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The Influence of Development on Habitat Fragmentation, Animal Behavior and Movement

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By

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Professor Justin Brashares, Chair
Professor Adina Merenlender
Professor Arthur Middleton

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Abstract

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Protecting ecosystems, corridors, and working landscapes is critical to addressing rapid global change. Given the pervasiveness of the human footprint, managers and policy-makers often seek a clearer picture of how development affects habitat conservation and species persistence. This dissertation used a combination of remote sensing, data synthesis, and empirical data collection to examine how protected areas have been impacted by development within and beyond their borders, as well as how terrestrial species have behaviorally responded to anthropogenic features in altered landscapes. This work measured ecosystem change spanning three scales, from global protected areas, to community-level ecological interactions, to individual-level change in animal behavior.

Habitat connectivity between protected areas and surrounding land influences protected area effectiveness. More isolated protected areas often exhibit reduced species movement, dispersal, and genetic diversity, resulting in wildlife decline. To quantify protected area isolation globally, in Chapter 2, I developed a habitat-edge detection approach to measure change between protected areas and surrounding land over time. I found a significant 20-year loss in habitat continuity along the borders of the world's largest protected areas — the strongest evidence to date that protected areas have begun to resemble habitat islands in a human-dominated world. While habitat discontinuity may have negatively affected wild animals by disrupting patterns of movement or behavior, others may have used human-altered environments to gain resources or safety, with each type of response resulting in distinct outcomes for species interactions and wildlife persistence. In Chapter 3, I delved into this topic with a framework I used to examine the behavioral effects of human activity on 178 predator-prey pairs from published camera trap studies. I found four primary patterns of predator-prey response to people, highlighting the context-dependency of development on species interactions. While some wildlife species likely displayed a consistent behavioral response to disturbance, many species may have adjusted their behavior based on the level, frequency, or length of exposure to disturbance. To measure how behaviorally flexible species navigate landscapes with both development and natural features, in Chapter 4, I evaluated coyote (*Canis latrans*) habitat selection in a mixed-use agricultural landscape. I found that coyotes avoided development, but selected for roads and agricultural areas despite possible persecution and conflict. This study revealed a few of the risks, rewards, and tradeoffs that behaviorally plastic carnivores face in developed landscapes. To conclude, I summarize the conservation implications of this research, and call for incorporating the social, economic, and political drivers of land-use into wildlife ecology to promote effective and socially-conscious conservation into the future.

To my grandmother, Nancy —
who had a fierce love
of people and critters.

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Acknowledgements

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I have been so fortunate and I am so grateful.

Chapter 1.

Introduction

Human activities have reduced landscape connectivity for wildlife, resulting in population declines and biodiversity loss worldwide (Powers & Jetz, 2019). To date, human pressure on the environment has accelerated vertebrate extinctions to nearly one-hundred times the background extinction rate (Barnosky et al., 2011; Ceballos et al., 2015). Such drastic restructuring of ecological communities over the past century has had devastating consequences for ecosystem dynamics (Estes et al., 2011), and in turn, for human livelihoods, food systems, and health (Brashares et al., 2014; Dirzo et al., 2014; Ollerton et al., 2011). International conservation efforts have responded to the mounting biodiversity crisis by protecting ecosystems, corridors, and working landscapes for wildlife (Kremen & Merenlender, 2018). While these conservation actions have been critical to protecting species and habitat, protecting ecosystem processes requires a mechanistic understanding of how humans alter the environment. In this dissertation, I examine the influence of human activity and development on ecosystem change spanning three scales: from global-level change across protected landscapes, to community-level change in ecological interactions, to individual-level change in animal movement and behavior.

Protected areas are expected to preserve nature and maintain ecosystem function by serving as reservoirs of genetic diversity and providing landscape linkages that allow plants and animals to move (Butchart et al., 2015; Margules & Pressey, 2000). However, protected areas were not designed in a systematic approach (Venter et al., 2018; Visconti et al., 2019; Watson et al., 2014), and as a result reserves are often insufficient for safeguarding the ecosystem processes (Maxwell et al., 2020), riverine habitats (Moravek et al., 2023), species ranges (Butchart et al., 2015), dispersal corridors (Brennan et al., 2022), breeding grounds, or migratory paths (Runge et al., 2015) that extend beyond their borders. Extensive research has shown that as protected area habitats become isolated by development and land-use change, species and populations can become vulnerable to extinction, especially by humans (Hilborn & Sinclair, 2021; Woodroffe & Ginsberg, 1998) or climatic events (Anderson et al., 2023; Elsen et al., 2020), despite protection. If modern protected area networks are to serve as ‘biodiversity banks’ or nature-based climate solutions, then the fate of reserves and their surrounding land cannot be considered separately.

Conservation science has long recognized the importance of identifying and restoring habitat mosaics, corridors, and working lands (Kremen & Merenlender, 2018; Soulé, 1985) to fill ecological gaps in protected area networks (Davis et al., 1990) and buffer ecosystem processes (Franklin, 1993). In fact, global initiatives, such as the Convention on Biological Diversity Aichi Target 11 and the more recent Kunming-Montreal Global Biodiversity Framework have committed to integrating protected areas into the wider landscape and seascape (CBD, 2010; CBD, 2022). However, much of the research on protected area gaps has focused on forests (Bowker et al., 2017; Curtis et al., 2018; DeFries et al., 2005; Haddad et al., 2015; Leberger et al., 2020; Wolf et al., 2021) leaving out a vast diversity of terrestrial systems on the planet. Furthermore, there are no proposed indicators to assess the continuity of protected areas within the broader landscape (Bacon et al., 2019; CBD, 2022; Gannon et al., 2019).

In Chapter 2, I aim to fill this gap by measuring habitat change between protected areas and surrounding land in biomes across the globe. I ask, have protected areas begun to resemble habitat islands in human-dominated landscapes? To quantify a loss in habitat continuity, I designed an edge-detection approach and used satellite imagery to exhaustively sample for habitat edges (e.g., the abrupt margin between two types of habitat, such as forest and farmland) in 10-km transects across protected area boundaries. I evaluate changes in habitat continuity along the boundaries of 4,471 protected areas over 20 years (2001-2020), and discuss how the broader management, socioeconomic, and political context of a protected area can impact its conservation.

While habitat loss is a major threat to biodiversity, human activity and development have also caused marked shifts in animal behavior, with equally severe consequences for the long-term conservation of wildlife (Ciuti et al., 2012; Sih et al., 2011). In 2020, the onset of the global COVID-19 pandemic and corresponding lock-down restrictions highlighted how a reduction of human activity resulted in an increase in wildlife activity in urban centers, as well as protected areas (Anderson et al., 2023; Gordo et al., 2021; Schofield et al., 2021). This global event confirmed extensive findings that many wild animals have been avoiding humans by changing patterns of movement (Tucker et al., 2018), activity (Gaynor et al., 2018), or consumption (Smith et al., 2015). Nonetheless, some animals preferentially use areas with human activity to gain resources (Newsome & Van Eeden, 2017) or safety (Berger, 2007; Geffroy et al., 2015). The various behavioral responses of wildlife to human activities can have distinct downstream effects on predators, competitors, or prey species (Estes et al., 2011), ultimately restructuring ecological dynamics (Gaynor et al., 2019). The field of wildlife ecology has begun to integrate humans into ecological theory to more accurately predict the growth or collapse of wildlife populations (Miller & Schmitz, 2019). However, understanding how people influence species interactions may be key to discerning the mechanisms that regulate wildlife populations in an increasingly human-dominated world.

In Chapter 3, I explore the influence of humans on animal behavior and species interactions. In this chapter, entitled "The influence of human activity on predator-prey spatiotemporal overlap", I ask, how might human activity influence the encounters between a predator and its prey in space and time? I draw on ecological theory to create a framework with four primary pathways for how humans alter the behavior of wildlife, and ultimately, predator-prey interactions. I assess the validity of this framework with hypothesis-testing, using data from 19 published camera trap studies to compare predator and prey activity in settings of high and low human use. I discuss how changes in predator-prey overlap may influence predation rates to grow or shrink wildlife populations.

Measuring human impacts on animal behavior remains challenging because humans can play multiple roles in ecosystems, acting as neutral interactors, facilitators, competitors, and predators. Similarly, human activities can produce multiple sensory stimuli (e.g., smell, sound, light, movement, and physical infrastructure) that can reshape animal perceptions of risk (Ditmer et al., 2021; Francis & Barber, 2013; Nickel et al., 2020). While some wildlife species display a consistent behavioral reaction to human disturbance, many animals exhibit the flexibility to vary their behavior in response to the type, level, or frequency of a disturbance. Thus, a single species might avoid humans (Sih et al., 2011), coexist with humans (Bateman & Fleming, 2012), or incite conflict with humans (i.e., crop damage, property damage, loss of livestock, and injury; (Richardson et al., 2020; Treves et al., 2006) depending on the context. Studies that identify how wildlife balance the use of anthropogenic and natural features at different thresholds of disturbance remain critical to wildlife management.

In Chapter 4, I ask how does a behaviorally-flexible species balance the risks and rewards of living in a moderately developed landscape? I use GPS collars over a 3-year period to examine the winter habitat selection of coyotes (*Canis latrans*) in a mixed-use agricultural landscape in Mendocino County, CA, USA. To infer whether coyotes tolerate or avoid diurnal human use of anthropogenic features, I test whether coyotes partition their selection for development, roads, and agricultural land by time of day or by behavioral state (resting, foraging, and traveling). Finally, I discuss how studies of animal risk tolerance are critical to predicting and managing areas of conflict and coexistence between wildlife and people.

Taken together, I hope this dissertation contributes to our understanding of how human activity and development influence landscape change, ecological interactions, and animal behavior. This work outlines several practical approaches for measuring human influence on wildlife and the environment, as well as highlighting several new avenues of future research. By improving our understanding of the interactions among humans, wildlife, and land, I hope we can endeavor to conserve biodiversity alongside the needs of people.

Chapter 2.

The islandization of terrestrial protected areas

This chapter has been prepared for publication and is reproduced here with kind permission of the contributing authors Wenjing Xu and Justin S. Brashares.

ABSTRACT

Recent global commitments to biodiversity conservation focus on expanding the protected area (PA) network to improve connectivity and safeguard landscape-scale ecological processes. Yet, habitat changes within and beyond PA boundaries threaten to isolate PAs from surrounding landscapes, reducing PA effectiveness and the capacity for adaptation to rapid global change. Our ability to recognize and mitigate the isolation of PAs is limited by a weak understanding of where and at what rate this process occurs. Here, I empirically measured the 'islandization' of PAs, that is, the loss of habitat continuity at PA boundaries, across all the world's biomes. I used MODIS satellite imagery and a spectral angle mapper to calculate the difference and change in the spectral gradient of PA boundaries relative to interior and exterior land. Nearly half of the world's PAs (43.14%) showed a significant loss in habitat continuity across their boundaries over a 20-year period (2001-2020) ($n = 4,471$; $p < 0.05$). The global pattern of PA islandization was the result of multiple processes, including habitat modification, management, degradation, and ecosystem recovery. PAs in grassland and shrubland biomes showed the greatest increase in islandization over time ($\beta = 0.00034$, $R^2 = 0.76$, $F(1, 18) = 55.3$, $p < 0.001$, $n = 1,353$). The pervasive loss of habitat continuity at PA boundaries suggests PAs are losing connectivity with surrounding landscapes relative to their baseline. These findings highlight the challenges and opportunities of using PAs as the backbone of post-2020 initiatives for large-landscape conservation.

INTRODUCTION

For more than half a century conservation science has cautioned that the continued expansion of human activities will ultimately reduce our terrestrial protected areas (PAs) to habitat islands in a sea of development (Gilpin & Diamond, 1980; Wilson & MacArthur, 1967). Human settlement, land conversion, and resource extraction outside of PA boundaries (Hilborn & Sinclair, 2021; Jones et al., 2018; Ward et al., 2020; Wittemyer et al., 2008), as well as habitat preservation, ecosystem recovery, and management practices within PAs (Aslan et al., 2021; Cadenasso et al., 2003) may all serve to disrupt habitat continuity between PAs and their surrounding landscapes. This process of PA 'islandization' (Gilpin & Diamond, 1980; Myers, 1987) has been observed to reduce habitat connectivity, affecting the demography, genetics, and survival of isolated populations, rendering species, and large-landscape processes such as migrations, vulnerable to extinction (Anderson et al., 2023; Margules & Pressey, 2000; Runge et al., 2015; Woodroffe & Ginsberg, 1998).

Though well-trod in conservation science and planning, the concerns surrounding PA islandization have received new life in recent conservation initiatives such as the CBD Aichi Target 11 which prioritized the integration of PAs into larger land and seascapes (CBD, 2010).

More recently, the Kunming-Montreal Global Biodiversity Framework committed to restoring and supporting sustainable use of land surrounding PAs to retain wider ecosystem function and improve the adaptive potential of species facing rapid climate change (CBD, 2022). Yet, while several landmark studies have quantified changes in forest cover to highlight the gaps in habitat connectivity and potential isolation of PAs (Bowker et al., 2017; Curtis et al., 2018; DeFries et al., 2005; Leberger et al., 2020; Wolf et al., 2021), there remain no general assessments of PA islandization across biomes nor indicators for measuring progress toward the integration of protected areas into larger landscapes (Bacon et al., 2019; CBD, 2022; Gannon et al., 2019).

Here, I devised and applied a metric to quantify the global rate and extent of islandization for 4,471 terrestrial PAs over a 20-year period, across the world's biomes. To achieve this, I characterized the habitat continuity along PA frontiers, defined as where PAs boundaries met unprotected land. To characterize habitat continuity, I used the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra MOD09A1 product to compare the spectral differences between each PA interior and its surroundings. Specifically, the method measured the habitat continuity by using the integrated spectral signature from all seven MODIS land surface reflectance bands to examine whether landcover transitions coincided with PA boundaries (**Figure 1**). My analysis included protected areas of all designations (e.g., wilderness, active management) in order to test whether biome, size, or type of protection influenced the habitat continuity across PA boundaries.

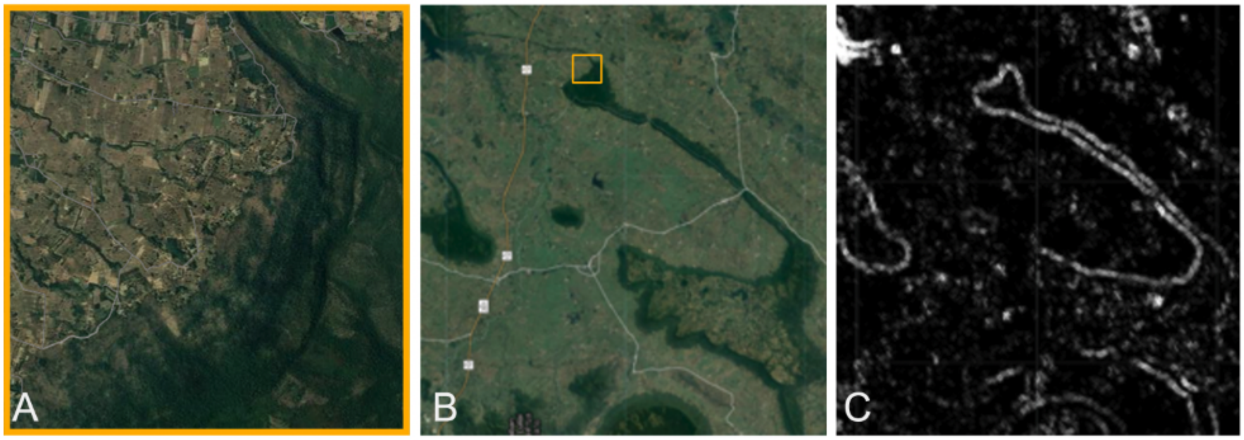

Figure 1. Demonstration of habitat discontinuity detection using spectral gradient differencing across protected area boundaries. (**A-B**) Original Google Earth satellite image of a protected area. (**C**) Spectral gradient image using 7-band Terra MODIS surface spectral reflectance imagery (MOD09A1) and a spectral angle mapper.

METHODS

Protected Area Data

First, I obtained data for protected area geometries using the June 2021 World Database on Protected Areas (UNEP-WCMC, 2020). Following other global protected area studies (Butchart et al., 2015; Jones et al., 2018), I removed PAs that were marine, lacked a reported area, did not include detailed geographic information (i.e. those represented as a single point), or with a

"UNESCO-MAB Biosphere Reserve" designation. Following the WDPA best practice guidelines, I eliminated overlap in protected area geometries using the '*wdpar*' package in R (Hanson, 2022) and only included PAs with status of "designated", "established", or "inscribed".

From this terrestrial protected area geometry dataset, I selected PAs with an area larger than 200 km^2. This enabled me to match the resolution of the satellite imagery to the PA size, and to include PAs that were wide enough to sample with transects. I assigned biomes to each PA using the global ecoregion layer (Dinerstein et al., 2017). When multiple biomes were present I retained the biome label with the largest area.

Transect Sampling

For each terrestrial protected area, I created sampling transects perpendicular to the PA boundary to compare change in the spectral differences between the PA's interior, exterior, and boundary. Transects extended 10km across the PA boundary to represent the central value of the log-transformed reference range of bird and terrestrial mammal dispersal distances (1–100 km) (Saura et al., 2017), and were spaced 500m apart to allow for exhaustive sampling of the boundary, given that I used satellite imagery with a 500m pixel size (Figure S1). Each transect contained five sample points spaced 2.5-km apart: two interior points, two exterior points, and one boundary point. I removed transects that intersected water bodies, that bisected other parts of the PA boundary in curved or narrow sections, and that fell within neighboring protected areas. When multiple PAs directly neighbored each other, I only evaluated the outer footprint of the entire protected region, defined here as the 'PA frontier' (Figure S1). I excluded PAs with frontiers that were less than 30% of the total boundary, to ensure that each PA frontier was representative of the larger PA.

Satellite Imagery

To characterize the habitat continuity along the transects bisecting PA frontiers, I created global annual median composites from MODIS/Terra Surface Reflectance 8-Day L3 Global 500-m SIN Grid (MOD09A1) imagery for each year, from 2001 to 2020. The 500-m MODIS imagery had the most consistent data quality and coverage for this 20-year analysis and was more adept than 30-m Landsat imagery at capturing the broad landcover patterns while reducing noise from fine-scale spectral heterogeneity (Figure S2). From each seven-band global MODIS annual composite, I derived a single-band spectral gradient image by computing the per pixel difference between spectral erosion and dilation using the *Image.spectralGradient* function (Plaza et al., 2002) with a 3x3 square kernel in Google Earth Engine (Gorelick et al., 2017). Because this technique combined spectral information from all seven bands it allowed me to detect habitat characteristics important to forest and non-forest biomes including vegetation cover, soil cover, moisture, and vegetation water content (e.g. certain types of woody plant encroachment in grasslands; (Soubry & Guo, 2022). Larger spectral gradient values represented a greater spectral difference among pixels in the 3x3 kernel (i.e., greater spectral heterogeneity), indicating higher landcover heterogeneity. I extracted the spectral gradient value of every transect point for each of the 20 MODIS composite images.

Quantifying Habitat Discontinuity

Ecological boundaries are created when habitat patches are distinguished by distinct habitat characteristics, thus "*the gradient [of] that characteristic is steeper in the boundary than in either of the neighboring patches*" (Cadenasso et al., 2003). Following this logic, if a PA boundary coincided with habitat discontinuity, we would expect higher spectral gradient values at the PA boundary than on either side of the PA boundary (Figure S3). Thus, I compared the spectral gradient of each boundary point to the interior and exterior points in the same transect. When a boundary point had a larger gradient value than any combination of its interior-exterior pairs, I classified the transect as exhibiting habitat discontinuity (Figure S3).

I measured protected area islandization as an increase in the number of transects showing habitat discontinuity overtime. I summarized the percent of all transects showing habitat discontinuity for each of 20 years and estimated global-level and biome-level trends in using linear regression. I also used linear regression to estimate the trend in each PA's boundary gradient values over 20-years. I determined significant PA trend estimates using a *p-value* < 0.05 and summarized significant PA-level trends by biome. Last, I summarized the percent of transects showing habitat discontinuity in each protected area in 2020. All statistical analyses were conducted using R (R Core Team, 2022).

Validation

To test whether the pattern of habitat discontinuity at the protected area boundaries was different from random, I compared the measured distribution to a null model. Given the first law of geography that nearer objects are more similar (Tobler, 1970), support for the null model would find the mean number of transects showing habitat discontinuity to be higher when calculated with randomly paired points than with points along the same transect. Thus, I used a paired t-test to compare the measured distribution of habitat discontinuity to a null distribution of habitat discontinuity created with randomly paired points (Figure S4). I found that the measured distribution had significantly higher percent of transects showing habitat discontinuity than the null model, in support of our hypothesis that the distribution of habitat discontinuity along PA boundaries was non-random (Figure S4).

RESULTS

The final dataset included 4,471 protected areas, ranging from 200.4 km^2 to 961,673.2 km^2 in size (median = 862.2 km^2). The analysis included all terrestrial PAs larger than 200 km^2 and with at least 30% of their boundary bordering unprotected land. Restricting PA size to greater than 200-km^2 excluded 225,353 PAs, most of which were in Europe, but only reduced the total area analyzed by 7.66%. In total, there were 1,516,412 transects (7,582,060 points) bisecting the protected area frontiers, with a median of 224 transects and a range of 7 to 7,628 transects evaluated per protected area.

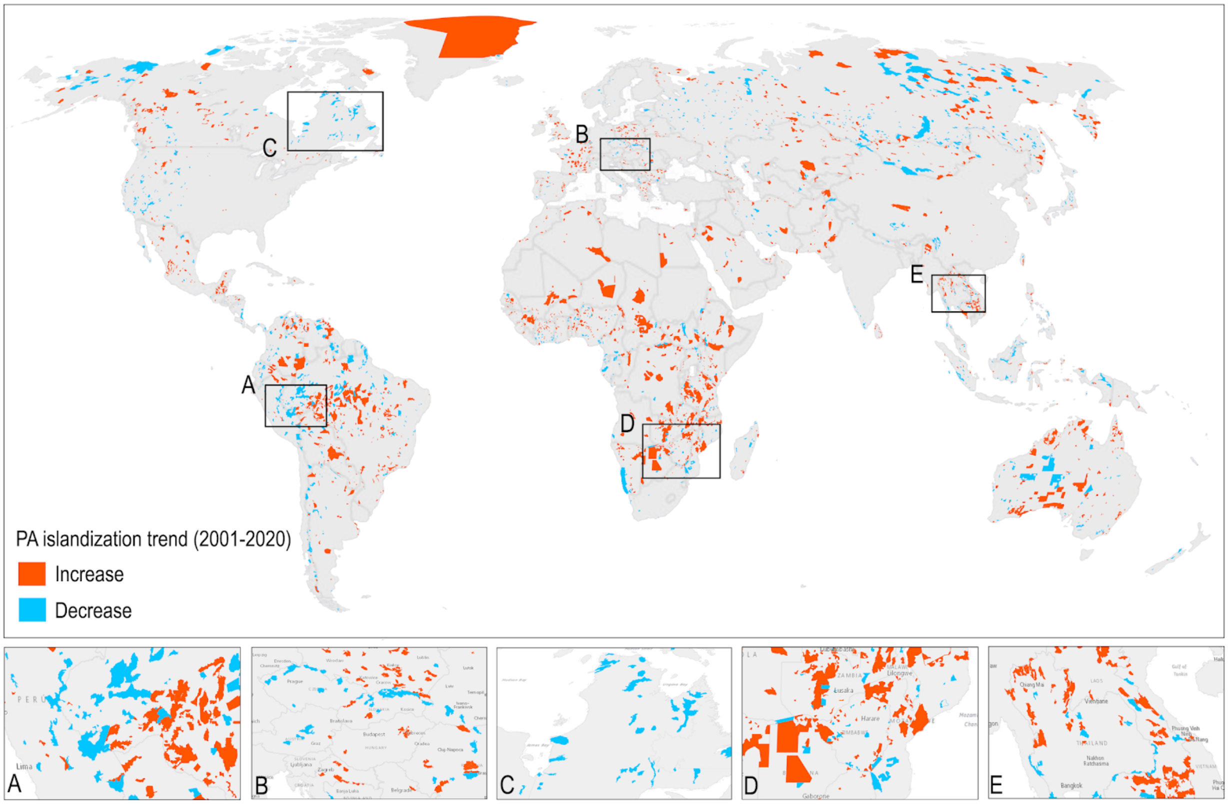

Figure 2. Global islandization of protected areas. Twenty-year trends in islandization were estimated for each of 4,471 protected areas, as measured by the change in the spectral gradient values of boundary points over a 20-year period. The map illustrates significant estimates using a *p-value* < 0.05. From 2001-2020, nearly half of protected areas (43.14%) exhibited a significant increase in habitat discontinuity with surrounding land, that is, islandization coinciding with PA boundaries. A quarter of protected areas (26.65%) exhibited a significant decrease in islandization, while the remainder showed no change.

Nearly half of the world's largest terrestrial PAs exhibited a significant increase in islandization over a 20-year period from 2001-2020 (**Figure 2**). Specifically, 43.14% of PAs showed a significant increase in the percent of sampled transects in which the gradient value of the PA boundary was greater than its neighboring internal and external habitats (Figure S3). The analysis detected widely-documented cases of increasing PA isolation in Amazonia's deforestation frontier (Curtis et al., 2018; **Figure 2A**), increasing habitat continuity in eastern Europe's agricultural abandonment frontier (Levers et al., 2018; **Figure 2B**) and boreal tree encroachment in northeastern North America (Langdon et al., 2020; **Figure 2C**). Moreover, PA islandization trends were found to be consistent at a global level when pooling samples from all PAs (n = 1,516,412 total transects sampled), with 51.4% of cumulative PA boundaries identified as habitat edges in 2020, representing a slight but significant increase over the last 20-years ($\beta = 0.00019$, $R^2 = 0.75$, $F(1, 18) = 55.38$, $p < 0.001$; **Figure 3A**, Table S1).

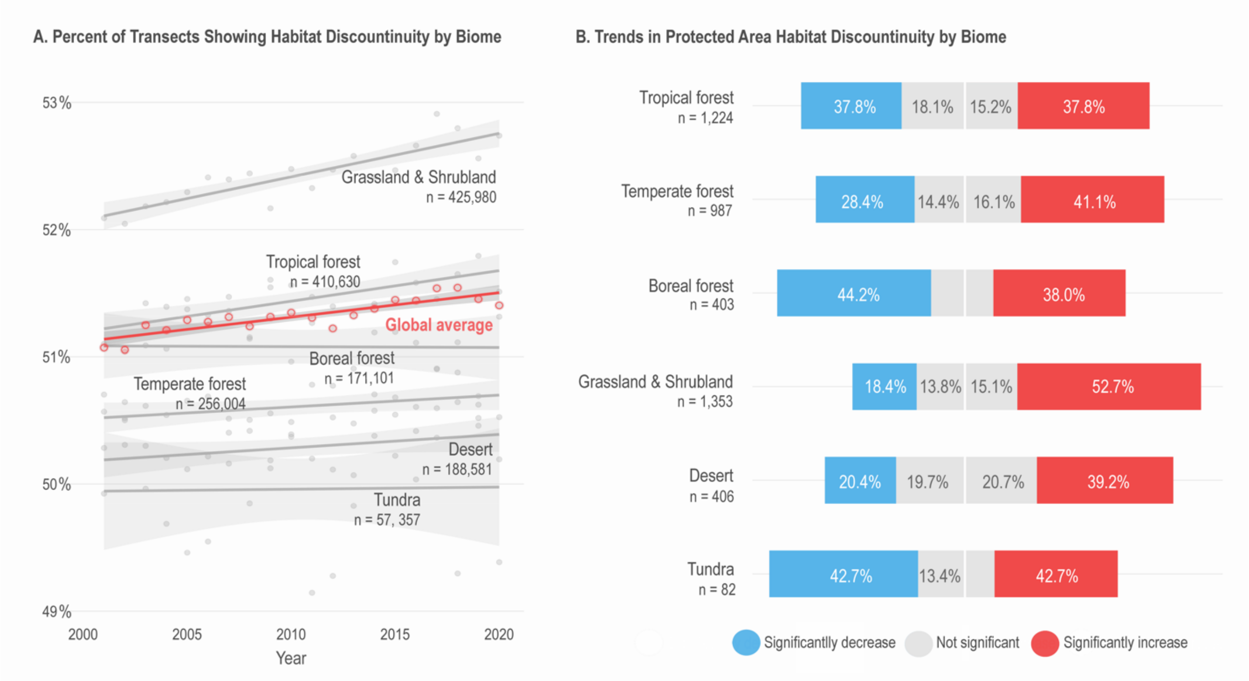

Figure 3. Protected area islandization across the world's biomes. From 2001 to 2020, the percent of transects exhibiting habitat discontinuity at protected area boundaries increased across major terrestrial biomes when pooled (**A**) globally ($\beta = 0.00019$, $R^2 = 0.75$, $F(1, 18) = 55.38$, $p = 0.026$, $n = 1{,}516{,}412$ transects), and by (**B**) protected area ($n = 4{,}471$). Grassland-shrubland biomes and protected areas showed the highest levels of habitat discontinuity and the greatest increase of islandization over time (rock-ice and mangrove biomes are not shown due to low sample sizes, see Table S1). Shown percentages are rounded to the nearest tenth and significant estimates were determined using a *p-value* < 0.05.

While research on deforestation (DeFries et al., 2005; Wolf et al., 2021) might suggest forest habitats would show the most striking change at PA boundaries, in fact, PAs showed islandization in nearly all biomes (**Figure 3A**). In particular, grassland-shrubland biomes, typically omitted from global habitat analyses, demonstrated the greatest rate of islandization over time, followed by tropical forest and desert (**Figure 3A**; Table S1). These trends were consistent when habitat discontinuity was calculated for individual PAs (**Figure 3B**), and matched the published rates of 0.5% habitat loss over the past 20-years in tropical forests (Hansen et al., 2020; Wade et al., 2020). Islandization trends also varied by IUCN protection category (ANOVA; $F(6, 3056) = 3.89$, $p < 0.001$). PAs that prioritized sustainable use (Category VI) had a significantly higher percentage of transects showing habitat discontinuity at the boundary than for PAs that prioritized active management (Category IV; post-hoc Tukey test; $p = 0.01$). Finally, PA size significantly, though weakly, influenced islandization trends from 2001-2020, such that larger PAs had higher percentages of habitat discontinuity at the boundary ($\beta = 0.003$, $R^2 = 0.001$, $F(1{,}4469) = 5.10$, $p < 0.05$, $n = 4{,}471$).

This approach allowed inference on the spatial and temporal dynamics of islandization at the scale of individual PAs, and even within a given PA. Such high resolution may tempt site-by-site analysis of the drivers of islandization for each PA, region or country. However, such analyses could easily confuse correlation for causation and ultimately be harmful to landowners, residents, or park personnel if interpreted without local or regional context. Instead, I provide a global snapshot of PA islandization, by measuring habitat discontinuity across all PAs in 2020. These results showed that in 2020, more than half of all PAs (54.84%) exhibited habitat discontinuity along a majority of their boundary (**Figure 4**).

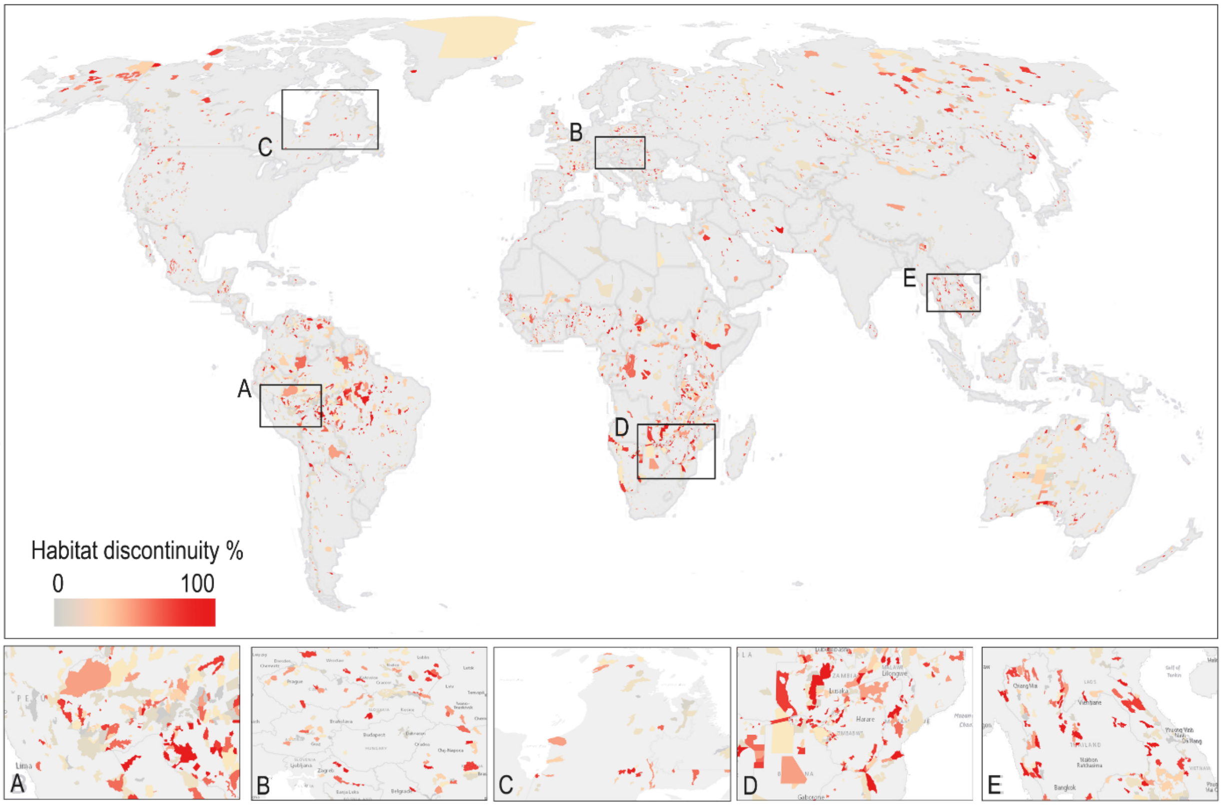

Figure 4. The extent of protected area habitat discontinuity in 2020. Characterizing each terrestrial protected area based on the percentage of boundary transects that showed habitat discontinuity in 2020 reveals great variation in islandization, even among neighboring parks (n = 4,471).

In 2020, there was substantial spatial variation in habitat continuity among PAs. For instance, biome strongly influenced the percent of habitat discontinuity along PA boundaries (ANOVA; $F(7, 4463) = 18.69$, $p < 0.001$). Grassland-shrubland biomes showed a significantly greater extent of habitat discontinuity than desert (post-hoc Tukey test; $p < 0.001$), all forests ($p < 0.01$), and tundra ($p < 0.05$; Figure S5). As in the 2001-2020 change analysis, geographic patterns of PA isolation varied by IUCN protection category in 2020 (ANOVA; $F(6, 3056) = 2.4$, $p < 0.05$), but with the percent of habitat discontinuity along actively managed PAs (Category IV) significantly higher than PAs designated as wilderness (Category Ib; post-hoc Tukey test; $p < 0.05$). The size of the PA did not significantly influence the percent of habitat discontinuity along its boundary ($\beta = 0.00025$, $R^2 = 0.000$, $F(1,4469) = 0.039$, $p = 0.84$, $n = 4471$). However, there was a weak but significant effect such that the earlier the PA was established the higher the percent of habitat discontinuity in 2020 ($\beta = -0.0003$, $R^2 = 0.003$, $F(1,4048) = 12.83$, $p < 0.001$, $n = 4050$).

DISCUSSION

The global pattern of PA islandization that I observed can be explained as the result of habitat modification, as well as management differences and ecological recovery. In the land surrounding PAs, there was evidence of agriculture, resource extraction, grazing pressure, industrial logging, and urbanization (**Figure 5**). This was not unexpected, given that human impacts have altered 77% of Earth's terrestrial land with more than half under moderate or intense human pressure (Allan et al., 2017; Jones et al., 2018; Williams et al., 2020). Additionally, land management approaches, such as fire, invasive species, or water use, may drive habitat discontinuity from within PAs (Aslan et al., 2021). For instance, long-held policies of fire suppression have aided forest succession within many PAs, altering habitat continuity outside boundaries where fire may be less managed (Kelly et al., 2020). Finally, islandization can indicate ecological recovery within PAs, such as the regrowth of riparian vegetation (Beschta & Ripple, 2016). Nonetheless, while habitat discontinuity at PA boundaries may signal overall ecological recovery or management effectiveness of PAs in preventing deforestation, agriculture, and other forms of development within their boundaries (Bowker et al., 2017), it also signals isolation and a growing vulnerability of PAs to edge effects and environmental shocks, such as floods, frost, or fire (Haddad et al., 2015; Kremen & Merenlender, 2018).

Grassland-shrubland ecosystems exhibited the highest percentage and most rapid rate of islandization between 2001-2020, followed by tropical forests and deserts. Grasslands are considered one of the most imperiled ecosystems on Earth (Cowie, 2021). Today, 60% of the world's grasslands are less than 20% intact (Scholtz & Twidwell, 2022), in part, because grasslands often coincide with human activities (Newbold et al., 2016) on easy to develop, flat land. Additionally, biophysical changes, such as desertification and shrub encroachment (de Souza et al., 2022; Li et al., 2006), fire (Schmidt & Eloy, 2020), or grazing (Veldhuis et al., 2019) may have led to islandization of grassland-shrubland PAs over the past 20-years. Previous research supports our finding that grassland habitat change outpaces that of forests (Boakes et al., 2010), yet, international grassland conservation lags behind that of forests (Carbutt et al., 2017). Preserving grasslands remains critical for protecting endemic species, the world's many herbivore migrations which track greening vegetation over expanses of savannahs, steppes, and grasslands (Abraham et al., 2022; Harris et al., 2009), and for absorbing atmospheric carbon in response to global emissions (Chang et al., 2021).

Overall, trends in PA islandization likely represent several global and divergent land-use processes, such as afforestation and agricultural abandonment in the global North, as well as grazing and agricultural expansion in the global South (Winkler et al., 2021). In some cases, habitat discontinuity could represent positive outcomes for PAs (e.g., prescribed fire) and habitat continuity could represent negative outcomes for PAs (e.g., shrub encroachment in grasslands or spread of invasive species across boundaries). Thus, the percent habitat discontinuity should not be interpreted as an index of PA effectiveness. To avoid oversimplifying and misrepresenting local context, this analysis does not include global-scale correlations between percent habitat discontinuity, and landcover type, economic indices such as Gross Domestic Product (GDP), human population density, or livestock density. However, future conservation efforts would benefit from further research on the individual causes and consequences of islandization for each desert, grassland, tundra, and forested ecosystems.

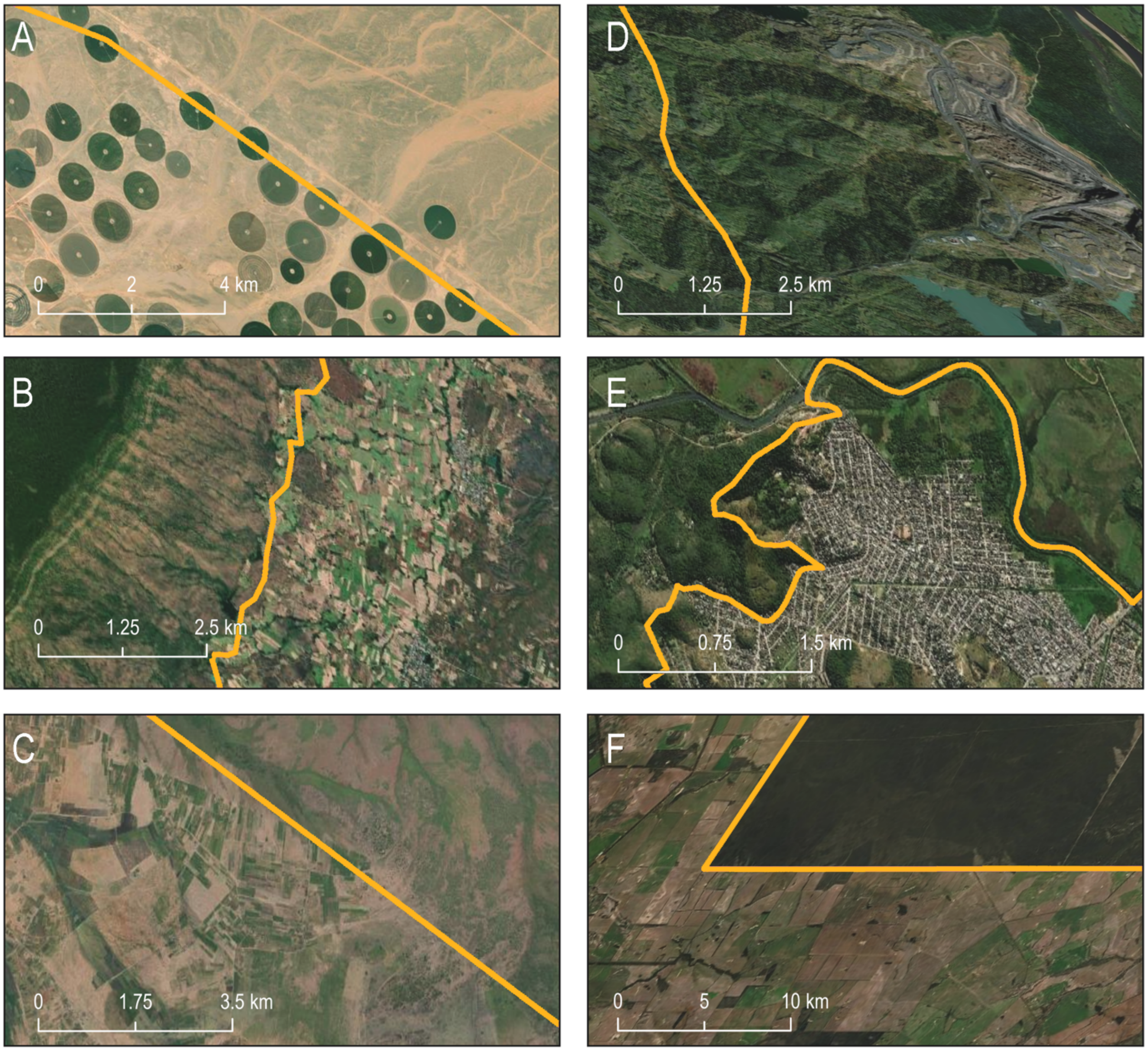

Figure 5. Examples of protected area islandization created by land-use practices at protected area boundaries. (**A**) Agricultural irrigation in the desert along Harrat al Harrah Conservation Area, Saudi Arabia. (**B**) Farmland densification and a natural boundary (mountain range) in tropical forest near the Phu Khiew Wildlife Sanctuary, Thailand. (**C**) Livestock grazing in tropical savannah outside of Serengeti National Park, Tanzania. (**D**) Copper mining in boreal forest outside of Naryskiy protected area, Russia. (**E**) Urbanization in coastal scrub along the Alto Iguaçu protected area near Rio de Janiero, Brazil. (**F**) Industrial logging in temperate forest outside of Lake Magenta protected area, Australia.

A number of broader economic, social, and political factors are known to drive land-use change within and beyond PA boundaries. Economically, PAs can retained rich and biodiverse resources to promote sustainable livelihoods and grow nearby communities, but can result in a loss of habitat continuity (Corson et al., 2014; Wittemyer et al., 2008). The social exclusion and removal of people from PAs has been found to concentrate human settlement and resource-use at PA boundaries, accelerating the loss of habitat continuity (Brandt & Spierenburg, 2014; Spierenburg & Wels, 2006; Veldhuis et al., 2019). Politically, conservation offsets in one landscape have justified the over-extraction of resources in nearby landscapes (Feeney, 2023). It is well understood that the concept of a boundary and land-ownership can create visible differences in management, human behavior, and land-use (Aslan et al. 2021; Schonewald-Cox & Bayless 1986). But how or whether these sociopolitical land-use drivers should be addressed, requires decision-making by local communities with support from ecologists, social scientists, and state actors.

Limitations

This analysis provides a global assessment of the presence and rate of PA islandization over the past two decades, but has a few limitations. By combining all seven MODIS bands to detect the spectral gradient of PA boundaries, this approach detected changes in habitat continuity across landcover types and biomes. However, the approach is limited in that it cannot distinguish which spectral bands, and corresponding landscape features, contributed the most to trends in islandization. To understand which landcover features underlie a given habitat discontinuity, such as a forest-urban or forest-grassland transition, future research could target islandized PAs for detailed analysis, and use specific sets of spectral bands to quantify the landcover of interest.

Similarly, this study provided a simple but effective measurement of the global PA islandization trend by using linear regression. However, landcover change is not always linear. For example, large-scale fire may lead to abrupt islandizing effects, and be followed by rapid recovery due to post-fire succession. Future studies that aim to capture landcover dynamics across a single PA boundary can adopt detailed landcover change analysis approaches such as LandTrendr (Kennedy et al., 2010) or Continuous Change Detection and Classification (Zhu & Woodcock, 2014).

Finally, habitat continuity is highly scale-dependent (Cadenasso et al., 2003). MODIS satellite imagery was appropriate for quantifying coarse-scale islandization processes along the boundaries of the world's largest PAs, as it could detect the presence of ecological boundaries with a width of 500m or greater. Smaller PAs, associated with fine-scale habitat heterogeneity might be better suited to using remote sensing imagery with finer resolution, such as Landsat (30 m), Sentinel (10 – 60 m), or Planet (0.5 m).

CONCLUSION

The pervasive islandization of PAs—spanning forests, deserts, and grasslands—challenges our hopes and assumptions about the capacity of protected areas to serve as biodiversity banks and climate refugia within large, mixed-use landscapes. Yet, as we enter an era of unprecedented commitments and investment in land protection, we are presented with a rare opportunity to take targeted action against the effects of islandization. To sustainably protect our investment in PAs, we must understand their historical complexity and use equitable, inclusive, and morally-just forms of land protection inside and outside of their borders. First, shifting investment targets from solely PA expansion toward ecological enhancement of buffer areas and working landscapes will improve connection among PAs and surrounding habitat. Second, investment in PA management through local staffing and capacity building are linked to greater community benefits and conservation outcomes (Oldekop et al., 2016). Third, targeting investment toward connecting ecosystem flows (e.g., water quality, migration corridors, pollinator host plants, climate migration and adaptation) will enhance ecosystem features that integrate PAs into wider landscapes and, in doing so, advance goals for biodiversity conservation and climate change mitigation. If PAs are to help alleviate biodiversity loss, it is essential we act quickly and pragmatically to restore the ecological integrity of landscapes beyond their borders.

ACKNOWLEDGEMENTS

I am grateful to M.W. Brunson, C.E. Aslan, W. Ji , and I. Dronova for their thoughts on an early version of this study. A special thanks to A. Merenlender, A. Middleton, and the Brashares Lab at UC Berkeley for insightful feedback and edits. AV was funded an NSF Graduate Research Fellowship.

DATA AVAILABILITY STATEMENT

All data are available in the supplementary materials and on GitHub: https://github.com/wx-ecology/PA_Boundary.

SUPPLEMENT TO CHAPTER 2:

Figures S1 – S4
Table S1

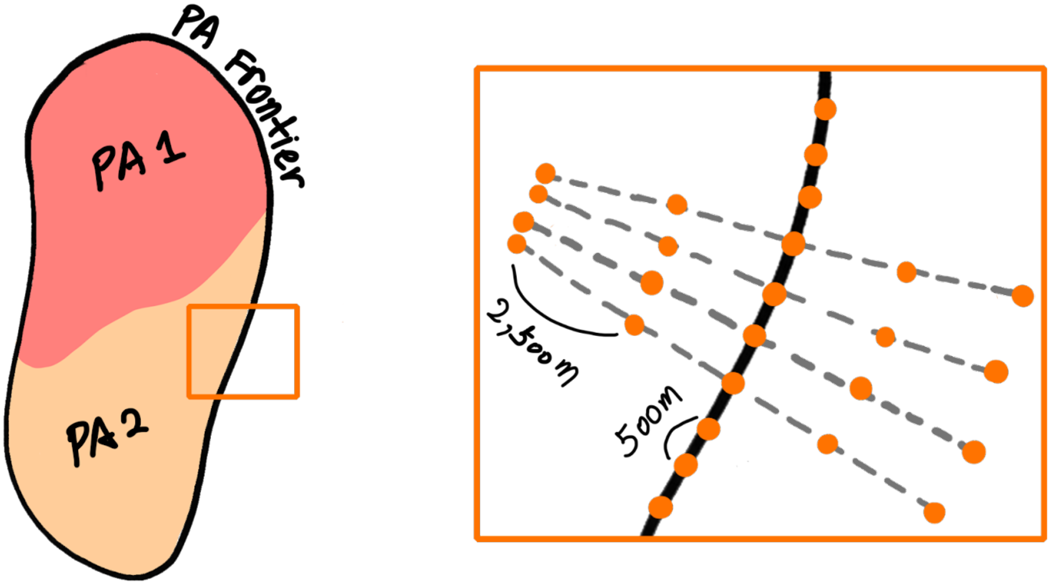

Figure S1. Illustration of exhaustive exterior-to-interior transect sampling, with 10-km transects separated by 500-meter spacing to accommodate MODIS 500-meter pixel size. Transects were sampled perpendicular to the PA frontier, defined as the outermost footprint of the protected region.

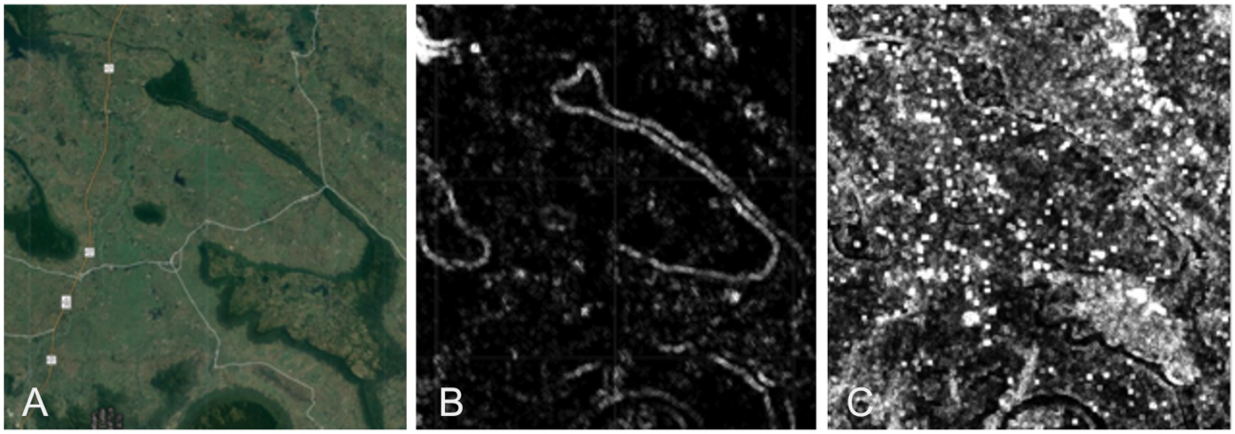

Figure S2. Example of (**a**) an original protected area satellite image, alongside a 3x3 kernel image gradient of (**b**) MODIS 500-meter pixel size, and (**c**) Landsat 30-meter pixel size. A MODIS 500-meter pixel size was most sufficient to reduce fine-scale heterogeneity while retaining broad-scale patterns.

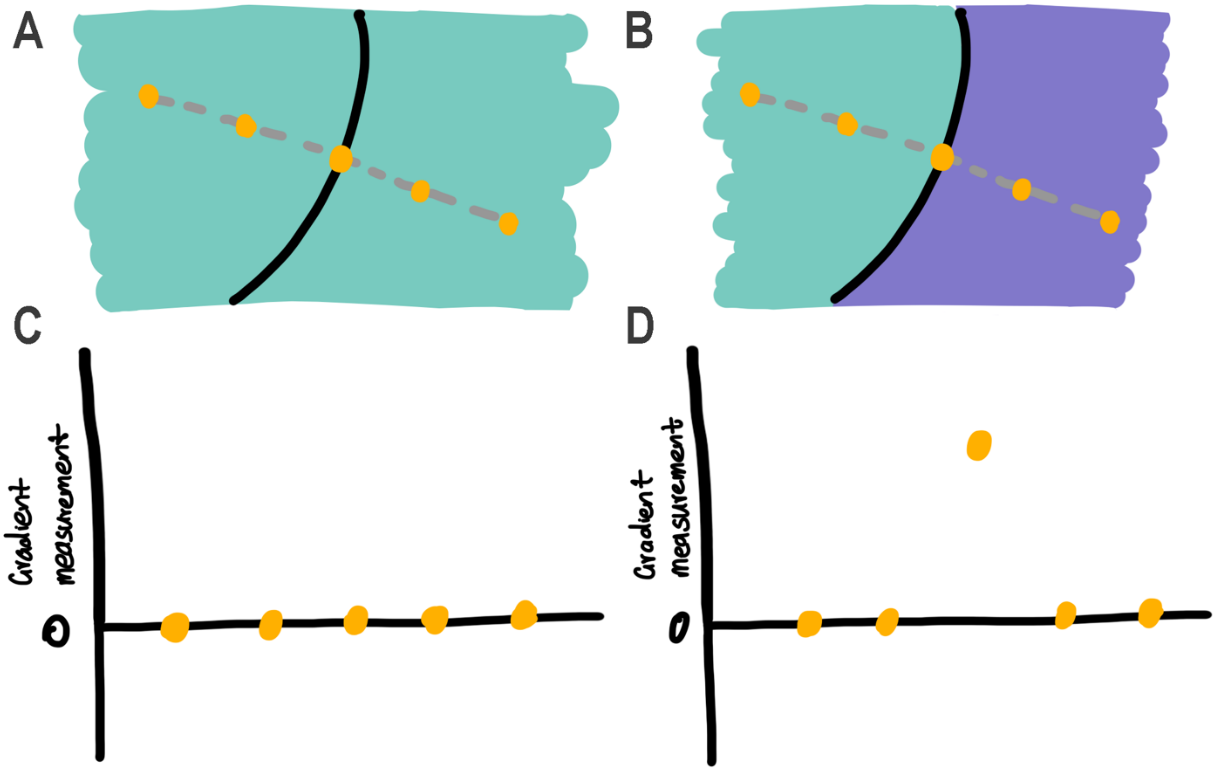

Figure S3. Conceptual illustration of detecting habitat discontinuity along protected area boundaries for areas with (**A**, **C**) continuous habitat, and (**B**, **D**) discontinuous habitat. Satellite image pixel gradient values were sampled using a 3x3 kernel at five points along transects (dotted line), perpendicular to protected area boundaries (solid line). If the boundary point had a larger gradient value than any combination of its interior-exterior pairs, the transect was classified as showing habitat discontinuity.

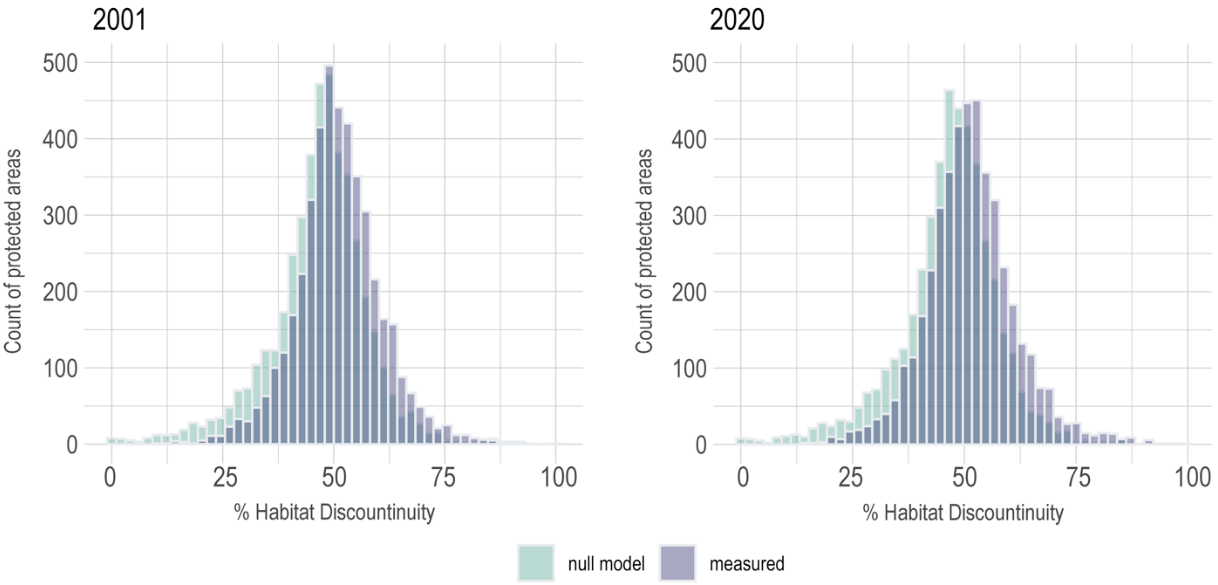

Figure S4. Comparison of measured protected area habitat discontinuity with a null model (*paired t-test*, $p < 0.001$). Percent habitat discontinuity is summarized per protected area as the percent of transects classified as having boundary point spectral gradient values greater than those of any interior-exterior point pair on the same transect. The null model was constructed by comparing boundary point spectral gradient values to those of interior-exterior point pairs from random transects within the same protected area.

Table S1. Estimates of global protected area (PA) islandization by biome from 2001-2020 using annual percent of habitat discontinuity for all transects perpendicular to protected area boundaries (n = 1,516,412).

Biome	**β (*10,000)**	**R^2**	***SE* (*10,000)**	**F (1,18)**	***p***	***n* (transects)**	***n* (PAs)**
Desert	1.054	0.153	0.585	3.246	0.088	188,581	406
Grassland & shrubland	3.414	0.755	0.459	55.320	$< 0.001^{***}$	425,980	1,353
Tropical forest	2.403	0.519	0.545	19.430	$< 0.001^{***}$	410,630	1,224
Temperate forest	0.933	0.158	0.508	3.376	0.083	256,004	987
Boreal forest	-0.065	< 0.001	1.097	0.003	0.954	171,101	403
Tundra	0.167	< 0.001	1.978	0.007	0.934	57,357	82
Mangrove	-1.003	< 0.001	8.770	0.013	0.910	885	7
Rock & Ice	6.719	0.155	3.692	3.313	0.085	5,874	9
Global	1.923	0.7547	0.258	55.380	$< 0.001^{**}$	1,516,412	4,471

Abbreviations: SE, standard error; $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Chapter 3.

The influence of human activity on predator-prey spatiotemporal overlap

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Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K., & Brashares, J. S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, 00, 1– 11. https://doi.org/10.1111/1365-2656.13892.

ABSTRACT

Despite growing evidence of widespread impacts of humans on animal behavior, our understanding of how humans reshape species interactions remains limited. Here, we present a framework that draws on key concepts from behavioral and community ecology to outline four primary pathways by which humans can alter predator-prey spatiotemporal overlap. We suggest that predator-prey dyads can exhibit similar or opposite responses to human activity with distinct outcomes for predator diet, predation rates, population demography, and trophic cascades. We demonstrate how to assess these behavioral response pathways with hypothesis testing, using temporal activity data for 178 predator-prey dyads from published camera trap studies on terrestrial mammals. We found evidence for each of the proposed pathways, revealing multiple patterns of human influence on predator-prey activity and overlap. Our framework and case study highlight current challenges, gaps, and advances in linking human activity to animal behavior change and predator-prey dynamics. By using a hypothesis-driven approach to estimate the potential for altered species interactions, researchers can anticipate the ecological consequences of human activities on whole communities.

INTRODUCTION

Human activity can alter the behavior of animals by amplifying or dampening perceptions of risk, food availability, or safety (Gaynor et al., 2019; Geffroy et al., 2020; Hammond et al., 2020; Sih et al., 2011). Yet, complex behavioral feedbacks among multiple ecological players (i.e., predators, prey, competitors) have limited our ability to establish links between human-altered animal behavior and broader ecological change, such as altered predator diet, predation rate, population demography, competitive exclusion, or trophic cascades. Although human activity—defined broadly here as human presence and infrastructure—is known to affect animal populations by changing species interactions, including predation (Gaynor et al., 2021), knowledge of these dynamics is largely anecdotal or context-specific (Wilson et al., 2020). Formally recognizing the effect of humans on predator-prey interactions is necessary to align hypothesis testing with the range of potential effects of increasing human activity on the persistence and coexistence of wild animals (Mumma et al., 2018; Sinclair et al., 2003).

The field of behavioral ecology has long demonstrated that predators and prey influence each other's spatial distributions (Brown et al., 1999; MacArthur & Pianka, 1966) in a behavioral response race, whereby predators seek to encounter prey while prey seek to avoid predators (Lima & Dill, 1990; Sih, 1984). Considerable research has established that contextual factors (e.g., patch size, habitat complexity, resources, and species functional traits) can give an advantage to either player in the predator-prey response race (Fretwell, 1972; Laundré, 2010; Luttbeg et al., 2020; Schmidt & Kuijper, 2015; Sih et al., 1998; Smith, Donadio, et al., 2019). These conceptual models have allowed ecologists to predict changes to the consumptive (e.g., predation) and non-consumptive (e.g., risk effects) dynamics of ecological communities. However, although classic behavioral response models have been extended to communities with multiple predators (Sih et al., 1998) surprisingly few models have been broadened to describe how human activity influences the contest between predator and prey (but see Miller & Schmitz, 2019 and Muhly et al., 2011).

Understanding how human activity affects animal behavior and species interactions is complex because animal responses to humans are rarely uniform. Many wild animals avoid humans by changing patterns of movement, activity, or consumption (Gaynor et al., 2018; Smith et al., 2015; Tucker et al., 2018), whereas others preferentially use settings of human activity to gain resources or safety (Berger, 2007; Geffroy et al., 2015; Newsome & Van Eeden, 2017). Accounting for this variation in animal responses could be key to anticipating shifts in predation and potential cascading trophic effects (Kuijper et al., 2016; Yovovich et al., 2021). Each player's (i.e., predator or prey) response to humans can vastly influence the ecological outcome. For example, if a predator avoids human activity but its prey does not, predator and prey may encounter each other less often (Berger, 2007; Rogala et al., 2011) possibly reducing predation and/or non-consumptive effects. Alternatively, if both predator and prey perceive human activity as a threat, mutual avoidance of humans may force prey and predator to share space and time. The loss of spatiotemporal refuges that previously stabilized predator-prey coexistence (Schoener, 1974; Shamoon et al., 2018) may lead to the increase of predation and its non-consumptive effects.

Here, we present a framework that draws on theory and empirical literature to conceptualize the behavioral pathways by which human activity can reshape the overlap between predators and prey. As a proof of concept, we review the literature to evaluate evidence for each pathway in terrestrial mammal predator-prey dyads, and conduct an analysis to test how human activity influenced predator-prey temporal overlap. Further, we highlight current challenges, gaps, and advances in linking animal behavior change to predator-prey interactions and ecological dynamics in settings with human activity. Our goal is to provide a testable framework that allows researchers to evaluate hypotheses and assess the potential for human-altered species interactions.

HUMAN-ALTERED PREDATOR-PREY OVERLAP

Humans are dominant actors in ecological communities around the world. Human presence and infrastructure, which we collectively refer to as human activity, alter sensory stimuli that animals may perceive as associated with risk or reward (e.g., smell, sound, light, movement; (Ditmer et al., 2021; Francis & Barber, 2013). Varied stimuli can differentially reshape animals' perceptions of risk-reward trade-offs. For instance, different types of human activity can influence species differently, as when large mammal predators spatially avoided building density and temporally avoided human presence, whereas smaller mammal predators temporally avoided human presence but did not spatially avoid building density (Nickel et al., 2020). Animals may also only perceive altered risk-reward cues at a certain threshold of human activity. For instance, mule deer (*Odocoileus hemionus*) rarely used areas with greater than 3% surface disturbance from energy development during migration (Sawyer et al., 2020). An animal's experience with human activity (e.g., prior events, duration of exposure) and its functional traits (e.g., body size, propensity for learning, memory, boldness) may also influence perception of risk-reward cues and its corresponding behavioral response (Moiron et al., 2020; Ross et al., 2019). For instance, many species have learned to associate human activity with increased foraging opportunities (e.g., garbage, agriculture; Newsome et al., 2015).

In response to risk-reward cues, animals can adjust their spatial distribution or temporal activity to avoid or seek out human activity. If individuals in a given animal population consistently alter their spatiotemporal distribution, we might expect reverberating impacts on closely interacting species, such as predators and their prey (Muhly et al., 2011; Wilson et al., 2020). Because predators and their prey can each respond to human activity along a continuum of attraction to avoidance, there are four behavioral pathways by which humans can increase or decrease predator-prey spatiotemporal overlap (hereafter, 'overlap') (**Figure 1**).

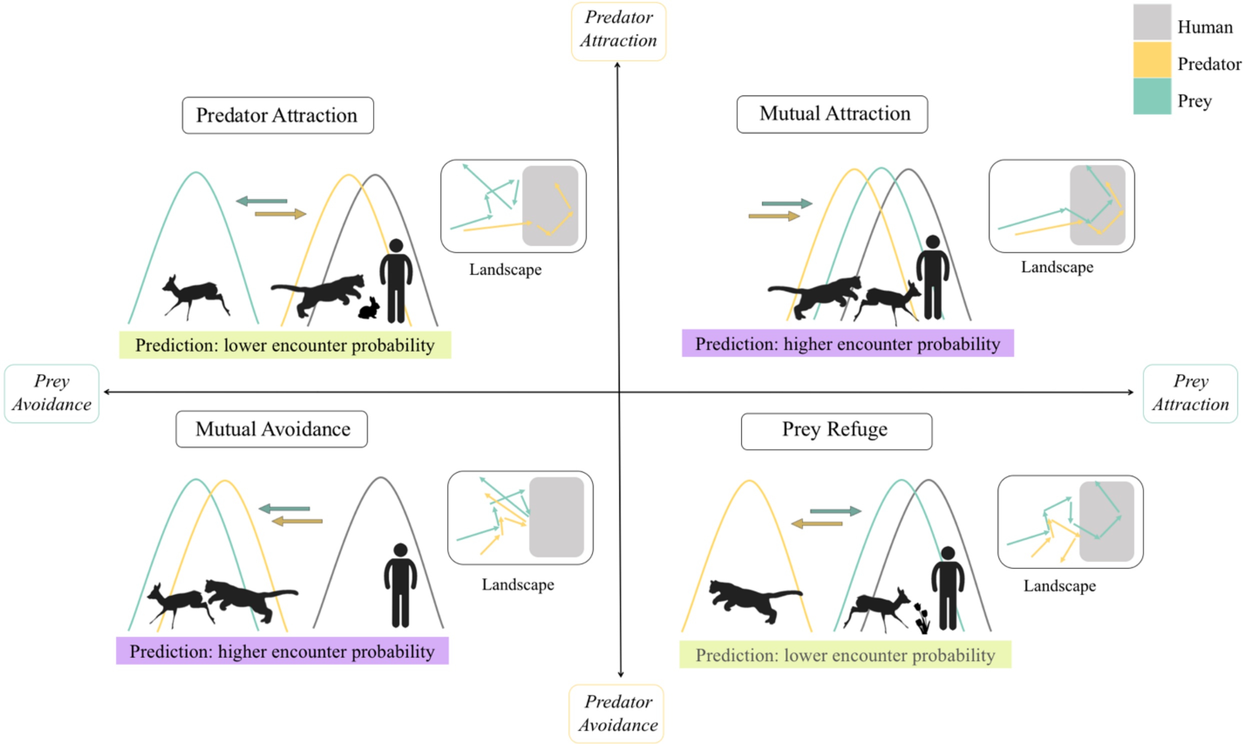

Figure 1. Humans can alter predator and prey behavior, spatiotemporal overlap, and encounter probability via four major pathways: mutual attraction, mutual avoidance, prey refuge, and predator attraction. Predator (y-axis) and prey (x-axis) respond to human activity along a continuum of attraction to avoidance. Similar responses of predator and prey to human activity are predicted to result in increased predator-prey overlap and possible encounters, whereas opposite responses are predicted to reduce overlap and possible encounters.

Changing the degree of overlap between predator and prey may tip the behavioral response race in favor of one player to affect consumptive or non-consumptive dynamics. Although linking predator-prey overlap to predation requires evaluating the full predation sequence (i.e., the encounter, pursuit, and successful capture of prey; Guiden et al., 2019; Lima & Dill, 1990; Suraci et al., 2022; Wootton et al., 2023), a predator and prey first must occupy the same space at the same time for an encounter to occur. We reduce this complexity to consider overlap a necessary precursor to any predator-prey encounter (Prugh et al., 2019). While human activity can also change the densities of both predator and prey species through non-behavioral pathways (e.g., direct mortality, habitat degradation), here we focus on behaviorally-mediated effects of humans on predators and prey.

Human activity increases predator-prey overlap

There are two behavioral pathways through which human activity can increase the overlap between a predator and its prey, potentially tipping the behavioral response race in favor of the predator. First, mutual attraction to human activity (i.e., synanthropy) may increase predator-prey encounter rates (**Figure 1, quadrant I**). For example, the attraction of black bears (*Ursus americanus*) to human-associated food led to increased predation of mutually attracted red-backed voles (*Clethrionomys gapperi*) feeding nearby (Morris, 2005). Second, mutual avoidance of human activity may cause a predator and prey to increase overlap to avoid a shared perceived risk (**Figure 1, quadrant III**). For instance, in Manas National Park, India, tigers (*Panthera tigris*) and ungulate prey constrained their spatiotemporal activity to avoid humans in the park, thus increasing overlap with one another (Lahkar et al., 2020). If mutual attraction or mutual avoidance transpire in both space and time, the realized niche (Hutchinson, 1957) between predator and prey will be compressed and encounter rates may be amplified. This change may lead to increased predation rates or phenomena such as ecological traps (Gates & Gysel, 1978).

Human activity decreases predator-prey overlap

There are two behavioral pathways by which human activity can decrease the overlap between a predator and its prey, potentially tipping the behavioral response race in favor of prey. First, predators may avoid human activity while prey do not, creating a spatial or temporal prey refuge (**Figure 1, quadrant IV**; Berger, 2007; Muhly et al., 2011). Prey refuges (also called 'human shields') occur in environments where the absence of large predators for fear of people allows prey species to reduce their anti-predator behavior (Shannon et al., 2014) or selectively use human-occupied habitats that predators avoid (Gaynor et al., 2022). Second, prey may avoid human activity while predators do not (Fleming & Bateman, 2018). This case may entail predator attraction (**Figure 1, quadrant II**), whereby predators select settings of high human activity, affording human-avoidant prey a refuge. Predator use of human settings may be driven by prey switching and the selection for synanthropic or domestic prey, or other human food subsidies, such as garbage or agriculture (Murdoch & Oaten, 1975; Murdoch, 1969; Newsome et al., 2015). For instance, in Maharashtra, India, 87% of leopard (*Panthera pardus*) diet in human-dominated areas consisted of domestic animals, reducing consumption of wild species (Athreya et al., 2016). If prey refuge or predator attraction transpire in both space and time, the realized niche (Hutchinson, 1957) between predator and prey will be relaxed, and predation encounter rates may be reduced. This can lead to decreased predation rates, altered population dynamics, or phenomena such as mesopredator release (Crooks & Soulé, 1999).

Human activity does not alter predator-prey overlap

Human activity may have no clear effect on the overlap among predators and prey, obscuring “winners” or “losers” in the predator-prey behavioral response race. This condition is likely to emerge when neither ecological player responds to human activity. Such lack of response could indicate at least four underlying mechanisms (Smith et al., 2021) including, but not limited to, high tolerance thresholds for human activity, perception of humans as non-threatening, intrinsic or extrinsic constraints on behavioral adjustments, and temporary transitions between avoidance and attraction. A true lack of response can only be measured when an animal does not alter its behavior despite consistency in the density of competitors, predators, and resources across a human-use gradient. Because community composition also generally varies with anthropogenic disturbances (Ordeñana et al., 2010), fully characterizing the conditions underlying non-response to humans may require additional non-observational approaches, such as experiments (e.g., (Suraci, Clinchy, et al., 2019) or simulations (e.g.,(Thompson et al., 2018). Comparative studies of predator and prey spatiotemporal overlap in settings with and without human activity, or along gradients of human activity, may help to shed light on which behavioral pathways are most common. Such studies may also reveal whether functional traits, such as body size, influence an animal’s behavioral response.

CASE STUDY: MEASURING HUMAN INFLUENCE ON PREDATOR-PREY TEMPORAL OVERLAP

Our framework formalizes four behavioral pathways for how human activity may alter predator-prey overlap; yet, it remains important to test support for related hypotheses. To demonstrate how researchers can apply empirical data to our framework, we evaluated these four hypotheses in a literature review and analysis, and tested whether the behavioral response patterns were generalizable based on functional traits of each predator and its prey. We selected studies that measured temporal activity and overlap of predators and prey at paired settings of high and low human activity (for full Methods see Supplementary Information). Briefly, we limited our analysis to terrestrial mammals with a body mass >1kg in line with recent research suggesting that medium and large-bodied terrestrial mammals exhibit varied responses to human activity (Frey et al., 2020; Suraci et al., 2021). We focused our review on published camera trap studies that reported predator-prey temporal overlap, given that the temporal dimension is often overlooked, more easily standardized than the spatial dimension, and is potentially more critical to predicting a predation event (Moll et al., 2017). In total, we reviewed 6,646 abstracts and 405 papers to identify available data for 178 predator-prey dyads from 19 camera trap studies. These 19 studies spanned five continents and included forest, savanna, shrubland, and desert ecosystems (see Supplementary Information).

For each species in each study, we calculated the relative difference in the diurnal activity ratio (i.e., the proportion of daytime activity) at paired settings of high and low human activity. This calculation allowed us to visualize the difference between the temporal niche of each predator and its prey, relative to the diurnal human niche. Next, given that functional traits can influence an animal’s perception of risk-reward cues, we tested whether functional traits (including prey order, body size, predator hunting mode, trophic level, predator guild, and circadian rhythm) influenced the difference in diurnal activity of predator-prey dyads between paired settings of low and high human activity. Finally, to estimate how human activity altered the overlap between predator and prey, we calculated the difference in temporal overlap coefficients of predator-prey dyads between paired settings of low and high human activity (see Supplementary Information).

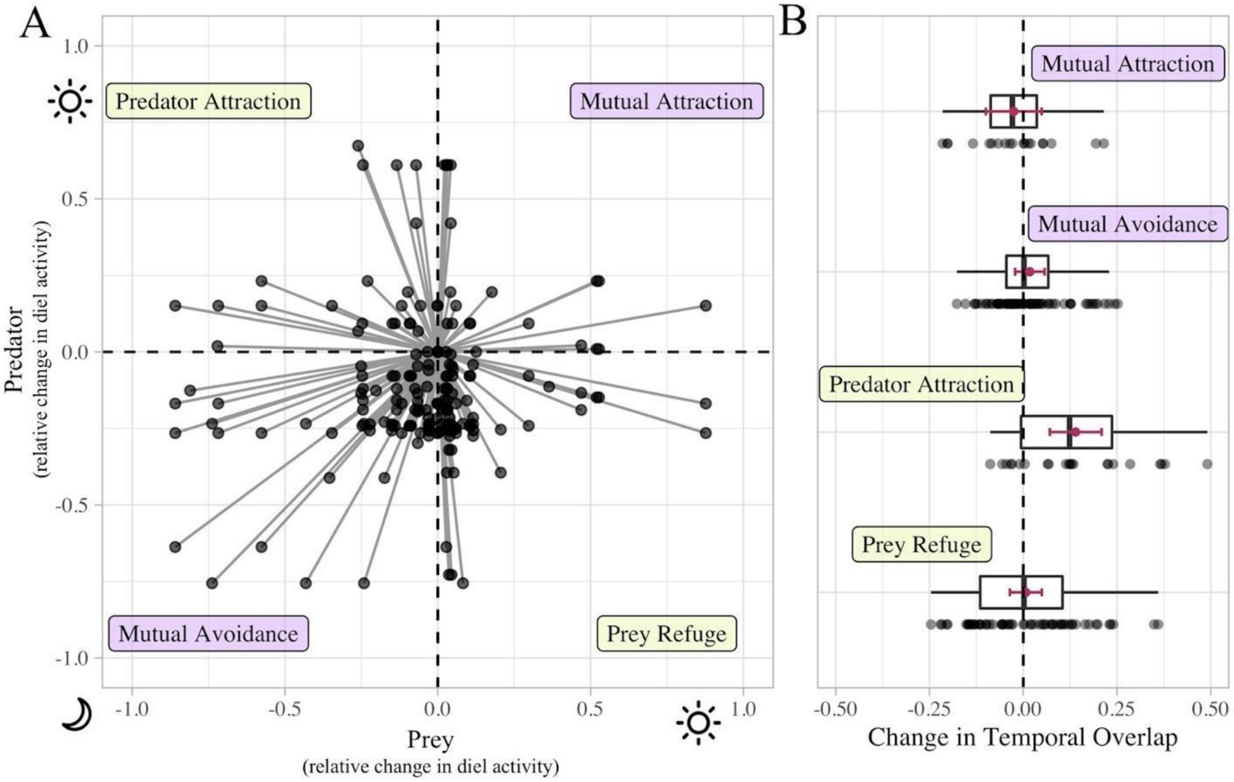

Figure 2. Human influence on predator-prey dyad (**A**) temporal activity and (**B**) temporal overlap based on review of camera trap studies between paired settings of low and high human use. (**A**) Lines reflect the relative magnitude and direction of the diel activity ratio toward nocturnality (-1) or diurnality (1) for each predator-prey dyad in paired settings of low to high human use (n = 178 predator-prey dyads, 19 studies) to indicate the behavioral response pathway (e.g., mutual attraction, mutual avoidance, prey refuge, predator attraction). (**B**) Black dots represent the change in predator-prey dyad temporal overlap (Δ) between paired settings of low and high human use, as grouped by corresponding behavioral response pathway (n = 167 predator-prey dyads, 16 studies). Red error bars represent estimated marginal means and ± 95% confidence interval.

We found evidence to suggest that mammalian predator-prey dyads respond to human activity in each of our proposed behavioral response pathways (**Figure 2A**). In settings of high human activity, 70 predator-prey dyads showed temporal patterns of mutual avoidance, while 60 exhibited prey refuge, 23 predator attraction, and 19 mutual attraction to human activity. Six predator-prey dyads showed no change. Only half of the predator-prey dyads that exhibited mutual attraction (44%) and mutual avoidance (51%) increased temporal overlap with each other. Similarly only 49% of dyads exhibiting prey refuge and 27% exhibiting predator attraction decreased temporal overlap with each other in settings of high human use. Thus, temporal overlap did not consistently increase among predator-prey dyads exhibiting congruent activity shifts (i.e., mutual attraction to or avoidance of human activity), and likewise, temporal overlap did not consistently decrease among predator-prey dyads exhibiting divergent activity shifts (**Figure 2B**), as per our framework's expectations.

One explanation for why many predator-prey dyads had higher overlap with one another despite opposite responses to humans (i.e., prey refugia or prey switching; one ecological player becomes more nocturnal while the other becomes more diurnal) may be that human-avoidant prey can tolerate high overlap with a predator rather than tolerate high human activity (see (Zbyryt et al., 2017). For instance, although black-tailed jackrabbits (*Lepus californicus*) had lower diurnal activity and bobcats (*Lynx rufus*) had higher diurnal activity in settings of high human activity, these species exhibited higher overlap with each other (see Supplementary Information; (Baker & Leberg, 2018). More than 70% of the predator-prey dyads that exhibited predator attraction reflected this phenomenon. Thus, hypothesis testing within our framework can highlight differences in risk tradeoffs for predators and their prey in settings of high human activity.

Our analyses also revealed that some predator-prey dyads exhibited similar diel responses to human activity (i.e., mutual avoidance or mutual attraction; both predator and prey become more diurnal or nocturnal) yet decreased overlap with one another (**Figure 2B**). This finding may show maintenance of temporal partitioning between predators and prey at a fine scale, despite human-induced activity shifts (Ferreiro-Arias et al., 2021). For instance, while leopards (*Panthera pardus*) and spotted deer (*Axis axis*) exhibited decreased diurnal activity to mutually avoid high human activity, spotted deer avoided human activity to a lesser degree, ultimately reducing overlap between spotted deer and leopards (see Supplementary Information; Carter et al., 2015). For prey, maintaining fine-scale spatiotemporal partitioning with both natural and human predators could come at the cost of altered stress and fecundity (Tuomainen & Candolin, 2011) or increased overlap among competitors (Manlick & Pauli, 2020; Sévêque et al., 2020; Smith et al., 2018). Ecological outcomes for these scenarios might include increased intraspecific competition (Carter et al., 2015; Wang et al., 2015) and resource limitation (Muhly et al., 2011) rather than increased predation encounter risk, as key drivers of population dynamics.

We found no effect of functional traits on the change in diurnal activity ratios for terrestrial mammal predators and prey between paired settings of high and low human activity (**Figure 3**; n = 49 predators, n = 76 prey, 19 studies). It is possible that the variability of human activity across the studies obscured underlying behavioral response patterns, especially given the relatively small number of studies (n = 19). It is also possible that in mammals, behavioral responses to humans are more strongly driven by in-situ learning and experience than by the functional traits we tested. To examine these possibilities, researchers could use this framework to test how different types, magnitudes, and frequencies of human activity influence the behavioral response of the same predator-prey dyads. Similarly, researchers might consider whether morphology or past experience with humans drives the behavior of the focal animals.

Future applications of this framework should ensure that change in animal activity and predator-prey overlap is measured relative to peak human activity. The published studies in our analysis exhibited diurnal human activity, but the peak impacts of human presence and infrastructure can also be crepuscular or nocturnal. For instance, lights or generators may turn on at night, or humans may tend agriculture at dawn and dusk, leaving fields unattended during the heat of the day. If the onset of peak human activity coincides with either a predator or prey's peak in activity, human impacts on predator-prey overlap may be greater.

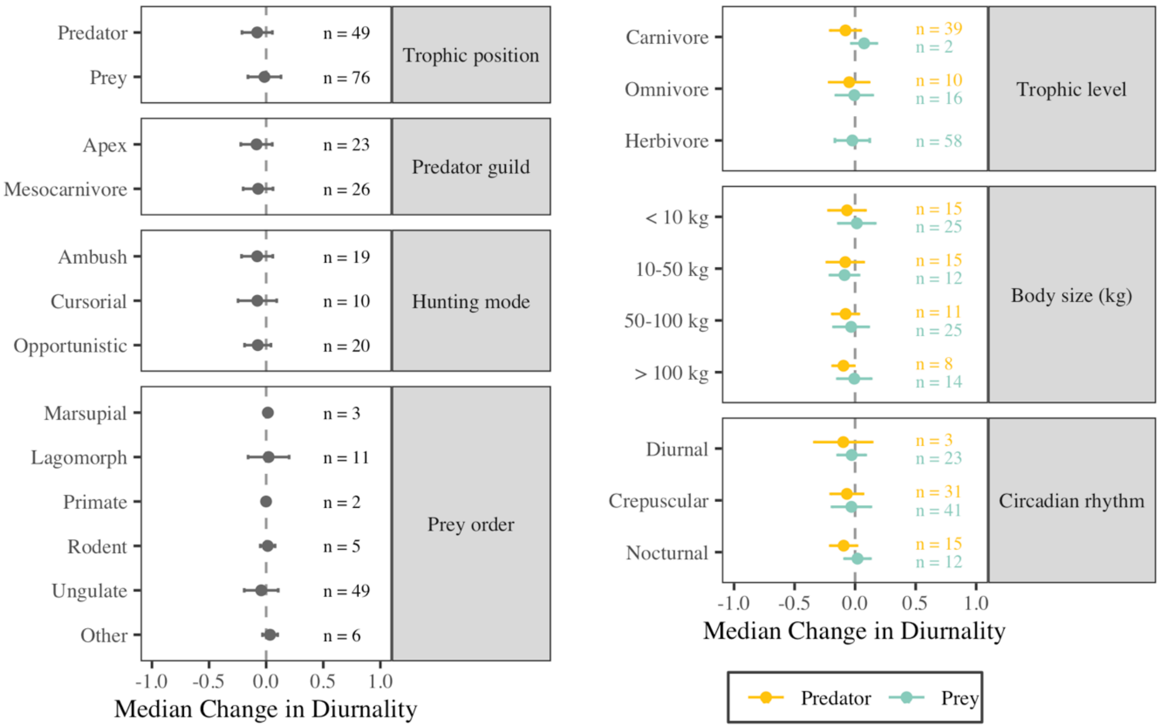

Figure 3. The influence of functional traits on the change in diurnal activity of terrestrial mammals, based on a review of paired camera trap studies. The change in diurnal activity ratio was calculated between paired settings of low and high human activity for each species in each study (n = 49 predators, n = 76 prey, 19 studies).

While our analysis revealed that, in paired settings of high human activity, predator-prey activity resembled all four predicted behavioral pathways, such an analysis is incomplete without concurrent measures of animal responses in space and time. In our review, we found that studies seldom reported both temporal and spatial impacts of human activity on animal behavior. Paired research designs that measured human impacts on both predators and their prey were similarly rare. Out of the 405 abstracts that warranted a full review, we excluded 155 studies that did not use camera trap array study designs, 75 studies for lacking concurrent data on mammal predators and prey, 80 studies that did not adequately distinguish between high and low human use, 28 studies that had fewer than 10 camera sites or did not include temporal data, and 48 studies with temporal data in the wrong format for our analysis. We suggest researchers apply this framework to local empirical data to test for site-specific or species-specific patterns in both space and time.

LINKING PREDATOR-PREY OVERLAP TO ECOLOGICAL OUTCOMES

Our framework (**Figure 1**) provides testable hypotheses regarding the influence of humans on predator-prey behavior and overlap. However, the measurement of human impacts on predator-prey overlap is only a first step to identifying whether species interactions may change. Taken together, these concepts, as well as a few key considerations and additional empirical methods, can help researchers link human-altered predator-prey overlap to broader ecological outcomes including predator diet, predation rates, competitive exclusion, trophic interactions.

Most importantly, it is difficult to infer how altered behavior and spatiotemporal overlap influence predation encounter rate without accounting for differences in predator and prey population density. Predator consumption relies heavily on prey density (Holling, 1959; Solomon, 1949). Recent extensions of density estimation methods, such as the Random Encounter Staying Time model, can allow for robust estimation of animal density without individual recognition (Nakashima et al., 2018). However, such methods rely on accounting for variation in detection by study, site, survey design, or species, which can vary widely (Moll et al., 2020). To be considered robust, human-impact studies that link animal behavior to predation would ideally collect data on a wide array of metrics, beginning with behavioral response as a first step but also including demography, density, and abundance.

Another key consideration in linking predator-prey overlap to ecological outcomes is that altered overlap of dyads may not predict where or when predation events occur (Suraci et al., 2022). Prey might continue to avoid predators at fine scales, maintaining spatiotemporal partitioning despite high overlap. In such cases, non-consumptive effects (i.e., stress that leads to lower fecundity) may emerge if prey employ energetically costly anti-predator behaviors to avoid both humans and predators (Frid & Dill, 2002; Soudijn et al., 2020). Pairing multi-species behavioral studies with demographic or physiological studies will be needed to determine whether consumptive or non-consumptive effects of predation change as a result of human-altered predator-prey overlap (e.g., Zbyryt et al., 2017).

Measuring human impacts on animal responses at the appropriate scale can also be key to accurately identifying ecological outcomes of behavioral shifts. Conceivably, predators and prey may respond to different human stimuli (including various auditory, olfactory, and visual cues), and at different scales. This can lead to situations where one species may be attracted to human activity at a broad spatial scale (for example, to forage on anthropogenic food sources), but both predator and prey avoid humans at fine spatial scales (e.g., Rogala et al., 2011). When possible, studies that measure animal behavior across spatiotemporal scales will be most informative. When this is not feasible, researchers might consider how the goal of the study and the ecology of the system correspond to tradeoffs associated with choosing various sampling designs (e.g., see Steidl & Powell, 2006).

Comprehensive assessments of human influence on predator-prey interactions consider both spatial and temporal dimensions of predator-prey overlap, because prey may avoid predators in one dimension (i.e., space or time) despite high overlap in another dimension. If human activity increases predator-prey overlap in space, prey may still safely exploit risky places by foraging during predator downtimes (Beauchamp, 2007), though non-optimal foraging times may be energetically costly to prey (Kronfeld-Schor & Dayan, 2003). Methods like GPS telemetry and camera trapping facilitate inference on both spatial and temporal distribution simultaneously. Furthermore, using indices that simultaneously estimate predator-prey overlap in space and time, such as occupancy models with a continuous-time detection process (Kellner et al., 2022) or Bayesian time-dependent observation models (Ait Kaci Azzou et al., 2021) can avoid these issues and provide more accurate estimates of human impact on encounter probabilities. Applying our proposed framework to such inferences would provide a rigorous test of how humans influence predator-prey outcomes across dimensions.

As humans modify the contest between predators and prey, complex feedbacks among multiple players can obscure the true mechanisms driving an observed pattern. Human activity can influence each ecological player, while predator and prey simultaneously influence each other. As a result, it is often difficult to disentangle, for instance, whether a prey refuge pattern is the consequence of (a) prey attraction to human activity, or (b) prey exploitation of a predator-free zone. To resolve these types of uncertainty, researchers may consider using additional controlled experiments to further isolate and test the hypothesized drivers of an observed response to human activity (e.g., Sarmento & Berger, 2017).

While our framework explicitly considers predator-prey relationships as dyads, rarely are predators and prey in obligate pairings. Human activity may influence prey choice, for example when predators have multiple prey, or reshape multi-predator effects on prey with more than one predator (Sih et al., 1998). To advance predictions of how human activity will affect species interactions, it will be beneficial to apply this framework to combinations of predators, prey, and competitors (Mills & Harris, 2020). One promising avenue of research lies in comparing how species richness, composition, and food web structure influence predator-prey responses to human activity (e.g., see Sévêque et al., 2020). Researchers can deploy these research designs to identify whether predators, prey, competitors, or human disturbance are driving the predominant patterns of dietary preference and predation rate.

Future research might consider further investigation into how human influence on predator-prey overlap, encounter, or predation, is linked to the functional traits (e.g., body size, hunting mode, circadian rhythm) of each interactor. For instance, nocturnal prey may outperform diurnal human-avoidant predators forced to hunt at night, limiting encounter risk despite high overlap between predator and prey (Beauchamp, 2007). One successful approach to clarifying whether altered overlap results in altered predation is using multispecies camera trap studies in tandem with diet composition studies (e.g., Smith et al., 2018). Pairing camera and diet data can allow researchers to connect overlap to predation non-invasively, avoiding the more costly and effort-intensive research designs that use GPS telemetry clusters and animal necropsy data to estimate predation.

In certain cases, human influence on predator-prey overlap may be temporary and without lasting consequences for ecological communities. For instance, if predators and prey habituate to human activity over time (Blumstein, 2016) encounter rates may be maintained, and the predator-prey response race may continue unaltered by humans. Yet in this case, the rise of human-wildlife conflict and use of lethal or non-lethal deterrents may in turn affect animal behavior and predator-prey overlap (Manlick & Pauli, 2020). Researchers can use iterative experiments that measure how multiple ecological players habituate or sensitize to human disturbance (e.g., (Uchida & Blumstein, 2021) to better capture which of the four possible human-induced response pathways predict shifts in encounter risk over time.

Identifying thresholds of human activity that alter animal behavior will be key to drawing useful inference from human impact studies and improving our understanding of when altered interactions may have reverberating impacts across ecosystems. Examples of such studies include comparison of animal response to motorized versus non-motorized recreation (Larson et al., 2016), leashed versus unleashed domestic dogs (Reed & Merenlender, 2011), exurban versus suburban development (Merenlender et al., 2009; Smith, Duane, et al., 2019), dense versus dispersed oil development (Sawyer et al. 2020), and the influence of human presence versus the human footprint (Nickel et al., 2020; Suraci et al., 2021). Such measurements can aid in creating specific guidelines for human activity near wildlife. Ultimately, these research designs will help anticipate how predators and prey respond to human activity in rapidly changing landscapes.

CONCLUSION

Behavioral ecology is increasingly recognized as a valuable aspect of population and ecosystem management (Gaynor et al., 2021) yet complex behavioral interactions among predators, prey, and humans (Kuijper et al., 2016) challenge the application of theory to practical solutions. Nonetheless, understanding species interactions remains key to the coexistence and persistence of wildlife, and ecosystem function, in settings with high human activity. For example, anthropogenic effects on prey may sometimes need to be minimized before predator recovery and predator-prey interactions can be restored (Lahkar et al., 2020). Unfortunately, the daunting task of studying or modeling complex behavioral feedbacks among players in this ecological game has deterred progress in understanding the ecology of landscapes characterized by high human activity. Investment in models that explain how humans modify species interactions, rather than solely species richness or abundance, is critical to fundamental ecology and the implementation of science-based management and conservation practice. Adopting our framework can help researchers test for patterns of human influence on strongly interacting species and identify possible mechanisms driving broader ecological outcomes.

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DATA AVAILABILITY STATEMENT

A list of data sources used in the study are provided in the Data sources section. The authors confirm that any data that was not available from published sources was used and cited with permission of the data's original authors. Data used to produce Figure 2 and Figure 3 are available from the Dryad Digital Repository: https://doi.org/10.6078/D1FQ42 (Van Scoyoc et al., 2023).

SUPPLEMENT TO CHAPTER 3:

Supplementary Methods
Tables S1 – S3

Supplementary Methods

We conducted systematic and snowball literature reviews to gather empirical data and examine how human activity affected the activity and overlap of predator-prey dyads. For the systematic review, we used Web of Science to search the published literature from 2000 – 2020, using the query "TS = ("activity pattern*" OR "temporal*" OR "diel" OR "nocturnal*" OR "diurnal*" OR "time of day" OR "camera trap*" OR "overlap*" OR "co-occurrence" OR "cooccurrence" OR "occupancy") AND ("human*" OR "people" OR "anthropogenic" OR "touris*" OR "recreat*" OR "disturb*") AND ("wildlife" OR "mammal*" OR "animal*" OR "*carnivor*" OR "herbivor*" OR "ungulate*" OR "predator*" OR "prey" OR "commun*") NOT ("marine*" OR "*fish*")" to match titles, abstracts, and keywords within the topics of Environmental Sciences & Ecology, Zoology, or Biodiversity & Conservation. We read the resulting paper titles and abstracts (n = 6,646) and read the full study if it showed potential to meet our criteria (n = 405).

We retained studies that (1) measured the diel activity of at least one terrestrial mammal predator and terrestrial mammal prey dyad <1 kg in body mass, and (2) used camera traps to compare animal activity at paired sites or treatments of high and low human use. We limited our review to camera trap studies given that the temporal dimension is often overlooked, easily standardized, and eliminates confounding lethal or density effects of spatial indices. For our analysis, we defined "human activity" as sustained, non-lethal presence of humans. Targeting studies that measured non-lethal human activity allowed us to examine behavioral effects rather than the numerical effects of humans on wildlife. Our definition of human activity was intentionally broad (e.g., people on foot, motorized and non-motorized recreation, pastoralism, energy infrastructure, housing, roads, urban areas) as our aim was to capture and compare the multiple pathways of animal response to disturbance. We distinguished high and low human use according to author descriptions in each peer-reviewed paper (Table S1). We designated predator-prey dyads based on predator diet as listed in the paper, expert advice, or the Encyclopedia of Life (Parr et al., 2014; see Table S2 and Table S3 for the list of included predator-prey dyads).

To examine predator-prey temporal activity, we extracted day and night image counts of each species at each high and low human use to calculate the ratio of diurnal activity. When these metrics were not available, we used the raw data with author permission, filtered for image independence as greater than 30-minutes apart (Sollmann, 2018) and classified images based on sun-time (Nouvellet et al., 2012); see Table S1 for detailed methods on each study). We discarded any dyads for which there were fewer than 10 total images of a species. We centered the diurnal activity ratio on zero and standardized it so that -1 represented complete nocturnality and 1 complete diurnality. Then, we set the rescaled diurnal activity ratios at low human use to zero and calculated the relative difference for diurnal activity ratios at high human use across predator-prey dyads. This allowed us to simultaneously compare the relative magnitude of diurnal activity changes across all predator-prey dyads (**Figure 2A**). We made the assumption that the majority of human activity was diurnal across studies, thus, we considered any difference in activity between low and high human use to be in response to diurnal human activity.

To examine predator-prey temporal overlap, we compared temporal overlap coefficients of each species pair at low and high human use. Overlap coefficients (Δ) are widely used metrics to report temporal partitioning of animals from camera trap surveys and are calculated using kernel density estimation that range from 0 (no overlap) to 1 (complete overlap) (Ridout & Linkie, 2009). When these metrics were not available, we used published datasets or the raw data with author permission to estimate Δ using the 'overlap' R package. We calculated Δ using Dhat4, according to the protocol of Ridout & Linkie (2009). We were able to include or calculate overlap coefficients for 17 of the studies and 172 dyads. We calculated the change in overlap as the difference between predator-prey overlap at high and low human use (**Figure 2B**).

Out of the 405 abstracts that warranted a full review, we excluded 155 studies that did not use camera trap array study designs, 75 studies for lacking concurrent data on mammal predators and prey, 80 studies that did not adequately distinguish between high and low human use, 28 studies that had fewer than 10 camera sites or did not include temporal data, and 48 studies with temporal data in the wrong format for our analysis. Ultimately, there were 19 studies that had data that fit our criteria for inclusion, with 178 predator-prey dyads included in the temporal activity analysis (**Figure 2A**). Of these, we included 167 predator-prey dyads from 17 studies in the temporal overlap analysis (**Figure 2B**). We eliminated 11 dyads for the overlap analysis, given that 5 dyads did not include data to calculate overlap coefficients, and 6 dyads exhibited a neutral activity response and thus did not warrant further testing via our framework's approach.

We examined how functional traits (prey order, body size, predator hunting mode, trophic level, predator guild, and circadian rhythm) influenced temporal activity of predator and prey species (unique to each study) between settings of high and low human activity (**Figure 3**).

Table S1. Site descriptions, human activity level, and method used to calculate predator-prey activity ratio and overlap coefficient of each study in analysis (n = 19).

Reference	Location	Habitat Type	Human activity type	Data acquisition and human activity	Activity ratio	Overlap coefficient
Baker & Leberg 2018	USA	Desert	Human presence (on foot, vehicles, human density)	Acquired record table from authors. We used the author's classification of SAGU site as high human activity and CHIR site as low human activity.	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Barrueto *et al.* 2014	Canada	Forest	Human presence (on foot), Roads	Acquired data from Figure 2. We used the authors classification of backcountry and wildlife crossings as low and high human activity.	We digitized percent data from Figure 2, transformed it into image counts using the image totals from the paper, then calculated day/night activity ratios based on sun-time for the study period.	We digitized percent data from Figure 2, transformed it into image counts using the image totals from the paper, then estimated the overlap coefficient with the 'overlap' package in R (delta 4, bootstrap 1000).
Caldwell *et al.* 2020	USA	Shrubland, Woodland	Human presence (on foot, vehicles)	Accquired record table from authors. We classified low human activity as less than 25 total human and/or vehicle detections (2 sites, cameras 35 & 33), and high human activity as greater than 25 total human and/or vehicle detections (4 sites, remaining).	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to calculate hourly counts and estimate the overlap coefficient with the 'overlap' package in R (delta 4, bootstrap 1000).
Carter *et al.* 2015	Nepal	Forest	Inside vs. outside National Park	Acquired record table from authors. We used the author's classification of high human activity as sites outside the park, and low human activity as sites inside the park, as well as the author's classification of day/night.	We used the raw record table to calculate day/night image counts by species for 2010 & 2011 to calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Dawson *et al.* 2018	Australia	Savanna, Woodland	Energy infrastructure (seismic lines)	Acquired data from Table S3 and Figure 6. We used the author's classification of control and seismic line camera placement.	The author provided image counts from Appendix S2, as broken down by day/night to calculate diel activity ratios.	We used values in Table S3 and Figure 6.
Díaz-Ruíz *et al.* 2016	Spain	Savanna	Agriculture, Housing	We used the author's classification of agricultural sites as high human activity and shrubland sites as low human activity.	We digitized Figure 3 to estimate the proportion of hourly activity, we averaged hourly activity for agricultural and shrubland sites which we used to calculate day/night activity ratios.	We used data from Table 2. We averaged the overlap coefficients for agricultural sites with both species present (1, 3, 4, and 8) and shrubland sites (5, 6, 10, and 11)
Gallo *et al.* 2019	USA	Urban	Urban housing	Acquired data from Dryad. We replicated the authors' procedure of distinguishing high/low human activity sites using a PCA of the site covariates mean canopy, mean housing, and mean impervious, and counted values <= 0 as high human activity.	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Gray *et al.* 2011	Cambodia	Forest	Human presence (on foot), Resource extraction	Activity ratios aqcuired with permission from Gaynor et al. 2018.	Acquired activity ratios with permission from Gaynor et al. 2018.	No overlap data available.
Kays *et al.* 2017	USA	Forest	Human presence (on foot, vehicles, dogs, horses)	Accquired study data from Dryad. We classified low human activity as 'off trail' sites (50 or 200m from trails), and high human activity as 'on trail' sites.	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).

Lendrum *et al.* 2017	USA	Forest	Human presence, Energy infrastructure	Accquired study data from Table 2 and Figure 2. We used the authors site classifications as developed (high human activity) and undeveloped (low human activity) based on the presence of energy infrastructure and human activity.	We used activity data from Table 2. We evenly divided dawn/dusk crepuscular activity into the nocturnal/diurnal categories.	We digitized the plots in Figure 2 to estimate the overlap of the density curves using the overlapTrue() function in the 'overlap' package in R. (CIs could not be calculated without raw data).
Mills & Harris 2020	Burkina Faso, Benin, Niger	Savanna, Woodland	Human presence (on foot)	Accquired study data from Figure 3 and Figure 4. We used the author's classification of high human activity as > 0.54 mean occupancy of humans.	We extracted the nocturnal activity for each species by digitizing Figure 4, we then calculated the proportion of diurnal activity as 1 - nocturnal activity.	We digitized the plots in Figure 3 to estimate the overlap of the density curves using the overlapTrue() function in the 'overlap' package in R. (CIs could not be calculated without raw data).
Nix *et al.* 2018	USA	Forest	Human presence (on foot, camping)	Record table acquired with permission from Gaynor et al. 2018. We used the authors classification of low human activity as the weekday (Monday - Thursday), and high human activity as the weekend (Friday - Sunday).	We used the record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the record table to filter independent detections and estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Oberosler *et al.* 2017	Italy	Forest	Human presence, Logging, Roads	Acquired data from Figure 4.	We digitized Figure 4 to estimate the proportion of hourly activity at sites of high and low human activity, which we used to calculate day/night activity ratios.	No overlap data available.
Reilly *et al.* 2017	USA	Savanna	Human presence (on foot, horses, vehicles)	Acquired record table from authors. We used the author's classification of high and low human activity, but combined high/medium and low/none categories.	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Rich *et al.* 2016	Botswana	Savanna	Human presence (on foot, livestock, vehicles)	Acquired record table from authors. We used the authors recommendation to classify high human activity as the livestock grazing area and low human activity as the wildlife management area and game reserves.	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Smith *et al.* 2019	South Africa	Woodland, Shrubland	Land use type (residential, agricultural, reserve)	Accquired data from Figure 4, Figure 5, and Figure 6. We used the author's classification of agricultural as high human activity sites, and reserve land as low human activity sites.	We used activity data from Table 2. We evenly divided dawn/dusk crepuscular activity into the nocturnal/diurnal categories.	We used the overlap coefficients in Figure 4, Figure 5, and Figure 6.
Wang *et al.* 2015	USA	Forest	Human presence (on foot)	Acquired record table from authors. We used the author's classification of high and low human activity.	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the overlap coefficients in Table 3.
Wilkinson *et al.* 2021	Kenya	Savanna	Human presence (on foot, livestock)	Acquired record table from authors. We used the author's classification as sites of high human activity (>= 1 detection/trap night, n = 8 sites), and low human activity (< 1 detection/trap night, n = 11 sites)	We used the raw record table to filtered images for independence, classified day/night using sun-time for species, and calculate activity ratios.	We used the raw record table to estimate overlap coefficients with the 'overlap' package in R (delta 4, bootstrap 1000).
Xiao *et al.* 2018	China	Forest	Human presence (on foot), Housing, Roads, Logging	Acquired data from Figure 8. We used the author's classification of the summer season as high human activity and the winter season as low human activity.	We used the authors breakdown of percent of daytime and night time images for each species.	We used the overlap coefficients in Figure 8.

Table S2. Predator-prey activity ratios at high and low human use for 19 studies and 178 predator-prey dyads.

Reference	Predator	Prey	Predator diurnal activity		Prey diurnal activity	
			(low)	(high)	(low)	(high)
Baker & Leburg 2018	Bobcat	Black-Tailed Jackrabbit	0.316	0.241	0.044	0.304
		Desert Cottontail			0.165	0.429
	Coyote	Black-Tailed Jackrabbit	0.1	0.216	0.044	0.304
		Desert Cottontail			0.165	0.429
		Deer spp.			0.578	0.463
		Javelina			0.538	0.25
	Gray Fox	Black-Tailed Jackrabbit	0.035	0.04	0.044	0.304
		Desert Cottontail			0.165	0.429
Barrueto et al. 2014	Black Bear	Mule Deer	0.744	0.646	0.631	0.599
	Brown Bear	Elk	0.748	0.679	0.378	0.253
		Mule Deer			0.631	0.599
		Moose			0.474	0.498
	Coyote	Mule Deer	0.563	0.481	0.631	0.599
	Puma	Mule Deer	0.411	0.262	0.631	0.599
	Wolf	Elk	0.463	0.44	0.378	0.253
		Mule Deer			0.631	0.599
		Moose			0.474	0.498
Caldwell & Klip 2020	Bobcat	Lagomorph spp.	0	0.337	0.762	0.631
	Coyote	Lagomorph spp.	0.5	0.534	0.762	0.631
		Mule Deer			0.35	0.318
Carter et al. 2015	Leopard	Chital	0.535	0.157	0.743	0.527
		Muntjac			0.648	0.527
		Wild Boar			0.624	0.254
		Sambar			0.074	0.115
	Tiger	Chital	0.19	0.073	0.743	0.527
		Muntjac			0.648	0.527
		Wild Boar			0.624	0.254
		Sambar			0.074	0.115
Dawson et al. 2018	Dingo	Agile Wallaby	0.7	0.336	0.267	0.285
		Greater Bilby			0	0.022
	Domestic Cat	Agile Wallaby	0.302	0.142	0.267	0.285
		Greater Bilby			0	0.022
Díaz-Ruíz et al. 2016	Red Fox	European Rabbit	0.26	0.181	0.889	0.937
Gallo et al. 2019	Coyote	Eastern Cottontail	0.209	0.152	0.247	0.23
		White-Tailed Deer			0.54	0.722
Gray et al. 2011	Leopard	Muntjac	0.613	0.55	0.713	0.612
		Wild Boar			0.838	0.432
	Black Bear	Eastern Fox Squirrel	0.781	0.663	0.986	0.971
		Virginia Opossum			0.013	0
		White-Tailed Deer			0.577	0.502
		Wild Boar			0.444	0.333
		Eastern Cottontail			0.03	0.088
		Eastern Gray Squirrel			0.962	0.982

Kays et al. 2017		Raccoon			0.054	0.06
	Bobcat	Eastern Fox Squirrel	0.53	0.423	0.986	0.971
		Eastern Cottontail			0.03	0.088
		Eastern Gray Squirrel			0.962	0.982
	Coyote	Eastern Fox Squirrel	0.284	0.156	0.986	0.971
		Virginia Opossum			0.013	0
		White-Tailed Deer			0.577	0.502
		Wild Boar			0.444	0.333
		Eastern Cottontail			0.03	0.088
		Eastern Gray Squirrel			0.962	0.982
		Raccoon			0.054	0.06
	Gray Fox	Eastern Fox Squirrel	0.107	0.086	0.986	0.971
		Eastern Cottontail			0.03	0.088
		Eastern Gray Squirrel			0.962	0.982
	Red Fox	Eastern Fox Squirrel	0.27	0.133	0.986	0.971
		Eastern Cottontail			0.03	0.088
		Eastern Gray Squirrel			0.962	0.982
Lendrum et al. 2017	Bobcat	Lagomorph spp.	0.346	0.232	0.25	0.163
	Coyote	Lagomorph spp.	0.588	0.382	0.25	0.163
		Mule Deer			0.686	0.509
Mills & Harris 2020	Leopard	Aardvark	0.366	0.412	0.165	0.314
		Hartebeest			0.726	0.78
		Kob			0.826	0.878
		Oribi			0.861	0.885
		Waterbuck			0.819	0.834
		Bushbuck			0.599	0.528
		Duiker spp.			0.625	0.551
		Reedbuck			0.592	0.468
		Roan Antelope			0.787	0.742
		Warthog			0.987	0.941
	Lion	Bushbuck	0.561	0.44	0.599	0.528
		Cape Buffalo			0.578	0.534
		Duiker spp.			0.625	0.551
		Reedbuck			0.592	0.468
		Roan Antelope			0.787	0.742
		Warthog			0.987	0.941
		Aardvark			0.165	0.314
		Hartebeest			0.726	0.78
		Kob			0.826	0.878
		Oribi			0.861	0.885
		Waterbuck			0.819	0.834
		Bushbuck			0.599	0.528
		Cape Buffalo			0.578	0.534
		Duiker spp.			0.625	0.551
		Reedbuck			0.592	0.468
		Roan Antelope			0.787	0.742

	Spotted Hyena	Warthog	0.453	0.413	0.987	0.941
		Aardvark			0.165	0.314
		Hartebeest			0.726	0.78
		Kob			0.826	0.878
		Oribi			0.861	0.885
		Waterbuck			0.819	0.834
Nix et al. 2018	Puma	Beaver	0	0	0.047	0.061
		Raccoon			0.018	0.08
		Mule Deer			0.578	0.561
Oberosler et al. 2017	Red Fox	Brown Hare	0.239	0.248	0.6	0.239
Reilly et al. 2017	Bobcat	Brush Rabbit	0.38	0.314	0.494	0.729
	Coyote	Mule Deer	0.459	0.364	0.615	0.585
		Raccoon			0.097	0.078
		Brush Rabbit			0.494	0.729
	Gray Fox	Brush Rabbit	0.049	0.059	0.494	0.729
Rich et al. 2016	Black-backed Jackal	Springhare	0.162	0.372	0.097	0.118
		Cape Hare			0.213	0.177
	Caracal	Cape Hare	0.14	0.136	0.213	0.177
		Springhare			0.097	0.118
	Leopard	Duiker	0.333	0.254	0.554	0.432
		Warthog			0.887	0.819
		Greater Kudu			0.584	0.6
		Impala			0.735	0.746
	Lion	Buffalo	0.417	0.322	0.313	0.275
		Duiker			0.554	0.432
		Warthog			0.887	0.819
		Greater Kudu			0.584	0.6
		Impala			0.735	0.746
		Zebra			0.511	0.526
	Spotted Hyena	Buffalo	0.239	0.179	0.313	0.275
		Duiker			0.554	0.432
		Warthog			0.887	0.819
		Greater Kudu			0.584	0.6
		Impala			0.735	0.746
		Zebra			0.511	0.526
	Wild Dog	Greater Kudu	0.443	0.748	0.584	0.6
		Impala			0.735	0.746
		Springhare			0.097	0.118
		Zebra			0.511	0.526
		Cape Hare			0.213	0.177
		Duiker			0.554	0.432
		Warthog			0.887	0.819
Smith et al. 2019	Black-backed Jackal	Blue Duiker	0.52	0.49	0.665	0.65
		Duiker			0.71	0.735
	Caracal	Blue Duiker	0.6	0.475	0.665	0.65
		Bushbuck			0.625	0.655

		Duiker			0.71	0.735
Wang et al. 2015	Coyote	Mule Deer	0.503	0.305	0.525	0.551
		Raccoon			0.067	0.17
		Virginia Opossum			0.028	0.043
	Puma	Mule Deer	0.263	0.136	0.525	0.551
		Raccoon			0.067	0.17
		Virginia Opossum			0.028	0.043
Wilkinson et al. 2021	Black-backed Jackal	Kirk's Dikdik	0.382	0.063	0.789	0.359
		Thomsons Gazelle			1	0.712
		African Hare			0	0.014
	Leopard	Common Zebra	0.164	0.08	0.254	0.195
		Impala			0.927	0.568
		Kirk's Dikdik			0.789	0.359
		Olive Baboon			1	0.999
		Vervet			1	0.999
		Aardvark			0	0
		Warthog			0.953	0.983
		Waterbuck			0.167	0.605
	Lion	Warthog	0	0.075	0.953	0.983
		Waterbuck			0.167	0.605
		Aardvark			0	0
		Buffalo			0.058	0.03
		Common Zebra			0.254	0.195
		Eland			0.651	0.477
		Impala			0.927	0.568
		Kirk's Dikdik			0.789	0.359
		Olive Baboon			1	0.999
		Thomsons Gazelle			1	0.712
	Serval	African Hare	0.093	0.053	0	0.014
	Spotted Hyena	Buffalo	0.152	0.019	0.058	0.03
		Common Zebra			0.254	0.195
		Eland			0.651	0.477
		Impala			0.927	0.568
		Kirk's Dikdik			0.789	0.359
		Olive Baboon			1	0.999
		Thomsons Gazelle			1	0.712
		Aardvark			0	0
		Warthog			0.953	0.983
		Waterbuck			0.167	0.605
	Striped Hyena	Olive Baboon	0.13	0.021	1	0.999
Xiao et al. 2018	Tiger	Roe Deer	0.295	0.392	0.577	0.665
		Sika Deer			0.635	0.655
		Wild Boar			0.633	0.584

Table S3. Summary of predator and prey overlap coefficients at high and low human use for 17 studies and 172 predator-

Reference	Predator	Prey	Overlap (low)	CI	Overlap (high)	CI	Change in overlap
Baker & Leburg 2018	Bobcat (*Lynx rufus*)	Black-Tailed Jackrabbit	0.641	0.464-0.851	0.806	0.718-0.981	0.165
		Desert Cottontail	0.758	0.652-0.97	0.814	0.728-0.982	0.056
	Coyote (*Canis latrans*)	Black-Tailed Jackrabbit	0.664	0.486-0.933	0.879	0.827-0.993	0.215
		Deer spp.	0.517	0.312-0.752	0.757	0.624-0.86	0.24
		Desert Cottontail	0.815	0.714-1.137	0.767	0.67-0.841	-0.048
		Javelina	0.451	0.217-0.761	0.82	0.736-0.949	0.369
	Gray Fox (*Urocyon cinereoargenteus*)	Black-Tailed Jackrabbit	0.768	0.669-0.911	0.772	0.692-0.85	0.004
		Desert Cottontail	0.857	0.79-0.963	0.655	0.557-0.703	-0.202
Barrueto et al. 2014	Black Bear (*Ursus americanus*)	Mule Deer	0.742	0.66-0.793	0.821	0.778-0.857	0.079
	Brown Bear (*Ursus arctos*)	Elk	0.647	0.592-0.679	0.58	0.54-0.605	-0.067
		Moose	0.724	0.656-0.771	0.797	0.737-0.85	0.073
		Mule Deer	0.834	0.792-0.866	0.852	0.817-0.886	0.018
	Puma (*Puma concolor*)	Mule Deer	0.672	0.579-0.738	0.668	0.601-0.7	-0.004
	Coyote (*Canis latrans*)	Mule Deer	0.871	0.836-0.917	0.84	0.806-0.861	-0.031
	Wolf (*Canis lupus*)	Elk	0.865	0.824-0.904	0.804	0.771-0.823	-0.061
		Moose	0.884	0.835-0.949	0.888	0.839-0.939	0.004
		Mule Deer	0.821	0.776-0.857	0.852	0.823-0.876	0.031
Caldwell & Klip 2020	Bobcat (*Lynx rufus*)	Lagomorph spp.	0.276	0.104-0.429	0.641	0.544-0.713	0.365
	Coyote (*Canis latrans*)	Lagomorph spp.	0.75	0.645-1.018	0.741	0.679-0.819	-0.009
		Mule Deer	0.742	0.607-0.962	0.807	0.728-0.872	0.065
Carter et al. 2015	Leopard (*Panthera pardus*)	Wild Boar	0.767	0.687-0.909	0.808	0.712-0.924	0.041
		Chital	0.656	0.533-0.742	0.557	0.402-0.612	-0.099
		Muntjac	0.597	0.443-0.69	0.571	0.415-0.645	-0.026
		Sambar	0.492	0.351-0.604	0.841	0.774-0.964	0.349
	Tiger (*Panthera tigris*)	Wild Boar	0.481	0.387-0.52	0.71	0.6-0.807	0.229
		Chital	0.453	0.379-0.479	0.495	0.369-0.553	0.042
		Muntjac	0.545	0.447-0.59	0.511	0.375-0.593	-0.034
		Sambar	0.735	0.625-0.781	0.756	0.652-0.856	0.021
Dawson et al. 2018	Dingo (*Canis lupus dingo*)	Agile Wallaby	0.62	0.42-0.83	0.86	0.79-0.93	0.24
		Greater Bilby	0.3	0.08-0.46	0.66	0.57-0.75	0.36
	Domestic Cat (*Felis catus*)	Agile Wallaby	0.75	0.64-0.85	0.81	0.74-0.85	0.06
		Greater Bilby	0.55	0.42-0.68	0.68	0.58-0.78	0.13
Díaz-Ruíz et al. 2016	Red Fox (*Vulpes vulpes*)	European Rabbit	0.425	-	0.3975	-	-0.0275
Gallo et al. 2019	Coyote (*Canis latrans*)	Eastern Cottontail	0.828	0.771-0.857	0.853	0.814-0.858	0.025
		White-Tailed Deer	0.726	0.693-0.734	0.48	0.427-0.488	-0.246
Gray et al. 2011	Leopard (*Panthera pardus*)	Red Muntjac	-	-	-	-	-
		Wild Boar	-	-	-	-	-
	Black Bear (*Ursus americanus*)	Eastern Cottontail	0.405	0.325-0.433	0.581	0.483-0.648	0.176
		Eastern Fox Squirrel	0.63	0.57-0.669	0.548	0.448-0.588	-0.082
		Eastern Gray Squirrel	0.697	0.664-0.729	0.549	0.489-0.582	-0.148
		Raccoon	0.33	0.273-0.333	0.419	0.343-0.433	0.089
		Virginia Opossum	0.29	0.212-0.288	0.339	0.225-0.345	0.049
		White-Tailed Deer	0.801	0.767-0.825	0.825	0.781-0.859	0.024
		Wild Boar	0.634	0.495-0.746	0.743	0.632-0.832	0.109
	Bobcat (*Lynx rufus*)	Eastern Cottontail	0.627	0.539-0.709	0.728	0.634-0.804	0.101
		Eastern Fox Squirrel	0.486	0.387-0.554	0.438	0.335-0.473	-0.048

Kays et al. 2017		Eastern Gray Squirrel	0.529	0.445-0.612	0.417	0.354-0.445	-0.112
	Coyote (*Canis latrans*)	Eastern Cottontail	0.757	0.677-0.803	0.856	0.774-0.923	0.099
		Eastern Fox Squirrel	0.309	0.225-0.32	0.241	0.144-0.249	-0.068
		Eastern Gray Squirrel	0.348	0.292-0.375	0.216	0.175-0.219	-0.132
		Raccoon	0.748	0.702-0.789	0.854	0.82-0.882	0.106
		Virginia Opossum	0.697	0.633-0.733	0.763	0.682-0.797	0.066
		White-Tailed Deer	0.748	0.699-0.779	0.705	0.66-0.713	-0.043
		Wild Boar	0.723	0.585-0.817	0.71	0.609-0.784	-0.013
	Gray Fox (*Urocyon cinereoargenteus*)	Eastern Cottontail	0.863	0.806-0.974	0.824	0.727-0.914	-0.039
		Eastern Fox Squirrel	0.151	0.02-0.173	0.173	0.041-0.176	0.022
		Eastern Gray Squirrel	0.18	0.069-0.22	0.148	0.054-0.159	-0.032
	Red Fox (*Vulpes vulpes*)	Eastern Cottontail	0.757	0.7-0.851	0.835	0.765-0.918	0.078
		Eastern Fox Squirrel	0.302	0.199-0.328	0.232	0.131-0.244	-0.07
		Eastern Gray Squirrel	0.345	0.268-0.387	0.209	0.16-0.219	-0.136
Lendrum et al. 2017	Bobcat (*Lynx rufus*)	Lagomorph spp.	0.55	-	0.794	-	0.244
	Coyote (*Canis latrans*)	Lagomorph spp.	0.748	-	0.915	-	0.167
		Mule Deer	0.838	-	0.84	-	0.002
Mills & Harris 2020	Spotted Hyena (*Crocuta crocuta*)	Aardvark	0.656	-	0.796	-	0.14
		Buffalo	0.763	-	0.777	-	0.014
		Bushbuck	0.726	-	0.779	-	0.053
		Duiker	0.776	-	0.778	-	0.002
		Hartebeest	0.584	-	0.466	-	-0.118
		Kob	0.428	-	0.312	-	-0.116
		Oribi	0.386	-	0.333	-	-0.053
		Reedbuck	0.78	-	0.813	-	0.033
		Roan Antelope	0.541	-	0.509	-	-0.032
		Warthog	0.289	-	0.291	-	0.002
		Waterbuck	0.523	-	0.394	-	-0.129
	Leopard (*Panthera pardus*)	Aardvark	0.776	-	0.74	-	-0.036
		Bushbuck	0.613	-	0.839	-	0.226
		Duiker spp.	0.661	-	0.795	-	0.134
		Hartebeest	0.524	-	0.538	-	0.014
		Kob	0.385	-	0.385	-	0
		Oribi	0.349	-	0.402	-	0.053
		Reedbuck	0.69	-	0.812	-	0.122
		Roan Antelope	0.467	-	0.581	-	0.114
		Warthog	0.234	-	0.363	-	0.129
		Waterbuck	0.414	-	0.466	-	0.052
	Lion (*Panthera leo*)	Aardvark	0.547	-	0.78	-	0.233
		Buffalo	0.906	-	0.862	-	-0.044
		Bushbuck	0.897	-	0.858	-	-0.039
		Duiker spp.	0.831	-	0.849	-	0.018
		Hartebeest	0.769	-	0.549	-	-0.22
		Kob	0.608	-	0.391	-	-0.217
		Oribi	0.562	-	0.41	-	-0.152
		Reedbuck	0.899	-	0.874	-	-0.025
		Roan Antelope	0.715	-	0.592	-	-0.123
		Warthog	0.462	-	0.375	-	-0.087
		Waterbuck	0.682	-	0.478	-	-0.204
		Beaver	0.843	0.72-0.973	0.758	0.62-0.886	-0.085

Nix et al. 2018	Puma (*Puma concolor*)	Mule Deer	0.361	0.194-0.423	0.291	0.143-0.33	-0.07
		Raccoon	0.825	0.697-0.943	0.731	0.617-0.859	-0.094
Oberosler et al. 2017	Red Fox (*Vulpes vulpes*)	Brown Hare	-	-	-	-	-
Reilly et al. 2017	Bobcat (*Lynx rufus*)	Brush Rabbit	0.632	0.496-0.707	0.576	0.434-0.623	-0.056
	Coyote (*Canis latrans*)	Brush Rabbit	0.764	0.654-0.87	0.619	0.496-0.691	-0.145
		Mule Deer	0.841	0.773-0.909	0.784	0.728-0.829	-0.057
		Raccoon	0.638	0.511-0.725	0.724	0.653-0.767	0.086
	Gray Fox (*Urocyon cinereoargenteus*)	Brush Rabbit	0.44	0.293-0.485	0.373	0.237-0.405	-0.067
Rich et al. 2016	Black-backed Jackal (*Canis mesomelas*)	Cape Hare	0.849	0.753-0.932	0.793	0.737-0.846	-0.056
		Springhare	0.9	0.839-1.085	0.685	0.598-0.738	-0.215
	Caracal (*Caracal caracal*)	Cape Hare	0.868	0.788-0.967	0.851	0.774-0.944	-0.017
		Springhare	0.826	0.719-0.997	0.767	0.648-0.855	-0.059
	Leopard (*Panthera pardus*)	Common Duiker	0.724	0.612-0.843	0.744	0.65-0.82	0.02
		Greater Kudu	0.665	0.552-0.748	0.584	0.46-0.647	-0.081
		Impala	0.533	0.45-0.59	0.388	0.298-0.407	-0.145
		Warthog	0.292	0.158-0.316	0.259	0.146-0.272	-0.033
	Lion (*Panthera leo*)	Buffalo	0.556	0.412-0.665	0.742	0.636-0.833	0.186
		Common Duiker	0.536	0.37-0.623	0.754	0.638-0.819	0.218
		Greater Kudu	0.487	0.367-0.573	0.608	0.485-0.682	0.121
		Impala	0.357	0.246-0.408	0.401	0.309-0.438	0.044
		Warthog	0.186	0.075-0.236	0.255	0.13-0.274	0.069
		Zebra	0.489	0.364-0.568	0.619	0.492-0.677	0.13
	Spotted Hyena (*Crocuta crocuta*)	Buffalo	0.735	0.642-0.828	0.581	0.465-0.65	-0.154
		Common Duiker	0.531	0.393-0.603	0.564	0.44-0.597	0.033
		Greater Kudu	0.479	0.361-0.534	0.425	0.301-0.467	-0.054
		Impala	0.324	0.245-0.333	0.225	0.159-0.224	-0.099
		Warthog	0.135	0.035-0.14	0.108	0.024-0.103	-0.027
		Zebra	0.517	0.419-0.567	0.476	0.371-0.528	-0.041
	Wild Dog (*Lycaon pictus*)	Cape Hare	0.433	0.29-0.461	0.4	0.301-0.446	-0.033
		Common Duiker	0.662	0.498-0.682	0.617	0.538-0.721	-0.045
		Greater Kudu	0.57	0.408-0.58	0.486	0.39-0.568	-0.084
		Impala	0.553	0.418-0.53	0.419	0.339-0.455	-0.134
		Springhare	0.336	0.148-0.37	0.307	0.192-0.345	-0.029
		Warthog	0.318	0.146-0.308	0.23	0.118-0.252	-0.088
		Zebra	0.628	0.489-0.645	0.426	0.33-0.501	-0.202
Smith et al. 2019	Black-backed Jackal (*Canis mesomelas*)	Blue Duiker	0.74	0.59-0.86	0.72	0.62-0.81	-0.02
		Gray Duiker	0.66	0.48-0.83	0.66	0.55-0.76	0
	Caracal (*Caracal caracal*)	Blue Duiker	0.82	0.75-0.87	0.69	0.54-0.80	-0.13
		Bushbuck	0.86	0.64-0.89	0.72	0.64-0.89	-0.14
		Gray Duiker	0.76	0.61-0.89	0.67	0.50-0.83	-0.09
Wang et al. 2015	Puma (*Puma concolor*)	Mule Deer	-	-	-	-	-
		Virginia Opossum	0.659	0.554-0.730	0.771	0.680-0.850	0.112
		Raccoon	0.793	0.774-0.937	0.844	0.725-0.866	0.051
	Coyote (*Canis latrans*)	Mule Deer	-	-	-	-	-
		Virginia Opossum	0.454	0.389-0.464	0.653	0.594-0.672	0.199
		Raccoon	0.545	0.485-0.557	0.739	0.681-0.781	0.194
	Black-backed Jackal (*Canis mesomelas*)	Kirk's Dikdik	0.523	0.407-0.561	0.65	0.55-0.69	0.127
		African Hare	0.606	0.483-0.669	0.836	0.771-0.86	0.23
		Thomsons Gazelle	0.213	0.031-0.258	0.338	0.152-0.366	0.125
		Aardvark	0.78	0.683-0.914	0.601	0.388-0.719	-0.179

Wilkinson et al. 2021	Leopard (*Panthera pardus*)	Kirk's Dikdik	0.332	0.158-0.347	0.511	0.298-0.603	0.179
		Impala	0.221	0.093-0.265	0.473	0.333-0.582	0.252
		Olive Baboon	0.151	0.051-0.206	0.085	-0.219	-0.066
		Vervet	0.137	0.026-0.184	0.108	-0.233	-0.029
		Warthog	0.202	0.066-0.241	0.103	-0.222	-0.099
		Waterbuck	0.36	0.134-0.471	0.439	0.26-0.551	0.079
		Common Zebra	0.675	0.519-0.69	0.867	0.794-1.024	0.192
	Lion (*Panthera leo*)	Aardvark	0.617	0.362-0.795	0.742	0.622-0.826	0.125
		Buffalo	0.575	0.308-0.635	0.579	0.517-0.632	0.004
		Kirk's Dikdik	0.12	-0.175	0.611	0.475-0.648	0.491
		Eland	0.256	0.112-0.307	0.381	0.22-0.365	0.125
		Impala	0.028	-0.101	0.406	0.293-0.39	0.378
		Olive Baboon	0.001	-0.06	0.069	0.022-0.089	0.068
		Thomsons Gazelle	0.01	-0.151	0.295	0.097-0.305	0.285
		Warthog	0.015	-0.1	0.09	0.029-0.103	0.075
		Waterbuck	0.27	0.052-0.445	0.464	0.327-0.546	0.194
		Common Zebra	0.508	0.272-0.6	0.733	0.608-0.728	0.225
	Serval (*Leptailurus serval*)	African Hare	0.736	0.622-0.793	0.756	0.614-0.881	0.02
	Spotted Hyena (*Crocuta crocuta*)	Aardvark	0.674	0.526-0.73	0.664	0.529-0.731	-0.01
		Buffalo	0.799	0.757-0.799	0.671	0.649-0.675	-0.128
		Kirk's Dikdik	0.432	0.363-0.459	0.631	0.549-0.689	0.199
		Eland	0.481	0.403-0.516	0.304	0.203-0.307	-0.177
		Impala	0.254	0.205-0.246	0.381	0.325-0.351	0.127
		Olive Baboon	0.129	0.076-0.109	0.018	0.004-0.011	-0.111
		Thomsons Gazelle	0.158	0.036-0.198	0.33	0.176-0.407	0.172
		Warthog	0.247	0.19-0.243	0.045	0.019-0.036	-0.202
		Waterbuck	0.38	0.199-0.478	0.41	0.279-0.504	0.03
		Common Zebra	0.821	0.77-0.829	0.81	0.776-0.809	-0.011
	Striped Hyena (*Hyaena hyaena*)	Olive Baboon	0.117	0.048-0.101	0.02	-0.019	-0.097
Xiao et al. 2018	Tiger (*Panthera tigris*)	Roe Deer	0.84	0.76-0.92	0.75	0.68-0.82	-0.09
		Sika Deer	0.69	0.61-0.76	0.71	0.63-0.78	0.02
		Wild Boar	0.78	0.70-0.86	0.75	0.68-0.83	-0.03

Chapter 4.

Coyote movement patterns reveal a tolerance of humans in a mixed-use agricultural landscape

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ABSTRACT

Identifying which landscape features wildlife species select or avoid remains critical to understanding animal risk tolerance, habitat preferences, and the potential for human-wildlife conflict in altered environments. Here, I examined how anthropogenic and natural features influenced coyote (*Canis latrans*; n = 13) habitat selection in a mixed-use, agricultural landscape in Mendocino County, California, USA. I used resource selection functions and hidden Markov models to test whether coyote selection for anthropogenic and natural features differed by time of day or by behavioral state (resting, foraging, and traveling). I found that coyotes avoided development, but, contrary to my expectations, that coyotes selected for roads, agriculture, and areas used by rifle hunters regardless of diel period or behavioral state. While traveling, coyotes increased selection for roads and avoided ruggedness, indicating that unpaved roads may enhance connectivity for coyotes in mixed-use landscapes. Finally, I found that coyotes selected for mountain lion habitat when resting and at night, signifying that risk from natural predators was not a factor in habitat selection at coarse scales. Evidence that coyotes selected for most anthropogenic features at times when humans were also active suggests that the region may have high conflict potential given many people perceive coyotes as a nuisance.

INTRODUCTION

Human activity has modified landscapes worldwide, contributing to wildlife range contractions and decline (Ceballos et al., 2017). Yet, some species successfully navigate human-modified environments, either by exploiting anthropogenic resources or by making behavioral adjustments that outpace novel threats (Geffroy et al., 2020; Newsome et al., 2015; Sih et al., 2011). Behaviorally flexible species can even achieve robust populations in human-modified landscapes (Bateman & Fleming, 2012), inciting conflict with humans (i.e., crop damage, property damage, loss of livestock, and injury; Richardson et al., 2020; Treves et al., 2006) or causing outsized change to community structure via predation (Geffroy et al., 2015) or interference competition (Shochat et al., 2010). Efforts to understand how wildlife balance the use of anthropogenic and natural features remain critical to wildlife management and coexistence, especially as humans continue to alter landscapes around the world.

Animal survival depends on the ability to maximize reward, while reducing risk (Charnov, 1976; Lima & Bednekoff, 1999). Rewards are resources that increase animal fitness (e.g., forage, mates), while risk represents the challenges an animal faces (e.g., energy expenditure, predation; Sih, 1980). In human-modified landscapes, wildlife often encounter a novel portfolio of risks and rewards such as food subsidies (Oro et al., 2013), infrastructure, and intensification of human activities such as hunting and recreation (Schell et al., 2021), alongside the risks and rewards with which they evolved. This is especially true in mixed-use landscapes, characterized by mosaics of low-density development, agriculture, and wildlands. Because mixed-use landscapes experience a low to moderate level of disturbance, these areas can retain natural predators, competitors, and prey, alongside a variety of anthropogenic risks and foods (Ferreira et al., 2018; Gascon et al., 1999; Kremen & Merenlender, 2018). In mixed-used landscapes, the choice between anthropogenic and natural landscape features can reveal an animal's risk tolerance, habitat preferences, and potential constraints on an animal's behavior.

Animals that successfully navigate human-modified landscapes are known to alter diel activity, space use, behavior, or diet in response to cues, to take advantage of rewards and avoid spatial or temporal risks (Gaynor et al., 2018; Geffroy et al., 2020; Smith et al., 2015; Tucker et al., 2018). For example, lions (*Panthera leo*) avoided areas near livestock pens during the day, but selected for livestock areas at night to exploit prey when the risk of encountering humans was lower (Suraci, Frank, et al., 2019). Animals can also modify their behavior to navigate human-modified landscapes. For instance, African wild dogs (*Lycaon pictus*) selected for roads while running to maximize ease of travel, but avoided roads when walking, resting, and denning to minimize time spent in locations with vehicles (Abrahms et al., 2016). With the onset of the global COVID-19 pandemic in 2020, a decrease in diurnal human activity resulted in increased diurnal wildlife activity in both highly-developed and undeveloped landscapes (Anderson et al., 2023; Gordo et al., 2021; Schofield et al., 2021). Thus, factors regulating fitness, like the risk of encountering humans, non-human predators, or food resources, should be important factors in shaping animal risk perception and habitat selection (Rettie & Messier, 2000).

Coyotes are widely regarded as a behaviorally flexible species and can take advantage of various seasonal resources, including fruits, berries, insects, young animals or anthropogenic food, while avoiding predation themselves (Fedriani et al., 2001; Sacks, 1996). Although coyotes are known to successfully navigate a variety of landscapes (Atwood et al., 2004), including dense urban areas (Breck et al., 2019), coyote habitat selection in mixed-use landscapes is less understood (but see Atwood et al., 2004). In some cases, food availability is the primary factor driving coyote habitat selection (Mills & Knowlton, 1991) and density (Fedriani et al., 2001). Alternatively, human-related risk factors, including vehicles, domestic dogs, and human presence (Breck et al., 2019), can drive coyote habitat selection, as some evidence suggests coyotes use dense vegetation to avoid development and agricultural fields (Atwood et al., 2004).

Here, I examined how anthropogenic and natural features influenced coyote (*Canis latrans*) habitat selection in a mixed-use, agricultural landscape in Mendocino County, California, USA. I hypothesize that coyotes partition their use of anthropogenic features to maximize rewards while minimizing risk. I expect that coyotes avoid anthropogenic features during the day, (including roads, development, agriculture, grasslands with livestock, and areas with risk of lethal removal) but select for these features at night to exploit food rewards and minimize human encounters. If coyote selection for anthropogenic features changes by diel period, it would indicate a behaviorally flexible response to a perceived risk of diurnal human activity.

Additionally, coyotes may avoid roads, development, agriculture, grasslands with livestock, and lethal removal risk while foraging and resting, but select for these features while traveling to minimize human encounters. If selection for anthropogenic features changes by behavioral state, it may reveal constraints on when and how coyotes can use anthropogenic features.

Finally, in addition to human-related risks, natural risks and rewards may drive aspects of coyote habitat selection. I anticipate that coyotes avoid habitats with mountain lion (*Puma concolor*) encounter risk (hereafter 'mountain lion encounter risk') because coyotes comprise 30% of mountain lion diet in this area (Sacks, 1996). Specifically, I expect coyotes will avoid mountain lion encounter risk while resting, and at night when mountain lions in the area are most active (Gaynor et al., 2022). Vegetation and terrain may also influence coyote habitat selection. I expect coyotes select woodlands for cover, and grasslands at night to avoid humans. I also expect coyotes will avoid rugged terrain for ease of travel, but not while resting or foraging.

METHODS

Study Area

I conducted this study in the Sanel Valley of Mendocino County, California (39°0' 1.14N, -123°4'45.86W; **Figure 1**). The region is situated at the southern end of the Mayacamas mountains in the California Coast Range and is composed of a mosaic of rural agriculture, livestock pasture, residential areas, and wildlands dominated by oak savanna and chaparral habitat. The primary agricultural products in the valley are wine grapes and pears, while livestock operations for cattle and sheep are situated in grasslands in the surrounding hillsides. The valley is bisected by a major road corridor (US 101) on the banks of the Russian river and flanked by 25000 ha of Bureau of Land Management land with Mendocino National Forest to the north. The landscape has a moderate level of human pressure with motorized and non-motorized recreation. Coyote diet in the area consists of native prey species, including lagomorphs, rodents, birds, insects, reptiles, manzanita berries, as well as livestock and domestic fruit (Benjamin Nicholas Sacks, 1996). The region is also home to a host of potential coyote predators and competitors, including mountain lion (*Puma concolor*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), and gray fox (*Urocyon cinereoargenteus*) (Gaynor et al., 2022). The climate is typically Mediterranean, with mild rainy winters and hot dry summers.

In this study area, humans often hunt and trap coyotes or use guardian dogs to prevent crop raiding and livestock depredation. While cattle are too large to be prey species to coyotes, coyotes pose the greatest threat to sheep and lambs (McInturff et al., 2021). In 2013, Mendocino County had over 10,000 sheep and lambs, although some ranchers have since switched to cattle as a result of conflicts with coyotes (Blackwell, 2021; R. Sagehorn, pers. comm., June 2022). One study on a Mendocino County sheep ranch estimated that up to 5% of lambs were killed annually by coyotes (Conner et al., 1998). Through Mendocino County's contract with the United States Department of Agriculture's (USDA) Wildlife Services, the county was called upon to conduct 4,119 coyote removals between 1997 – 2017, using poison, leg hold traps, and snares (Blackwell, 2021). The County voted to end the Wildlife Services contract with the USDA in 2021 (Blackwell, 2021), however, ranchers and landowners continue to protect livestock by trapping and shooting coyotes on site. While these individual statistics are not available, it is estimated that sheep ranches may kill up to 20-30 coyotes annually (T. McWilliams, pers. comm., November 2020; Anderson, 2015). Nonetheless, growing popularity of non-lethal deterrents among ranchers (Rifkin, 2020) and research spurring a transition to targeted coyote removal (Sacks et al., 1999) has likely reduced the overall mortality of coyotes in the county.

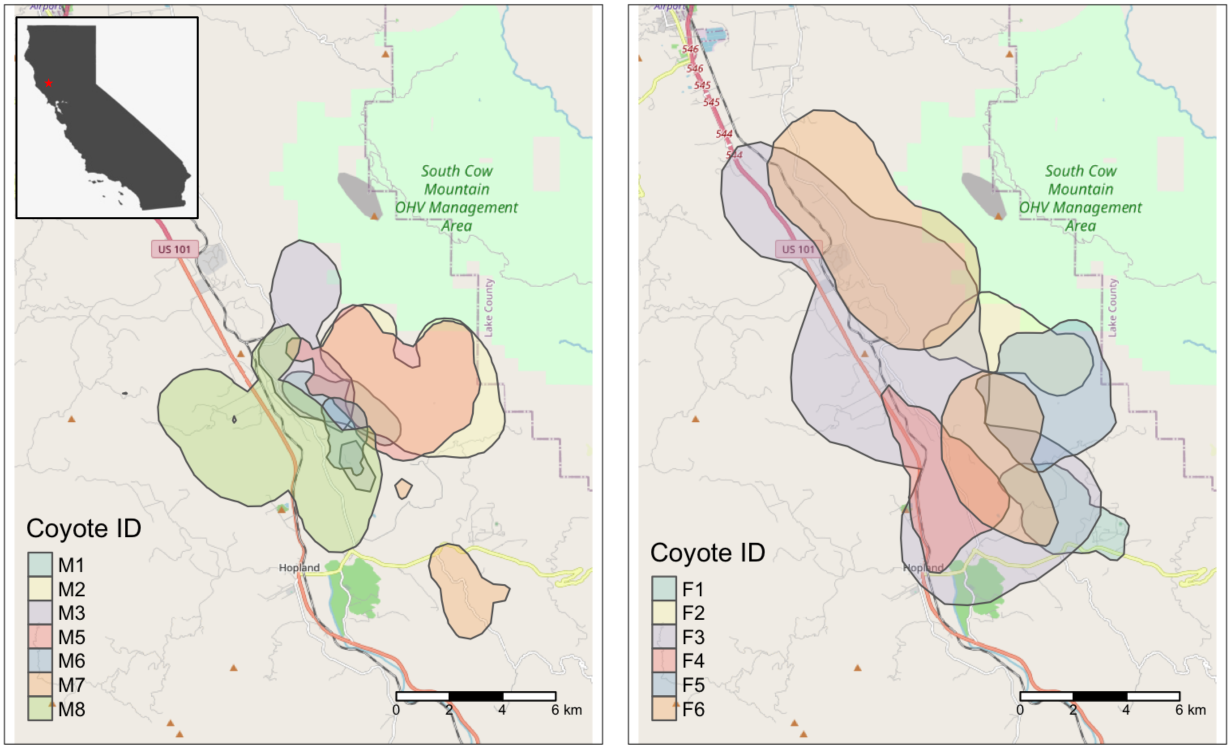

Figure 1. Study area in Sanel Valley, Mendocino County, California, USA. Maps depict 95% kernel utilization home range for male (M) and female (F) coyotes (*Canis latrans*; n = 13) derived from hourly GPS locations for a total of 265 unique days (mean 60 days per individual) between late November and early March of 2020-2021, 2021-2022, and 2022-2023.

Data Collection

All coyotes were live-captured at the University of California's 5,358 acre Hopland Research and Extension Center (HREC), fitted with GPS collars (Vertex Lite 1C, Vectronic Aerospace, Iowa, USA), and released at the point of capture. All captures were conducted using cable snares and processed within a 30-minute period in accordance with the protocol approved by the Institutional Animal Care and Use Committee at the University of California Berkeley (protocol # AUP-2016-04-8723-2). No complications were observed for any of the collared individuals.

The GPS collars recorded spatial locations hourly. Movement data were obtained for fourteen coyotes (six females and eight males) across three field seasons from late November to early March of 2020-2021, 2021-2022, and 2022-2023. I excluded one adult male from the analysis due to death five days after capture, likely due to a vehicle collision. To reduce possible post-capture behavioral bias, I excluded the first three days of GPS data for all individuals. Ultimately, thirteen coyotes were tracked for a total of 265 unique days (mean 60 days per individual).

Environmental Data

I examined coyote habitat selection for anthropogenic and natural features, including development, roads, agriculture, lethal removal risk, mountain lion encounter risk, terrain, and vegetation type (**Table 1**).

Table 1. Predicted relationship of coyote (*Canis latrans*) habitat selection with anthropogenic and natural features in the Sanel Valley, Mendocino County, California, USA.

Covariate	Description	Predicted Relationship
Development	distance to low, medium, high development; highway	avoid
Road	distance to secondary and tertiary roads	select (night, travel)
Agriculture	distance to agriculture	select (night, forage)
Lethal removal risk	open viewshed, proximity to roads, ruggedness (*from Gaynor et al. 2022)*	select (night, forage)
Mountain lion encounter risk	shrubland, far from agriculture (*from Gaynor et al. 2022)*	avoid (night)
Ruggedness	terrain ruggedness index	avoid (travel)
Vegetation type	grassland woodland shrubland	select (night) select avoid

To obtain data on covariates, I used the 2016 National Land Cover Dataset (NLCD) to reclassify development, roads, and agriculture into distance rasters, and to obtain vegetation type at 30-meter resolution (Dewitz, 2016). I chose the 2016 NLCD because it more closely resembled the vegetation cover of the study area in the 2020-2023 seasons. The 2019 NLCD (Dewitz, 2019) was not used because the 2018 River Fire burned a large section of chaparral to grassland, and the 2016 NLCD was more representative of the chaparral density in 3-4 years of post-fire vegetation growth. To measure terrain ruggedness, I used the NASA SRTM Digital Elevation 30m (Farr et al., 2007) and calculated the topographic ruggedness index, which reflects the elevational difference between eight adjacent cells of a digital elevation model (Riley et al., 1999). To characterize lethal removal risk for coyotes, I modeled the results of a recent study on deer hunters in the region (Gaynor et al., 2022). While coyote removal is often opportunistic, uses various tactics (i.e., trapping, shooting, poisoning), and is likely less common than deer hunting, I adopted the top model coefficients for deer hunting (proximity to roads, clear viewshed, and high ruggedness) as sufficient to create a predictive raster of gun use in the study area. I excluded areas within 150-yards of buildings to reflect local gun laws (Mendocino County Code of Ordinances, 1974). Last, I modeled the spatial distribution of mountain lions in the study area with the results of a nearby camera trap study (Gaynor et al., 2022), using the top model coefficients (distance to agriculture and high elevation) as spatial predictors for mountain lions at the study site.

I ensured that there was no collinearity ($|r| \leq 0.7$; Dormann et al., 2013) among environmental covariates using Pearson correlation coefficients (Table S1). The shrubland vegetation type was highly correlated with mountain lion encounter risk. As a result, I measured coyote habitat selection for vegetation type in a separate model (Table S5). All environmental covariates were centered and scaled (Figure S1). I extracted covariates to coyote spatial locations using the "raster" package in R (Hijmans et al., 2013).

Behavioral Segmentation

To determine if coyote habitat selection varied by behavioral state, I used hidden Markov models (HMMs) to label GPS data with three ecologically relevant behavioral states: resting, foraging, and traveling (e.g. Abrahms et al., 2016)). HMMs are a class of sequence-dependent models that use an observed process to infer an unobserved, underlying state process (Langrock et al., 2012). I developed HMMs using turning angle (the angle between locations) and step length (the distance between locations) of GPS fixes within the 'moveHMM' package in R (Michelot & Langrock, 2016). To maximize the likelihood of the data fit, I iterated 25 models from a randomized set of plausible parameters for each behavioral state (Table S2). I chose the model with the smallest negative log-likelihood and assigned the most likely sequence of states to each individual track using the Viterbi algorithm (Zucchini, MacDonald, & Langrock, 2017). GPS points were then segmented into resting, foraging, and traveling datasets to examine differences in habitat selection by behavior.

Habitat Selection Modeling

To estimate the influence of environmental variables on coyote habitat selection, I fit single-season resource selection functions (RSFs) to each individual's home range (i.e., third order selection; Johnson, 1980). I fit three types of RSFs for each coyote home range to directly compare habitat selection using 1) the full dataset, 2) behavioral state datasets, and 3) diel period datasets. Behavioral state (i.e. resting, foraging, and traveling datasets) was derived from aforementioned HMMs, while day-night datasets were segmented using the local, daily sunset and sunrise times with the 'lubridate' package in R (Grolemund & Wickham, 2013). To generate the RSFs, I obtained used points and available points from within 95% kernel home range polygon of each individual, using the 'kernelUD' function in the 'adehabitatHR' package in R (Calenge, 2006; R Core Team, 2022). For each RSF I randomly generated five times as many available points as used points to reduce bias (Table S3; Northrup et al., 2013; Stears et al., 2019).

I used generalized linear mixed effects models with a binomial error distribution and log-link function to model coyote habitat selection for development, roads, terrain, agriculture, lethal removal risk, and mountain lion encounter risk. I fit a separate generalized linear mixed effects model (logistic) to model coyote habitat selection for vegetation type. I included random intercepts in the models to account for individual differences in sample size (Hebblewhite & Merrill, 2007). This allowed us to compare how selection for covariates differed between resting, foraging, and traveling datasets and the full model, as well as how selection differed between day and night datasets and the full model. I tested the influence of year on the covariates in the full model, by using year as a nested random effect. I estimated beta coefficients and calculated odds ratios for each model and estimated 95% confidence intervals. I identified differences in habitat selection between models as being estimates with non-overlapping 95% confidence intervals.

RESULTS

Behavioral State Allocation

I found that the top hidden Markov model adequately estimated three state-distributions for coyote foraging, resting, and traveling, using the step length and turning angle distributions of GPS points (Figure S2). The traveling state was associated with longer step lengths and turning angles centered on 0 (i.e., directed movement), whereas resting was associated with shorter step lengths and wide turning angles (i.e., undirected movement). All iterated models converged with little variation between models (*Maximum Log Likelihood* = 152963.6, *mean* = 149767.4, *SD* = 2259.1, *n* = 25). I found that on average, coyotes spent 41% of time resting, 33% foraging, and 26% traveling each day (**Figure 2**). There was little variation in activity budget between years, except that in 2022-2023 coyotes exhibited significantly more resting than foraging or traveling (ANOVA; *F*(2, 10) = 19.04, $p < 0.001$; post-hoc Tukey test; $p < 0.01$). The variation in resting was likely due to likely individual differences between coyotes. There was a tendency to increase resting behavior at night (18:00 - 0:00), and foraging and traveling behavior at pre-dawn (01:00 - 07:00) and pre-dusk (14:00 - 16:00), which was consistent among years.

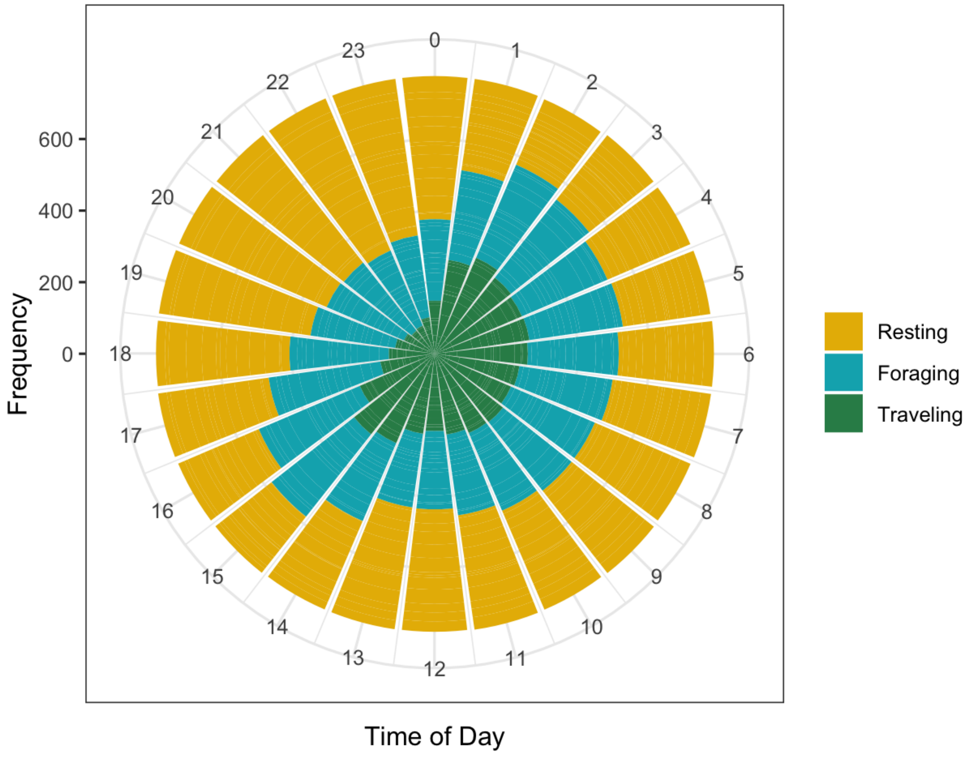

Figure 2. Diel state-activity budget for resting, foraging, traveling behaviors of coyotes (*Canis latrans*; n = 13) from the Sanel Valley, Mendocino County, California, USA, from November - March between 2020-2023 seasons. The diel state-activity budget was estimated by the top hidden Markov model (*Maximum Log Likelihood* = 152963.6, *mean* = 149767.4, *SD* = 2259.1, *n* = 25). Frequency indicates number of GPS relocations over a period of total of 265 unique days (mean 60 days per individual).

Coyote habitat selection

Using resource selection functions, I found that coyotes have a complex response to natural and anthropogenic features in mixed-use landscapes. Overall, the full dataset showed that coyotes avoided development, but selected for roads, agriculture, lethal removal risk, mountain lion encounter risk, and ruggedness (**Figure 3**; Table S4). Coyotes also avoided shrubland and woodland relative to grassland (Figure S3). I found no difference in the full model across years, when using year as a nested random effect.

Behavioral partitioning of habitat selection

I found that models partitioned by behavioral state differed from the full model and each other in several key ways (**Figure 3**; Table S4). Consistent with my hypotheses, coyotes avoided ruggedness while traveling (OR$_{full}$ = 1.02, 95% CI [1.00, 1.04]; OR$_{travel}$ = 0.84, 95% CI [0.81, 0.87]). In support of my expectations, coyotes also had significantly stronger selection for roads while traveling and foraging than resting (OR$_{travel}$ = 0.82, 95% CI [0.78, 0.85], OR$_{forage}$ = 0.82, 95% CI [0.79, 0.85], OR$_{rest}$ = 0.92, 95% CI [0.89, 0.95]). I found that coyotes avoided development consistently, but significantly more while foraging than resting or traveling (OR$_{forage}$ = 1.17, 95% CI [1.12, 1.21], OR$_{rest}$ = 1.06, 95% CI [1.02, 1.09], OR$_{travel}$ = 1.06, 95% CI [1.02, 1.11]). Coyote selection for agriculture was stronger while resting and foraging than traveling (OR$_{rest}$ = 0.73, 95% CI [0.69, 0.77], OR$_{forage}$ = 0.83, 95% CI [0.80, 0.87], OR$_{travel}$ = 0.94, 95% CI [0.89, 0.98]). Coyotes selection for lethal removal risk was weaker while traveling (OR$_{full}$ = 1.11, 95% CI [1.09, 1.13; OR$_{travel}$ = 1.05, 95% CI [1.02, 1.08]. Contrary to my hypothesis, selection for mountain lion encounter risk was strongest while resting (OR$_{full}$ = 1.20, 95% CI [1.18, 1.22]; OR$_{rest}$ = 1.38, 95% CI [1.34, 1.43]). Finally, coyotes avoided shrublands overall, but interestingly selected for shrublands while resting (OR$_{full}$ = 0.93, 95% CI [0.90, 0.97]; OR$_{rest}$ = 1.25, 95% CI [1.17, 1.33]; Figure S3; Table S5).

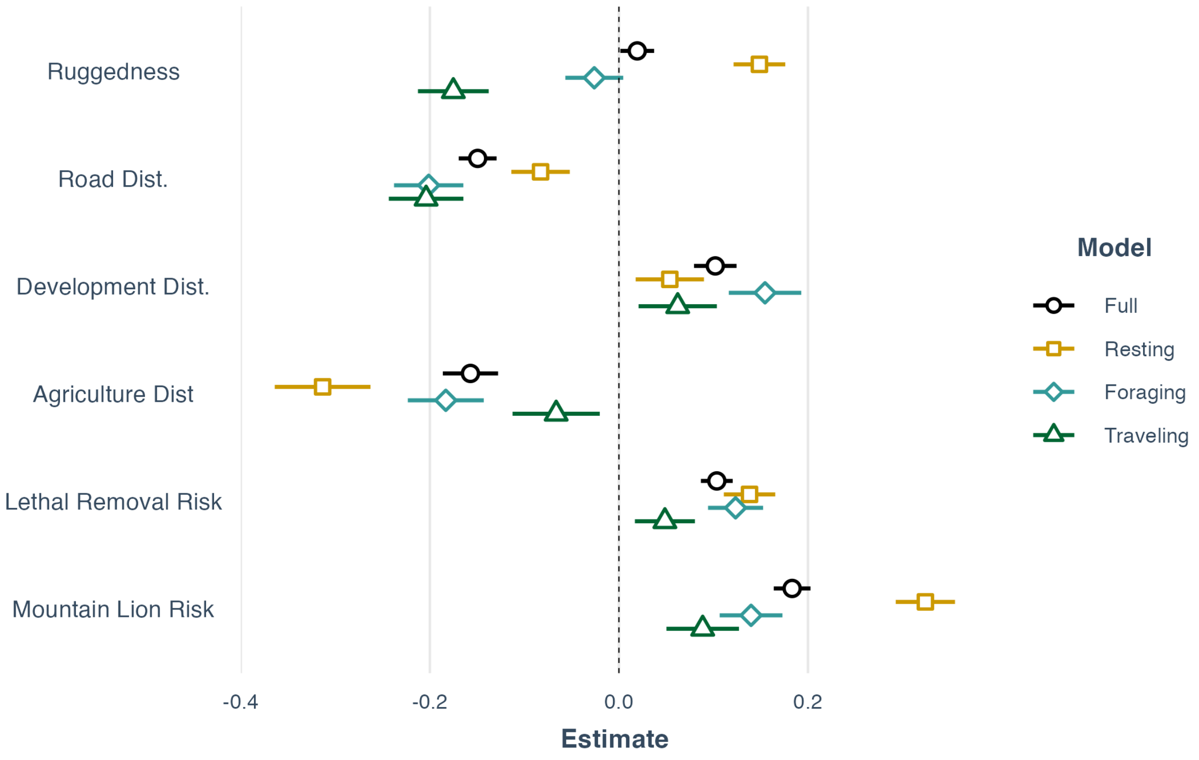

Figure 3. Estimates of coyote (*Canis latrans*; n = 13) habitat selection in the Sanel Valley, Mendocino County, California, USA, using a full model with all GPS locations, and three models partitioned by resting, foraging, and traveling behavior estimated by the top hidden Markov model. All covariates were standardized prior to modelling. For covariates corresponding to the distance to a feature (Dist.), a negative estimate means that selection was higher closer to that feature.

Diel partitioning of habitat selection

I expected that coyotes would more often select for roads, agriculture, and grasslands with lethal removal risk at night to exploit rewards, while minimizing human encounters. However, for roads, development, lethal removal risk, and mountain lion encounter risk, there was no significant difference between coyote selection for features at day or night (**Figure 4**; Table S4). Opposite of my expectations, coyotes selected for agriculture slightly more during the day than at night (OR_{day} = 0.80, 95% CI [0.77, 0.84], OR_{night} = 0.87, 95% CI [0.84, 0.90]). Coyote use of vegetation also did not match my hypotheses, as coyotes avoided shrublands during the day, with no effect at night, when mountain lions are most active in shrublands (OR_{day} = 0.86, 95% CI [0.80, 0.90], OR_{night} = 1.00, 95% CI [0.95, 1.05]; Figure S4; Table S5). I found that coyotes avoided woodlands significantly more during the day (OR_{day} = 0.45, 95% CI [0.41, 0.50], OR_{full} = 0.56, 95% CI [0.52, 0.59]; Figure S4; Table S5). Finally, I expected coyotes would select for ruggedness during the day, to avoid places and times humans are active in the area, but instead, coyotes selected for ruggedness at night, with no effect during the day (OR_{night} = 1.05, 95% CI [1.03, 1.08]; OR_{day} = 0.98, 95% CI [0.95, 1.00]).

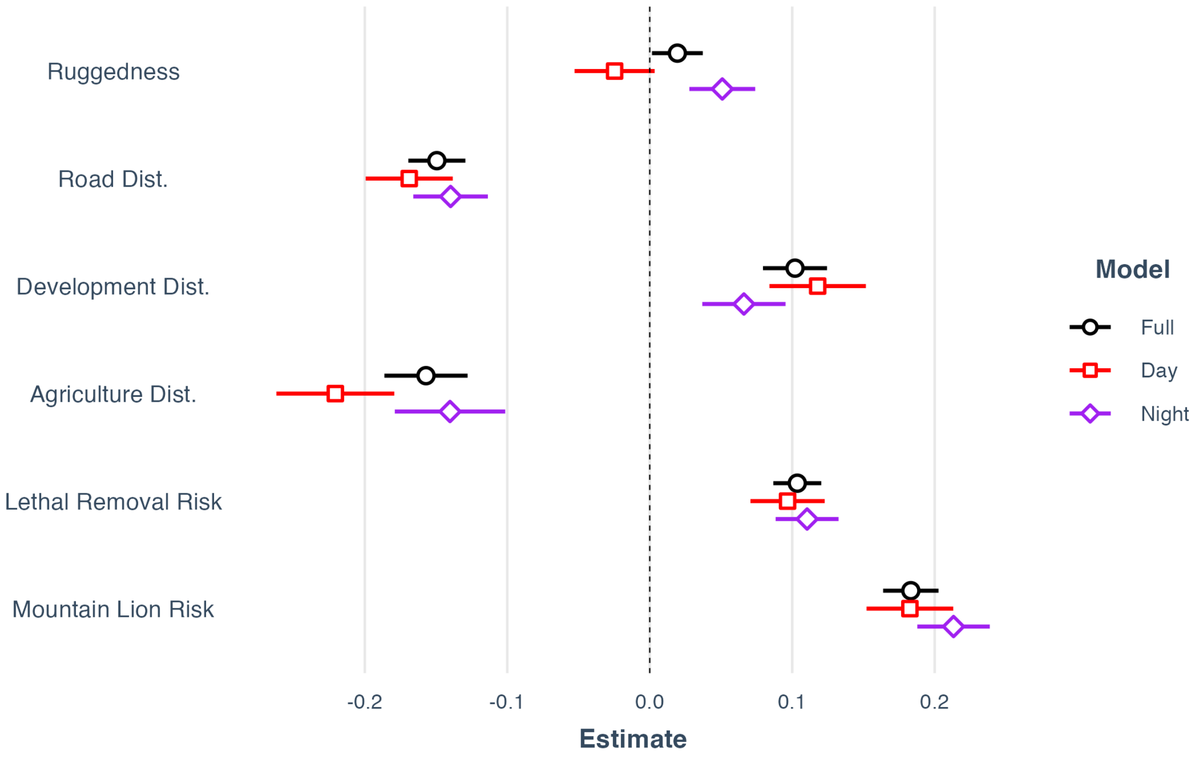

Figure 4. Estimates of coyote (*Canis latrans*; n = 13) habitat selection in the Sanel Valley, Mendocino County, California, USA, using a full model with all GPS locations, and two models partitioned by day and night. All covariates were standardized prior to modelling. For covariates corresponding to the distance to a feature (Dist.), a negative estimate means that selection was higher closer to that feature.

DISCUSSION

As humans modify landscapes worldwide, assessing how wildlife use altered environments is critical to wildlife management and to enhancing coexistence. Although some carnivores are known to exhibit increased behavioral flexibility (Gaynor et al., 2018; Šálek et al., 2015) and take advantage of anthropogenic resources (Gámez et al., 2022) in rural and urban environments, the drivers and thresholds of behavior change may be most representative at intermediate gradients of development (McDonnell & Pickett, 1990). The results show that coyotes exhibited behavioral and diel partitioning in a mixed-use landscape, but not to the degree of altering selection in places or times associated with human persecution (i.e., agriculture, development, roads, grasslands, and areas with lethal removal risk) as expected.

It might appear that coyotes perceive anthropogenic features a low risk, given that coyotes selected for areas with roads, crops, livestock, and open viewsheds. However, the pull of associated food rewards may have been sufficient to attract coyotes despite perceived risk — especially given that the data were collected in early winter, following the wine grape harvest and as young livestock went out to pasture. As a result, it is difficult to disentangle whether habitat selection was in response to low risk, high reward, or both. Previous work found that coyote foraging was opportunistic and used anthropogenic features to minimize time spent on food acquisition (Sacks & Neale, 2002). Additional research on fine-scale responses to known risk factors, including livestock guardian dogs or hunters, may help to better identify coyote risk perception driving habitat selection. For instance, using a spatiotemporal point process or continuous-time Markov chain (CTMC) modelling framework (Buderman et al., 2018) paired with telemetry data for both coyotes and their predators (i.e., humans, livestock guardian dogs, or mountain lions) would allow a more detailed exploration of how coyotes use landscapes with and without potential risks. Similarly, diet studies and research on coyote-livestock interactions also shed light on whether coyote used anthropogenic features for food. Ultimately, coyote use of less-developed anthropogenic areas, without diurnal avoidance, may underscore the potential for human-coyote coexistence — that is if livestock and crops are adequately protected and minimize conflict using non-lethal tools (Scasta et al., 2018; Young et al., 2019).

The results showed that coyotes avoided the development covariate (composed of low, medium and high-intensity development and highways), in support of my hypothesis. Coyote avoidance of development was significant across all diel periods and behavioral states. This may indicate that development is largely impermeable to coyotes, consistent with previous work that coyotes avoid developed areas where possible (Gehrt et al., 2009; Riley et al., 2003). Coyotes may have avoided development because of associated risks, such as humans, vehicles, or domestic dogs, or because of unfamiliar features such as infrastructure, noise, or lighting. Alternatively, coyotes may have avoided development because it had fewer food rewards, preferring to use agriculture and grassland habitats for foraging in this region. I found coyotes in this region selected for agriculture significantly more while resting, foraging, and during the day. This likely indicates that coyotes were, more often than not, moving through agricultural fields slowly to forage and had a low perceived risk of diel human activity in these open spaces. In an urban environment in Southern California, USA, coyotes had larger home-ranges and moved farther and faster to acquire food than in low-development environments (Riley et al., 2003), which is consistent with how coyotes used agricultural fields versus development in the region.

While coyote habitat selection for anthropogenic features was largely consistent across models, the strength of selection did vary some by diel period and behavioral state. Coyote selection for roads (i.e., secondary and tertiary roads) was significantly stronger while traveling and foraging, consistent with previous studies indicating that mammalian carnivores use anthropogenic linear features to move (Abrahms et al., 2016; Andersen et al., 2017; Latham et al., 2011). However, coyote selection for roads did not differ by diel period. It is possible that the vehicle traffic and human presence on secondary and tertiary roads was not high enough to cause diel variation in coyote use, as previous studies find that wildlife activity on and near roads can vary with human activity (Anton et al., 2020; Barrueto et al., 2014; Kautz et al., 2021). Instead, unpaved roads appeared to allow coyotes to opportunistically travel quickly to avoid rugged terrain. This aligned with the result that coyotes selected for ruggedness while resting, but avoided ruggedness while traveling. Rural and unpaved roads are often used in carnivore scent-marking (Barja & List, 2014), hunting (Latham et al., 2011), and can improve visibility. Thus, rural or unpaved roads may enhance landscape connectivity for coyotes in mixed-use landscapes.

In addition to anthropogenic features, I expected natural features to drive aspects of coyote habitat selection. Coyotes selected for mountain lion encounter risk across diel periods, including at night when mountain lions at this study site were most active (Gaynor et al., 2022). As a result, coarse-scale predator risk did not appear to be a factor in coyote habitat selection. In fact, coyotes had an overall positive association with mountain lion encounter risk, which was predicted using distance to agriculture and high elevation as described by Gaynor and colleagues (2022). While coyotes have, at times, composed a large fraction of mountain lion diet (Sacks, 1996), coyotes are not obligate prey of mountain lions, which can exhibit diet flexibility in response to prey availability (Karandikar et al., 2022). Similarly, mountain lions may not be a major source of mortality to coyotes due to the naturally low densities, sprawling home ranges, and infrequent site revisits of mountain lions in this region (see Gaynor et al., 2022). Reduced mountain lion detections following the 2018 River fire near the study area, may have allowed further coyote expansion into these habitats (Calhoun et al., 2022). However, it is still possible that coyotes continue to avoid mountain lions at fine-scales and by using indirect perception (Brunet et al., 2022). Ultimately, coyotes may be using mountain lion habitat to hunt for similar prey species, scavenge on the kills of larger predators, or to seek dense shrubland cover in areas of low human use. Although, mountain lion encounter risk was highly correlated with shrubland, mountain lion encounter risk still shows value as an estimate because coyotes avoided shrubland overall, but selected for mountain lion encounter risk. Follow up studies on the diet composition of coyotes will help to disentangle whether coyotes co-occur in areas with large predators for food, vegetation cover, or perceived safety.

Finally, I found that coyotes avoided woodlands and shrublands relative to grassland. Grasslands and other open vegetation types are known to be important resources to coyotes for hunting (Stevenson et al., 2019), and use of open viewsheds (i.e., grasslands, agriculture) did not appear to be impacted by the potential exposure to mortality factors, such as humans and livestock guardian dogs. Interestingly, the finding that coyotes select grasslands more than expected (based on availability) is in contrast to what Sacks & Neale (2002) found at this study site 28 years prior. Renewed coyote use of grasslands may be a response to lower densities of livestock and correspondingly reduced human-related risk factors within grasslands at this site (McInturff et al., 2021; Sacks, 1996). In support of this explanation, coyotes also consistently selected for lethal removal risk areas, which was parameterized using estimates of gun use near grasslands, roads and rugged terrain. Besides reduced risk factors, grasslands may be attractive habitats in that they that allow for high-visibility, giving coyotes an advantage in detecting risk from afar (Aben et al., 2018). This alternative explanation is supported by the finding that coyotes avoided low-visibility habitats (i.e., shrublands and woodlands). Reduced ability to detect risk, difficulty of travel in dense understory, and lower prey densities may equally explain why coyotes avoided dense vegetation cover. Furthermore, coyote avoidance of woodlands was reduced at night and while resting, possibly indicating that dense vegetation cover is safest when coyotes are inactive.

I found that coyote habitat selection varied across several anthropogenic and natural features, however, the approach had several limitations. First, it is challenging to disentangle whether habitat selection was driven by risk or reward, as the factors were often intertwined. To address this, future work could conduct experiments to manipulate the relative levels of risk and reward associated with different habitats, such as altering food availability or human use along roads or hiking trails, and measuring the corresponding changes in coyote behavior. Second, the habitat selection models did not measure coyote responses to fine-scale risk, such as presence or absence of mountain lions or livestock guardian dogs. To detect subtle coyote responses to fine-scale risk, researchers could use higher-resolution data on coyote in tandem with predator movements. Similarly, our habitat selection model did not account for heterogeneous patterns of risk, such as distinguishing among livestock pastures using lethal removal versus non-lethal deterrents. Future studies might observe how coyotes select habitat differently when lethal and non-lethal deterrents occur within their home ranges. Researchers could also measure coyote responses to manipulated auditory risk cues (such as recordings of human voices, barking dogs, and gunshots) and olfactory risk cues (such as scent lures for humans, dogs, and livestock). Finally, this study did not account for coyote mortality or prey availability, which may ultimately drive coyote habitat selection. I used deer hunting as a surrogate for gun use, although patterns of mortality among deer and coyotes likely differ. Going forward, researchers could track coyote mortality rates in different habitats, interview landowners, and conduct surveys of prey abundance, to better understand how these factors influence coyote habitat selection.

Overall, additional research is needed to disentangle the complex interplay of risk and reward on coyote behavior. My results suggest that human activity and persecution were not proximate factors in coyote habitat selection in a mixed-use agricultural landscape. However, research on wildlife habitat preferences and thresholds of behavioral flexibility should be incorporated into landscape-level monitoring and connectivity planning, especially with any intensification of road or residential development. Important questions remain as to whether coyote selection for anthropogenic and natural features changes with seasonally available crops, drought, and fire to determine whether coyotes are opportunistically maximizing rewards, or risking use of these features during seasons of scarcity. Such research would inform future management approaches in response to declining wild prey, drought, and extreme climatic events, which are known to increase human-wildlife conflict and wildlife use of agricultural areas across the globe (Abrahms, 2021).

CONCLUSION

This research supports a growing body of literature indicating that carnivores can navigate human-modified landscapes to balance use of anthropogenic and natural features (Geffroy et al., 2020; Newsome et al., 2015; Sih et al., 2011). My comparison of behavioral and diel aspects of coyote habitat selection suggest that coyotes are resilient to low-development anthropogenic features in mixed-use landscapes, however, we lack information on how habitat selection ultimately influences mortality or conflict. The finding that coyotes appear undeterred by roads, agriculture, and open viewsheds underscores the importance of managing livestock and agricultural resources and considering the use of non-lethal tools to avoid coyote conflict. Future studies on seasonal or disturbance-related shifts in coyote diet and habitat selection may further illuminate how coyotes interact with livestock, agriculture, and influence community structure. Considering the risk-reward tradeoffs that drive animal habitat selection will ultimately help to improve fate of adaptable predators in altered environments.

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DATA AVAILABILITY STATEMENT

Coyote movement data and scripts used to conduct habitat selection analyses are available from GitHub: https://github.com/avanscoyoc/coyote-movement.

SUPPLEMENT TO CHAPTER 4:

Figures S1 – S4
Tables S1 – S5

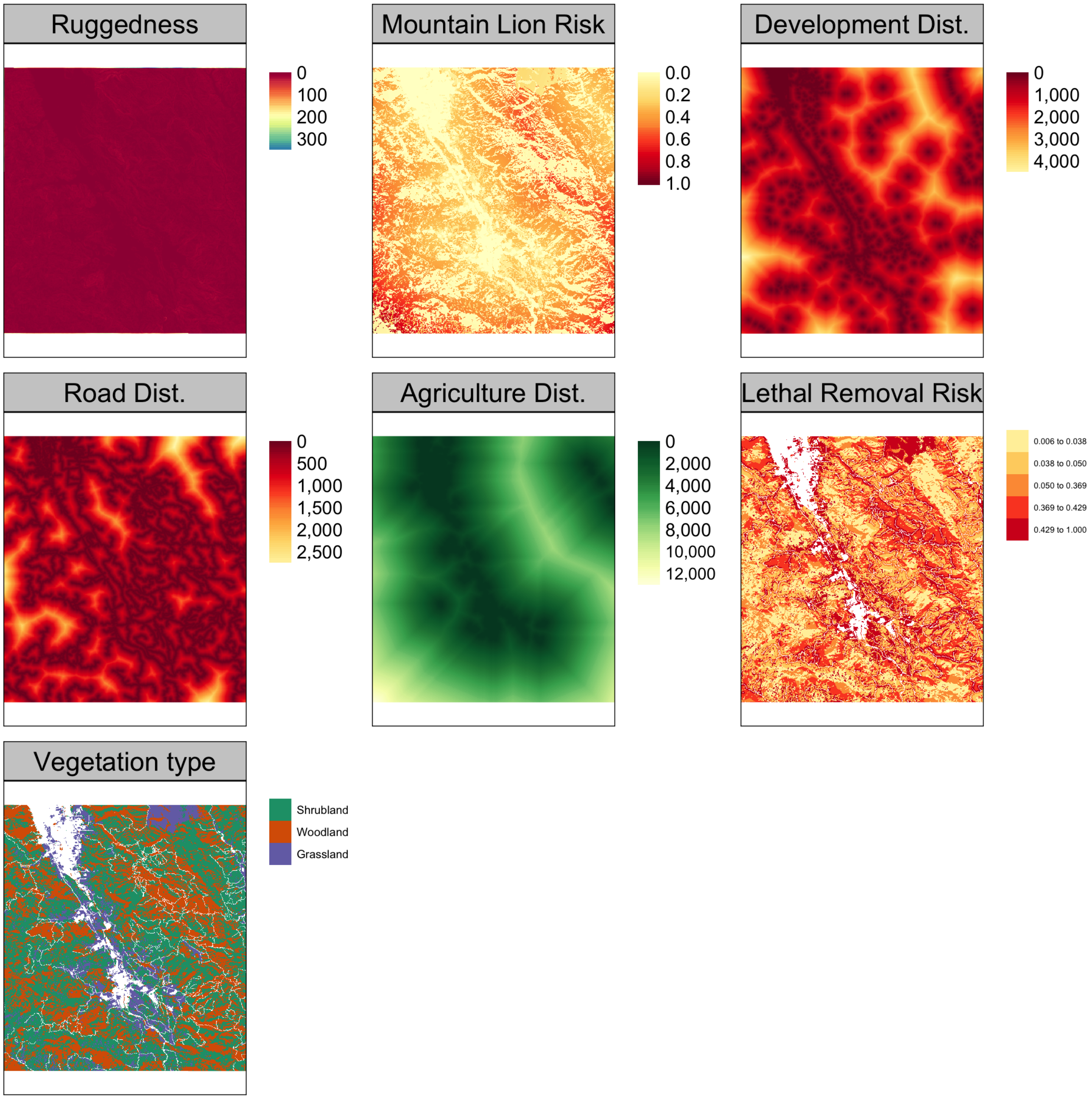


Figure S1. Environmental covariates used in coyote habitat selection models in the Sanel Valley, Mendocino County, CA, USA. Covariates include elevation (m), ruggedness, mountain lion encounter risk (scaled 0-1), distance to development (m), distance to roads (m), distance to agriculture (m), lethal removal risk (scaled 0-1), and vegetation type (woodland, grassland, shrubland). All covariates were scaled and centered prior to modelling.

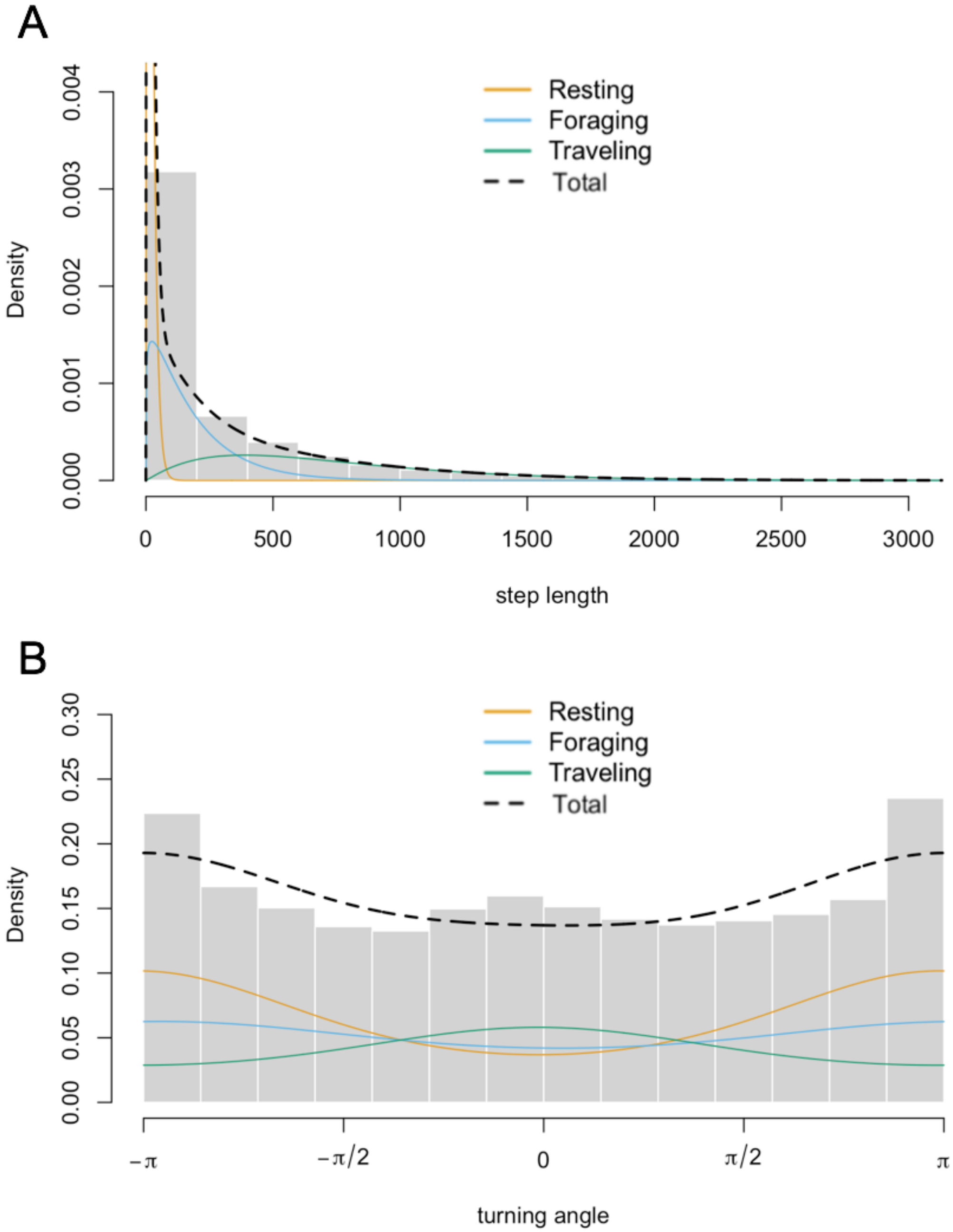


Figure S2. Histograms of (**A**) step lengths and (**B**) turning angles overlaid with three state-dependent movement distributions (Resting, Foraging, Traveling) estimated by top hidden Markov model for coyotes (n = 13) from the Sanel Valley, Mendocino County, California, USA.

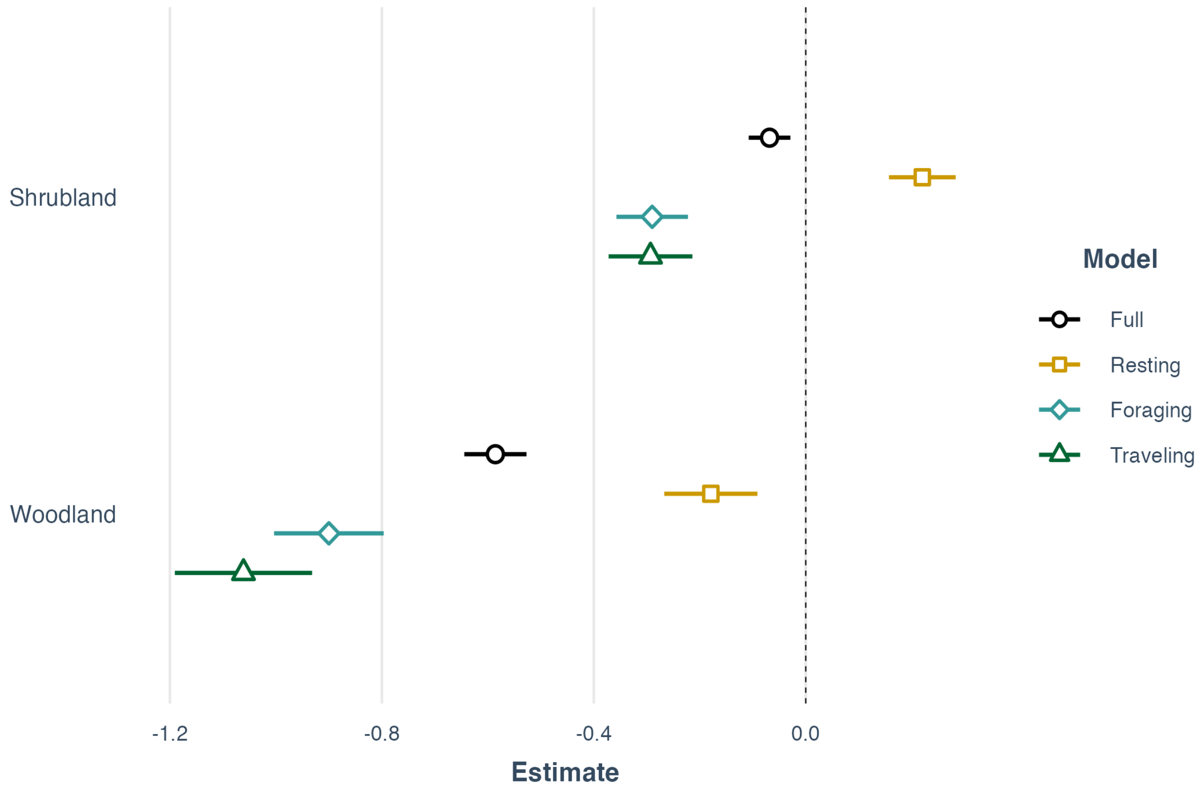


Figure S3. Estimates of coyote habitat selection for vegetation type (grassland, woodland, and shrubland) in the Sanel Valley, Mendocino County, California, USA, using a full model with all GPS locations, and three models partitioned by resting, foraging, and traveling behavior estimated by the top hidden Markov model. The reference value for the vegetation layer is grassland (the most open habitat with highest visibility), thus, negative estimates indicate that selection was lower in woodland (intermediate habitat) and shrubland (most dense habitat) as compared to grassland as determined from a generalized linear model (logistic).

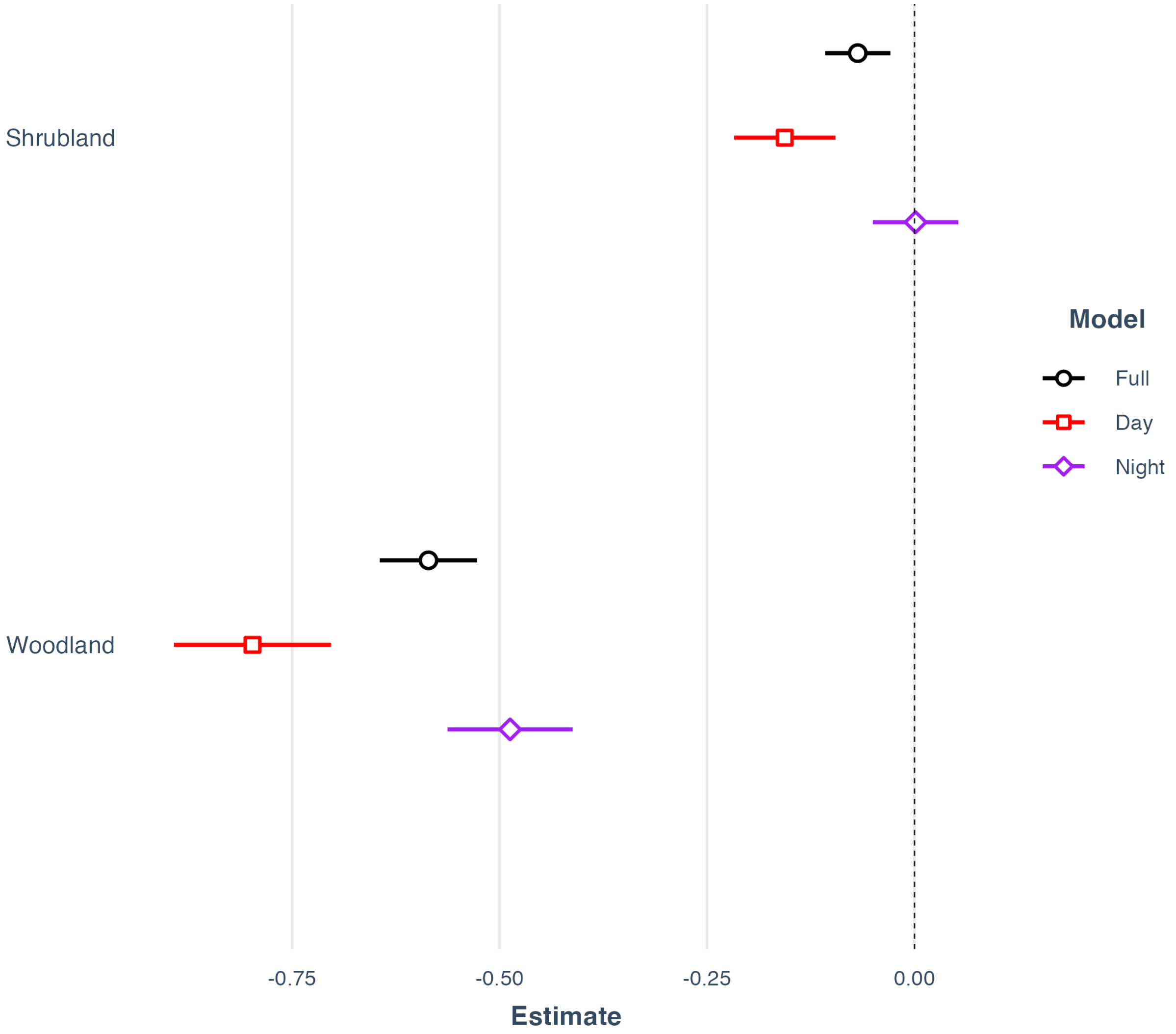
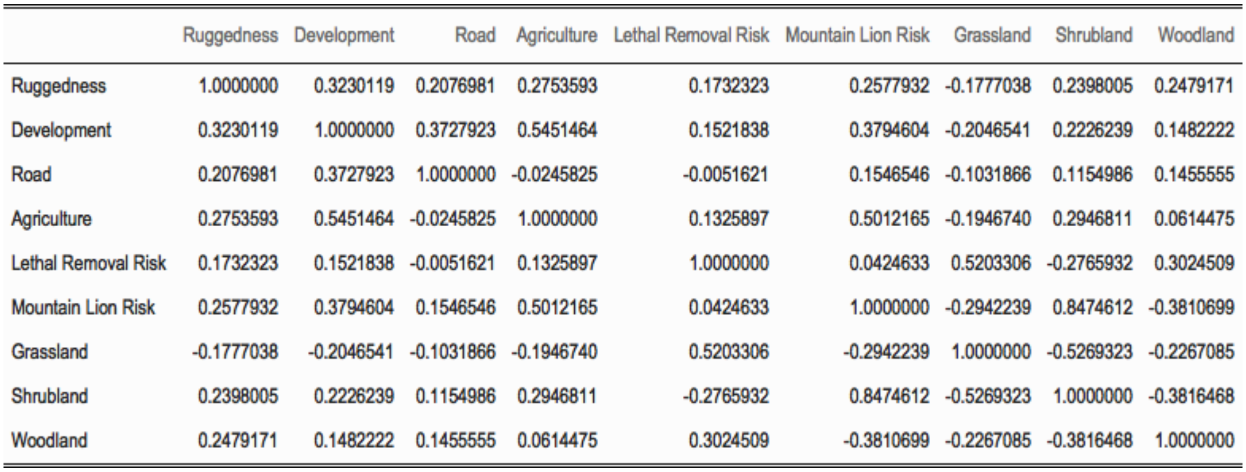


Figure S4. Estimates of coyote habitat selection for vegetation type (grassland, woodland, and shrubland) in the Sanel Valley, Mendocino County, California, USA, using a full model with all GPS locations, and two models partitioned by day and night. The reference value for the vegetation layer is grassland (the most open habitat with highest visibility), thus, negative estimates indicate that selection was lower in woodland (intermediate habitat) and shrubland (most dense habitat) as compared to grassland as determined from a generalized linear model (logistic).

Table S1. Pearson correlation coefficients for environmental covariates in the Sanel Valley, Mendocino County, CA, USA. The shrubland vegetation type was highly correlated with mountain lion encounter risk. As a result, vegetation type was modelled separately from the other covariates.



	Ruggedness	Development	Road	Agriculture	Lethal Removal Risk	Mountain Lion Risk	Grassland	Shrubland	Woodland
Ruggedness	1.0000000	0.3230119	0.2076981	0.2753593	0.1732323	0.2577932	-0.1777038	0.2398005	0.2479171
Development	0.3230119	1.0000000	0.3727923	0.5451464	0.1521838	0.3794604	-0.2046541	0.2226239	0.1482222
Road	0.2076981	0.3727923	1.0000000	-0.0245825	-0.0051621	0.1546546	-0.1031866	0.1154986	0.1455555
Agriculture	0.2753593	0.5451464	-0.0245825	1.0000000	0.1325897	0.5012165	-0.1946740	0.2946811	0.0614475
Lethal Removal Risk	0.1732323	0.1521838	-0.0051621	0.1325897	1.0000000	0.0424633	0.5203306	-0.2765932	0.3024509
Mountain Lion Risk	0.2577932	0.3794604	0.1546546	0.5012165	0.0424633	1.0000000	-0.2942239	0.8474612	-0.3810699
Grassland	-0.1777038	-0.2046541	-0.1031866	-0.1946740	0.5203306	-0.2942239	1.0000000	-0.5269323	-0.2267085
Shrubland	0.2398005	0.2226239	0.1154986	0.2946811	-0.2765932	0.8474612	-0.5269323	1.0000000	-0.3816468
Woodland	0.2479171	0.1482222	0.1455555	0.0614475	0.3024509	-0.3810699	-0.2267085	-0.3816468	1.0000000

Table S2. Starting parameter ranges for iterating 25 three-state hidden Markov models (resting, foraging, and traveling) for coyotes in the Sanel Valley, Mendocino County, CA, USA.

Starting parameter		**Resting**	**Foraging**	**Traveling**
Step length mean	*min*	50m	500m	1000m
	max	100m	1000m	3000m
Step length standard deviation	*min*	25m	250m	500m
	max	50m	500m	1500m
Turning angle mean		pi	$pi/2$	0
Turning angle concentration	*min*	0.2	0.5	0.7
	max	0.5	0.7	3
Zero mass parameter		0.002356343	0.002356343	0.002356343

Table S3. Total number of used and available coyote GPS locations in the full, resting, foraging, traveling, day, and night datasets. Available points were randomly generated for each coyote home range at five times the number of used GPS locations. Resource selection functions were estimated for individual coyote home ranges (n = 13).

Model	**Used**	**Available**
Full	18,673	93,365
Rest	4,788	23,940
Forage	3,641	18,205
Travel	3,164	15,820
Day	7,656	38,280
Night	11,017	55,085

Table S4. Estimates of coyote habitat selection in the Sanel Valley, Mendocino County, California, USA, using all covariates, except vegetation type, in a combined model with all GPS locations, and models partitioned by resting, foraging, and traveling behavior states, as well as by day and night locations. All covariates were standardized prior to modelling. For covariates corresponding to the distance to a feature, a negative estimate means that selection was higher closer to that feature, as determined from a generalized linear model (logistic).

	Full model		**Rest**		**Forage**		**Travel**		**Day**		**Night**	
Covariates	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*
Intercept	0.20 ***	0.19 – 0.20	0.19 ***	0.18 – 0.20	0.20 ***	0.19 – 0.20	0.20 ***	0.19 – 0.20	0.20 ***	0.19 – 0.20	0.19 ***	0.19 – 0.20
Ruggedness	1.02 *	1.00 – 1.04	1.16 ***	1.13 – 1.19	0.97	0.94 – 1.00	0.84 ***	0.81 – 0.87	0.98	0.95 – 1.00	1.05 ***	1.03 – 1.08
Road distance	0.86 ***	0.84 – 0.88	0.92 ***	0.89 – 0.95	0.82 ***	0.79 – 0.85	0.82 ***	0.78 – 0.85	0.84 ***	0.82 – 0.87	0.87 ***	0.85 – 0.89
Development distance	1.11 ***	1.08 – 1.13	1.06 **	1.02 – 1.09	1.17 ***	1.12 – 1.21	1.06 **	1.02 – 1.11	1.13 ***	1.09 – 1.16	1.07 ***	1.04 – 1.10
Agriculture distance	0.85 ***	0.83 – 0.88	0.73 ***	0.69 – 0.77	0.83 ***	0.80 – 0.87	0.94 **	0.89 – 0.98	0.80 ***	0.77 – 0.84	0.87 ***	0.84 – 0.90
Lethal Removal Risk	1.11 ***	1.09 – 1.13	1.15 ***	1.12 – 1.18	1.13 ***	1.10 – 1.16	1.05 **	1.02 – 1.08	1.10 ***	1.07 – 1.13	1.12 ***	1.09 – 1.14
Mountain Lion Risk	1.20 ***	1.18 – 1.22	1.38 ***	1.34 – 1.43	1.15 ***	1.11 – 1.19	1.09 ***	1.05 – 1.14	1.20 ***	1.16 – 1.24	1.24 ***	1.21 – 1.27
Observations	112038		45936		36444		29658		45936		66102	
Marginal R^2 / Conditional R^2	0.015 / 0.016		0.039 / 0.042		0.018 / 0.018		0.021 / 0.022		0.017 / 0.017		0.018 / 0.019	

* *p<0.05* ** *p<0.01* *** *p<0.001*

Table S5. Estimates of coyote habitat selection for vegetation (grassland, woodland, shrubland) in the Sanel Valley, Mendocino County, California, USA, comparing a combined model with all GPS locations, and models partitioned by resting, foraging, and traveling behavior states, as well as by day and night locations. The reference value for the vegetation layer is grassland (the most open habitat with highest visibility), thus, negative estimates indicate that selection was lower in woodland (intermediate habitat) and shrubland (most dense habitat) as compared to grassland as determined from a generalized linear model (logistic).

	Full model		**Rest**		**Forage**		**Travel**		**Day**		**Night**	
Covariates	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*	*Odds Ratios*	*CI*
Intercept	0.23 ***	0.22 – 0.24	0.19 ***	0.18 – 0.20	0.26 ***	0.24 – 0.28	0.26 ***	0.24 – 0.28	0.24 ***	0.23 – 0.26	0.22 ***	0.21 – 0.23
Shrubland	0.93 ***	0.90 – 0.97	1.25 ***	1.17 – 1.33	0.75 ***	0.70 – 0.80	0.75 ***	0.69 – 0.81	0.86 ***	0.80 – 0.91	1.00	0.95 – 1.05
Woodland	0.56 ***	0.52 – 0.59	0.84 ***	0.77 – 0.91	0.41 ***	0.37 – 0.45	0.35 ***	0.30 – 0.39	0.45 ***	0.41 – 0.50	0.61 ***	0.57 – 0.66
Observations	95177		39237		32020		24165		38897		56068	
Marginal R^2 / Conditional R^2	0.012 / 0.013		0.007 / 0.007		0.026 / 0.028		0.036 / 0.037		0.022 / 0.023		0.010 / 0.011	

* *$p<0.05$* ** *$p<0.01$* *** *$p<0.001$*

Chapter 5.

Conclusion

Humans have a vast influence on ecological communities across the globe, by altering the structure and composition land cover, as well as the patterns of animal movement and behavior. Therefore, research that advances our understanding of human influence on species persistence is a critical component of any conservation effort. The work presented in this dissertation offers several new approaches for assessing these influences, including methods to identify land cover change at the margins of protected areas, to measure human influence on species interactions, and to assess behavioral change in wildlife habitat selection within human-modified landscapes.

My results demonstrate several key patterns of ecosystem change, but often exhibit divergent trends, yielding new questions and opportunities for research. For instance, in Chapter 2, I find that most protected areas have begun to resemble habitat islands, yet a great many exhibited the opposite pattern. In Chapter 3, as expected, many animals avoided high human activity, but many animals did not, and these differences were responsible for the broad range in temporal overlap among predators and their prey. And finally, in Chapter 4, even individual animals appeared to vary in their habitat selection for anthropogenic and natural features. These complex and often conflicting patterns are undoubtedly driven, in part, by the broad diversity of human-nature interactions. Humans are ecosystem engineers, competitors, predators, and facilitators, all of which may serve to benefit or harm to wildlife species. A great future challenge lies in disentangling the relative influence of these co-occurring roles to predict which species will die, survive, or thrive, in order to anticipate the consequences of our great ecological reshuffling.

A few compelling directions for future research emerge from the results of this work, with direct applications to conservation. First, connectivity research on forests has outpaced research in a vast diversity of terrestrial systems on the planet. Chapter 1 extended what we know about habitat connectivity and isolation beyond forests, to deserts, grasslands, and other critical ecosystems, highlighting, in particular, threats to habitat connectivity in grasslands. Indeed, grasslands are considered one of the most imperiled ecosystems on Earth (Cowie, 2021), and today 60% of the world's grasslands are less than 20% intact (Scholtz & Twidwell, 2022). While my approach revealed and compared biome-wide changes in landcover, the method is limited in that it cannot differentiate between the predominant types and causes of land-cover change. To effectively guide global conservation investment in diverse ecosystems, critical future work lies in comparing land-use changes by biome. Future research might use detailed land-use change analyses to more closely examine rates of, for instance, urbanization, shrub encroachment, or grazing in grassland and desert protected areas experiencing rapid islandiziation. In addition to research on the biophysical correlates of landcover change, research into the socioeconomic correlates of local land cover change near protected areas (e.g., land sales and subdivision, changes in global trade, political turnover) may help to shift conservation investment from land protection toward also identifying and supporting at-risk industries that benefit wildlife in working lands or buffer zones.

Beyond deciphering the causes of land cover change, additional research is required to uncover the consequences of islandization on wildlife. Habitat edges are known to alter abiotic conditions (e.g., wind, light, microclimate) and species composition, with both positive and negative outcomes on wildlife (Hilty et al., 2019). Future work could compare animal movement and behavior across the boundaries of protected areas with different causes and levels of islandization to identify whether these habitat edges correspond to shifts in the spatial and temporal activity of wildlife, or influences the success of certain species over others. Additionally, while protected area designation has often opportunistically set aside land for biodiversity, new conservation strategies might quantify and prioritize ecosystem flows (i.e., migratory paths, rivers, metapopulations, and animal movements), especially to support the adaptive capacity of species to respond to climate change. For instance, tracking source-sink dynamics of pollinators or plants across protected area boundaries may help us strategize how to safeguard ecosystem processes that extend beyond protected area borders.

Extensive research suggests that global change has led to considerable shifts in the spatial and temporal activity of animals, yet we lack an understanding of how these shifts affect species interactions. Chapter 2 outlined several possibilities for how human activities may influence predator-prey interactions, by affecting overlap and encounter rates. Although I found support for at least four patterns, my analysis was based on a limited amount of empirical evidence. In 2020, only 19 studies measured the temporal responses of terrestrial mammal predators-prey pairs to humans, and even fewer studies reported the change in predator and prey overlap across both space and time. This dearth of research signals an important opportunity for designing studies that measure human impacts on predators, prey, and competitor interactions. Future work might measure changes in encounter rate alongside predator diet or prey survival to quantify how human-altered overlap affects predation. Controlled experiments could, for instance, compare how various types, frequencies, or levels of disturbance affect the overlap, encounter rate, and predation in a given predator-prey pair to predict changes in populations.

Ultimately, as we enter an era of human-dominated ecosystems, the question of whether and how animals respond to anthropogenic features has become more important than ever before. In 2020, while this research was in progress, the global COVID-19 pandemic and ensuing restrictions on human activity revealed that a reduction in human activity was tightly linked to an increase in wildlife activity in many places across the world (Anderson et al., 2023; Gordo et al., 2021; Schofield et al., 2021). Designing ecological models that test whether humans are modifying predation or competition, rather than simply species activity, will be critical to accurately predicting wildlife population dynamics into the future.

Finally, many species tolerate ecosystem change in developed landscapes, but these landscapes can also present hidden tradeoffs for wildlife species. Chapter 4 identified that coyotes (*Canis latrans*) select habitat in working landscapes, such as ranchlands or agriculture, over development or woodlands. However, coyotes may also face higher lethal risk in these areas if humans perceive these animals as a risk to livestock or crops. My study did not quantify how coyote mortality risk is associated with various land cover types, but pairing coyote GPS data with high resolution data on landscape risk factors, such as presence of hunters or livestock guardian dogs, would allow researchers to quantify how or whether coyotes can avoid fine-scale risks in working landscapes. Future research could also conduct experiments to manipulate the relative levels of risk and reward associated with different habitats, such as altering food availability or human use along roads or hiking trails, and measuring the corresponding changes in coyote behavior.

Ultimately, by studying the movements of behaviorally flexible species, we can predict what challenges wildlife may face in their effort to survive in human-altered landscapes. Important questions remain as to whether animals modify habitat selection for anthropogenic features with seasonally available crops, drought, or fire to maximize rewards and reduce risk during times of scarcity. Such research would enable us to predict whether and how species will respond to declining wild prey, drought, and climatic events, and can aid in the development of conservation strategies that better account for the tradeoffs presented by various land uses.

Overall, this work explores a few intricate connections between human-induced global change, protected areas, and wildlife. There is much that is still unknown about how human activities influence ecosystem dynamics to affect the individual fitness, populations, and evolution of wildlife species. The integration of wildlife research with economic, political, and social sciences will be essential for guiding inclusive, ethical, and socially-just conservation actions. Considering humans as key players in ecological systems is not only critical to understanding biodiversity change, but also to stewarding the relationship between people and nature into the future.

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