**-1.83 (0.61)**	2015
250m*	-	-	-1.94 (1.2)	-	**1.02 (0.33)**	**-0.70 (0.41)**	2015

Chilla	Ψ covariates			p covariates			
Scale	Forest	Patch isolation	Edge/area	Camera type	Dog occupancy	Understory	**Year**
1000m	1.39 (1.17)	**2.84 (1.36)**	–	–	**0.81 (0.16)**	**-0.81 (0.16)**	2011
500m	–	–	–	–	**-**	**-**	**-**
250m*	–	–	0.66 (0.46)	–	**0.65 (0.16)**	**-0.75 (0.18)**	1986

Chapter V

Mismatched Movement Responses to Habitat Loss and Fragmentation Alters Encounter Rates Between Predator and Prey

Preamble: This chapter is currently in preparation for submission to the journal American Naturalist. The citation for this chapter is: Malhotra, R., Harris, N. C., Avgar T. (2022) Mismatched movement responses to habitat loss and fragmentation alters encounter rates between predator and prey

Abstract

Human-modifications to the landscape such as habitat loss, fragmentation, and urbanization disrupt the movement of animals. Furthermore, there is considerable evidence that altered movement affects a range of interspecific interactions. Surprisingly, these two areas of research remain largely disconnected. To demonstrate that habitat loss and configuration can alter interactions through the movement responses of the interacting species, we developed an agent-based model in which a predator and prey are assigned various combinations of boundary crossing behavior. Using a simple yet flexible framework to classify the relative movement response of the predator and prey, we demonstrate that the movement behavior has a strong effect on the time to predation (TTP). We confirm that the effect of the movement behavior on the time until first encounter is dependent on both the habitat amount and configuration. Notably, we find that mismatched movement responses drastically increase the TTP, which favors the prey; the only scenario that favors that predator (a lower TTP) is if the boundary crossing

behavior of the predator and prey are similar, and that higher fragmentation tips this scenario back in favor of the prey. Our findings highlight that in human-modified systems the extirpation of species is not necessary for interactions between species to be significantly altered. Importantly, our general model is simple to parameterize with empirical data and provides a set of expectations against which the outcomes of more complex movement responses can be compared. By understanding how relative movement responses translate into encounter rates, we can more generally determine the consequences for species interactions as humans alter landscapes.

Introduction

Habitat loss and fragmentation are pervasive and threaten biodiversity (Foley 2005). One of the major impacts of these anthropogenic changes to the landscape is the potential to alter movement of organisms on a global scale depending on species habitat preference and mobility (Doherty and Driscoll 2018; Tucker et al. 2018). For example, fragmentation can reduce movement probability or cause avoidance of the novel habitat type, or alternatively increase movement and lead to larger home ranges (Fahrig 2007; Beasley and Rhodes 2010). Examples of altered habitat configuration leading to altered movement exist across systems and taxa, including fish (Rahel and McLaughlin 2018), insects (Collinge 2000; Fitch and Vaidya 2021), birds (Silveira et al. 2016; Ramos et al. 2020; Londe et al. 2022), mammals (Beasley and Rhodes 2010; Habib et al. 2021), amphibians (Mazerolle 2001; Popescu and Hunter Jr. 2011), reptiles (Jiménez-Franco et al. 2022b), and even microbes (Laurent et al. 2020). This altered movement can lead to extirpation and changes in biodiversity because of altered population and metapopulation

dynamics (Hanski and Gilpin 1991; Hansson 1991; Russell et al. 2003; Doherty and Driscoll 2018).

Even without the extirpation of species, altered movement can result in changes in interspecific interactions. Altered movement of one or both species can change host-parasite interactions, (Elzinga et al. 2007; Tracey et al. 2014; White et al. 2018), seed dispersal (Emer et al. 2018; Nield et al. 2020; Tucker et al. 2021), pollination mutualisms (Cheptou and Avendaño V 2006), and predation (Vander Vennen et al. 2016). Despite the considerable amount of research linking altered movement with disrupted interactions and a similarly large body of literature linking heterogenous landscapes with altered movement, there is surprisingly little work bridging these two areas of research (Wosniack et al. 2014). A complementary area of research links habitat loss and fragmentation to altered species interactions (e.g. García and Chacoff 2007), but few of these studies explored altered movement as the causative mechanism (but see Dickie 2019, Tucker 2021).

Encounter rates provide an ideal way to examine the impacts of movement responses on interactions since they are both the result of movement decisions that animals make, as well as a key component of interactionssuch as predation or parasitism (Gurarie 2013). For example, Scharf and colleagues (2006) showed that movement characteristics (velocity) of predators relative to prey can drive the success of the interaction as measured by the capture rate (also see Avgar et al. 2008). Avgar and colleagues (2011) demonstrated that these encounter rates can be linked to the spatial aggregation of resources. This connection to resources is key to understanding how changes in habitat amount and configuration can alter the frequency of an interaction via movement. For a predator-prey interaction, if habitat loss or fragmentation alters the movement of the prey (the resource) such that it results in prey aggregation within a habitat

type, it should result in higher time until first encounter (assuming the predator is not also aggregating in that habitat type). However, predators do not move through all habitat types similarly and may either aggregate in the same habitat type as the prey, in a different habitat type, or show no preference (Dickie 2019, Yang 2017). Thus, in terms of movement, the encounter rate between the predator and prey should be driven by the relative responses of the predator and prey to the habitat types present in the landscape. Conceptually, this is applicable to both classic predator-prey (e.g. spider and grasshopper prey) as well as intraguild predation (e.g. antagonistic size-based hierarchies, such as those common among species of Canidae). We present a simple, general framework that examines predator-prey movement responses relative to each other in novel/anthropogenic landscapes:

Neutral response (null model): neither predator nor prey show a habitat preference

Matched response: predator and prey preferentially use the same habitat type

Partially mismatched response: either predator or prey preferentially uses a habitat type, while the other species does not alter movement based on habitat type

Mismatched response: predator and prey preferentially use different habitat types

To determine what effects these different paired movement responses have on first encounter rates, we used a simulation model to test different scenarios that fall within each paired response in a simple landscape. We hypothesized that:

1. Broadly, the movement behavior of the predator and prey relative to each other would determine the shape of the correlation between landscape metrics and first encounter rate.

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2. Regardless of the shape of the relationship between landscape metrics and time until

first encounter rate, the mismatched response would result in the greatest increase in

time until first encounter relative to the neutral response, followed by the partial

mismatch, while a matched response would result in a decrease in time until first

encounter.

Determining how mismatched movement responses translate into encounter rates is key to be

able to more generally predict how interactions between species are impacted by alterations to

landscapes.

Methods

We constructed a 48x48 (-24 to 24 distance units on x axis, and -24 to 24 distance units on the y

axis) 2D agent-based model in Netlogo (vers. 6.2.0) to test different combinations of predator

and prey movement responses across a variety of landscapes on time until first encounter.

Netlogo is a program for implementing agent-based models that is commonly used for ecological

inquiry. Within Netlogo, agents (an individual, i.e. each individual predator and prey in this case)

can move with a heading between 0 and 360 degrees at a given step length, which can be

fractions of units. Starting at the origin, the landscape was partitioned into grid cells ('patches')

of area 1 distance unit^2. Each patch was assigned either a 'forest' habitat or 'matrix' habitat

designation (see Figure 1 for examples of resultant landscapes). It is important to note that agents

were not restricted to centroid-to-centroid movement between patches; based on step length and

heading, they could end a time step anywhere within a given patch. A single predator and a

single prey moved across the landscape where both started at randomly assigned locations and

moved across the grid in simultaneous time steps. Either the predator, prey, or both were

designated as 'forest-preference', 'matrix-preference' or 'no preference', as described below.

The base detection range for each agent (predator or prey) was 3 distance units. If prey landed within 2 distance units of the predator, there was a base chance of predation of 50% (this can also be thought of as a 50% survival or evasion rate for the prey). If the prey survived, in the next time step it moved 1 distance unit directly away from the predator. This 'prey escape' was undertaken before accounting for the normal movement of the prey item (so the prey could move a maximum of 2 distance units within a time step). The time-to-predation (TTP) was recorded for every simulation, up to a maximum of 100,000 time steps. A single time step is defined as a single full run through of the model (prey escape if relevant, movement of predator and prey, predation/survival if relevant). TTP was used as a response variable because it is the time until first encounter scaled by the attack success rate (50%, as stated earlier). Each combination of parameters (movement behavior) was simulated 10,000 times for each landscape.

Movement behavior of predator and prey

Habitat preference was reflected in the movement behavior of each agent as boundary crossing behavior (Kuefler et al. 2010). Note that 'forest' can represent any native vegetation cover type, and 'matrix' can represent any human modified habitat type. For each simulation, the predator and the prey were each designated one of the following habitat preferences:

'neutral' – An unbiased random walk without any correlation. Regardless of the patch type, at every time step a random degree heading (0-360 degrees) was picked for the agent (predator or prey), and the agent moved 1 distance unit in that direction.

'forest-preference' – A base random walk, with a tendency to move into forest habitat from matrix habitat (positive correlated random walk), or remain within native habitat (negative correlated random walk). If the agent was in a native habitat patch and reached an edge (the next

time step would result in entering a matrix habitat patch), a new heading between 90 and 270 degrees was randomly picked for the next time step. If the agent was in matrix habitat , and there was forest habitat in front of it within the detection radius (in the direction of the heading), it retained that heading for the next time step.

'matrix-preference' – A base random walk, with a tendency to move into matrix habitat from forest habitat (positive correlated random walk), or remain within matrix habitat (negative correlated random walk). If the agent was in a matrix habitat patch and reached an edge (the next time step would result in entering a forest habitat patch), a new heading between 90 and 270 degrees was randomly picked for the next time step. If the agent was in forest habitat, and there was matrix habitat in front of it within the detection radius (in the direction of the heading), it retained that heading for the next time step.

Habitat dependency of attack success

Habitat can influence other aspects of the predation interaction, such as success of the attack based on both the detection distance and obstacles that may favor the escape behavior of the prey (Wheatley et al. 2020). We incorporated attack success as a simple interacting factor with habitat type:

Treatment 1. Capture probability independent of habitat type

Regardless of which type of habitat each agent was in, the capture probability remained at base rates (50%).

Treatment 2. Probability of capture varies with habitat type

We varied the probability of capture for the prey, depending on the habitat type. If the prey was in matrix habitat, the probability of capture was left at the base capture rate (50%). If the prey was in forest habitat, the capture probability was reduced to 25%.

Disentangling habitat loss and fragmentation

Fragmentation and loss of habitat often happen simultaneously in landscapes. These confounding factors have fueled the debate over the impacts of fragmentation on biodiversity requiring the distinction of 'fragmentation *per se*' to distinguish between the effects of habitat configuration and amount (Fahrig 2017). Both amount and configuration can impact the predator-prey interaction (Burger et al. 1994; Vanlandeghem et al. 2021). We modeled two scenarios to account for this distinction: one with decreasing habitat, and one in which a fixed amount of habitat (50%) breaks into an increasing number of patches (fragmentation *per se*):

Treatment 1. Habitat amount

We started with an intact landscape (100% of the patches were forest habitat), and increased the amount of matrix habitat by 5% for each simulation. The forest habitat was restricted to a single square patch (Fig. 4-1A).

Treatment 2. Habitat configuration

To disentangle the effects of habitat amount and habitat configuration, we also tested all parameter combinations in three landscapes that were 50% native habitat and 50% matrix

habitat, but with increasing amounts of fragmentation (Fig. 4-1B)

<center>*Results*</center>

Movement behavior of predator and prey

The movement behavior of the predator and prey relative to each other determined how a given landscape impacted time-to-predation (TTP), supporting our hypothesis. Time-to-predation was not sensitive to the amount or configuration of forest habitat when neither predator nor prey exhibited a habitat type preference, as expected (null model; TTP mean at 50% habitat: 2141, CI: 2099-2184) (Fig. 4-2A,B). Adding a forest habitat or matrix habitat preference to either predator or prey altered the time-to-predation as function of both the habitat amount and configuration (Fig. 4-3, 4-4). Similarly, adding a habitat dependency for the attack rate of the predator altered the relationship between the TTP and the amount of each type of habitat (Fig. 4-3, 4-4A-C). Generally, the sensitivity of TTP to changes in forest habitat amount and configuration seemed to correspond with how matched the habitat type preference of the predator and prey were; matched responses exhibited the smallest magnitude of difference in TTP from an intact system, with a partially mismatched habitat type preference (either predator or prey with a habitat type preference, and the other neutral) showing greater changes to TTP as the landscape changed, and opposite habitat type preferences showing the greatest changes to TTP with changes in the landscape.

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Habitat dependency of attack success

A lower change of successful predation in forest habitat did not change the general shape of the relationship between TTP and habitat amount or configuration in any scenario, but generally increased the TTP as the amount of forest habitat increased (Fig. 4-4D-F). Essentially, the effect on TTP scaled linearly as a function of the magnitude of the difference in attack rate between habitat types (0.25) multiplied by the amount of habitat.

Habitat amount

We note that the total amount of edge increased with increasing proportion of forest habitat (albeit at a decreasing rate). TTP changed with the amount of forest habitat in every scenario where either or both predator and prey exhibited a habitat type preference, with the shape of the correlation varying depending on whether the movement was matched, partially matched, or mismatched. For the matched scenario, the correlation between TTP and habitat amount was parabolic; for a partial mismatch, linear, and for mismatched, cubic. If only the predator exhibited a forest habitat preference (partial mismatch), the magnitude of the change in TTP was the smallest (TTP mean at 50% habitat: 2329, CI: 2282-2375), decreasing with the proportion of forest habitat (Fig. 4-3A). When both predator and prey exhibited the same habitat preference (matched response) the TTP decreased (TTP mean at 50% habitat: 1284, CI:1271-1297) below the rate for intact forest habitat/both predator and prey exhibiting no habitat type preference (null model; TTP mean at 50% habitat: 2141 ,CI: 2099-2184). However, this was only for low levels of forest habitat, with increasing forest habitat causing increasing TTP (TTP mean at 75% habitat: 1995, CI: 1955-2034) (Fig. 4-3B). Opposite habitat preferences for predator and prey

caused the greatest magnitude of change in TTP, more than tripling the time at medium levels of habitat loss (TTP mean at 50% habitat: 12568, CI:12306-12830), but with similar levels of TTP at high forest habitat amounts or high matrix habitat amounts (Fig. 4-3C).

Habitat configuration

In all cases where predator or prey exhibited a habitat type preference, the amount of edge was important as a driver of TTP, with 50% forest habitat leading to significantly different TTP depending on the number of patches. For only the predator exhibiting a forest habitat preference, medium levels of fragmentation caused higher TTP (mean and CI for TTP 4 patches: 2530; 2478-2582), comparable to rates for lower amounts of forest habitat (Fig. 4-4A, 4-3A). If both predator and prey exhibited native habitat preference, the TTP was drastically increased (mean and CI for TTP 4 patches: 7447; 7267-7626) reversing the lowered TTP in unfragmented 50% habitat (Fig. 4-4B). This effect was lessened in the most fragmented scenario (mean and CI for TTP 16 patches: 3128; 3065-3190), but still had higher TTP than in the intact forest habitat scenario/no predator or prey habitat preference scenario. Opposing habitat preferences for predator and prey was also sensitive to habitat configuration, with the sharp increase in TTP at 50% forest habitat decreasing considerably with increasing fragmentation (mean and CI for TTP 4 patches: 6541; 6412-6669; 16 patches: 3483; 3415-3551), (Fig. 4-4C).

Discussion

While changes to habitat amount and configuration can alter movement, and altered movement can change interactions, there is little work that uses the movement process to link the landscape structure to the fate of an interaction. Focusing on a predator-prey interaction, we demonstrate

that habitat mediated movement can translate to an altered interaction, as measured by the time-to-predation. The time-to-predation (TTP) varied if the predator or prey displayed a habitat preference in their boundary crossing behavior. Furthermore, mismatched responses to the changes in the landscape produced drastically different TTP, demonstrating that even if a predator and prey can persist in a landscape with fragmentation and habitat loss, the predator-prey interaction will be altered based on species-specific sensitivities.

Broadly, the amount of forest habitat governed TTP if either the predator or the prey exhibited a habitat type preference. Habitat type preference and associated boundary responses led to aggregation within the preferred habitat (Fortin et al. 2013). As expected, in our 'matched' response in which both predator and prey preferred the same habitat type, TTP decreased as the preferred habitat type decreased. The positive relationship between TTP and preferred habitat type is consistent with increased encounter rates due to crowding that can lead to higher killing and predation of conspecifics (Cubaynes et al. 2014; Kotze et al. 2021) and prey (Holbrook and Schmitt 2002). Generally, the only habitat loss scenario which favored the predator was if the predator movement was governed by a matrix preference, or if the prey had a matched response (same habitat preference) to the predator. The dependency of TTP on the relative movement response of predator and prey has implications for the conservation of the predator or prey depending on which is favored, and for human-wildlife conflict. For example, encounter rates between predators and their native prey species would be reduced if they have mismatched movement responses; however, for matrix-preferring predators this could be offset by higher encounter rates with livestock as an alternative source of prey. While wild prey may actively switch habitat preference to avoid predators (Schmitz et al. 2017), livestock may be more

bounded by their association with humans and have lost many antipredator behaviors (Mignon-Grasteau et al. 2005) .

Fragmentation altered the expectations from habitat amount considerably, even reversing the effects. While 50% forest habitat would favor the predator for a forest habitat-selecting predator and prey if the habitat is aggregated into a single patch, a more fragmented landscape shifts the favor to the prey, with TTP rates far exceeding those in an undisturbed landscape. Fragmentation was not entirely unfavorable for predators however – in our mismatched scenario, which was the least favorable for predators, high fragmentation reduced TTP to levels closer to an undisturbed landscape. For example, our mismatched results would predict that in a landscape where wolves (*Canis lupus*) use the matrix to move and moose the patches of forest (e.g. Droghini and Boutin 2018), the moose (*Alces alces*) would be favored to avoid predation at middling amounts of habitat loss with low fragmentation. Increasing or decreasing the habitat to extremes or increasing fragmentation would reduce this advantage for the moose. However, this type of mismatched aggregation highlights the role of cognition and fear in driving the movement of predator or prey. By aggregating in the opposite patch type as the predator, the prey is avoiding the 'matched-response' scenario we presented (Fortin et al. 2005), which is the only (Codling et al. 2008) case we found for which the TTP was reduced. This scenario was explored by Dickie et al. (2020), who found that predators did preferentially use matrix (specifically, anthropogenic linear features), while prey aggregated in habitat patches. However, their work also highlights how increased complexity in real systems can alter our expectations – if predators are using matrix to move more efficiently between habitat patches (rather than simply selecting for matrix), this would potentially increase the encounter rate and subsequently, predation. This latter scenario is consistent with our simulation model, where the increased TTP

for predator and prey selecting different habitat types is offset as fragmentation is increased, even though we did not incorporate increased speed through the matrix. Vanlandeghem et al. (2021) further confirm this result using an agent-based model parameterized with collar data; while wolves and woodland caribou (*Rangifer tarandus*) selected for different types of habitat, caribou mortality increased under systems with extensive networks of roads (highly fragmented).

Our model has several assumptions that simplify reality, both in the composition of the landscape and in animal movement. Real landscapes have additional heterogeneity and complexity beyond binary habitat and matrix distinctions, and the type of land-use change can determine the movement response (Jiménez-Franco et al. 2022b). Animal movement is better approximated by a correlated random walk than completely diffusive movement (Codling et al. 2008); however, adding correlation to both predator and prey should not change the patterns we have found as increasing correlation from an uncorrelated random walk reduces the variance but does not affect the mean encounter rate (Hutchinson and Waser 2007). Our model used a binary distinction between habitat and matrix. Matrix composition is an important determinant of species response to habitat loss and fragmentation (Ricketts 2001; Abouelezz et al. 2018), and the heterogeneity within the matrix likely has consequences for animal movement. Additional complexity in the matrix and the landscape in general are easily implemented into agent-based models through the implementation of GIS datasets (e.g. Lane-deGraaf et al. 2013). Lastly, incorporating other habitat-dependent movement characteristics in addition to boundary crossing behavior is a particularly promising future direction as animals change directionality and speed of movement depending on habitat associated factors such as resource density (Kuefler and Haddad 2006) and perceived risks (Nickel et al. 2021). This direction is particularly important to

explore since other movement metrics such as total displacement and tortuosity may not be independent of boundary crossing behavior (Kuefler et al. 2010).

Animal movements are not driven solely by the physical landscape but also by myriad factors associated with the heterogeneity in that landscape. Our model does not test how habitat loss and fragmentation impact the components of movement (Nathan et al. 2008); instead, it examines the effect of a particular external factor (the physical structure of the landscape) on the movement path, and the resultant first encounter rate (Fig. 4-5). Thus we can either consider the effect of the physical landscape on movement either in isolation (just the physical structure) or as a summed response to the physical landscape and the entirety of the associated perceived distribution of resources and threats. Essentially, the movement path is an emergent result from interaction between the three movement components (internal state, movement capacity, and navigational capacity) and several external factors – the spatial distribution of resources, competitors, and antagonists (Nathan et al. 2008). In other words, the movement behavior that leads to the encounter rate between predator and prey in our model (and in general) is in part driven by the perceived probability of said encounter. However, the movement of the predator and prey will also be influenced by several other factors such as the avoidance of other natural predators (e.g. Scheuerell and Schindler 2003; Hebblewhite and Merrill 2009), humans (Ciuti et al. 2012; Prokopenko et al. 2017), competitors (Leone and Estévez 2008; Laskowski and Bell 2013) and pursuit of resources or alternate prey (Mueller et al. 2011; Abrahms et al. 2021). For example, while movement for prey may be driven in part by the avoidance of predators, Fortin et al (2013) found that the overall movement behavior is also driven by the avoidance of humans which results in aggregation near disturbed areas which puts prey at higher risk of encountering predators. If we consider intraguild predation, the movement behavior of the predator is more

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likely to track other prey species rather than the intraguild subordinate species (Lima 2002).

Boundary responses such as those we modeled for our different scenarios are inherently based in the physical, risk, and resource landscapes that each species evolved in (Fahrig 2007), and if the summed movement path (i.e. any real-world movement path) shows aggregation within habitat types, our framework can be used to assess the encounter rate. The further along the spectrum the considered predator and prey are from habitat preference to habitat dependence (generalists to specialists, as per Keinath et al. 2017, or specialists to dependents, as per Chetcuti et al. 2020), our model becomes more directly applicable to real-world scenarios even considering solely the physical landscape and excluding associated factors. Alternatively, based on predator-prey habitat tolerances our model provides null expectations against which deviations due to factors such as fear can be measured.

While our model provides expectations for predation outcomes based on several simple movement response scenarios, the effects of changing landscapes on predation (or more generally, encounter rates) can be determined for real systems empirically. Agent-based models can incorporate considerable further complexity to better fit specific real-world predator-prey systems, and are a particularly useful tool for determining long-term outcomes (Grimm et al. 2005). Vanlandeghem and colleagues (2021) provide an excellent example of using an ABM to determine how predation rates are impacted by the landscape, by parameterizing agents with GPS collar data. Alternatively, predator and prey biologger data can be used to determine the effect of habitat heterogeneity on movement through approaches such as integrated step-selection (Avgar et al. 2016; Dickie et al. 2020) and paired with mortality surveys. Given advancements in biologger technology and modeling methods that allow fine-scale

characterization of animal movement, we can more definitively translate anthropogenic land use change into their effects on species interactions.

Conclusions

Our simple comparative framework based on a commonly derived movement metric (habitat selection) will allow researchers to use movement data to build expectations for how a changing landscape could affect predator-prey interactions. We demonstrate the consequences that habitat loss/fragmentation mediated movement can have even without the loss of species, and we highlight the need to empirically quantify changes to interaction rates.

Acknowledgements
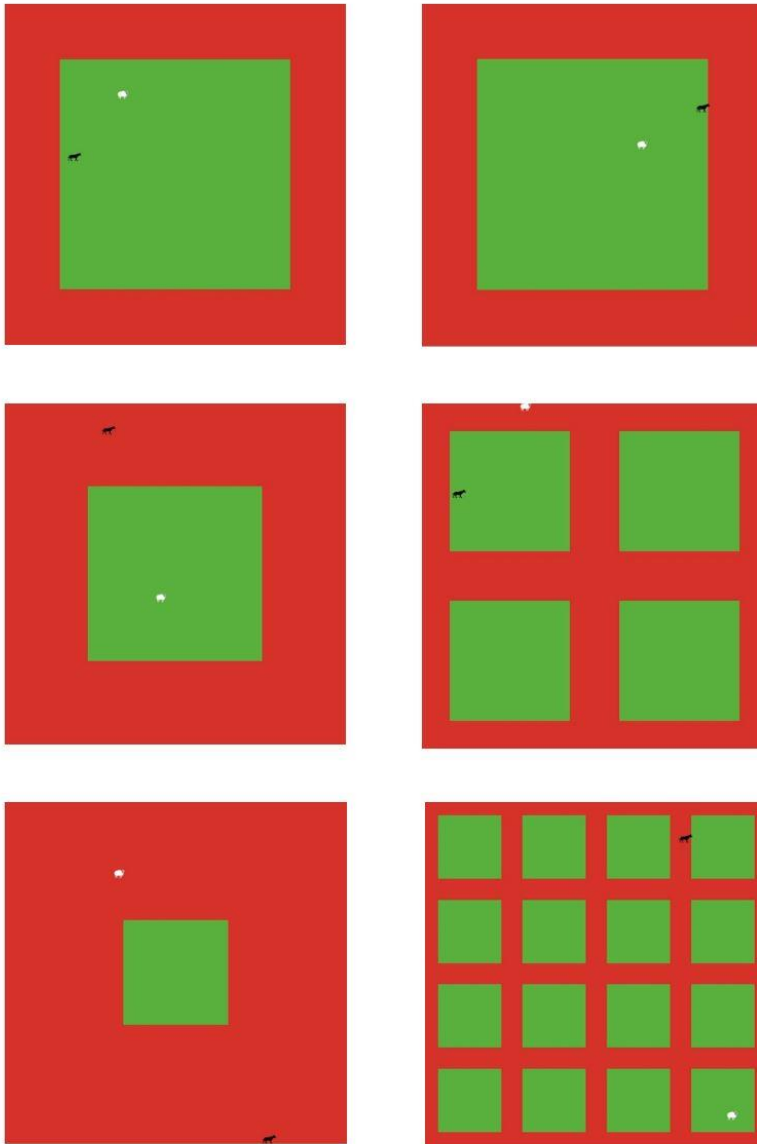
Fig. 4-1. Habitat (green) was modeled as a square patch of forest within matrix (red) in a torus. For habitat amount, the habitat was modeled as a single square forest patch. For example, column A shows 50%, 25% and 10% forest respectively. For habitat configuration, 50% forest was modeled with different amounts of edge, with column B showing the three different configurations from least fragmented (least edge) to most fragmented (most edge)
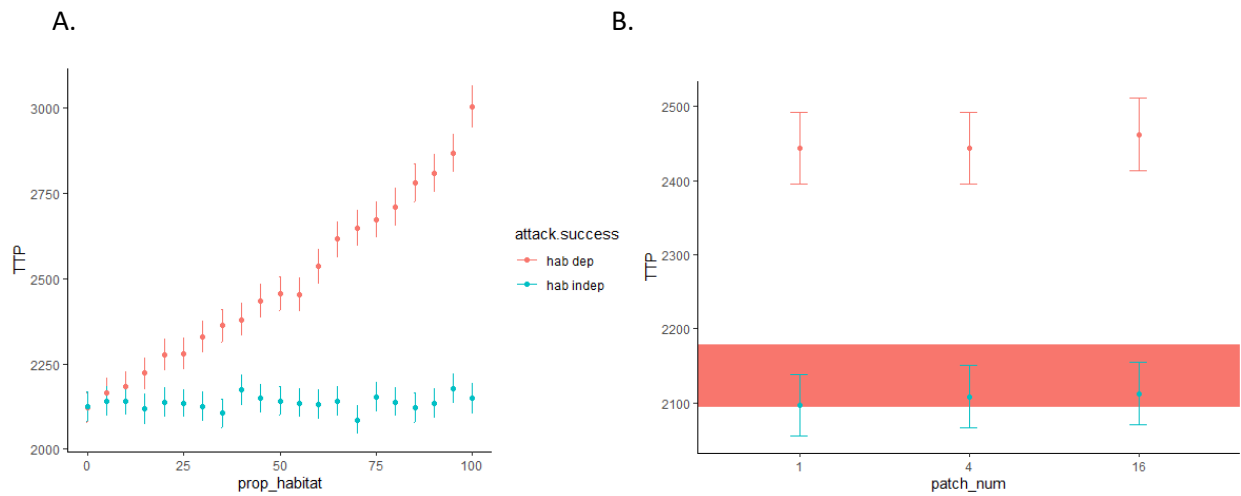
Fig. 4-2. Null models: time-to-predation (TTP) plotted with 95% confidence intervals for both predator and prey with no habitat preference. A. TTP measured with increasing forest B. TTP compared across different amounts of fragmentation (50% habitat). If the attack rate was habitat independent ('hab indep') there was a 50% chance of destruction upon encounter regardless of habitat type; for 'hab dep' there was a lower chance of successful attack (25% instead of 50%) in forest compared to matrix.
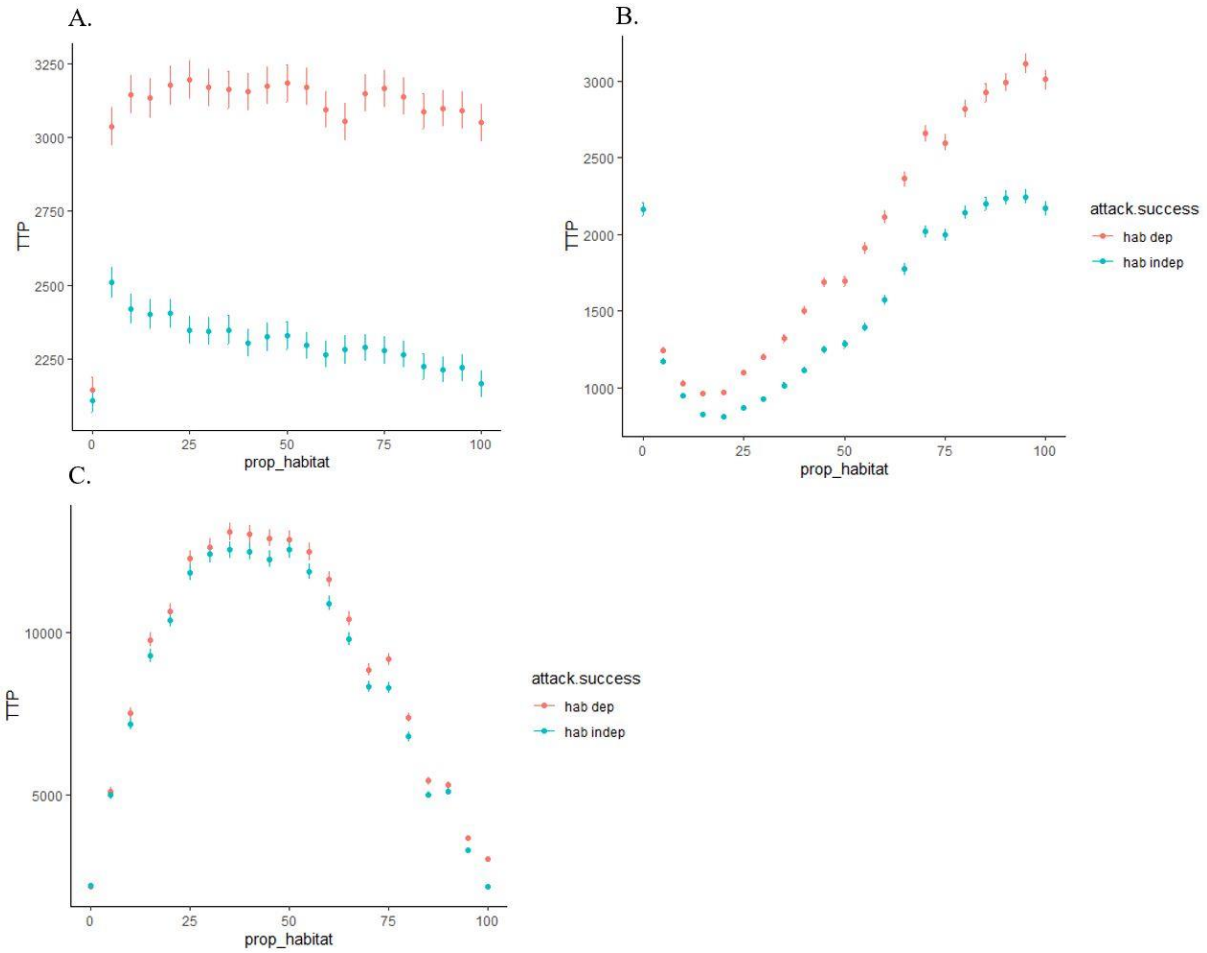
Fig. 4-3. The effect of habitat <u>amount</u> on TTP. A. Predator forest preference, prey no preference; B. predator forest preference, prey forest preference; C. predator matrix preference, prey forest preference. If the attack rate was habitat independent ('hab indep') there was a 50% chance of destruction upon encounter regardless of habitat type; for 'hab dep' there was a lower chance of successful attack (25% instead of 50%) in forest compared to matrix.

Habitat independent attack rate   Habitat dependent attack rate
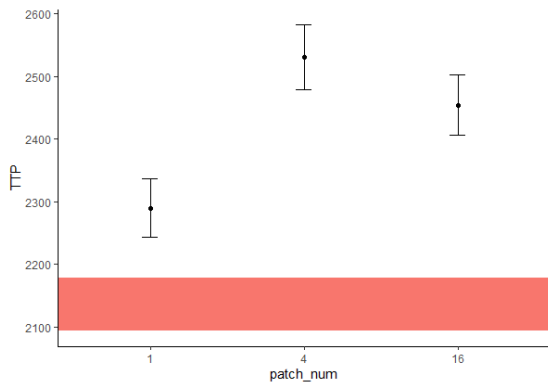
A.   D.
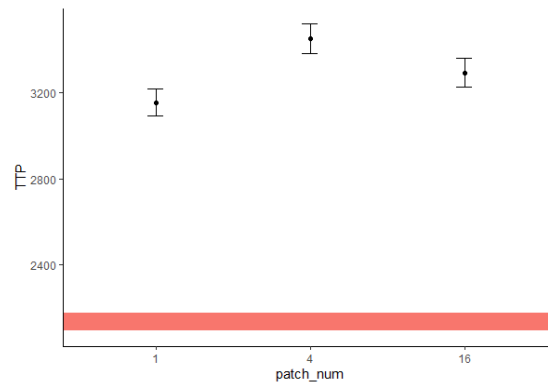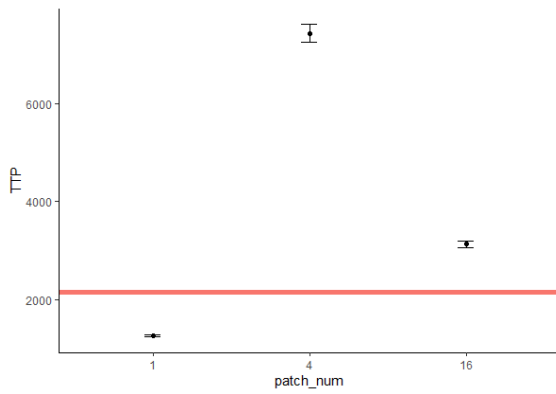
B.   E.
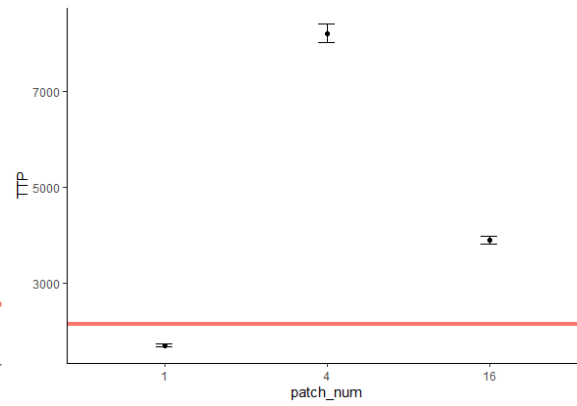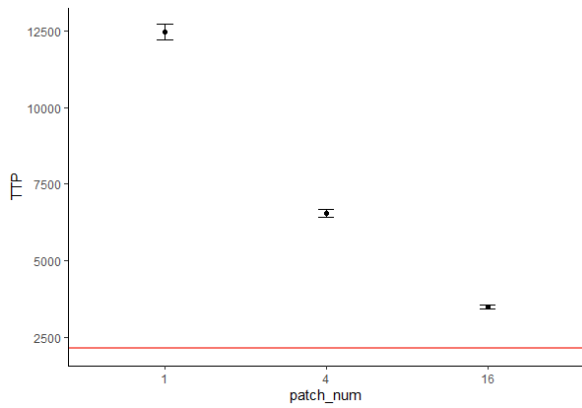
C.   F.
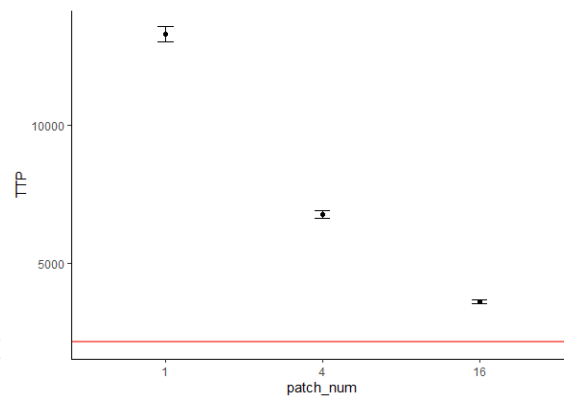
Fig. 4-4. The effect of habitat <u>configuration</u> on TTP. A. Predator habitat preference, prey no

preference; B. predator habitat preference, prey habitat preference; C. predator matrix

preference, prey habitat preference. D-F. The same as A-C, but with a lower probability of successful attack in habitat (0.25) vs matrix (0.50). The reference point is 95% confidence interval for TTP with a neutral response (no habitat preference) predator and prey.
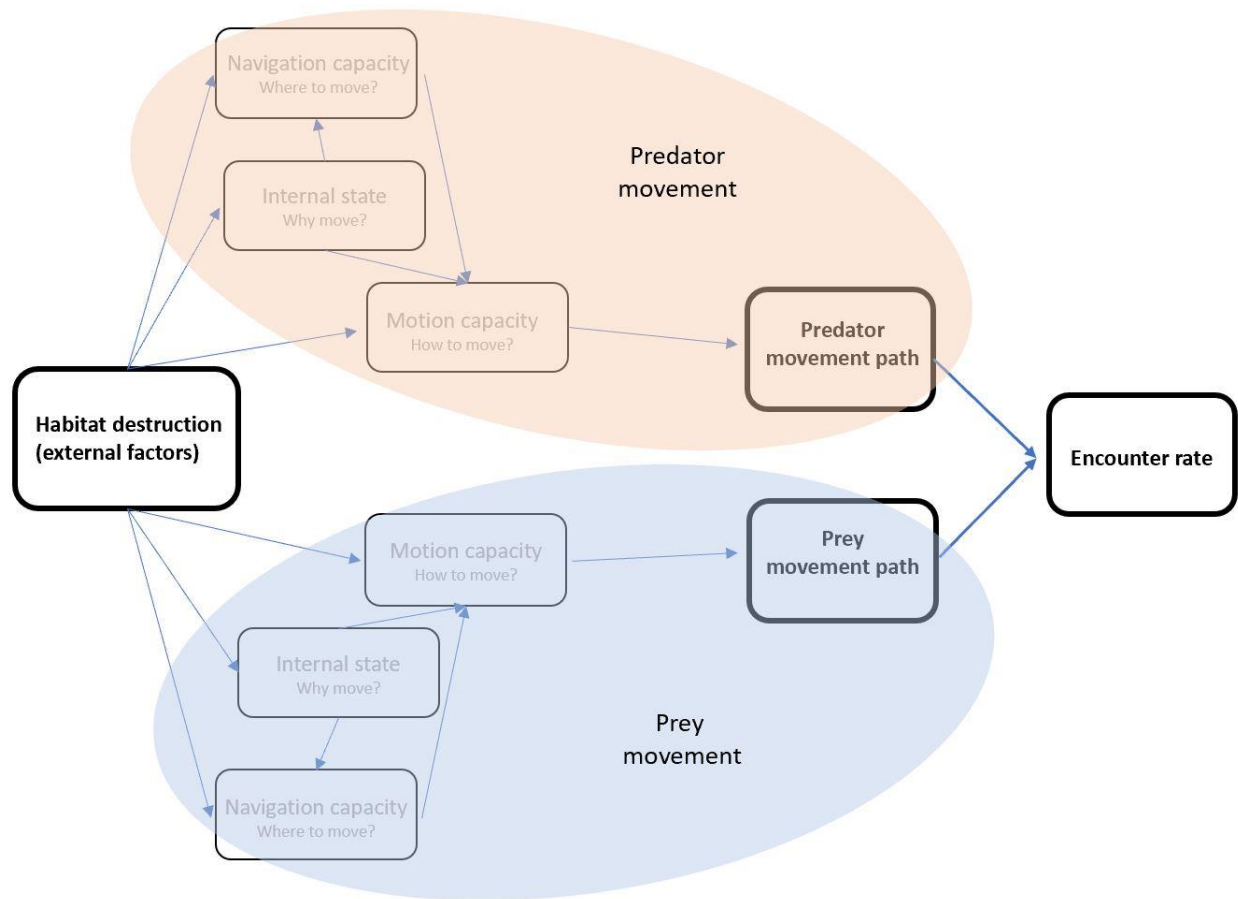
Fig. 4-5. The general movement ecology conceptual framework adapted from Nathan et al. (2008) to examine the effects of habitat destruction (a specific external factor) on the predator-prey interaction via encounter rates. This framework represents the movement of an individual, and we can use it to examine the encounter rate between an overlapping predator and prey individuals. To expand it to population level consequences for the predator-prey interaction we can generalize the habitat-dependent movement behavior for each species (in our simulations: 'neutral', 'forest', or 'matrix' preference).

Chapter VI

Conclusions

This dissertation explores mesocarnivore species' responses and sensitivity to anthropogenic landscape changes at both spatial and temporal dimensions. Chapters II and III explore temporal aspects, across an urban-rural gradient (Chapter II) and in an agricultural system (Chapter III). Chapters III and IV focus on spatial responses, including time lagged responses to habitat, and habitat-mediated response to domestic dogs. Chapter V examines the finer scale outcomes for species interactions that can occur given spatiotemporal overlap based on different movement behaviors.

Key take-home messages

The spatial components of this dissertation highlight that the correlation between the human-modified landscape structure (such as remnant habitat amount and configuration) and habitat generalist mesocarnivore space use may be hidden. It is tempting to think of habitat generalist species as being resilient to fluctuations in the landscape composition; after all, they persist or expand into areas where many other species are excluded. Indeed, this seems to be the initial takeaway from the Chapter III results. However, the finding that dog occupancy was a driver of culpeo occupancy demonstrated that the landscape structure was indeed reflected in culpeo space use, even though the effect was hidden by a mediating antagonist (the dogs). Chapter IV provided evidence of another hidden driver in the form of a time lag, further supporting the idea that the spatial use of even habitat generalists can be affected by changes to the landscape.

Taken together, the results from the Chile system highlight the multiple drivers that species must balance with potential tradeoffs such as different sources of risk (e.g., multiple predator species) and obtaining resources in human-modified landscape. If occupancy of a native species and an antagonist are characterized by different amounts of time lag areas of the current landscape may pose as risky areas with higher encounter probability. For example, if native species occupancy is best described by a past landscape, and an introduced predator of that species instead tracks the current landscape, the mismatch could lead to zones with higher predation risk. Even considering current landscape drivers in isolation, the resilience to one aspect of anthropogenic change could mean susceptibility to another. For example, the resilience of chillas to forest loss results in higher spatial overlap with dogs, and thus increased susceptibility to predation and disease spillover. The risks that come with human-modified landscapes may be even more pronounced at the extreme of urban systems, which bring higher exposure to mortality from roads, exposure to toxicants, and dogs (Murray et al. 2019; Leighton et al. 2022). While human-modified landscapes may lessen the impacts of larger natural antagonists on mesocarnivores, these areas should not be assumed to be safe the wildlife that inhabit them.

Mesocarnivores may be able to mitigate threats that are spatially unavoidable through the partitioning of time (Broekhuis et al. 2013; Bischof et al. 2014); this is a major mechanism for wildlife to avoid humans in human-modified landscapes (Podgórski et al. 2013; Gaynor et al. 2018). However, when there are many competing drivers that wildlife must balance, even antagonists may show broad overlap in space and time (Smith et al. 2018). The temporal results from Chapters II and III provided corroborating evidence in two different systems. In both urban Michigan and agricultural Los Lagos, the low overlap with peak human or human associate

activity also meant that temporal overlap between native species was high. This could either mean that the overlapping species will interact with potentially negative consequences, or that there is avoidance at a finer scale that we are unable to detect (Hammond et al. 2012; Suraci et al. 2022).

Future directions

Presence-absence data paired with appropriate modeling methods provide a powerful and noninvasive methodology for assessing drivers of space and time use (Broennimann et al. 2012; Cusack et al. 2017; Zanni et al. 2021). The relative ease of obtaining presence-absence data for multiple species across large geographic areas noninvasively makes it a valuable part of the conservation toolkit. In a multispecies context, we can use presence-absence data to determine spatial and temporal overlap or cooccurrence patterns as useful metrics for determining potential consequences for interactions between species (Cusack et al. 2017; Karanth et al. 2017), which we can extend to determine the implications that anthropogenic pressures have for interactions (Moll et al. 2018). However, establishing general overlap in space and time does not definitively mean that two species are interacting, as the perception and response to cues between species play out at finer scales that we are able to detect with noninvasive methods (Suraci et al. 2022). Finer scale movement data, which condenses the various stimuli (perceptions of risks, detection of resources) to a single measurable response, allows us to bridge the gap between the broader patterns we find through presence-absence data and the encounter rates which are more informative metrics of interactions (Deuel et al. 2017; Rafiq et al. 2020). Chapter V is a simulated example of a future direction in which we can test how variation in finer scale metrics (movement) can confirm or demonstrate deviations from the expectations that we derive from spatiotemporal overlap. Movement data that can be collected at increasingly higher resolutions,

giving us a window into finer scale use of space and time of wildlife (Walker et al. 2015; Magowan et al. 2022). Pairing movement data with presence-absence data provide a powerful combination for studying human impacts on wildlife. An initial occupancy-based approach can identify important spatiotemporal drivers and potential community consequences. A subsequent targeted movement approach can then be used to explore the finer scale mechanisms driving spatiotemporal patterns, or to examine the interaction consequences.

While digging into finer scale dynamics of the presented study systems will yield valuable insights into interactions, it is important to consider how generally applicable the results from this dissertation are across different mesocarnivore communities in a variety of human-modified landscapes. Presence-absence or movement datasets for mesocarnivores exist in other agricultural systems, and the impacts of dogs are increasingly being recorded (e.g. Zapata-Ríos and Branch 2018; Carricondo-Sanchez et al. 2019). For example, Indian foxes and golden jackals in Maharashtra, India present a similar system to the chillas and culpeos I surveyed in Los Lagos, with documented impacts of dogs on the Indian fox (*Vulpes bengalensis*) (Vanak et al. 2009; Katna et al. 2022). Looking for similar drivers across a variety of systems will allow us to build a better understanding of where mesocarnivores are within human-modified landscapes, and how their distributions will change as landscapes continue to change. For example, comparing the sensitivity of the spatial use of culpeos, coyotes, golden jackals, and black-backed jackals to past landscapes or the presence of dogs would elucidate if mid-sized carnivores globally respond a similar way as landscapes are converted from natural systems into agricultural ones. Comparing the spatiotemporal drivers of the same mesocarnivore community across different landscapes is as important as comparing different analogous mesocarnivores across systems. While limited to temporal use, the results of Chapter II clearly demonstrated that variation in both individual

species use and overlap between species exists across a gradient of landscapes, including when comparing different types of human-dominated landscapes. This lesson should be applied when examining systems for hidden drivers of spatial use as well. For example, we could hypothesize that in an urban system, time lags would be practically nonexistent given the harshness of the matrix compared to an agricultural system. Such a comparison could easily be implemented with currently available datasets in North America (e.g., Snapshot USA), including with the dataset that was used for Chapter II.

Implications

The implications of understanding the different pathways through which the human-modified landscapes drive habitat generalist mesocarnivore space and time use are rooted in conservation. This may be surprising since common and widespread generalist mesocarnivores (e.g. most study species described in this dissertation) are not typical conservation targets (Marneweck et al. 2021). However, I make an argument for studying mesocarnivores in the context of conservation for two reasons. First, habitat generalist mesocarnivores may not actually be faring as well as we often assume. Second, mesocarnivores are linked to wildlife in more pristine areas. I expand on each of these points below.

Despite the potential benefits humans bring (food subsidies, exclusion of larger predators and competitors), mesocarnivore can incur high costs in human-modified landscapes in the form of novel sources of mortality (Vanak and Gompper 2010; Acosta-Jamett et al. 2011; Serieys et al. 2019; Nieszała and Klich 2021). Additionally, as I outlined above in the key takeaways, avoidance of humans can cause increased pressure on smaller mesocarnivores because of reduced niche partitioning (Smith et al. 2018). To persist in human-modified landscapes, even generalist mesocarnivores use habitat refuges (Nickel et al. 2020). Discerning how habitat

generalist species are linked to these refuges in the landscape, whether it is through human associated species or a delayed response, may help us uncover sensitivities which would otherwise go unnoticed. Broekman et al. (2022) corroborated this idea by showing that accounting for the effects of time lags can result in meeting the criteria for a higher (greater conservation priority) IUCN red list category, even for two species that are not habitat specialists. In an era of rapid global change, it may be particularly fruitful to be vigilant in areas where wildlife are already facing numerous stressors (i.e. in human-modified landscapes).

Species that are more typical conservation targets are often linked to mesocarnivores, and so understanding the impacts that human pressures have on the persistence, abundance, and interactions of mesocarnivores are of importance for protecting these species (León et al. 2017; Figueiredo et al. 2021). Generalist mesocarnivores are a particularly important link between the human world and less human tolerant species since they use and move between highly human-modified areas and habitat refuges (Andersen et al. 2017; Rodriguez et al. 2021). Mesocarnivores are more likely to interact with human associates (i.e. cats, dogs) that are reservoirs of pathogens in more modified areas of the landscape, and are thus are intermediaries that 'translate' human pressures such as the heightened disease spillover risk or transmission of parasites to other wildlife that would normally have lower exposure to human associates (Allen et al. 2009; Velasco-Villa et al. 2017; Figueiredo et al. 2021; Malmberg et al. 2021). Determining the amount of spatiotemporal overlap between mesocarnivores and both of these key groups (human associates, other wildlife) thus has implications for conservation in the face of changing landscapes. For example, based on the results from Chapter III, we would expect increased deforestation in the coastal forests of Los Lagos to both increase the occupancy of chilla and the exposure of chillas to dogs. This would also likely lead to higher overlap between chillas and the

endangered Darwin's fox (*Lycalopex fulvipes*). The potential negative consequences for the Darwin's fox in this hypothetical situation are twofold: 1) through competition and intraguild predation by chillas on the smaller Darwin's fox and 2) the increase overlap between chillas and dogs would have disease transmission implications for the Darwin's fox as well, since chillas use both open habitats and forest refuges. Movement data for the species in question would allow us to approximate encounter rates and better translate potential consequences into actual consequences.

Summary

Despite habitat generality being a key trait for species such as many mesocarnivores to survive or even thrive in human-modified landscapes, it is habitat driven space and time use that is a key part of their ecology in these systems. Finding these habitat sensitivities are difficult because they may be dependent on other species, be obscured by time lags, or manifest at fine scales that are hard to detect. However, doing so will improve our understanding of how wildlife use human-modified landscapes. This more comprehensive understanding is key to maintaining the positive impacts that mesocarnivores while mitigating the negative impacts on other wildlife and humans within and around landscapes that are increasingly modified by humans.

Fig. S1.1 Concurrent surveys between sites used in analysis. At least two surveys were

conducted at each site between 2015 and 2020. Surveys run chronologically from right to left;

those surveys that have two survey periods within a year are surveys that were run through

December, into the following year (e.g. HMC 2017 ran from July 2017 through May 2018).

Table S1.1. Raccoon activity between sites using Mardia-Watson-Wheeler test. W is the test statistic (approximately Chi-sq distributed), and associated degrees of freedom and *p* value are included. Temporal overlap (Δ) coefficients and 95% confidence intervals are also included to assess the overlap in activity patterns between sites. Raccoon activity at each site was based off the aggregated raccoon triggers for all surveys with that site.

Site Comparison	W	*df*	*pvalue*	$\Delta_{overlap}$	Δ (CI)
HMC vs UMBS	50.001	2	**0.00**	0.79	0.75-0.83
HMC vs SNWR	40.358	2	**0.00**	0.84	0.79-0.87
HMC vs DMP	80.085	2	**0.00**	0.76	0.72-0.80
UMBS vs SNWR	9.654	2	**0.01**	0.90	0.88-0.93
UMBS vs DMP	9.54	2	**0.01**	0.94	0.91-0.96
SNWR vs DMP	63.218	2	**0.00**	0.88	0.87-0.90
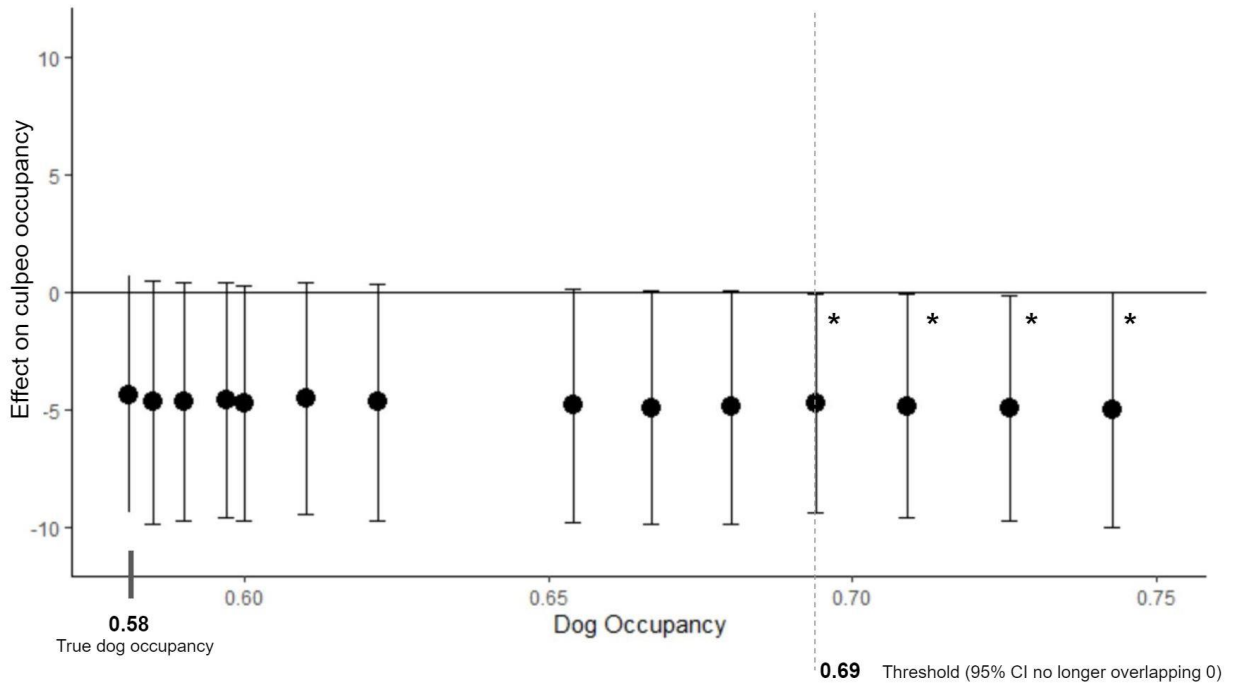
Figure S2.1. The effect of a simulated increase in dog occupancy across the landscape on the

beta coefficient and 95% confidence interval for the *dogo* covariate in the culpeo occupancy

model. *represents a significant beta coefficient.
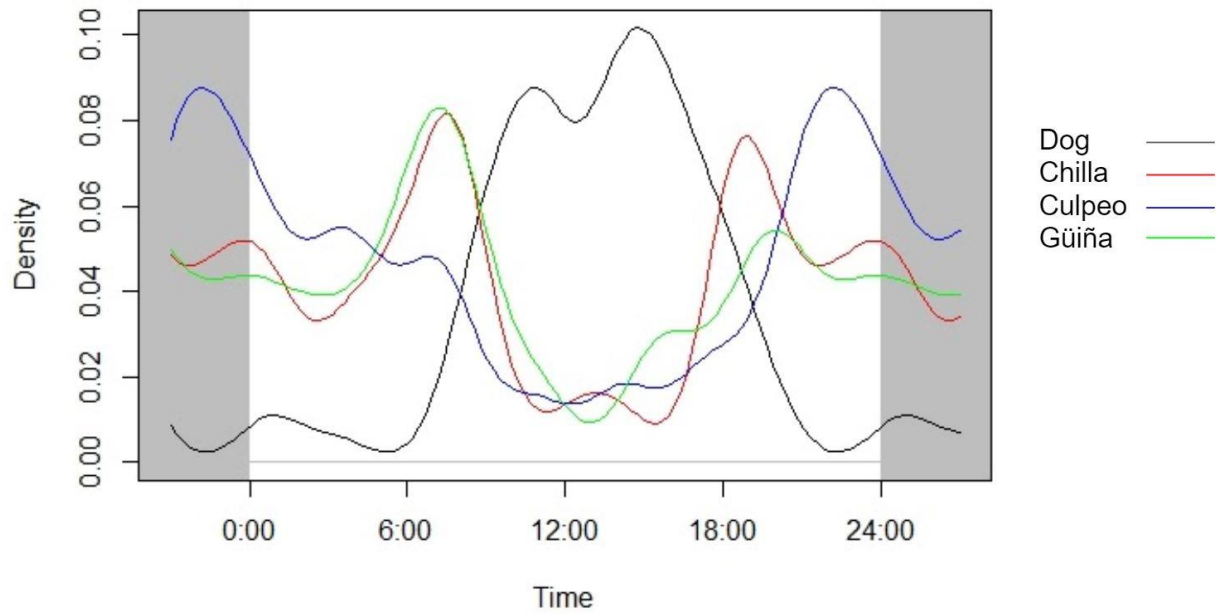
Figure S2.2. 24-hour activity patterns of all four study species. Dogs are distinct from native species in having a clearly diurnal activity pattern.

Table S2.1. Overlap coefficients (Δ) and Mardia-Watson-Wheeler test for homogeneity of means for every pairwise combination of the study species. Δ_4 was used for every comparison except for those pairs containing the culpeo, where Δ_1 was used to account for lower number of triggers.

Comparison	Δ Overlap (95% CI)	W statistic	*p-value*
Chilla-Dog	0.40 (0.25-0.44)	83.62	<0.001
Culpeo-Dog	0.35 (0.22-0.48)	42.96	<0.001
Guigna-Dog	0.43 (0.30-0.56)	47.84	0.001
Chilla-Culpeo	0.78 (0.66-0.89)	5.02	0.08
Chilla-Guina	0.89 (0.80-0.97)	0.47	0.79
Guina-Culpeo	0.78 (0.75-1.03)	4.79	0.09

Appendix C.
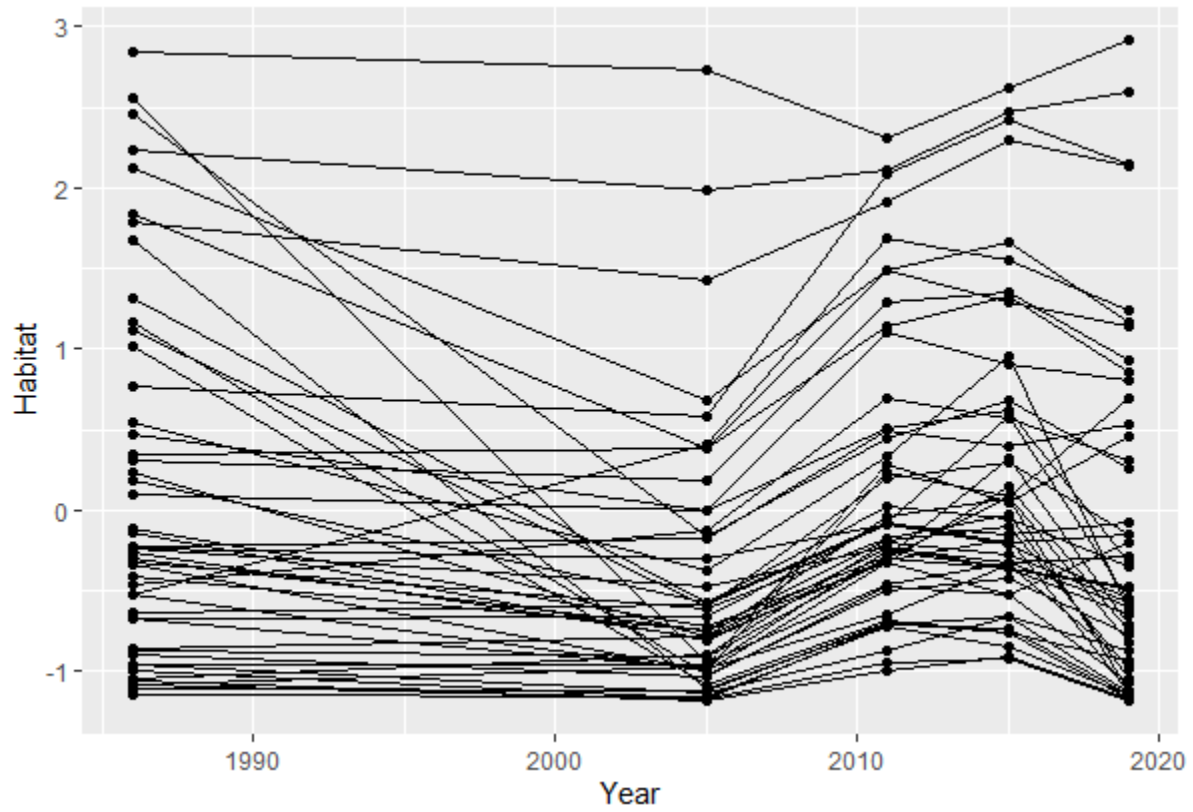
Fig. S3.1. Habitat amount within 1km buffer of each camera. Habitat amount (measured in m^2) was standardized.
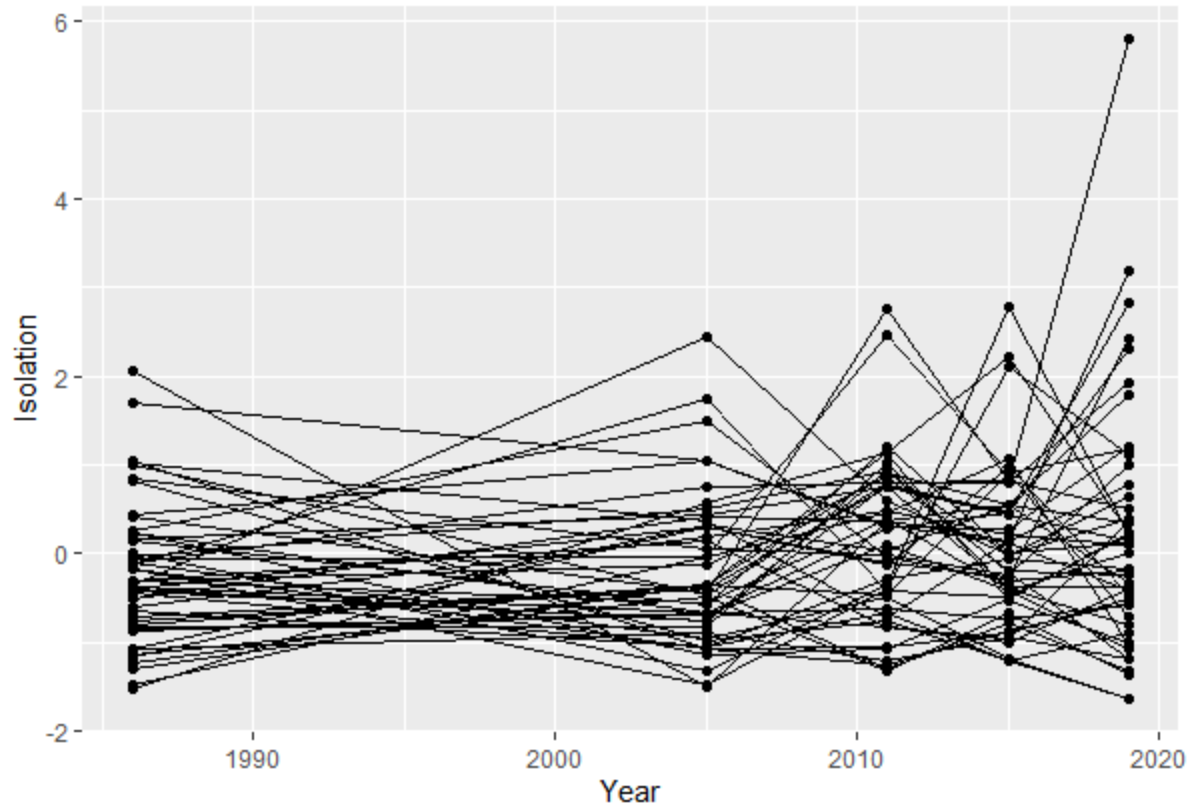
Fig. S3.2. Average patch isolation for patches within and intersecting 1km buffer of each

camera. Patch isolation (measured in m) was standardized.
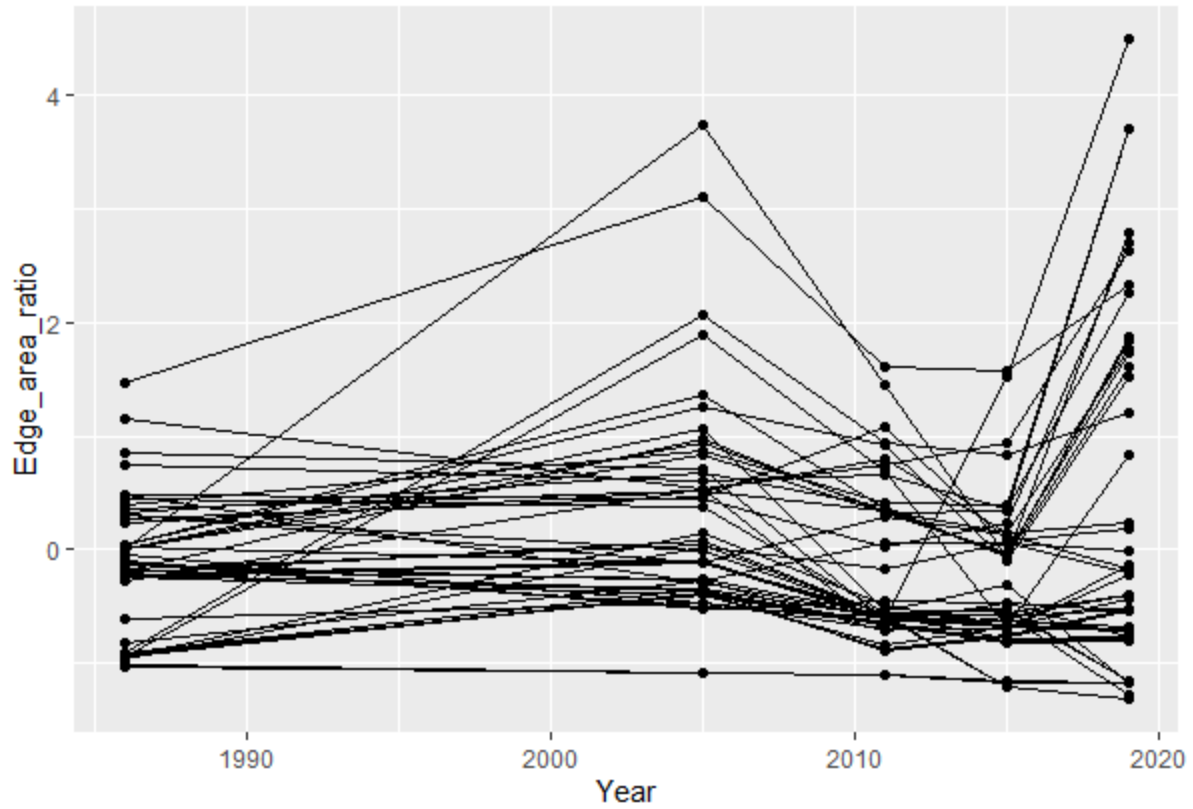
Fig. S3.3. Total edge/area ratio for patches within and intersecting 1km of each camera.

Edge/area ratio (measured in m/m^2) was standardized.

Appendix D.

Table S4.1. Summary statistics for habitat configuration (50% habitat) simulations. TTP: mean time to predation. Standard deviation, error, and confidence intervals are for variation in TTP.

attack success	predator	prey	# patches	# sims	TTP	sd	se	ci
hab indep	neutral	neutral	1	10000	2096.187	2128.933	21.28933	41.73136
hab indep	neutral	neutral	4	10000	2108.052	2132.436	21.32436	41.80005
hab indep	neutral	neutral	16	10000	2112.288	2169.436	21.69436	42.52531
hab dep	neutral	neutral	1	10000	2443.549	2481.691	24.81691	48.64615
hab dep	neutral	neutral	4	10000	2442.931	2469.661	24.69661	48.41032
hab dep	neutral	neutral	16	10000	2461.898	2500.049	25.00049	49.006
hab indep	forest	neutral	1	10000	2289.744	2382.826	23.82826	46.70818
hab indep	forest	neutral	4	10000	2530.434	2634.862	26.34862	51.64861
hab indep	forest	neutral	16	10000	2454.434	2477.512	24.77512	48.56423
hab dep	forest	neutral	1	10000	3152.577	3179.326	31.79326	62.32119
hab dep	forest	neutral	4	10000	3449.381	3438.867	34.38867	67.40871
hab dep	forest	neutral	16	10000	3290.88	3363.574	33.63574	65.93283
hab indep	forest	forest	1	10000	1253.555	1266.776	12.66776	24.83135
hab indep	forest	forest	4	10000	7447.358	9154.609	91.54609	179.4488
hab indep	forest	forest	16	10000	3128.007	3207.169	32.07169	62.86696
hab dep	forest	forest	1	10000	1684.739	1679.296	16.79296	32.91758
hab dep	forest	forest	4	10000	8212.193	9907.012	99.07012	194.1974
hab dep	forest	forest	16	10000	3883.647	4067.628	40.67628	79.7337
hab indep	matrix	forest	1	10000	12454	13146.95	131.4695	257.7066
hab indep	matrix	forest	4	10000	6541.08	6550.45	65.5045	128.402
hab indep	matrix	forest	16	10000	3483.725	3472.043	34.72043	68.05902
hab dep	matrix	forest	1	10000	13280.7	13955.73	139.5573	273.5603
hab dep	matrix	forest	4	10000	6754.658	6910.98	69.1098	135.4691
hab dep	matrix	forest	16	10000	3599.778	3694.275	36.94275	72.41523

Table S4.2. Summary statistics for habitat amount simulations. TTP: mean time to predation.

Standard deviation, error, and confidence intervals are for variation in TTP.

attack success	predator	prey	prop_habitat	#sims	TTP	sd	se	ci
hab indep	neutral	neutral	0	10000	2124.487	2162.137	21.62137	42.38224
hab indep	neutral	neutral	5	10000	2139.825	2196.246	21.96246	43.05085
hab indep	neutral	neutral	10	10000	2141.833	2159.102	21.59102	42.32274
hab indep	neutral	neutral	15	10000	2118.295	2190.16	21.9016	42.93155
hab indep	neutral	neutral	20	10000	2137.603	2218.63	22.1863	43.48961
hab indep	neutral	neutral	25	10000	2134.267	2126.3	21.263	41.67977
hab indep	neutral	neutral	30	10000	2125.237	2166.608	21.66608	42.46987
hab indep	neutral	neutral	35	10000	2105.695	2121.844	21.21844	41.59241
hab indep	neutral	neutral	40	10000	2173.252	2266.478	22.66478	44.42753
hab indep	neutral	neutral	45	10000	2148.335	2169.242	21.69242	42.52151
hab indep	neutral	neutral	50	10000	2141.925	2175.485	21.75485	42.64389
hab indep	neutral	neutral	55	10000	2135.158	2169.029	21.69029	42.51734
hab indep	neutral	neutral	60	10000	2130.965	2175.852	21.75852	42.65109
hab indep	neutral	neutral	65	10000	2141.905	2156.658	21.56658	42.27484
hab indep	neutral	neutral	70	10000	2085.169	2143.89	21.4389	42.02456
hab indep	neutral	neutral	75	10000	2153.31	2188.96	21.8896	42.90802
hab indep	neutral	neutral	80	10000	2138.792	2177.722	21.77722	42.68773
hab indep	neutral	neutral	85	10000	2122.414	2155.284	21.55284	42.24791
hab indep	neutral	neutral	90	10000	2133.569	2175.62	21.7562	42.64654
hab indep	neutral	neutral	95	10000	2176.851	2221.806	22.21806	43.55188
hab indep	neutral	neutral	100	10000	2150.268	2201.37	22.0137	43.15127
hab dep	neutral	neutral	0	10000	2121.837	2150.814	21.50814	42.16029
hab dep	neutral	neutral	5	10000	2165.48	2211.373	22.11373	43.34736
hab dep	neutral	neutral	10	10000	2184.423	2213.246	22.13246	43.38407
hab dep	neutral	neutral	15	10000	2223.435	2270.5	22.705	44.50636
hab dep	neutral	neutral	20	10000	2276.744	2305.152	23.05152	45.18562
hab dep	neutral	neutral	25	10000	2278.899	2350.385	23.50385	46.07228
hab dep	neutral	neutral	30	10000	2329.989	2363.284	23.63284	46.32513
hab dep	neutral	neutral	35	10000	2361.959	2403.454	24.03454	47.11254
hab dep	neutral	neutral	40	10000	2379.764	2444.147	24.44147	47.9102
hab dep	neutral	neutral	45	10000	2434.541	2488.003	24.88003	48.76987
hab dep	neutral	neutral	50	10000	2456.69	2534.036	25.34036	49.6722
hab dep	neutral	neutral	55	10000	2452.281	2497.859	24.97859	48.96306
hab dep	neutral	neutral	60	10000	2536.263	2591.391	25.91391	50.79649
hab dep	neutral	neutral	65	10000	2616.645	2604.466	26.04466	51.05277
hab dep	neutral	neutral	70	10000	2647.686	2682.133	26.82133	52.57521
hab dep	neutral	neutral	75	10000	2672.448	2680.943	26.80943	52.55187

hab dep	neutral	neutral	80	10000	2710.177	2782.218	27.82218	54.53708
hab dep	neutral	neutral	85	10000	2781.179	2821.271	28.21271	55.30259
hab dep	neutral	neutral	90	10000	2807.908	2850.7	28.507	55.87945
hab dep	neutral	neutral	95	10000	2868.15	2863.161	28.63161	56.12371
hab dep	neutral	neutral	100	10000	3005.642	3041.924	30.41924	59.62784
hab indep	forest	neutral	0	10000	2109.81	2158.53	21.5853	42.31154
hab indep	forest	neutral	5	10000	2507.881	2671.275	26.71275	52.36237
hab indep	forest	neutral	10	10000	2419.08	2539.856	25.39856	49.78628
hab indep	forest	neutral	15	10000	2401.856	2473.951	24.73951	48.49442
hab indep	forest	neutral	20	10000	2403.33	2492.986	24.92986	48.86755
hab indep	forest	neutral	25	10000	2346.412	2408.581	24.08581	47.21304
hab indep	forest	neutral	30	10000	2343.792	2440.234	24.40234	47.8335
hab indep	forest	neutral	35	10000	2348.269	2429.645	24.29645	47.62593
hab indep	forest	neutral	40	10000	2302.693	2370.72	23.7072	46.47089
hab indep	forest	neutral	45	10000	2323.769	2422.264	24.22264	47.48125
hab indep	forest	neutral	50	10000	2328.91	2384.978	23.84978	46.75036
hab indep	forest	neutral	55	10000	2295.071	2344.466	23.44466	45.95625
hab indep	forest	neutral	60	10000	2265.449	2309.471	23.09471	45.27027
hab indep	forest	neutral	65	10000	2283.122	2362.687	23.62687	46.31342
hab indep	forest	neutral	70	10000	2287.422	2327.6	23.276	45.62564
hab indep	forest	neutral	75	10000	2277.851	2325.489	23.25489	45.58426
hab indep	forest	neutral	80	10000	2265.649	2315.261	23.15261	45.38378
hab indep	forest	neutral	85	10000	2224.183	2289.017	22.89017	44.86935
hab indep	forest	neutral	90	10000	2212.836	2249.295	22.49295	44.0907
hab indep	forest	neutral	95	10000	2219.928	2284.786	22.84786	44.7864
hab indep	forest	neutral	100	10000	2167.458	2164.595	21.64595	42.43041
hab dep	forest	neutral	0	10000	2146.066	2168.35	21.6835	42.50402
hab dep	forest	neutral	5	10000	3036.52	3308.052	33.08052	64.84447
hab dep	forest	neutral	10	10000	3143.032	3339.694	33.39694	65.46473
hab dep	forest	neutral	15	10000	3133.23	3353.38	33.5338	65.73301
hab dep	forest	neutral	20	10000	3175.081	3465.89	34.6589	67.93842
hab dep	forest	neutral	25	10000	3193.225	3313.466	33.13466	64.9506
hab dep	forest	neutral	30	10000	3168.229	3258.155	32.58155	63.8664
hab dep	forest	neutral	35	10000	3161.039	3257.273	32.57273	63.84911
hab dep	forest	neutral	40	10000	3153.118	3250.648	32.50648	63.71925
hab dep	forest	neutral	45	10000	3173.67	3206.335	32.06335	62.85061
hab dep	forest	neutral	50	10000	3181.9	3252.588	32.52588	63.75727
hab dep	forest	neutral	55	10000	3170.835	3225.651	32.25651	63.22925
hab dep	forest	neutral	60	10000	3093.743	3176.694	31.76694	62.2696
hab dep	forest	neutral	65	10000	3052.909	3078.941	30.78941	60.35344
hab dep	forest	neutral	70	10000	3149.148	3210.372	32.10372	62.92975
hab dep	forest	neutral	75	10000	3164.183	3261.055	32.61055	63.92324

hab dep	forest	neutral	80	10000	3138.292	3155.764	31.55764	61.85932
hab dep	forest	neutral	85	10000	3087.713	3093.896	30.93896	60.64658
hab dep	forest	neutral	90	10000	3097.457	3142.395	31.42395	61.59727
hab dep	forest	neutral	95	10000	3090.882	3175.577	31.75577	62.2477
hab dep	forest	neutral	100	10000	3049.591	3067.797	30.67797	60.13499
hab indep	forest	forest	0	10000	2165.527	2195.606	21.95606	43.0383
hab indep	forest	forest	5	10000	1172.175	1080.213	10.80213	21.17434
hab indep	forest	forest	10	10000	945.5117	838.26	8.3826	16.43158
hab indep	forest	forest	15	10000	823.0832	664.9223	6.649223	13.03382
hab indep	forest	forest	20	10000	812.3072	642.8534	6.428534	12.60122
hab indep	forest	forest	25	10000	866.027	740.7959	7.407959	14.52109
hab indep	forest	forest	30	10000	926.0403	838.0788	8.380788	16.42803
hab indep	forest	forest	35	10000	1015.04	956.0931	9.560931	18.74135
hab indep	forest	forest	40	10000	1112.529	1084.7	10.847	21.2623
hab indep	forest	forest	45	10000	1248.876	1260.46	12.6046	24.70755
hab indep	forest	forest	50	10000	1284.272	1282.142	12.82142	25.13256
hab indep	forest	forest	55	10000	1395.674	1430.11	14.3011	28.03304
hab indep	forest	forest	60	10000	1571.963	1604	16.04	31.44162
hab indep	forest	forest	65	10000	1774.187	1865.932	18.65932	36.57603
hab indep	forest	forest	70	10000	2018.567	2046.115	20.46115	40.10797
hab indep	forest	forest	75	10000	1995.047	2015.771	20.15771	39.51317
hab indep	forest	forest	80	10000	2141.664	2207.906	22.07906	43.27941
hab indep	forest	forest	85	10000	2201.381	2252.133	22.52133	44.14633
hab indep	forest	forest	90	10000	2238.887	2308.903	23.08903	45.25914
hab indep	forest	forest	95	10000	2245.298	2288.145	22.88145	44.85224
hab indep	forest	forest	100	10000	2170.261	2186.87	21.8687	42.86705
hab dep	forest	forest	0	10000	2161.458	2179.627	21.79627	42.72507
hab dep	forest	forest	5	10000	1239.928	1127.79	11.2779	22.10694
hab dep	forest	forest	10	10000	1029.375	862.9105	8.629105	16.91478
hab dep	forest	forest	15	10000	960.621	756.5509	7.565509	14.82992
hab dep	forest	forest	20	10000	970.6101	788.1304	7.881304	15.44894
hab dep	forest	forest	25	10000	1096.942	953.0291	9.530291	18.68129
hab dep	forest	forest	30	10000	1199.42	1101.897	11.01897	21.5994
hab dep	forest	forest	35	10000	1320.032	1248.001	12.48001	24.46333
hab dep	forest	forest	40	10000	1504.421	1460.024	14.60024	28.61941
hab dep	forest	forest	45	10000	1686.315	1669.48	16.6948	32.72517
hab dep	forest	forest	50	10000	1693.976	1711.008	17.11008	33.5392
hab dep	forest	forest	55	10000	1909.576	1939.409	19.39409	38.01632
hab dep	forest	forest	60	10000	2111.226	2148.512	21.48512	42.11516
hab dep	forest	forest	65	10000	2362.934	2351.158	23.51158	46.08743
hab dep	forest	forest	70	10000	2659.514	2708.526	27.08526	53.09255
hab dep	forest	forest	75	10000	2598.871	2667.009	26.67009	52.27875

hab dep	forest	forest	80	10000	2821.204	2883.867	28.83867	56.52959
hab dep	forest	forest	85	10000	2923.601	2973.096	29.73096	58.27867
hab dep	forest	forest	90	10000	2991.741	3013.237	30.13237	59.06551
hab dep	forest	forest	95	10000	3114.935	3161.844	31.61844	61.9785
hab dep	forest	forest	100	10000	3011.226	3056.78	30.5678	59.91903
hab indep	matrix	forest	0	10000	2167.48	2186.744	21.86744	42.86459
hab indep	matrix	forest	5	10000	4974.823	5801.547	58.01547	113.722
hab indep	matrix	forest	10	10000	7165.082	8464.889	84.64889	165.9289
hab indep	matrix	forest	15	10000	9289.15	10379.51	103.7951	203.4594
hab indep	matrix	forest	20	10000	10407.87	11695.86	116.9586	229.2624
hab indep	matrix	forest	25	10000	11856.29	12627.72	126.2772	247.5286
hab indep	matrix	forest	30	10000	12431.44	13555.61	135.5561	265.7173
hab indep	matrix	forest	35	10000	12574.84	13361.37	133.6137	261.9097
hab indep	matrix	forest	40	10000	12525.77	13403.36	134.0336	262.7329
hab indep	matrix	forest	45	10000	12288.76	12868.61	128.6861	252.2506
hab indep	matrix	forest	50	10000	12568.46	13364.24	133.6424	261.9659
hab indep	matrix	forest	55	10000	11894.92	12501.1	125.011	245.0467
hab indep	matrix	forest	60	10000	10911.48	11331.97	113.3197	222.1295
hab indep	matrix	forest	65	10000	9801.624	10344.33	103.4433	202.7696
hab indep	matrix	forest	70	10000	8346.713	8880.374	88.80374	174.0732
hab indep	matrix	forest	75	10000	8313.878	8840.543	88.40543	173.2924
hab indep	matrix	forest	80	10000	6785.361	7200.472	72.00472	141.1437
hab indep	matrix	forest	85	10000	4975.098	5285.241	52.85241	103.6014
hab indep	matrix	forest	90	10000	5097.391	5460.251	54.60251	107.0319
hab indep	matrix	forest	95	10000	3283.125	3445.787	34.45787	67.54436
hab indep	matrix	forest	100	10000	2147.788	2228.669	22.28669	43.6864
hab dep	matrix	forest	0	10000	2137.606	2181.459	21.81459	42.76098
hab dep	matrix	forest	5	10000	5104.174	5976.28	59.7628	117.1471
hab dep	matrix	forest	10	10000	7503.637	8798.832	87.98832	172.4748
hab dep	matrix	forest	15	10000	9781.852	11096.91	110.9691	217.5217
hab dep	matrix	forest	20	10000	10661.24	11891.75	118.9175	233.1022
hab dep	matrix	forest	25	10000	12304	13136.28	131.3628	257.4974
hab dep	matrix	forest	30	10000	12658.23	13548.93	135.4893	265.5863
hab dep	matrix	forest	35	10000	13117.03	14077.28	140.7728	275.943
hab dep	matrix	forest	40	10000	13068.41	13855.15	138.5515	271.5889
hab dep	matrix	forest	45	10000	12935.83	13613.08	136.1308	266.8437
hab dep	matrix	forest	50	10000	12888.42	13484.3	134.843	264.3195
hab dep	matrix	forest	55	10000	12513.65	13198.01	131.9801	258.7077
hab dep	matrix	forest	60	10000	11667.13	12261.45	122.6145	240.3491
hab dep	matrix	forest	65	10000	10440.26	10844.56	108.4456	212.5751
hab dep	matrix	forest	70	10000	8860.27	9378.511	93.78511	183.8377
hab dep	matrix	forest	75	10000	9184.251	9655.634	96.55634	189.2699

hab dep	matrix	forest	80	10000	7380.633	7762.959	77.62959	152.1696
hab dep	matrix	forest	85	10000	5413.938	5617.438	56.17438	110.1131
hab dep	matrix	forest	90	10000	5296.875	5443.043	54.43043	106.6946
hab dep	matrix	forest	95	10000	3635.713	3747.447	37.47447	73.4575
hab dep	matrix	forest	100	10000	2993.884	3043.529	30.43529	59.65929

Bibliography

ABOUELEZZ, H. G., T. M. DONOVAN, R. M. MICKEY, J. D. MURDOCH, M. FREEMAN, AND K. ROYAR. 2018. Landscape composition mediates movement and habitat selection in bobcats (Lynx rufus): implications for conservation planning. Landscape Ecology 33:1301–1318.

ABRAHMS, B., E. O. AIKENS, J. B. ARMSTRONG, W. W. DEACY, M. J. KAUFFMAN, AND J. A. MERKLE. 2021. Emerging Perspectives on Resource Tracking and Animal Movement Ecology. Trends in Ecology & Evolution 36:308–320.

ACOSTA-JAMETT, G., W. S. K. CHALMERS, A. A. CUNNINGHAM, S. CLEAVELAND, I. G. HANDEL, AND B. DEC BRONSVOORT. 2011. Urban domestic dog populations as a source of canine distemper virus for wild carnivores in the Coquimbo region of Chile. Veterinary Microbiology 152:247–257.

ADAMS, R. A., AND K. M. THIBAULT. 2006. Temporal resource partitioning by bats at water holes. Journal of Zoology 270:466–472.

ALBERTI, M. 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends in Ecology & Evolution 30:114–126.

ALCOCER-RODRÍGUEZ, M. ET AL. 2021. Evaluating extinction debt in fragmented forests: the rapid recovery of a critically endangered primate. Animal Conservation 24:432–444.

ALLEN, L. J. S. ET AL. 2009. A habitat-based model for the spread of hantavirus between reservoir and spillover species. Journal of Theoretical Biology 260:510–522.

ANDERSEN, G. E., C. N. JOHNSON, L. A. BARMUTA, AND M. E. JONES. 2017. Use of anthropogenic linear features by two medium-sized carnivores in reserved and agricultural landscapes. Scientific Reports 7:11624.

Anon. no date. Osorno climate: Average Temperature, weather by month, Osorno weather averages - Climate-Data.org. <https://en.climate-data.org/south-america/chile/x-region-de-los-lagos/osorno-2047/> (26 July 2020a).

Anon. no date. camtrapR: an R package for efficient camera trap data management - Niedballa - 2016 - Methods in Ecology and Evolution - Wiley Online Library. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12600> (10 April 2021b).

ARMENTERAS, D., J. M. ESPELTA, N. RODRÍGUEZ, AND J. RETANA. 2017. Deforestation dynamics and drivers in different forest types in Latin America: Three decades of studies (1980–2010). Global Environmental Change 46:139–147.

ATHREYA, V., M. ODDEN, J. D. C. LINNELL, J. KRISHNASWAMY, AND U. KARANTH. 2013. Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. PLOS ONE 8:e57872.

AVGAR, T., J. R. POTTS, M. A. LEWIS, AND M. S. BOYCE. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

AVILÉS-RODRÍGUEZ, K. J., AND J. J. KOLBE. 2019. Escape in the city: urbanization alters the escape behavior of Anolis lizards. Urban Ecosystems 22:733–742.

BAI, W. ET AL. 2020. Microhabitat selection by giant pandas. Biological Conservation 247:108615.

BARTLETT, L. J., T. NEWBOLD, D. W. PURVES, D. P. TITTENSOR, AND M. B. J. HARFOOT. 2016. Synergistic impacts of habitat loss and fragmentation on model ecosystems. Proceedings of the Royal Society B: Biological Sciences 283:20161027.

BATZLI, G. O. 1992. Dynamics of Small Mammal Populations: A Review. Pp. 831–850 in Wildlife 2001: Populations (D. R. McCullough & R. H. Barrett, eds.). Springer Netherlands, Dordrecht.

BEASLEY, J. C., Z. H. OLSON, G. DHARMARAJAN, T. S. EAGAN, AND O. E. RHODES. 2011. Spatio-temporal variation in the demographic attributes of a generalist mesopredator. Landscape Ecology 26:937–950.

BEASLEY, J. C., AND O. E. RHODES. 2010. Influence of patch- and landscape-level attributes on the movement behavior of raccoons in agriculturally fragmented landscapes. Canadian Journal of Zoology 88:161–169.

BEKOFF, M., AND E. M. GESE. 2003. Coyote (Canis latrans). USDA National Wildlife Research Center-Staff Publications:224.

BERGER, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology letters 3:620–623.

BERGER, K. M. 2006. Carnivore-Livestock Conflicts: Effects of Subsidized Predator Control and Economic Correlates on the Sheep Industry. Conservation Biology 20:751–761.

BETTS, M. G. ET AL. 2020. Squeezed by a habitat split: Warm ocean conditions and old-forest loss interact to reduce long-term occupancy of a threatened seabird. Conservation Letters 13:e12745.

BROADBENT, E. N., G. P. ASNER, M. KELLER, D. E. KNAPP, P. J. C. OLIVEIRA, AND J. N. SILVA. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141:1745–1757.

BROADLEY, K., A. C. BURTON, T. AVGAR, AND S. BOUTIN. 2019. Density-dependent space use affects interpretation of camera trap detection rates. Ecology and Evolution 9:14031–14041.

BROEKHUIS, F., G. COZZI, M. VALEIX, J. W. MCNUTT, AND D. W. MACDONALD. 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? Journal of Animal Ecology 82:1098–1105.

BROEKMAN, M. J., J. P. HILBERS, A. M. SCHIPPER, A. BENÍTEZ-LÓPEZ, L. SANTINI, AND M. A. HUIJBREGTS. 2022. Time-lagged effects of habitat fragmentation on terrestrial mammals in Madagascar. Conservation Biology.

BROENNIMANN, O. ET AL. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21:481–497.

BROOK, B. W., N. S. SODHI, AND C. J. A. BRADSHAW. 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23:453–460.

BROWN, J. H. 1984. On the Relationship between Abundance and Distribution of Species. The American Naturalist 124:255–279.

BURGER, L. D., L. W. BURGER, AND J. FAABORG. 1994. Effects of Prairie Fragmentation on Predation on Artificial Nests. The Journal of Wildlife Management 58:249–254.

CARDILLO, M. ET AL. 2005. Multiple causes of high extinction risk in large mammal species. Science 309.

CARR, D. L. 2004. Proximate Population Factors and Deforestation in Tropical Agricultural Frontiers. Population and Environment 25:585–612.

CARRICONDO-SANCHEZ, D., M. ODDEN, A. KULKARNI, AND A. T. VANAK. 2019. Scale-dependent strategies for coexistence of mesocarnivores in human-dominated landscapes. Biotropica 51:781–791.

CHEN, D. M. ET AL. 2021. Lemur paparazzi: Arboreal camera trapping and occupancy modeling as conservation tools for monitoring threatened lemur species. American Journal of Primatology 83:e23270.

CHEN, Y., AND S. PENG. 2017. Evidence and mapping of extinction debts for global forest-dwelling reptiles, amphibians and mammals. Scientific Reports 7:44305.

CHEPTOU, P.-O., AND L. G. AVENDAÑO V. 2006. Pollination processes and the Allee effect in highly fragmented populations: consequences for the mating system in urban environments. New Phytologist 172:774–783.

CHEPTOU, P.-O., A. L. HARGREAVES, D. BONTE, AND H. JACQUEMYN. 2017. Adaptation to fragmentation: evolutionary dynamics driven by human influences. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160037.

CHETCUTI, J., W. E. KUNIN, AND J. M. BULLOCK. 2020. Habitat Fragmentation Increases Overall Richness, but Not of Habitat-Dependent Species. Frontiers in Ecology and Evolution 8.

CHITWOOD, M. C., M. A. LASHLEY, S. D. HIGDON, C. S. DEPERNO, AND C. E. MOORMAN. 2020. Raccoon Vigilance and Activity Patterns When Sympatric with Coyotes. Diversity 12:341.

ĆIROVIĆ, D., A. PENEZIĆ, AND M. KROFEL. 2016. Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. Biological Conservation 199:51–55.

CIUTI, S. ET AL. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PloS one 7:e50611.

CLINCHY, M. ET AL. 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behavioral Ecology 27:1826–1832.

COCHRANE, M. A. 2001. Synergistic Interactions between Habitat Fragmentation and Fire in Evergreen Tropical Forests. Conservation Biology 15:1515–1521.

CODLING, E. A., M. J. PLANK, AND S. BENHAMOU. 2008. Random walk models in biology. Journal of The Royal Society Interface 5:813–834.

COLBORN, A. S., C. C. KUNTZE, G. I. GADSDEN, AND N. C. HARRIS. 2020. Spatial variation in diet-microbe associations across populations of a generalist North American carnivore. Journal of Animal Ecology.

COLLINGE, S. K. 2000. Effects of Grassland Fragmentation on Insect Species Loss, Colonization, and Movement Patterns. Ecology 81:2211–2226.

COUSINS, S. A. O., H. OHLSON, AND O. ERIKSSON. 2007. Effects of historical and present fragmentation on plant species diversity in semi-natural grasslands in Swedish rural landscapes. Landscape Ecology 22:723–730.

COUSINS, S. A. O., AND D. VANHOENACKER. 2011. Detection of extinction debt depends on scale and specialisation. Biological Conservation 144:782–787.

CROOKS, K. R. 2002. Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. Conservation Biology 16:488–502.

CROOKS, K. R. ET AL. 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proceedings of the National Academy of Sciences 114:7635–7640.

CROOKS, K. R., C. L. BURDETT, D. M. THEOBALD, C. RONDININI, AND L. BOITANI. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2642–2651.

CROOKS, K. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

CUBAYNES, S., D. R. MACNULTY, D. R. STAHLER, K. A. QUIMBY, D. W. SMITH, AND T. COULSON. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). Journal of Animal Ecology 83:1344–1356.

CUNNINGHAM, C. X., V. SCOLERI, C. N. JOHNSON, L. A. BARMUTA, AND M. E. JONES. 2019. Temporal partitioning of activity: rising and falling top-predator abundance triggers community-wide shifts in diel activity. Ecography 42:2157–2168.

CUSACK, J. J. ET AL. 2017. Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: a comparison of spatiotemporal approaches. Oikos 126:812–822.

DE VOS, J. M., L. N. JOPPA, J. L. GITTLEMAN, P. R. STEPHENS, AND S. L. PIMM. 2015. Estimating the normal background rate of species extinction. Conservation biology 29:452–462.

DEUEL, N. R., L. M. CONNER, K. V. MILLER, M. J. CHAMBERLAIN, M. J. CHERRY, AND L. V. TANNENBAUM. 2017. Gray fox home range, spatial overlap, mated pair interactions and extra-territorial forays in southwestern Georgia, USA. Wildlife Biology 2017.

DEVICTOR, V., R. JULLIARD, AND F. JIGUET. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507–514.

DIAMOND, J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. Proceedings of the National Academy of Sciences 69:3199–3203.

DICKIE, M., S. R. MCNAY, G. D. SUTHERLAND, M. CODY, AND T. AVGAR. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology 89:623–634.

DOHERTY, T. S. ET AL. 2017. The global impacts of domestic dogs on threatened vertebrates. Biological Conservation 210:56–59.

DOHERTY, T. S., AND D. A. DRISCOLL. 2018. Coupling movement and landscape ecology for animal conservation in production landscapes. Proceedings of the Royal Society B: Biological Sciences 285:20172272.

DONADIO, E., AND S. W. BUSKIRK. 2006. Diet, morphology, and interspecific killing in Carnivora. The American Naturalist 167:524–536.

DROGHINI, A., AND S. BOUTIN. 2018. Snow conditions influence grey wolf (Canis lupus) travel paths: the effect of human-created linear features 96:9.

DUCATEZ, S., F. SAYOL, D. SOL, AND L. LEFEBVRE. 2018. Are urban vertebrates city specialists, artificial habitat exploiters, or environmental generalists? Integrative and Comparative Biology 58:929–938.

DUCATEZ, S., AND R. SHINE. 2017. Drivers of Extinction Risk in Terrestrial Vertebrates. Conservation Letters 10:186–194.

DYER, J. L. ET AL. 2014. Rabies surveillance in the United States during 2013. Journal of the American Veterinary Medical Association 245:1111–1123.

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ECHEVERRIA, C., D. A. COOMES, M. HALL, AND A. C. NEWTON. 2008. Spatially explicit models to analyze forest loss and fragmentation between 1976 and 2020 in southern Chile. Ecological Modelling 212:439–449.

ECHEVERRIA, C., D. COOMES, J. SALAS, J. M. REY-BENAYAS, A. LARA, AND A. NEWTON. 2006. Rapid deforestation and fragmentation of Chilean Temperate Forests. Biological Conservation 130:481–494.

ECHEVERRÍA, C., A. C. NEWTON, A. LARA, J. M. R. BENAYAS, AND D. A. COOMES. 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. Global Ecology and Biogeography 16:426–439.

ECHEVERRÍA, C., A. NEWTON, L. NAHUELHUAL, D. COOMES, AND J. M. REY-BENAYAS. 2012. How landscapes change: Integration of spatial patterns and human processes in temperate landscapes of southern Chile. Applied Geography 32:822–831.

ELLINGTON, E. H., AND S. D. GEHRT. 2019. Behavioral responses by an apex predator to urbanization. Behavioral Ecology 30:821–829.

ELLIS, E. C. ET AL. 2021. People have shaped most of terrestrial nature for at least 12,000 years. Proceedings of the National Academy of Sciences 118:e2023483118.

ELMHAGEN, B., AND S. P. RUSHTON. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecology letters 10:197–206.

ELZINGA, J. A., S. VAN NOUHUYS, D.-J. VAN LEEUWEN, AND A. BIERE. 2007. Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape. Basic and Applied Ecology 8:75–88.

EMER, C. ET AL. 2018. Seed-dispersal interactions in fragmented landscapes – a metanetwork approach. Ecology Letters 21:484–493.

FAHRIG, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003–1015.

FAHRIG, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40:1649–1663.

FAHRIG, L. 2017. Ecological Responses to Habitat Fragmentation Per Se. Annual Review of Ecology, Evolution, and Systematics 48:1–23.

FAHRIG, L. ET AL. 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230:179–186.

FARIAS, A. A., AND M. J. KITTLEIN. 2007. Small-scale spatial variability in the diet of pampas foxes (Pseudalopex gymnocercus) and human-induced changes in prey base. Ecological Research 23:543.

FARRIS, Z. J. ET AL. 2017. Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. Biological Conservation 210:116–124.

FARRIS, Z. J. ET AL. 2020. Exploring and interpreting spatiotemporal interactions between native and invasive carnivores across a gradient of rainforest degradation. Biological Invasions 22:2033–2047.

FARRIS, Z. J., M. J. KELLY, S. KARPANTY, AND F. RATELOLAHY. 2016. Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern Madagascar. Animal Conservation 19:189–198.

FEDRIANI, J. M., T. K. FULLER, R. M. SAUVAJOT, AND E. C. YORK. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

FENTON, S. ET AL. 2021. Movement, space-use and resource preferences of European golden jackals in human-dominated landscapes: insights from a telemetry study. Mammalian Biology 101:619–630.

FIGUEIREDO, A. M. ET AL. 2021. Parasites of the reintroduced Iberian lynx (Lynx pardinus) and sympatric mesocarnivores in Extremadura, Spain. Pathogens 10:274.

FIGUEIREDO, L., J. KRAUSS, I. STEFFAN-DEWENTER, AND J. SARMENTO CABRAL. 2019. Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research. Ecography 42:1973–1990.

FISCHER, J., AND D. B. LINDENMAYER. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265–280.

FISKE, I., AND R. CHANDLER. 2011. Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software 43.

FITCH, G., AND C. VAIDYA. 2021. Roads pose a significant barrier to bee movement, mediated by road size, traffic and bee identity. Journal of Applied Ecology 58:1177–1186.

FLETCHER, R. J. ET AL. 2018. Is habitat fragmentation good for biodiversity? Biological Conservation 226:9–15.

FLORES-MORALES, M., J. VÁZQUEZ, A. BAUTISTA, L. RODRÍGUEZ-MARTÍNEZ, AND O. MONROY-VILCHIS. 2019. Response of two sympatric carnivores to human disturbances of their habitat: the bobcat and coyote. Mammal Research 64:53–62.

FOLEY, J. A. 2005. Global Consequences of Land Use. Science 309:570–574.

FORD-THOMPSON, A. E. S., C. SNELL, G. SAUNDERS, AND P. C. L. WHITE. 2012. Stakeholder Participation in Management of Invasive Vertebrates. Conservation Biology 26:345–356.

FORTIN, D. ET AL. 2013. Movement Responses of Caribou to Human-Induced Habitat Edges Lead to Their Aggregation near Anthropogenic Features. The American Naturalist 181:827–836.

FUENTES, E. R., AND F. M. JAKSIĆ. 1979. Latitudinal Size Variation of Chilean Foxes: Tests of Alternative Hypotheses. Ecology 60:43–47.

FULLER, A. K., D. W. LINDEN, AND J. A. ROYLE. 2016. Management decision making for fisher populations informed by occupancy modeling. The Journal of Wildlife Management 80:794–802.

GALLARDO, G., L. F. PACHECO, R. S. RIOS, AND J. E. JIMÉNEZ. 2020. Predation of livestock by puma (Puma concolor) and culpeo fox (Lycalopex culpaeus): numeric and economic perspectives. Therya 11:359–373.

GALLO, T., M. FIDINO, E. W. LEHRER, AND S. MAGLE. 2019. Urbanization alters predator-avoidance behaviours. Journal of Animal Ecology 88:793–803.

GÁMEZ, S., AND N. C. HARRIS. 2021. Living in the concrete jungle: carnivore spatial ecology in urban parks. Ecological Applications 31:e02393.

GARCÍA, D., AND N. P. CHACOFF. 2007. Scale-Dependent Effects of Habitat Fragmentation on Hawthorn Pollination, Frugivory, and Seed Predation. Conservation Biology 21:400–411.

GAYNOR, K. M., C. E. HOJNOWSKI, N. H. CARTER, AND J. S. BRASHARES. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

GEHRT, S. D. 2010. Urban carnivores. Johns Hopkins university press,.

GEHRT, S. D., AND W. R. CLARK. 2003. Raccoons, coyotes, and reflections on the mesopredator release hypothesis. Wildlife Society Bulletin (1973-2006) 31:836–842.

GERBER, B. D., S. M. KARPANTY, AND J. RANDRIANANTENAINA. 2012. Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. Journal of Mammalogy 93:667–676.

GIBSON, L. ET AL. 2013. Near-Complete Extinction of Native Small Mammal Fauna 25 Years After Forest Fragmentation. Science 341:1508–1510.

GOMPPER, M. E. 2013. Free-Ranging Dogs and Wildlife Conservation. OUP Oxford.

GORDON, C. E., A. FEIT, J. GRÜBER, AND M. LETNIC. 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. Proceedings of the Royal Society B: Biological Sciences 282:20142870.

GRAMZA, A., T. TEEL, S. VANDEWOUDE, AND K. CROOKS. 2016. Understanding public perceptions of risk regarding outdoor pet cats to inform conservation action. Conservation Biology 30:276–286.

GRIMM, V. ET AL. 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. Science 310:987–991.

GUNTIÑAS, M., J. LOZANO, R. CISNEROS, E. LLORENTE, AND A. F. MALO. 2021. Ecology of the culpeo (Lycalopex culpaeus): a synthesis of existing knowledge:13.

HABIB, B., P. GHASKADBI, S. KHAN, Z. HUSSAIN, AND P. NIGAM. 2021. Not a cakewalk: Insights into movement of large carnivores in human-dominated landscapes in India. Ecology and Evolution 11:1653–1666.

HADDAD, N. M. ET AL. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

HAGEN, C. A., D. C. PAVLACKY, K. ADACHI, F. E. HORNSBY, T. J. RINTZ, AND L. L. MCDONALD. 2016. Multiscale occupancy modeling provides insights into range-wide conservation needs of Lesser Prairie-Chicken (Tympanuchus pallidicinctus). The Condor 118:597–612.

HALLEY, J. M., N. MONOKROUSOS, A. D. MAZARIS, W. D. NEWMARK, AND D. VOKOU. 2016. Dynamics of extinction debt across five taxonomic groups. Nature Communications 7:12283.

HANSKI, I., AND M. GILPIN. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

HANSKI, I., AND O. OVASKAINEN. 2002. Extinction Debt at Extinction Threshold. Conservation Biology 16:666–673.

HANSSON, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89–103.

HARRIS, N. C. 2022. Cities Build Better Biologists. *Scientific American*. <https://www.scientificamerican.com/article/cities-build-better-biologists/> (26 May 2022).

HARRISON, M. L. K., AND C. BANKS-LEITE. 2020. Edge effects on trophic cascades in tropical rainforests. Conservation Biology 34:977–987.

HEBBLEWHITE, M., AND E. H. MERRILL. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

HODY, A. W., R. MORENO, N. F. MEYER, K. PACIFICI, AND R. KAYS. 2019. Canid collision—expanding populations of coyotes (Canis latrans) and crab-eating foxes (Cerdocyon thous) meet up in Panama. Journal of Mammalogy 100:1819–1830.

HODY, J. W., AND R. KAYS. 2018. Mapping the expansion of coyotes (Canis latrans) across North and Central America. ZooKeys:81.

HOLBROOK, S. J., AND R. J. SCHMITT. 2002. Competition for Shelter Space Causes Density-Dependent Predation Mortality in Damselfishes. Ecology 83:2855–2868.

HUGHES, J., AND D. W. MACDONALD. 2013. A review of the interactions between free-roaming domestic dogs and wildlife. Biological Conservation 157:341–351.

HUTCHINSON, J. M. C., AND P. M. WASER. 2007. Use, misuse and extensions of "ideal gas" models of animal encounter. Biological Reviews 82:335–359.

HYLANDER, K., AND J. EHRLÉN. 2013. The mechanisms causing extinction debts. Trends in Ecology & Evolution 28:341–346.

INOUYE, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. Ecology 59:672–678.

JAKSIC, F. M. 1998. Vertebrate invaders and their ecological impacts in Chile. Biodiversity and Conservation 7:1427–1445.

JAMIN, A., M. PEINTINGER, U. GIMMI, R. HOLDEREGGER, AND A. BERGAMINI. 2020. Evidence for a possible extinction debt in Swiss wetland specialist plants. Ecology and Evolution 10:1264–1277.

JANECKA, J. E. ET AL. 2016. Genetic differences in the response to landscape fragmentation by a habitat generalist, the bobcat, and a habitat specialist, the ocelot. Conservation Genetics 17:1093–1108.

JESSEN, T., Y. WANG, AND C. C. WILMERS. 2018. Habitat fragmentation provides a competitive advantage to an invasive tree squirrel, Sciurus carolinensis. Biological Invasions 20:607–618.

JIMÉNEZ, J. E. 1993. Comparative ecology of Dusicyon foxes at the Chinchilla National Reserve in northcentral Chile. M.S., University of Florida.

JIMÉNEZ, J. E., AND A. J. NOVARO. 2004. Pseudalopex culpaeus. Pp. 44–49 in Canids: Foxes, wolves, jackals and dogs. Status survey and conservation action plan. (C. Sillero-Zubiri, M. Hoffmann & D. W. Macdonald, eds.). IUCN/SSC Canid Specialist Group., Gland, Switzerland and Cambridge, UK.

JIMÉNEZ, J. E., J. L. YÁÑEZ, E. L. TABILO, AND F. M. JAKSIĆ. 1995. Body size of Chilean foxes: a new pattern in light of new data. Acta Theriologica 40:321–326.

JIMÉNEZ, J. E., J. L. YANEZ, E. L. TABILO, AND F. M. JAKSIĆ. 1996. Niche-complementarity of South American foxes: reanalysis and test of a hypothesis. Revista Chilena de Historia Natural 69:113–123.

JIMÉNEZ-FRANCO, M. V. ET AL. 2022a. Problems seeded in the past: lagged effects of historical land-use changes can cause an extinction debt in long-lived species due to movement limitation. Landscape Ecology.

JIMÉNEZ-FRANCO, M. V. ET AL. 2022b. Problems seeded in the past: lagged effects of historical land-use changes can cause an extinction debt in long-lived species due to movement limitation. Landscape Ecology.

JOHNSON, W. E., AND W. L. FRANKLIN. 1994. Role of Body Size in the Diets of Sympatric Gray and Culpeo Foxes. Journal of Mammalogy 75:163–174.

KAMAL, S., M. GRODZIŃSKA-JURCZAK, AND G. BROWN. 2015. Conservation on private land: a review of global strategies with a proposed classification system. Journal of Environmental Planning and Management 58:576–597.

KARANTH, K. U., A. SRIVATHSA, D. VASUDEV, M. PURI, R. PARAMESHWARAN, AND N. S. KUMAR. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings of the Royal Society B: Biological Sciences 284:20161860.

KARL, J. W., S. E. McCORD, AND B. C. HADLEY. 2017. A comparison of cover calculation techniques for relating point-intercept vegetation sampling to remote sensing imagery. Ecological Indicators 73:156–165.

KATNA, A., A. KULKARNI, M. THAKER, AND A. T. VANAK. 2022. Habitat specificity drives differences in space-use patterns of multiple mesocarnivores in an agroecosystem. Journal of Zoology 316:92–103.

KAYS, R. 2018. Canis latrans. The IUCN Red List of Threatened Species: e. T3745A103893556. doi 10:2018–2.

KEINATH, D. A. ET AL. 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. Global Ecology and Biogeography 26:115–127.

KELLNER, K. F., N. L. FOWLER, T. R. PETROELJE, T. M. KAUTZ, D. E. BEYER JR., AND J. L. BELANT. 2022. ubms: An R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. Methods in Ecology and Evolution 13:577–584.

KOLBERT, E. 2014. The sixth extinction: An unnatural history. A&C Black.

KOTZE, R., J. P. MARSHAL, C. W. WINTERBACH, H. E. K. WINTERBACH, AND M. KEITH. 2021. Demographic consequences of habitat loss and crowding in large carnivores: A natural experiment. African Journal of Ecology 59:63–73.

KOWARIK, I. 2011. Novel urban ecosystems, biodiversity, and conservation. Environmental pollution 159:1974–1983.

KRAUSS, J. ET AL. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13:597–605.

KREMEN, C., AND A. M. MERENLENDER. 2018. Landscapes that work for biodiversity and people. Science 362.

KRONFELD-SCHOR, N., AND T. DAYAN. 2003. Partitioning of Time as an Ecological Resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181.

KUEFLER, D., AND N. M. HADDAD. 2006. Local versus landscape determinants of butterfly movement behaviors. Ecography 29:549–560.

KUEFLER, D., B. HUDGENS, N. M. HADDAD, W. F. MORRIS, AND N. THURGATE. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology 91:944–950.

KUUSSAARI, M. ET AL. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution 24:564–571.

LANE-DEGRAAF, K. E., R. C. KENNEDY, S. N. ARIFIN, G. R. MADEY, A. FUENTES, AND H. HOLLOCHER. 2013. A test of agent-based models as a tool for predicting patterns of pathogen transmission in complex landscapes. BMC Ecology 13:35.

LASKOWSKI, K. L., AND A. M. BELL. 2013. Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. Ecology Letters 16:746–753.

LAURANCE, W. F., J. SAYER, AND K. G. CASSMAN. 2014. Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution 29:107–116.

LAURENSON, K., C. SILLERO-ZUBIRI, H. THOMPSON, F. SHIFERAW, S. THIRGOOD, AND J. MALCOLM. 1998. Disease as a threat to endangered species: Ethiopian wolves, domestic dogs and canine pathogens. Animal Conservation 1:273–280.

LAURENT, E., N. SCHTICKZELLE, AND S. JACOB. 2020. Fragmentation mediates thermal habitat choice in ciliate microcosms. Proceedings of the Royal Society B: Biological Sciences 287:20192818.

LEIGHTON, G. R. M., J. M. BISHOP, J. MERONDUN, D. J. WINTERTON, M. J. O'RIAIN, AND L. E. K. SERIEYS. 2022. Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. Animal Conservation 25:244–258.

LEÓN, C. I. ET AL. 2017. Prevalence of selected pathogens in small carnivores in reintroduction areas of the Iberian lynx (Lynx pardinus). The Veterinary Record 180:252.

LEONE, E. H., AND I. ESTÉVEZ. 2008. Space Use According to the Distribution of Resources and Level of Competition. Poultry Science 87:3–13.

LESMEISTER, D. B., C. K. NIELSEN, E. M. SCHAUBER, AND E. C. HELLGREN. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern north America. Wildlife Monographs 191:1–61.

LEWIS, J. S., L. L. BAILEY, S. VANDEWOUDE, AND K. R. CROOKS. 2015. Interspecific interactions between wild felids vary across scales and levels of urbanization. Ecology and Evolution 5:5946–5961.

LIMA, S. L. 2002. Putting predators back into behavioral predator–prey interactions. Trends in Ecology & Evolution 17:70–75.

LINDENMAYER, D. 2019. Small patches make critical contributions to biodiversity conservation. Proceedings of the National Academy of Sciences 116:717–719.

LIRA, P. K., M. DE SOUZA LEITE, AND J. P. METZGER. 2019. Temporal Lag in Ecological Responses to Landscape Change: Where Are We Now? Current Landscape Ecology Reports 4:70–82.

LIU, G., J. J. L. ROWLEY, R. T. KINGSFORD, AND C. T. CALLAGHAN. 2021. Species' traits drive amphibian tolerance to anthropogenic habitat modification. Global Change Biology 27:3120–3132.

LÖFFLER, F., D. PONIATOWSKI, AND T. FARTMANN. 2020. Extinction debt across three taxa in well-connected calcareous grasslands. Biological Conservation 246:108588.

LONDE, D. W., R. D. ELMORE, C. A. DAVIS, T. J. HOVICK, S. D. FUHLENDORF, AND J. RUTLEDGE. 2022. Why did the chicken not cross the road? Anthropogenic development influences the movement of a grassland bird. Ecological Applications 32:e2543.

LOSS, S. R., T. WILL, AND P. P. MARRA. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396.

LOYD, K. A., AND C. A. MILLER. 2010. Factors Related to Preferences for Trap-Neuter–Release Management of Feral Cats Among Illinois Homeowners. The Journal of Wildlife Management 74:160–165.

LUCHERINI, M. 2016a. Lycalopex culpaeus. The IUCN Red List of Threatened Species e. T6929A85324366.

LUCHERINI, M. 2016b. Lycalopex griseus. The IUCN Red List of Threatened Species e. T6927A86440397.

MACKENZIE, D. I., J. D. NICHOLS, J. E. HINES, M. G. KNUTSON, AND A. B. FRANKLIN. 2003. Estimating Site Occupancy, Colonization, and Local Extinction When a Species Is Detected Imperfectly. Ecology 84:2200–2207.

MAGLE, S. B., V. M. HUNT, M. VERNON, AND K. R. CROOKS. 2012. Urban wildlife research: past, present, and future. Biological conservation 155:23–32.

MAGLE, S. B., L. S. SIMONI, E. W. LEHRER, AND J. S. BROWN. 2014. Urban predator–prey association: coyote and deer distributions in the Chicago metropolitan area. Urban Ecosystems 17:875–891.

MAGOWAN, E. A. ET AL. 2022. Dead-reckoning elucidates fine-scale habitat use by European badgers Meles meles. Animal Biotelemetry 10:10.

MALHOTRA, R., J. E. JIMÉNEZ, AND N. C. HARRIS. 2021. Patch characteristics and domestic dogs differentially affect carnivore space use in fragmented landscapes in southern Chile. Diversity and Distributions 27:2190–2203.

MALMBERG, J. L., L. A. WHITE, AND S. VANDEWOUDE. 2021. Bioaccumulation of Pathogen Exposure in Top Predators. Trends in Ecology & Evolution 36:411–420.

MANLICK, P. J., AND J. N. PAULI. 2020. Human disturbance increases trophic niche overlap in terrestrial carnivore communities. Proceedings of the National Academy of Sciences 117:26842–26848.

MARCUS ROWCLIFFE, J., C. CARBONE, P. A. JANSEN, R. KAYS, AND B. KRANSTAUBER. 2011. Quantifying the sensitivity of camera traps: an adapted distance sampling approach. Methods in Ecology and Evolution 2:464–476.

MARNEWECK, C. ET AL. 2021. Shining the spotlight on small mammalian carnivores: Global status and threats. Biological Conservation 255:109005.

MARZLUFF, J. M. 2001. Worldwide urbanization and its effects on birds. Pp. 19–47 in Avian ecology and conservation in an urbanizing world. Springer.

MASSARA, R. L., A. M. O. PASCHOAL, L. L. BAILEY, P. F. DOHERTY, AND A. G. CHIARELLO. 2016. Ecological interactions between ocelots and sympatric mesocarnivores in protected areas of the Atlantic Forest, southeastern Brazil. Journal of Mammalogy 97:1634–1644.

MATEO, M. ET AL. 2017. Occurrence and molecular genotyping of Giardia duodenalis and Cryptosporidium spp. in wild mesocarnivores in Spain. Veterinary Parasitology 235:86–93.

MAZEROLLE, M. J. 2001. Amphibian Activity, Movement Patterns, and Body Size in Fragmented Peat Bogs. Journal of Herpetology 35:13–20.

MCCLENNEN, N., R. R. WIGGLESWORTH, S. H. ANDERSON, AND D. G. WACHOB. 2001. The Effect of Suburban and Agricultural Development on the Activity Patterns of Coyotes (Canis Latrans). The American Midland Naturalist 146:27–36.

MCDONALD, R. I., B. GÜNERALP, C.-W. HUANG, K. C. SETO, AND M. YOU. 2018. Conservation priorities to protect vertebrate endemics from global urban expansion. Biological Conservation 224:290–299.

MCDONNELL, M. J., AND S. T. PICKETT. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232–1237.

METZGER, J. P. ET AL. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142:1166–1177.

MICHEL, V. T., M. V. JIMÉNEZ-FRANCO, B. NAEF-DAENZER, AND M. U. GRÜEBLER. 2016. Intraguild predator drives forest edge avoidance of a mesopredator. Ecosphere 7:e01229.

MIGNON-GRASTEAU, S. ET AL. 2005. Genetics of adaptation and domestication in livestock. Livestock Production Science 93:3–14.

MOLL, R. J. ET AL. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21:765–778.

MOLL, R. J., J. D. CEPEK, P. D. LORCH, P. M. DENNIS, T. ROBISON, AND R. A. MONTGOMERY. 2020. At what spatial scale(s) do mammals respond to urbanization? Ecography 43:171–183.

MONTGOMERY, F., S. M. REID, AND N. E. MANDRAK. 2020. Extinction debt of fishes in Great Lakes coastal wetlands. Biological Conservation 241:108386.

MONTIBELLER, B., A. KMOCH, H. VIRRO, Ü. MANDER, AND E. UUEMAA. 2020. Increasing fragmentation of forest cover in Brazil's Legal Amazon from 2001 to 2017. Scientific Reports 10:5803.

MOREIRA-ARCE, D., P. M. VERGARA, AND S. BOUTIN. 2015. Diurnal Human Activity and Introduced Species Affect Occurrence of Carnivores in a Human-Dominated Landscape. PLoS ONE 10.

MORIN, D. J., D. B. LESMEISTER, C. K. NIELSEN, AND E. M. SCHAUBER. 2018. The truth about cats and dogs: Landscape composition and human occupation mediate the distribution and potential impact of non-native carnivores. Global Ecology and Conservation 15:e00413.

MORMILE, J. E., AND C. M. HILL. 2017. Living with urban baboons: Exploring attitudes and their implications for local baboon conservation and management in Knysna, South Africa. Human Dimensions of Wildlife 22:99–109.

MUELLER, T. ET AL. 2011. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography 20:683–694.

MUHLY, T. B., C. SEMENIUK, A. MASSOLO, L. HICKMAN, AND M. MUSIANI. 2011. Human activity helps prey win the predator-prey space race. PLoS one 6:e17050.

MURRAY, M. H., C. A. SÁNCHEZ, D. J. BECKER, K. A. BYERS, K. E. WORSLEY-TONKS, AND M. E. CRAFT. 2019. City sicker? A meta-analysis of wildlife health and urbanization. Frontiers in Ecology and the Environment 17:575–583.

MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853.

NAHUELHUAL, L., A. CARMONA, A. LARA, C. ECHEVERRÍA, AND M. E. GONZÁLEZ. 2012. Land-cover change to forest plantations: Proximate causes and implications for the landscape in south-central Chile. Landscape and Urban Planning 107:12–20.

NATHAN, R. ET AL. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105:19052–19059.

NAUGLE, D. E., B. W. ALLRED, M. O. JONES, D. TWIDWELL, AND J. D. MAESTAS. 2020. Coproducing Science to Inform Working Lands: The Next Frontier in Nature Conservation. BioScience 70:90–96.

NEALE, J. C., AND B. N. SACKS. 2001. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. Canadian Journal of Zoology 79:1794–1800.

NEWBOLD, T. ET AL. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

NEWSOME, T. M. ET AL. 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography 24:1–11.

NEWSOME, T. M., AND W. J. RIPPLE. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. Journal of Animal Ecology 84:49–59.

NICKEL, B. A., J. P. SURACI, M. L. ALLEN, AND C. C. WILMERS. 2020. Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. Biological Conservation 241:108383.

NICKEL, B. A., J. P. SURACI, A. C. NISI, AND C. C. WILMERS. 2021. Energetics and fear of humans constrain the spatial ecology of pumas. Proceedings of the National Academy of Sciences 118.

NIELD, A. P., R. NATHAN, N. J. ENRIGHT, P. G. LADD, AND G. L. W. PERRY. 2020. The spatial complexity of seed movement: Animal-generated seed dispersal patterns in fragmented landscapes revealed by animal movement models. Journal of Ecology 108:687–701.

NIESZAŁA, A., AND D. KLICH. 2021. How far from the road should land cover be assessed? A case study on mesopredator mortality on roads. European Journal of Wildlife Research 67:23.

NIX, J. H., R. G. HOWELL, L. K. HALL, AND B. R. MCMILLAN. 2018. The influence of periodic increases of human activity on crepuscular and nocturnal mammals: Testing the weekend effect. Behavioural Processes 146:16–21.

NOH, J., C. ECHEVERRÍA, A. PAUCHARD, AND P. CUENCA. 2019. Extinction debt in a biodiversity hotspot: the case of the Chilean Winter Rainfall-Valdivian Forests. Landscape and Ecological Engineering 15:1–12.

NOVARO, A., M. FUNES, AND J. E. JIMÉNEZ. 2004. Patagonian foxes. Selection for introduced prey and conservation of culpeo and chilla foxes in Patagonia. Pp. 239–250 in Biology and conservation of wild canids (D. W. McDonald & C. Sillero-Zubiri, eds.). OUP Oxford, Oxford, UK.

NOVARO, A. J., M. C. FUNES, AND R. SUSAN WALKER. 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. Biological Conservation 92:25–33.

OCCDOWNLOAD GBIF.ORG. 2022. Occurrence Download. The Global Biodiversity Information Facility. <https://doi.org/10.15468/dl.kb724c>.

OEHLER, J. D., AND J. A. LITVAITIS. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070–2079.

ORO, D., M. GENOVART, G. TAVECCHIA, M. S. FOWLER, AND A. MARTÍNEZ-ABRAÍN. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology letters 16:1501–1514.

OVASKAINEN, O., AND I. HANSKI. 2002. Transient Dynamics in Metapopulation Response to Perturbation. Theoretical Population Biology 61:285–295.

PALMEIRIM, A. F., M. SANTOS-FILHO, AND C. A. PERES. 2020. Marked decline in forest-dependent small mammals following habitat loss and fragmentation in an Amazonian deforestation frontier. PLOS ONE 15:e0230209.

PALOMARES, F., AND T. M. CARO. 1999. Interspecific Killing among Mammalian Carnivores. The American Naturalist 153:492–508.

PALOMARES, F., P. GAONA, P. FERRERAS, AND M. DELIBES. 1995. Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits. Conservation Biology 9:295–305.

PASCHOAL, A. M. O. ET AL. 2018. Anthropogenic Disturbances Drive Domestic Dog Use of Atlantic Forest Protected Areas. Tropical Conservation Science 11:1940082918789833.

PERES, C. A. 2001. Synergistic Effects of Subsistence Hunting and Habitat Fragmentation on Amazonian Forest Vertebrates. Conservation Biology 15:1490–1505.

PÉRON, G. ET AL. 2017. Periodic continuous-time movement models uncover behavioral changes of wild canids along anthropization gradients. Ecological Monographs 87:442–456.

PFEIFER, M. ET AL. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551:187–191.

POESSEL, S. A., S. W. BRECK, AND E. M. GESE. 2016. Spatial ecology of coyotes in the Denver metropolitan area: influence of the urban matrix. Journal of Mammalogy 97:1414–1427.

POPESCU, V. D., AND M. L. HUNTER JR. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. Ecological Applications 21:1283–1295.

POWERS, R. P., AND W. JETZ. 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nature Climate Change 9:323–329.

PRANGE, S., S. D. GEHRT, AND E. P. WIGGERS. 2003. Demographic Factors Contributing to High Raccoon Densities in Urban Landscapes. The Journal of Wildlife Management 67:324–333.

PRESLEY, S. J., L. M. CISNEROS, B. T. KLINGBEIL, AND M. R. WILLIG. 2019. Landscape ecology of mammals. Journal of Mammalogy 100:1044–1068.

PROKOPENKO, C. M., M. S. BOYCE, AND T. AVGAR. 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. Journal of Applied Ecology 54:470–479.

PRUGH, L. R. ET AL. 2009. The rise of the mesopredator. Bioscience 59:779–791.

PRUGH, L. R., K. E. HODGES, A. R. E. SINCLAIR, AND J. S. BRASHARES. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences 105:20770–20775.

QI, J., M. HOLYOAK, Y. NING, AND G. JIANG. 2020. Ecological thresholds and large carnivores conservation: Implications for the Amur tiger and leopard in China. Global Ecology and Conservation 21:e00837.

RAFIQ, K. ET AL. 2020. Spatial and temporal overlaps between leopards (Panthera pardus) and their competitors in the African large predator guild. Journal of Zoology 311:246–259.

RAHEL, F. J., AND R. L. MCLAUGHLIN. 2018. Selective fragmentation and the management of fish movement across anthropogenic barriers. Ecological Applications 28:2066–2081.

RAMOS, D. L., M. A. PIZO, M. C. RIBEIRO, R. S. CRUZ, J. M. MORALES, AND O. OVASKAINEN. 2020. Forest and connectivity loss drive changes in movement behavior of bird species. Ecography 43:1203–1214.

RANDA, L. A., AND J. A. YUNGER. 2006. CARNIVORE OCCURRENCE ALONG AN URBAN–RURAL GRADIENT: A LANDSCAPE-LEVEL ANALYSIS. Journal of Mammalogy 87:1154–1164.

RHODES, C., R. ATKINSON, R. ANDERSON, AND D. MACDONALD. 1998. Rabies in Zimbabwe: reservoir dogs and the implications for disease control. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 353:999–1010.

RICKETTS, T. H. 2001. The Matrix Matters: Effective Isolation in Fragmented Landscapes. The American Naturalist 158:87–99.

RIDDING, L. E., S. C. L. WATSON, A. C. NEWTON, C. S. ROWLAND, AND J. M. BULLOCK. 2020. Ongoing, but slowing, habitat loss in a rural landscape over 85 years. Landscape Ecology 35:257–273.

RIDOUT, M. S., AND M. LINKIE. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

RIELLY-CARROLL, E., AND A. L. FREESTONE. 2017. Habitat fragmentation differentially affects trophic levels and alters behavior in a multi-trophic marine system. Oecologia 183:899–908.

RIPPLE, W. J. ET AL. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343:1241484–1241484.

RIPPLE, W. J., C. WOLF, T. M. NEWSOME, M. HOFFMANN, A. J. WIRSING, AND D. J. MCCAULEY. 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. *PNAS*. <https://www.pnas.org/doi/abs/10.1073/pnas.1702078114> (6 March 2022).

ROCHA, D. G. ET AL. 2020. Wild dogs at stake: deforestation threatens the only Amazon endemic canid, the short-eared dog (Atelocynus microtis). Royal Society Open Science 7:190717.

RODRIGUEZ, J. T., D. B. LESMEISTER, AND T. LEVI. 2021. Mesocarnivore landscape use along a gradient of urban, rural, and forest cover. PeerJ 9:e11083.

ROEMER, G. W., M. E. GOMPPER, AND B. VAN VALKENBURGH. 2009. The Ecological Role of the Mammalian Mesocarnivore. BioScience 59:165–173.

ROWAN, J. ET AL. 2020. Geographically divergent evolutionary and ecological legacies shape mammal biodiversity in the global tropics and subtropics. Proceedings of the National Academy of Sciences 117:1559–1565.

RUBIO, A. V., R. ALVARADO, AND C. BONACIC. 2013. Introduced European rabbit as main prey of the native carnivore culpeo fox (*Lycalopex culpaeus*) in disturbed ecosystems of central Chile. Studies on Neotropical Fauna and Environment 48:89–94.

RUFFELL, J., M. N. CLOUT, AND R. K. DIDHAM. 2017. The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. Ecography 40:171–178.

RUSSELL, R. E., R. K. SWIHART, AND Z. FENG. 2003. Population consequences of movement decisions in a patchy landscape. Oikos 103:142–152.

RYALL, K. L., AND L. FAHRIG. 2006. Response of Predators to Loss and Fragmentation of Prey Habitat: A Review of Theory. Ecology 87:1086–1093.

SANTOS, F. ET AL. 2019. Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PloS one 14:e0213671.

SCHARF, I., E. NULMAN, O. OVADIA, AND A. BOUSKILA. 2006. Efficiency evaluation of two competing foraging modes under different conditions. The American Naturalist 168:350–357.

SCHEUERELL, M. D., AND D. E. SCHINDLER. 2003. Diel Vertical Migration by Juvenile Sockeye Salmon: Empirical Evidence for the Antipredation Window. Ecology 84:1713–1720.

SCHIPPER, J. ET AL. 2008. The Status of the World's Land and Marine Mammals: Diversity, Threat, and Knowledge. Science 322:225–230.

SCHMITZ, O. J., J. R. B. MILLER, A. M. TRAINOR, AND B. ABRAHMS. 2017. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. Ecology 98:2281–2292.

SCHUETTE, P., A. P. WAGNER, M. E. WAGNER, AND S. CREEL. 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation 158:301–312.

SEMPER-PASCUAL, A. ET AL. 2021. How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? Proceedings of the Royal Society B: Biological Sciences 288:20202466.

SERIEYS, L. E. K. ET AL. 2019. Widespread anticoagulant poison exposure in predators in a rapidly growing South African city. Science of The Total Environment 666:581–590.

SETO, K. C., M. FRAGKIAS, B. GÜNERALP, AND M. K. REILLY. 2011. A meta-analysis of global urban land expansion. PloS one 6:e23777.

SÉVÊQUE, A., L. K. GENTLE, J. VICENTE LÓPEZ-BAO, R. W. YARNELL, AND A. UZAL. 2021. Impact of human disturbance on temporal partitioning within carnivore communities. Mammal Review.

SHEDDEN, J. M., D. M. BUCKLIN, N. M. QUINN, AND P. STAPP. 2020. Do Coyotes Eat Mesocarnivores in Southern California? A Molecular Genetic Analysis. Proceedings of the Vertebrate Pest Conference 29.

SHORES, C. R., J. A. DELLINGER, E. S. NEWKIRK, S. M. KACHEL, AND A. J. WIRSING. 2019. Mesopredators change temporal activity in response to a recolonizing apex predator. Behavioral Ecology 30:1324–1335.

SILLERO-ZUBIRI, C., M. HOFFMANN, AND D. W. MACDONALD. 2004. Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan. IUCN Gland, Switzerland.

SILVA-RODRÍGUEZ, E. ET AL. 2016. Lycalopex fulvipes. The IUCN Red List of Threatened Species 2016: e. T41586A85370871.

SILVA-RODRÍGUEZ, E. A. ET AL. 2010a. Evaluating mortality sources for the Vulnerable pudu Pudu puda in Chile: implications for the conservation of a threatened deer. Oryx 44:97–103.

SILVA-RODRÍGUEZ, E. A., G. R. ORTEGA-SOLÍS, AND J. E. JIMÉNEZ. 2010b. Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile: INTERFERENCE OF CHILLAS FOXES BY DOGS IN CHILE. Austral Ecology 35:765–777.

SILVA-RODRÍGUEZ, E. A., AND K. E. SIEVING. 2012. Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. Biological Conservation 150:103–110.

SILVEIRA, N. S. D., B. B. S. NIEBUHR, R. DE L. MUYLAERT, M. C. RIBEIRO, AND M. A. PIZO. 2016. Effects of Land Cover on the Movement of Frugivorous Birds in a Heterogeneous Landscape. PLOS ONE 11:e0156688.

SMITH, J. A. ET AL. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences 284:20170433.

SMITH, J. A., T. P. DUANE, AND C. C. WILMERS. 2019. Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape. Landscape and Urban Planning 183:50–58.

SMITH, J. A., A. C. THOMAS, T. LEVI, Y. WANG, AND C. C. WILMERS. 2018. Human activity reduces niche partitioning among three widespread mesocarnivores. Oikos 127:890–901.

SMITH-RAMÍREZ, C. 2004. The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforests. Biodiversity and Conservation 13:373–393.

SMITH-RAMIREZ, C. ET AL. 2010. Habitat use of remnant forest habitats by the threatened arboreal marsupial Dromiciops gliroides (Microbiotheria) in a rural landscape of southern Chile. Wildlife Research 37:249–254.

SOVIE, A. R., D. U. GREENE, C. F. FROCK, A. D. POTASH, AND R. A. MCCLEERY. 2019. Ephemeral temporal partitioning may facilitate coexistence in competing species. Animal Behaviour 150:87–96.

STANTON, L. A., E. S. BRIDGE, J. HUIZINGA, S. R. JOHNSON, J. K. YOUNG, AND S. BENSON-AMRAM. 2021. Variation in reversal learning by three generalist mesocarnivores. Animal Cognition 24:555–568.

STARK, J. R., M. AIELLO-LAMMENS, AND M. M. GRIGIONE. 2020. The effects of urbanization on carnivores in the New York metropolitan area. Urban Ecosystems 23:215–225.

SURACI, J. P. ET AL. 2022. Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. Oikos:e09004.

SURACI, J. P., M. CLINCHY, L. M. DILL, D. ROBERTS, AND L. Y. ZANETTE. 2016. Fear of large carnivores causes a trophic cascade. Nature communications 7:1–7.

SURACI, J. P., M. CLINCHY, L. Y. ZANETTE, AND C. C. WILMERS. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecology letters 22:1578–1586.

SUSHINSKY, J. R., J. R. RHODES, H. P. POSSINGHAM, T. K. GILL, AND R. A. FULLER. 2013. How should we grow cities to minimize their biodiversity impacts? Global Change Biology 19:401–410.

SWIFT, T. L., AND S. J. HANNON. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biological Reviews 85:35–53.

TCHAICKA, L. ET AL. 2016. Molecular assessment of the phylogeny and biogeography of a recently diversified endemic group of South American canids (Mammalia: Carnivora: Canidae) Molecular assessment of the phylogeny and biogeography of a recently diversified endemic group of South American canids (Mammalia: Carnivora: Canidae). Genetics and Molecular Biology 39:442–451.

TILMAN, D., R. M. MAY, C. L. LEHMAN, AND M. A. NOWAK. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

TIMM, R., A. CUARÓN, F. REID, K. HELGEN, AND J. GONZÁLEZ-MAYA. 2017. Procyon lotor. The IUCN Red List of Threatened Species 2016: e. T41686A45216638.

TORRES, PC., AND PI. PRADO. 2010. Domestic dogs in a fragmented landscape in the Brazilian Atlantic Forest: abundance, habitat use and caring by owners. Brazilian Journal of Biology 70:987–994.

TRACEY, J. A., S. N. BEVINS, S. VANDEWOUDE, AND K. R. CROOKS. 2014. An agent-based movement model to assess the impact of landscape fragmentation on disease transmission. Ecosphere 5:art119.

TSCHARNTKE, T., A. M. KLEIN, A. KRUESS, I. STEFFAN-DEWENTER, AND C. THIES. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8:857–874.

TUCKER, M. A. ET AL. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359:466–469.

TUCKER, M. A., M. BUSANA, M. A. J. HUIJBREGTS, AND A. T. FORD. 2021. Human-induced reduction in mammalian movements impacts seed dispersal in the tropics. Ecography 44:897–906.

TURVEY, S. T., AND J. J. CREES. 2019. Extinction in the Anthropocene. Current Biology 29:R982–R986.

URBAN, M. C., D. K. SKELLY, D. BURCHSTED, W. PRICE, AND S. LOWRY. 2006. Stream communities across a rural–urban landscape gradient. Diversity and distributions 12:337–350.

URIBE, S. V., C. F. ESTADES, AND V. C. RADELOFF. 2020. Pine plantations and five decades of land use change in central Chile. PLOS ONE 15:e0230193.

VAN DONSELAAR, J. L., J. L. ATMA, Z. A. KRUYF, H. N. LaCROIX, AND D. S. PROPPE. 2018. Urbanization alters fear behavior in black-capped chickadees. Urban Ecosystems 21:1043–1051.

VANAK, A. T., AND M. E. GOMPPER. 2009. Dogs Canis familiaris as carnivores: their role and function in intraguild competition. Mammal Review 39:265–283.

VANAK, A. T., AND M. E. GOMPPER. 2010. Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. Journal of Applied Ecology 47:1225–1232.

VANAK, A. T., M. THAKER, AND M. E. GOMPPER. 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. Behavioral Ecology and Sociobiology 64:279–287.

VANDER VENNEN, L. M., B. R. PATTERSON, A. R. RODGERS, S. MOFFATT, M. L. ANDERSON, AND J. M. FRYXELL. 2016. Diel movement patterns influence daily variation in wolf kill rates on moose. Functional Ecology 30:1568–1573.

VANLANDEGHEM, V., P. DRAPEAU, M.-C. PRIMA, M.-H. ST-LAURENT, AND D. FORTIN. 2021. Management-mediated predation rate in the caribou–moose–wolf system: spatial configuration of logging activities matters. Ecosphere 12:e03550.

VEHTARI, A., A. GELMAN, AND J. GABRY. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.

VELASCO-VILLA, A. ET AL. 2017. The history of rabies in the Western Hemisphere. Antiviral Research 146:221–232.

VELLEND, M. ET AL. 2006. Extinction Debt of Forest Plants Persists for More Than a Century Following Habitat Fragmentation. Ecology 87:542–548.

WALD, D. M., S. K. JACOBSON, AND J. K. LEVY. 2013. Outdoor cats: Identifying differences between stakeholder beliefs, perceived impacts, risk and management. Biological Conservation 167:414–424.

WALKER, J. S. ET AL. 2015. Prying into the intimate secrets of animal lives; software beyond hardware for comprehensive annotation in 'Daily Diary'tags. Movement ecology 3:1–16.

WANG, Y., M. L. ALLEN, AND C. C. WILMERS. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

WATLING, J. I., A. J. NOWAKOWSKI, M. A. DONNELLY, AND J. L. ORROCK. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. Global Ecology and Biogeography 20:209–217.

WATTS, K. ET AL. 2020. Ecological time lags and the journey towards conservation success. Nature Ecology & Evolution 4:304–311.

WAY, J. G. no date. EASTERN COYOTE DENNING BEHAVIOR IN AN ANTHROPOGENIC ENVIRONMENT:13.

WEARN, O. R., D. C. REUMAN, AND R. M. EWERS. 2012a. Extinction Debt and Windows of Conservation Opportunity in the Brazilian Amazon. Science 337:228–232.

WEARN, O. R., D. C. REUMAN, AND R. M. EWERS. 2012b. Extinction Debt and Windows of Conservation Opportunity in the Brazilian Amazon. Science 337:228–232.

WHEATLEY, R., T. P. PAVLIC, O. LEVY, AND R. S. WILSON. 2020. Habitat features and performance interact to determine the outcomes of terrestrial predator–prey pursuits. Journal of Animal Ecology 89:2958–2971.

WHITE, L. A., J. D. FORESTER, AND M. E. CRAFT. 2018. Disease outbreak thresholds emerge from interactions between movement behavior, landscape structure, and epidemiology. Proceedings of the National Academy of Sciences 115:7374–7379.

WILSON, D. E., AND R. A. MITTERMEIER. no date. Handbook of the Mammals of the World. 2009th edition. Lynx Edicions, Barcelona.

WINTLE, B. A. ET AL. 2019. Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. Proceedings of the National Academy of Sciences 116:909–914.

WISE, M. E., F. J. SORVILLO, S. C. SHAFIR, L. R. ASH, AND O. G. BERLIN. 2005. Severe and fatal central nervous system disease in humans caused by Baylisascaris procyonis, the common roundworm of raccoons: a review of current literature. Microbes and Infection 7:317–323.

WOODROFFE, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal conservation 3:165–173.

WOSNIACK, M. E. ET AL. 2014. Unveiling a mechanism for species decline in fragmented habitats: fragmentation induced reduction in encounter rates. Journal of The Royal Society Interface 11:20130887.

WURTH, A. M., E. H. ELLINGTON, AND S. D. GEHRT. 2020. Golf Courses as Potential Habitat for Urban Coyotes. Wildlife Society Bulletin 44:333–341.

YOUNG, H. S., D. J. MCCAULEY, M. GALETTI, AND R. DIRZO. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. Annual Review of Ecology, Evolution, and Systematics 47:333–358.

YOUNG, J. K., K. A. OLSON, R. P. READING, S. AMGALANBAATAR, AND J. BERGER. 2011. Is Wildlife Going to the Dogs? Impacts of Feral and Free-roaming Dogs on Wildlife Populations. BioScience 61:125–132.

ZANNI, M., F. BRIVIO, S. GRIGNOLIO, AND M. APOLLONIO. 2021. Estimation of spatial and temporal overlap in three ungulate species in a Mediterranean environment. Mammal Research 66:149–162.

ZAPATA-RÍOS, G., AND L. C. BRANCH. 2018. Mammalian carnivore occupancy is inversely related to presence of domestic dogs in the high Andes of Ecuador. PLOS ONE 13:e0192346.