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# Carnivore Niche Partitioning in a Human Landscape

Mauriel Rodriguez Curras,<sup>1,\*</sup> Emiliano Donadio,<sup>2</sup> Arthur D. Middleton,<sup>3</sup> and Jonathan N. Pauli<sup>1</sup>

1. Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706; 2. Rewilding Argentina, Estancia La Ascensión, Los Antiguos, Santa Cruz 9041, Argentina; 3. Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720

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**ABSTRACT:** To minimize competitive overlap, carnivores modify one of their critical niche axes: space, time, or resources. However, we currently lack rules for how carnivore communities operate in human-dominated landscapes. We simultaneously quantified overlap in the critical niche axes of a simple carnivore community—an apex carnivore (*Puma concolor*), a dominant mesocarnivore (*Lycalopex culpaeus*), and a subordinate small carnivore (*Lycalopex griseus*)—in a human landscape featuring pastoralists and semidomestic carnivores (i.e., dogs, *Canis familiaris*). We found that dominant species had strong negative effects on the space use of subordinate ones, which ultimately created space for subordinate small carnivores. Humans and dogs were strictly diurnal, whereas the native carnivore community was nocturnal and exhibited high temporal overlap. Dietary overlap was high among the native carnivores, but dogs were trophically decoupled, largely because of human food subsidies. Our results show that in landscapes with evident human presence, temporal and dietary partitioning among native carnivores can be limited, leaving space as the most important axis to be partitioned among carnivores. We believe that these findings—the first to simultaneously assess all three critical niche axes among competing carnivores and humans and their associated species (i.e., domesticated carnivores)—are transferable to other carnivore communities in human-modified landscapes.

**Keywords:** carnivore guild, carnivore community, human-carnivore interactions, competition.

## Introduction

Competition is a fundamental organizing force of ecological communities (Gause 1934; Hardin 1960; Case and Gilpin 1974). Within the carnivore guild (Mammalia: Carnivora), competition is especially apparent because carnivores have evolved specialized morphology, physiology, and behaviors to effectively kill (Gittleman 1989). Interspecific competition between carnivores is typically manifested as interference competition, whereby dominant species prevent subordinate ones from accessing resources either di-

rectly, through aggressive and potentially lethal interactions (Palomares and Caro 1999), or indirectly, through displacement out of preferred habitats (Suraci et al. 2016). The outcome of such competitive interactions is costly to smaller-bodied species (Donadio and Buskirk 2006).

Fundamental to competition is a species niche (Hutchinson 1957). While the niche concept has undergone a recent resurgence and reform (Soberón 2007; Bolnick et al. 2010), the critical niche axes—space, time, and resources (Holt 2009)—remain central to understanding competitive overlap (Case and Gilpin 1974; Alley 1982). Indeed, species across the animal kingdom modify their space use (MacArthur 1958), diel activity (Carothers and Jaksic 1984), or resource consumption (Lack 1946) in response to competition, although research generally focuses on one or two of the critical niche axes at a time (Schoener 1974; Sévêque et al. 2020). Within carnivores, rarely have all major niche axes been explored concurrently to explain carnivore community structure and interactions (but see Thornton et al. 2004; Dröge et al. 2017; Miller et al. 2018). This limited body of work has shown that when high overlap occurs along two of the critical niche axes (e.g., space and resources), there is partitioning along the third (e.g., diel activity; see Dröge et al. 2017). Ultimately, niche partitioning among carnivores is structured by body size (Polis et al. 1989; Donadio and Buskirk 2006): apex carnivores limit mesocarnivores, which limit small carnivores (Newsome and Ripple 2014). Thus, apex carnivores often create ecological opportunities for small carnivores, although the particular axis that is made available varies by system (Prugh and Sivy 2020; Sévêque et al. 2020). Accordingly, understanding the mechanism structuring carnivore communities requires that all critical niche axes be quantified simultaneously.

The vast majority of studies on carnivore competition have been conducted in systems that do not feature humans (Kuijper et al. 2016) or where humans were present but not accounted for (e.g., Newsome and Ripple 2014; Flagel et al.

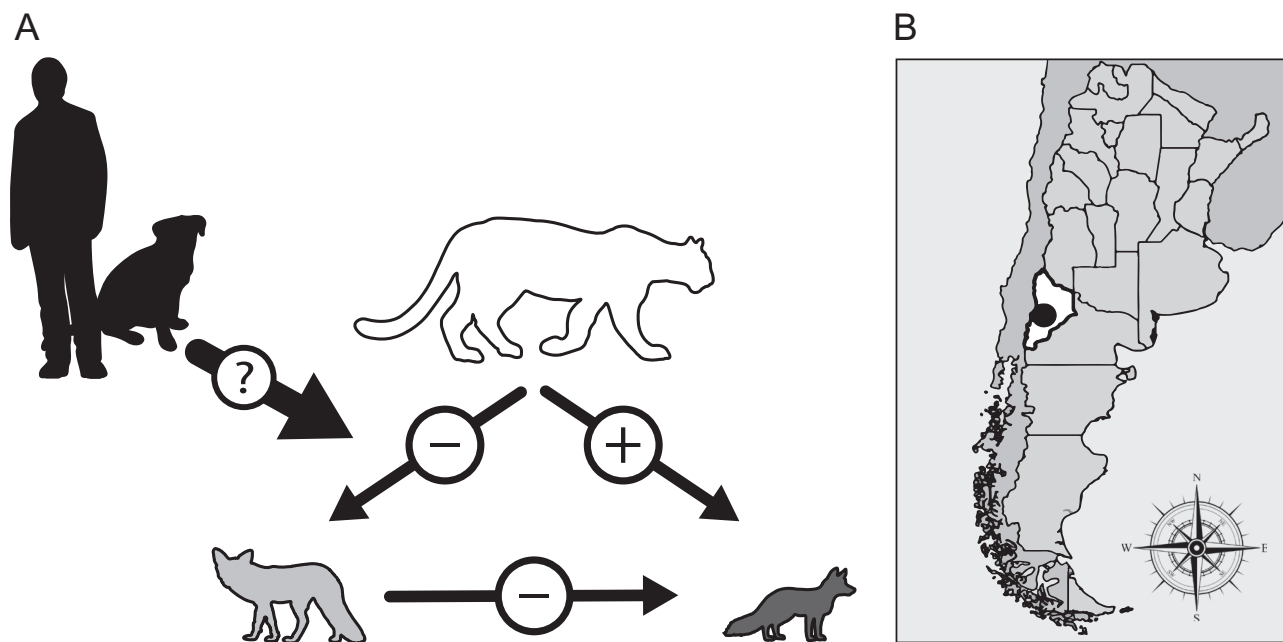
\* Corresponding author; email: [mrodriguezcu@wisc.edu](mailto:mrodriguezcu@wisc.edu).

ORCID: Rodriguez Curras, <https://orcid.org/0000-0003-2837-359X>.

2017). However, human presence can importantly alter carnivore interactions (Darimont et al. 2015; Dorresteijn et al. 2015) by adding an overarching level to a hierarchically structured community with varying, and sometimes unpredictable, effects (Sévêque et al. 2020). Carnivores perceive humans as “super predators” (Clinchy et al. 2016; Smith et al. 2016) and in response exhibit altered food-handling times and habitat selection (Smith et al. 2017). Such perceived risk has led to human-induced diel niche compression toward nocturnality (Gaynor et al. 2018). In contrast, some subordinate carnivores may use humans as “spatial shields” against dominant carnivores (Moll et al. 2018). At the same time, human foods often subsidize carnivore populations and can increase their local abundance and survival (Newsome et al. 2015) and enhance interspecific competition (Wilmers et al. 2003) and conflict with humans (Moss et al. 2016). In general, then, we currently lack rules governing carnivore communities in human-modified landscapes, which has limited our ability to predict how communities will respond to increasingly human-dominated ecosystems globally (Chapron et al. 2014; Venter et al. 2016).

To explore the mechanism of carnivore niche partitioning in a human-dominated landscape, we studied the spatial, temporal, and dietary overlap of a simple community of pumas (*Puma concolor*, an apex carnivore), culpeo foxes (*Lycalopex culpaeus*, a dominant mesocarnivore), and chilla foxes (*Lycalopex griseus*, a subordinate small carnivore)

within a diverse human-use landscape in Patagonia. These three carnivores are common throughout southern South America, where their distributions overlap, yet the effects of pumas on competing foxes or the role of humans on the overall native carnivore community has not been quantified. We accounted for humans and their domestic carnivores, dogs (*Canis familiaris*), given that these two are so tightly linked in this landscape and because of the growing conservation concerns of feral dogs altering community interactions across South America (Schüttler et al. 2018). Within the native carnivores, we hypothesized that the apex carnivore would facilitate the coexistence of subordinate guild members and mediate competitive interactions (fig. 1). Specifically, we predicted that this community of carnivores would be hierarchically nested, where subordinate carnivores would exhibit low spatial overlap with their dominant guild members, leading pumas to create a spatial refuge for chilla foxes. Furthermore, we predicted that pumas would provide resource subsidies to culpeo and chilla foxes in the form of carrion (i.e., livestock), resulting in high dietary niche overlap. We also hypothesized that humans have an overarching force on carnivore communities, with cascading effects on all community interactions (fig. 1). Specifically, we predicted that dominant native carnivores would exhibit low spatial overlap with humans, avoid times of the day that humans were active, and exhibit low dietary overlap with humans and domestic carnivores. Furthermore,



**Figure 1:** A, Conceptual figure of our hypothesized interactions within native carnivores (including pumas [*Puma concolor*], culpeo foxes [*Lycalopex culpaeus*], and chilla foxes [*Lycalopex griseus*]) based on the theoretical dominance hierarchy among species. The effects of humans and dogs (*Canis familiaris*) on niche overlap within native carnivores have received far less attention. B, Map showing the location of the study area: Laguna Blanca National Park, Neuquén, Argentina.

since humans are generally more tolerant of smaller carnivores, we predicted that humans would provide a spatial shield for chilla foxes. To our knowledge, this is the first study to simultaneously assess the overlap along all three critical niche axes—space, time, and resources—for a carnivore community while explicitly including humans and domestic carnivores in each analysis.

## Methods

### *Site Description*

We conducted fieldwork in and around Laguna Blanca National Park (LBNP; lat.  $-70.03$ , long.  $-39.05$ ), located in northern Patagonia, from late June to mid-October (fig. 1B). LBNP encompasses 11,250 ha, while our total study area was  $\sim 27,000$  ha. LBNP is home to a community of six native carnivores: pumas, culpeo foxes, chilla foxes, Geoffroy's cats (*Leopardus geoffroyi*), pampas cats (*Leopardus colocolo*), and skunks (*Conepatus* spp.). Our study focused on the three strongest interacting members of this community: pumas, culpeo foxes, and chilla foxes (de Oliveira and Pereira 2014). We did not consider Geoffroy's and pampas cats because, although present, they occur at very low local abundances and only in specialized rocky habitats (Walker et al. 2007; Palacios et al. 2012), insulating them from interactions with other community members, and skunks were not considered because of their smaller body size, which limits their interactions with the other carnivores. Although designated a national park, ranching of goats, sheep, cows, and horses is prominent within LBNP and its surrounding area; indeed, 30 pastoral households operate in the region with  $\sim 2,000$  head of livestock (mostly goats and sheep). Livestock roamed widely throughout the park and were generally accompanied by pastoralists and their dogs during the day.

### *Data Collection*

To assess spatial and temporal overlap among the three species, we deployed 46 camera traps (Bushnell Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS) within and around LBNP in a random design but buffered 300 m from dirt roads and highways and 500 m from pastoralists' houses to minimize conflict. Camera traps were spaced an average of 1.98 km apart, staked 0.75 m above the ground, and angled toward a reference stake  $\sim 3$  m from the camera. Cameras were programmed to collect a set of three pictures for every trigger, with 0-s delay between triggers. We checked camera traps two or three times a month. All data were analyzed using the program R (ver. 3.6 and 4.0; R Core Team 2020). Photos were processed and tagged (Adobe Bridge, Adobe Systems, San Jose, CA), and meta-data were created using the R package camtrapR (Niedballa et al. 2016).

At each camera station we measured habitat at four sampling plots; these plots were established by generating one random angle within each compass quadrant and a random distance between 5 and 25 m from the camera location. We measured low horizontal cover (LHC) by photographing a  $1 \times 1$ -m plain white sheet (at four random locations and distances) and visually estimated the percentage obscured by vegetation and rocks (e.g., low LHC values are sites with fewer obstructions). Our 5–25-m site-level LHC measurements were designed from the attack radius of pumas, who exhibit higher predation success between 5 and 25 m (Laundré and Hernández 2003). We expected that both chilla foxes and culpeo foxes could perceive predation risk within this distance and preemptively select habitat on the basis of horizontal cover. Using ArcGIS (Environmental Systems Research Institute 2011), we estimated the minimum distance to households, roads, cliffs, lakes, and rivers for each camera trap. Given the homogeneity and scale of the landscape within our study area, we deemed distance metrics adequate for analysis. For both spatial analyses and temporal analyses, we combined our detection data from the occurrence of humans and dogs (unless explicitly stated, we refer to humans as the combination of humans and their dogs; see the supplemental PDF, available online).

To assess dietary overlap, we opportunistically collected scat samples from native carnivores during our study for dietary scat analysis and collected hair from native carnivores and dogs for stable isotope analysis throughout the study season from roadkill and carcasses or obtained samples from pelts (collected by pastoralists before or during the study). All hair samples used for our stable isotope analysis were restricted to locations within 50 km of the study area (lat.  $-70.03$ , long.  $-39.05$ ), acquired from carcasses ( $N = 11$ ), live animals (dogs;  $N = 3$ ), or donated pelt samples ( $N = 12$ ). We supplemented the puma hair samples with two samples collected in the main canyon, where we observed pumas during our study period—one at a narrow pass on a cliff face with a catwalk and the other  $\sim 2$  m from a puma scrape. Although these samples were collected  $\sim 2$  months apart, they were collected within 2 km of each other, and determining whether they belonged to the same individual was not possible (see table S7; fig. S10; tables S1–S8, figs. S1–S11 are available online). All appropriate samples were collected under an approved institutional animal care and use committee through the University of Wisconsin–Madison (A006038-R01) and processed in the Pauli Lab (CONVE-2020-71252684-DNC#APCAC).

### *Space*

To assess the spatial drivers of carnivore community structure, we used a combination of single-species occupancy models (MacKenzie et al. 2006) and structural

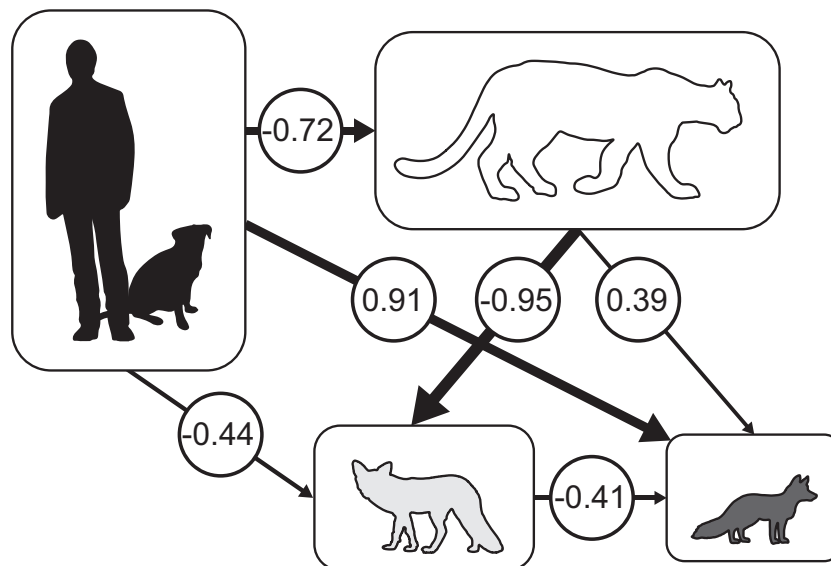
equation models (SEMs). Our sampling period (excluding a 2-week adjustment period) was from July 10 to October 10, 2018. We split camera trap surveys into 10-day intervals; if a species was photographed at a site on one or more days in an interval, we considered it a single detection. The survey periods were used to generate site-specific detection histories for each species. We assumed that sites were closed to changes in occupancy state over the entire sampling period. Because individuals did not have to be continually present at a site for it to be classified as occupied and because of the larger home ranges (HRs) of culpeo foxes and pumas, occupancy in our study should be interpreted as use (MacKenzie et al. 2006). We attempted to minimize sampling bias and limit the spatial autocorrelation with our trap placement; however, the larger carnivores and the humans in our study have HRs that covered the extent of several camera traps (e.g.,  $HR_{\text{Puma}} \approx 10,000$  ha,  $HR_{\text{CulpeoFox}} \approx 1,250$  ha). We tested for spatial autocorrelation between the detections of each species and the distance between cameras using correlograms (fig. S1).

We used three sequential stages of model fitting in the package unmarked (Fiske and Chandler 2011) to identify the best covariates of detection and occupancy from our list of a priori covariate candidates: (1) single-species detection, (2) single-species occupancy, and (3) global single-species occupancy. This approach enabled the modeling of species occupancies so that the same covariates for each species could be used in an SEM for interspecific comparisons. To determine survey-specific heterogeneity in detection probability, we used survey period, snow cover, moon phase, distance to road, LHC, and their additive effects as possible covariates. We held occupancy constant ( $\psi(\cdot)$ ) and fitted 23 models to explore the influence of the covariates and their additive combinations on the probability of detecting each species. We then carried the best detection covariates forward into a single-species single-season model, from which we determined the most important occupancy covariates for each species, considering distance from households, roads, rivers, lakes, and cliffs, as well as LHC and  $\psi(\cdot)$ . Last, we identified the best occupancy covariates for each single-species model and created a global single-species occupancy model featuring a combination of the best covariates for all species. We used our final global model (using the covariates distance to rivers, lakes, and cliffs) to determine site-specific occupancy probabilities and used these expected occupancy probabilities for the SEM.

We used estimates of the camera-specific occupancy probabilities from our global single-species occupancy models for each species in an SEM analysis using observed variables (a path analysis; Grace 2006; Sivy et al. 2017). Although co-occupancy models (e.g., Rota et al. 2016; Lombardi et al. 2020) can propagate uncertainty into the occupancy estimates (MacKenzie et al. 2006), they often cannot

provide inference on ecological interactions (Blanchet et al. 2020) and are less flexible than SEMs when dealing with direct, indirect, and net interactions (Sivy et al. 2017). Although combining occupancy models and SEMs likely resulted in an underestimation of the error surrounding the spatial effects between species, this approach enabled a mechanistic representation of the underlying drivers of species interactions (see Joseph et al. 2016) and the estimation of indirect interactions within the carnivore community and with humans. By deriving the site-specific occupancy probabilities from the global single-species models, we first accounted for habitat covariates that influence species distributions, and then we modeled how the estimated occupancy probabilities were influenced by interacting species using an SEM (i.e., we accounted for abiotic interactions and considered only biotic interactions). While the sample size of our SEM was sufficient for this analysis, it was too small to allow us to explore other potential mediating effects. We drew from previous literature on the interacting species (Jiménez et al. 1996; Novaro et al. 2005) and theoretical underpinnings of how these carnivore communities are structured (Donadio and Buskirk 2006; de Oliveira and Pereira 2014) to guide a multivariate hypothesis of the carnivore community structure in this system and how it is shaped by humans (fig. 2). We used a global estimation approach for our SEM, which compares the covariance matrices in the paths that we outlined in our a priori hypotheses (fig. 1). We used maximum likelihood for parameter estimation, where the relationships between covariance matrices are maximized with respect to model parameters. Overall model data fit was evaluated with Pearson's  $\chi^2$  test (West et al. 2012). Initially, we tested a direct effect from pumas to chilla foxes but found it to be nonsignificant, so we removed it from our final model. Our results are reported as standardized path coefficients for simpler interpretations across paths, where the values represent how a change in 1 SD of the exogenous (predictor) variable changes the endogenous (response) variable. Our data met the assumptions (e.g., sample size, normal distribution) for an SEM analysis (Grace 2006), and we used  $\alpha \leq .05$  to evaluate parameter relationships for each interaction. All SEM analyses were conducted using the R package lavaan (Rosseel 2012). We classify the strengths of interactions as weak ( $\leq 0.33$ ), moderate (0.34–0.66), and strong ( $\geq 0.67$ ). Because of our multimodel approach (building an SEM according to the expected occupancy probabilities from a suite of global single-species occupancy models), biases linked with the occupancy models would directly propagate to the SEM. To account for any potential bias in our conclusions, we implemented a multispecies occupancy model as a complementary analysis to the spatial interactions between species. Specifically, we used a build-up approach (Morin et al. 2020) using the best detection





**Figure 2:** Net effects of standardized path coefficients of our final structural equation model (each coefficient is reported within the circle) for pumas (*Puma concolor*), culpeo foxes (*Lycalopex culpaeus*), chilla foxes (*Lycalopex griseus*), and humans (including dogs, *Canis familiaris*). Note that line width is proportional to the effect size.

and occupancy covariates from the single-species occupancy models (tables S1, S2) to compose the individual species components of the multispecies occupancy model with all four species. We modeled the co-occurrence of all species pairs as constant (i.e., using  $\psi(\cdot)$ ) and with no higher-order interactions (i.e., three- or four-species interactions) to minimize the complexity of the model (for further details, see “Multi-Species Occupancy Model” in the supplemental PDF).

#### Time

To assess diel activity overlap of chilla foxes, culpeo foxes, pumas, and humans, we used the time stamp metadata from each camera trap. To ensure independence between captures, we limited temporal autocorrelation by considering detections only if  $>30$  min passed between camera captures. We tested for independence between detections for each species by minimizing the effect between minutes between detection and the average activity time, the standard deviation of activity time, and the total count of photos (fig. S5). We corrected for a shift in the recorded times of camera traps by regressing the number of photos taken and the difference between the recorded time on the camera and the actual time when the camera was checked (see fig. S3). We used the R package *overlap* (Ridout and Linkie 2009) and the *overlap* method for low samples sizes (i.e.,  $N_{\text{Culpeo}} = 35$  and  $N_{\text{Puma}} = 17$ ); both of these functions compare the vectors of fitted kernel densities at the times of the observations of the two species compared. We used

the bootstrap estimates of temporal overlap to have a more robust estimate of activity overlap (Ridout and Linkie 2009).

#### Resources

To assess dietary overlap between carnivores, we used two complementary methods: (1) the frequency of occurrence of dietary items in native carnivore scat and (2) the isotopic signature of hair collected from native carnivores and dogs in the field. We collected 25 chilla fox, 32 culpeo fox, and 24 puma scat samples; pseudoreplication was unlikely for culpeo and chilla foxes but likely for pumas (see “Scat Collection” in the supplemental PDF; table S6; fig. S7). We dried (48 h in  $65^{\circ}\text{C}$ ) and then rinsed the scat with hot water to facilitate manual separation of dietary items. We collected four to six clumps of hair, depending on how heterogeneous the scat appeared and on the presence of dissimilar bones, from each scat and analyzed it under a microscope to identify individual species (Chehebar and Martin 1989). When possible, we collected mandibles, teeth, and other bone material that could help identify species (Pearson 1995). We used the R package *EcoSimR* to estimate a bootstrap estimate ( $N = 1,000$ ) of Pianka’s index of overlap by resampling the frequency of occurrence of dietary items in each species’ scat; values of zero indicate complete dietary partitioning, and values of one indicate complete dietary overlap. To compare broader patterns in diet, we separated scat items into five different categories representing the major diet sources in LBNP: livestock (goats, sheep, horse, and cow), lagomorphs (European hares and European

rabbits), rodents (families Cricetidae, Ctenomidae, Octodontidae, and Caviidae), birds, and other (including unidentified arthropods, annelids, fish, reptiles, and amphibians). For each species, we estimated Levins' niche breadth index (Levins 1968).

We estimated carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) bulk isotopic signatures from hair samples from chilla foxes ( $N = 8$ ), culpeo foxes ( $N = 10$ ), pumas ( $N = 5$ ), and dogs ( $N = 5$ ). All samples analyzed were prepared following Pauli et al. (2009) and analyzed following standard techniques (see the supplemental PDF). To quantify the overlap in the isotopic niche of each species, we used the standard ellipses corrected for small sample size (SEAC; a measure of niche breadth) and calculated the area of overlap between ellipses in the R package SIBER (Parnell et al. 2010). To compare dietary niche overlap of native carnivores and dogs with humans, we used previously collected isotopic values of humans in South America (Hülsemann et al. 2015).

## Results

### Space

We conducted a total of 3,116 camera trap nights from July 10 to October 10, 2018; chilla foxes were the most common carnivore detected throughout the study area, with a naive occupancy of 59%, followed by culpeo foxes (26%) and finally pumas (20%). Naive occupancy of humans and dogs combined was 67%. We did not detect spatial autocorrelation for any of the species (fig. S1A), but we detected autocorrelation of chilla fox and human occupancy probability with distance between camera traps, likely because of the relatively high occupancy of these species within the study area (fig. S1B).

The detection probability of chilla foxes ( $0.28 \pm 0.04$ ;  $\pm 1$  SE throughout) was highest, followed by humans ( $0.26 \pm 0.03$ ), culpeo foxes ( $0.23 \pm 0.02$ ), and last pumas ( $0.13 \pm 0.04$ ). Covariates affecting detection probabilities differed by species (table S1). Specifically, we found that chilla fox detection decreased throughout the survey period and with increasing lunar luminosity, human detection increased with horizontal cover, and puma detection increased throughout the study period, likely as they acclimated to the camera traps (table S1). Culpeo fox detection decreased throughout the survey period and increased with horizontal cover; however, because of near-equal support and the minimal effect on the likelihood, we used the simpler model including only horizontal cover for subsequent modeling (see "Methods").

Chilla foxes were the most widespread carnivore species (occupying  $0.64 \pm 0.03$  of the study area). Surprisingly, pumas ( $0.34 \pm 0.04$  of the study area) were estimated to be more widespread than culpeo foxes ( $0.31 \pm 0.03$ ). Chilla fox predicted occupancy increased farther from rivers

(fig. S2D), culpeo fox predicted occupancy decreased farther from lakes (fig. S2C), and puma predicted occupancy decreased farther from cliffs (fig. S2B). Furthermore, we estimated that humans occupied most of the area in LBNP ( $0.76 \pm 0.02$  of the study area) and that their predicted occupancy increased farther from rivers (fig. S2A). The relationships for each of the single-species models were consistent with the global model (see "Methods") we used for the SEMs (table S3).

### Structural Equation Model

Chilla fox occupancy was moderately negatively influenced by culpeo fox space use and strongly positively influenced by human and dog space use. Furthermore, culpeo fox occupancy was moderately negatively influenced by human and dog space use and strongly negatively influenced by puma space use. The negative effect from pumas to culpeo foxes, in combination with the negative effect of culpeo foxes to chilla foxes, created an indirect, moderately strong, positive effect from pumas to chilla foxes (for all direct and indirect effects, see fig. S4). Last, humans and dogs had a strong negative effect on puma space use (fig. 2). Our final SEM (fig. 2) showed close fit to the observed data ( $\chi^2 = 1.42$ ,  $P = .23$ ). The results from our multispecies occupancy model supported our findings from our SEM: humans and chilla foxes exhibited the highest co-occurrence probability ( $0.53 \pm 0.04$ ), while puma and culpeo foxes had the lowest co-occurrence probability ( $0.08 \pm 0.01$ ). (See the supplemental PDF for further details.)

### Time

We used a total of 17 photos of pumas, 35 photos of culpeo foxes, 109 photos of chilla foxes, 68 photos of humans, and 49 photos of dogs to estimate the activity patterns of each species. Peak activity times of native carnivores varied by species, though they were mostly nocturnal. Pumas were found to be exclusively nocturnal, though their activity peaked twice, just before 00:00 and again before 06:00 (fig. 3A). Culpeo and chilla foxes, on the other hand, exhibited one distinct peak in activity. Culpeo fox activity increased after sunset and peaked just after 06:00, before it sharply decreased (fig. 3B). Chilla fox activity peaked around 20:00 (just after sunset) and remained relatively constant before a large decrease before 06:00 (fig. 3C). Human and dog activity times did not differ and were centered around midday (12:00; figs. 3D, S6).

There was no difference in the diel overlap between native carnivores (Puma–Culpeo Fox =  $0.76 \pm 0.09$ , Puma–Chilla Fox =  $0.75 \pm 0.09$ , and Culpeo–Chilla Fox =  $0.75 \pm 0.08$ ), although their peak activity times varied (fig. 3A–3C). Diel overlap between humans and dogs was much higher than overlap between any other pair of species (i.e.,

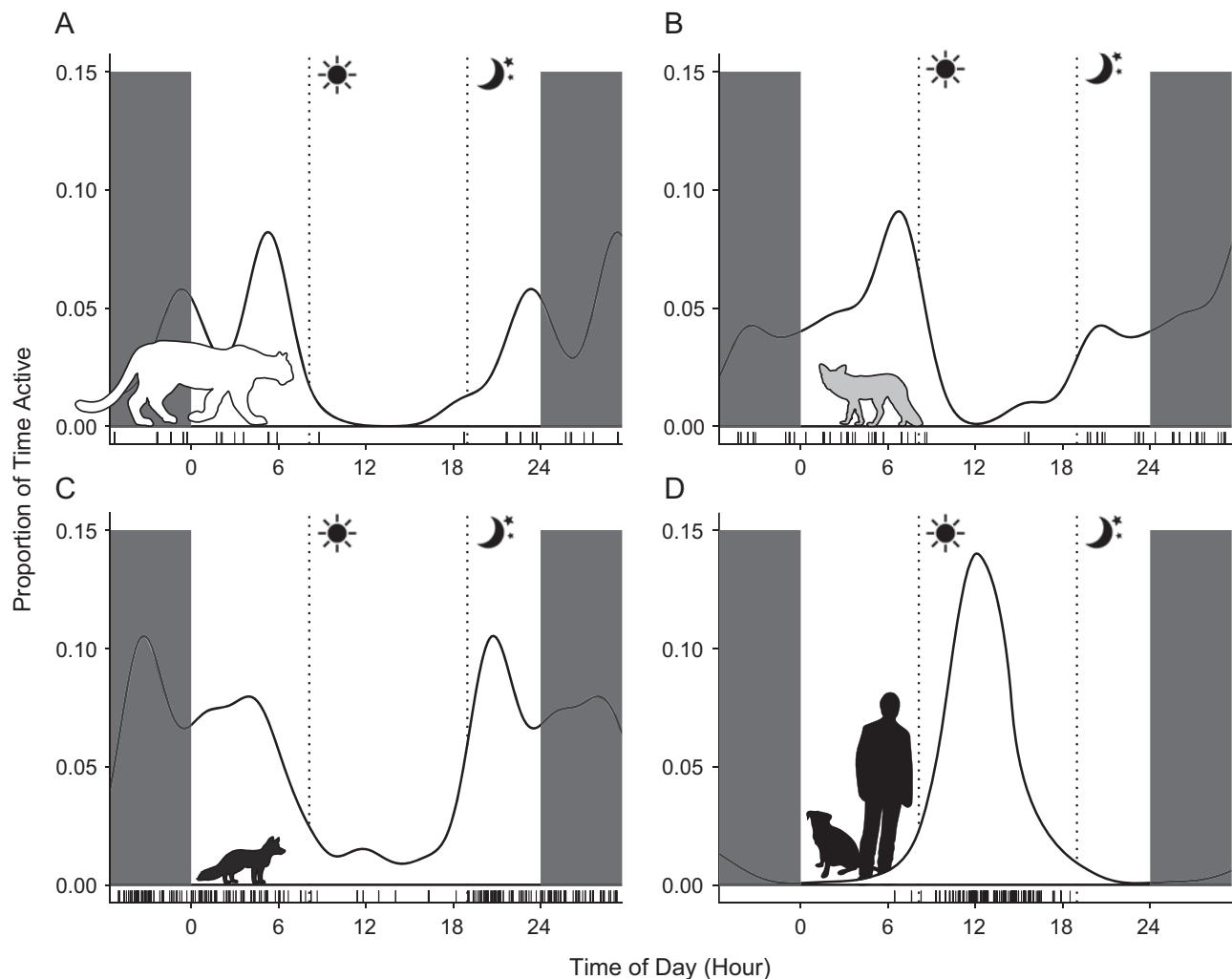
$0.96 \pm 0.01$ ; fig. S6) and was strictly diurnal (fig. 3D). Furthermore, the temporal overlap within native carnivores was significantly higher than it was between native carnivores and humans. The overlap between culpeo foxes and humans was highest ( $0.22 \pm 0.06$ ), followed by chilla foxes and humans ( $0.18 \pm 0.04$ ) and last by pumas and humans ( $0.15 \pm 0.06$ ).

### Resources

Puma scat primarily consisted of livestock remains ( $0.79 \pm 0.01$ ), followed by lagomorphs ( $0.18 \pm 0.04$ ). Culpeo foxes had the most diverse prey richness and evenness, including livestock ( $0.45 \pm 0.05$ ) and lagomorphs ( $0.21 \pm 0.04$ ), whereas chilla foxes consumed a majority of rodents ( $0.57 \pm 0.05$ ),

followed by livestock ( $0.23 \pm 0.04$ ; fig. 4A). Culpeo foxes had the highest measure of niche breadth ( $B = 3.52$ ), followed by chilla foxes ( $B = 2.62$ ) and pumas ( $B = 1.52$ ). Unexpectedly, puma and culpeo fox diets had the greatest overlap, while puma and chilla fox diets and culpeo fox and chilla fox diets exhibited low to moderate overlap (fig. 4C).

Culpeo foxes had the highest isotopic niche breadth ( $SEAc = 2.95$ ), followed by chilla foxes ( $SEAc = 1.72$ ), dogs ( $SEAc = 1.10$ ), and last pumas ( $SEAc = 0.80$ ; fig. 4B). Within native carnivores, the isotopic niche overlap was highest between culpeo foxes and chilla foxes, followed by pumas and culpeo foxes and then pumas and chilla foxes (fig. 4C). Isotopic niche overlap was very low between dogs and chilla foxes, culpeo foxes, and pumas. We found that



**Figure 3:** Temporal activity patterns of pumas (*Puma concolor*; A), culpeo foxes (*Lycalopex culpaeus*; B), chilla foxes (*Lycalopex griseus*; C), and humans (including dogs, *Canis familiaris*; D) from 0 (midnight) through 24 (midnight of the following day) in Laguna Blanca National Park, Argentina, 2018. Dotted vertical lines and emblems indicate average sunrise and sunset from July 15 to October 15 in our study area, and gray boxes indicate the repetition of activity from one day to the next. Lines near the base indicate occurrences of photos for each species.

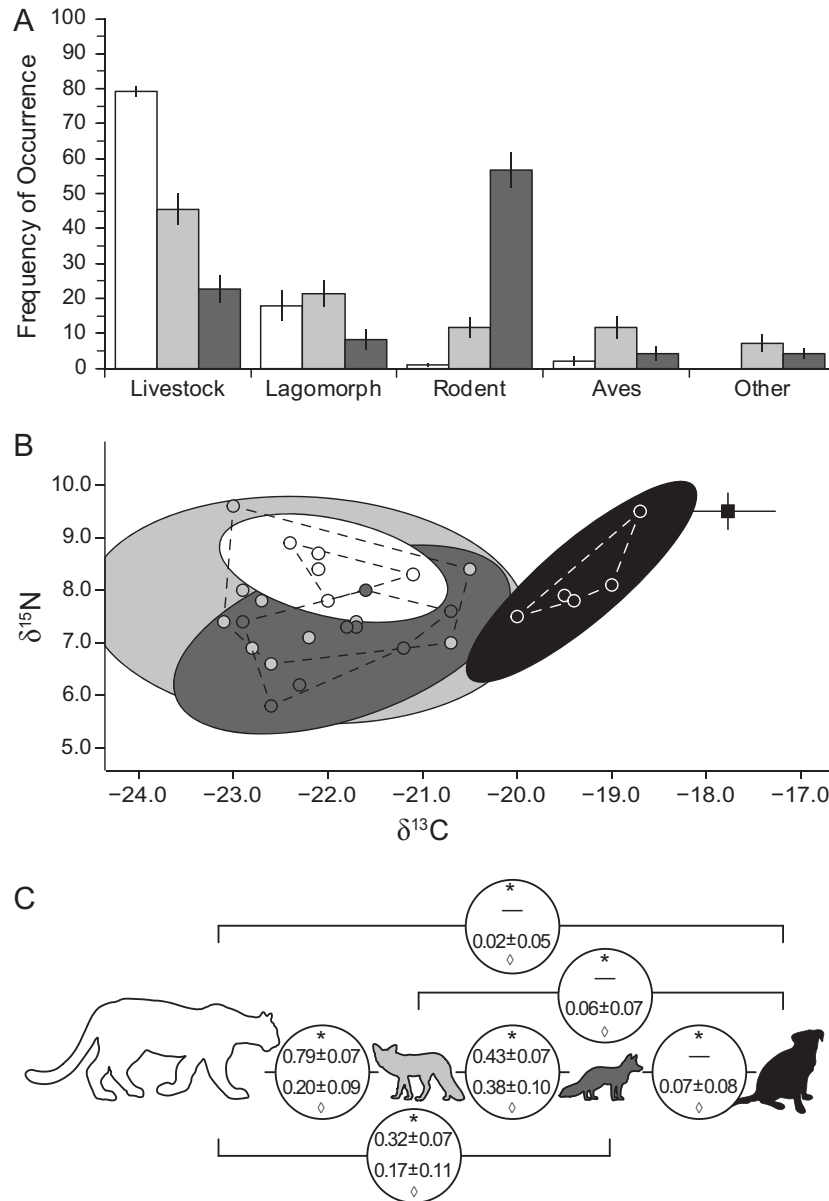


dogs foraged intermediately between humans and native carnivores (fig. 4).

**Discussion**

In agreement with our hypotheses, we found that the spatial, temporal, and resource drivers of community structure

differed for humans and apex carnivores, and their effects ultimately shaped the niche of mesocarnivores and small carnivores differently. Apex carnivores occupied areas not routinely used by humans, which created space for small carnivores. Native carnivores overlapped in activity times, and mesocarnivores and small carnivores did not appear to avoid the times that the apex carnivore was active, likely



**Figure 4:** Bootstrap mean ( $\pm$ SD) of scat analysis results (A) and SIBER ellipse areas corrected for small sample sizes (SEAc; B) of pumas (*Puma concolor*; white), culpeo foxes (*Lycalopex culpaeus*; light gray), chilla foxes (*Lycalopex griseus*; dark gray), and dogs (*Canis lupus familiaris*; black). C shows Pianka's index of overlap ( $\pm$ SD; asterisk at top of circles) and isotopic niche overlap ( $\pm$ SD; diamond at bottom of circles) between each species pair. SEAc's reported are 95% confidence intervals in a carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) biplot. The scat analysis is broken down into the frequency of occurrence of livestock, lagomorphs, rodents, aves, and other in carnivore scats. The expected mean ( $\pm$ SD) carbon and nitrogen isotope value of humans in South America (black square and error bars) is shown for reference (data from Hülsemann et al. 2015).

because they were also attempting to minimize temporal overlap with humans (Gaynor et al. 2018). Finally, domestic carnivores were trophically decoupled from native carnivores and thus somewhat insulated from the costs of niche compression and enhanced competition.

### Space

Native apex carnivores had strong effects on the space use of mesocarnivores and small carnivores. Unlike pumas, the habitat used by culpeo foxes contained long sight lines (i.e., farther from cliffs with lower LHC); the strong negative spatial effect from pumas to culpeo foxes is likely driven by a fear-mediated response, in which culpeo foxes are selecting against habitat that pumas utilize. Indeed, the “landscape of fear” for mesopredators may be especially steep, with little safety offered in risky places (Ritchie and Johnson 2009; Gaynor et al. 2019), and the response of culpeo foxes appeared to be greater than expected given the body size differences with pumas. On the other hand, although pumas kill chilla foxes (de Oliveira and Pereira 2014), the benefit they receive from decreased spatial pressure from culpeo foxes likely outweighs the risk from pumas. We also found a strong negative effect from mesocarnivores to small carnivores. Compared with culpeo foxes, chilla foxes are likely a superior exploitative competitor, so they can avoid culpeo foxes altogether by utilizing resource-poor areas (Johnson and Franklin 1994b).

Humans reinforce spatial structuring in carnivore communities (Kuijper et al. 2016). In general, the space use of apex carnivores is concentrated in areas unused by humans (Wilmers et al. 2013). This constriction in the space use of apex carnivores can create opportunities for mesocarnivores and small carnivores (Newsome and Ripple 2014). Indeed, we found a strong negative spatial effect of humans on pumas, which appears to have created space for both culpeo foxes and chilla foxes. However, this positive indirect effect of humans on culpeo foxes through pumas was overcome by a strong negative direct effect from humans to culpeo foxes. Thus, culpeo foxes were not benefiting from humans as a protective shield against pumas. In contrast, the positive effects that humans had on chilla foxes seemed to be at odds with the direct negative effects observed elsewhere (i.e., Silva-Rodríguez et al. 2010). Although we expected a net positive effect from humans to chilla foxes, we predicted that this would be largely driven by an indirect effect (via a spatial shield). Given our hypotheses, predictions, and previous literature on human and chilla fox interactions, the direct effect of humans on chilla foxes from our SEM does not seem to make biological sense. Mediating effects that were unaccounted for could have contributed to this (Grace 2006). For example, other predators and competitors—such as raptors and pampas or Geoffroy’s cats—or the spatial

distribution of small mammal prey could have mediated a human effect on chillas resulting in the observed positive effect. However, raptors rarely predate chilla foxes (Iriarte et al. 1990), and both pampas and Geoffroy’s cats were extremely rare in our study area. Furthermore, the small mammal prey that chilla foxes were consuming (e.g., *Ctenomys* spp. and Cricetine rodents) are not strongly associated with humans (Mapelli et al. 2020), and there was no pattern between the diet of chilla foxes and human space use. Instead, it is more likely that the underlying reason for net positive effects of humans on chilla fox spatial distribution is that humans and chilla foxes exhibited high co-occurrences across our study site. This statistical relationship (i.e., the high co-occurrence probabilities of these two interacting species) likely created a scenario where humans and chilla foxes exhibited a strong positive association and would explain the strong direct effect from humans to chilla foxes. Regardless, it appears that subordinate carnivores, like the chilla fox, may doubly benefit from the negative spatial effects that humans have on dominant members of the carnivore community. Our work further suggests that the spatial drivers of community structure differ for humans and apex carnivores, while the directionality of these effects on mesocarnivores and small carnivores may be similar.

### Time

Time was the most compressed niche axis (i.e., showed the highest overlap) for carnivores in our study. Recent work has shown that mammals, including carnivores, have increased their nocturnality in response to human disturbance (Gaynor et al. 2018). Although temporal avoidance may facilitate human-carnivore coexistence (Gaynor et al. 2018), temporal niche compression can intensify competition among carnivores by increasing the frequency of interspecific interactions (Cusack et al. 2017). Our study, however, is limited to broad activity patterns and does not address spatiotemporal partitioning, which can be an important mechanism for facilitating sympatry among carnivores (Karanth et al. 2017).

Puma diel activity is flexible (Franklin et al. 1999), generally influenced by the activity of prey (Smith et al. 2019). Pumas also appear to shift their activity to avoid humans and become increasingly more nocturnal when humans are present (Wang et al. 2015). Interestingly, humans, dogs, and livestock, the predominant prey species of pumas in our study, were all diurnal. If pumas attempted to maximize encounters with livestock, they would likely experience greater conflict with humans. Interestingly, in San Guillermo National Park, Argentina, a comparable system lacking human presence, puma activity times were concurrent with their primary prey in the area, vicuñas (*Vicugna vicugna*; Smith et al. 2019). Thus, it appears that the risk

of conflict with humans overwhelmed benefits of maximizing activity with prey.

Culpeo and chilla foxes overlapped greatly in their daily activity times, generally being nocturnal, and their activity patterns were similar to those found in previous research in Patagonia lacking humans (Johnson and Franklin 1994b; Jiménez et al. 1996). Our work thus aligns with previous research that suggests apex carnivores respond more strongly to human activity times compared with the response of mesocarnivores and small carnivores (Laporte et al. 2010). Furthermore, our work supports the idea that humans can compress the temporal niche of entire communities (Wang et al. 2015). Given that human activity indiscriminately increases nocturnality in carnivores (Gaynor et al. 2018), we propose that humans prevent mesocarnivores and small carnivores from responding to more nocturnal activity of apex carnivores (i.e., in response to humans) and through this mechanism increase temporal niche overlap among carnivores globally (i.e., mesocarnivores and small carnivores are conflicted between avoiding diurnal humans and nocturnal apex carnivores).

#### Resources

Humans and dogs were trophically decoupled from the carnivore community, with dogs foraging intermediately between humans and native carnivores. Indeed, dogs did not overlap in isotopic space with the native carnivore community—likely due to human subsidies—and were isotopically intermediate between the predicted isotope value of humans (Hülsemann et al. 2015) and our observed value of native carnivores. Food supplementation likely insulates domestic carnivores (i.e., dogs) from competition for resources and leads to a one-way competitive effect on native carnivores (Vanak et al. 2014). Notably, we found no evidence that native carnivores were being supplemented with human food sources, other than depredated livestock.

The high dietary overlap among native carnivores could be partly explained by landscape and resource homogenization; indeed, humans fundamentally alter the resource niche breadth and overlap of terrestrial carnivores across broad geographic regions (Manlick and Pauli 2020). The local extirpation of large herbivores (namely, guanacos, *Lama guanicoe*) compounded by the heavy grazing of domestic livestock has strongly altered the characteristics of the plant community and fundamentally restructured the prey base for carnivores (Novaro et al. 2017). Additionally, high densities of livestock provide an abundant and large-bodied prey, especially for apex carnivores. Livestock was the primary prey of pumas in our study area, and pumas likely provisioned livestock carrion to both fox species. However, culpeo foxes are large enough to prey on young live-

stock, and we were unable to determine how much livestock in their diet was from scavenging compared with predation.

While presence of humans can reduce puma foraging time at kill sites in North America (Smith et al. 2017), pumas there do not respond strongly to domestic dogs alone (Surraci et al. 2019). In our study system (and across much of rural South America; Silva-Rodríguez et al. 2010), dogs are somewhat feral; they are generally found with humans but will also hunt and scavenge. Dogs are likely to present a greater risk to native carnivores (Vanak and Gompper 2009, 2010), particularly since the strongest competitive interactions within carnivores occur at carcasses (Prugh and Sivy 2020). Given that dogs in LBNP were isotopically intermediate between humans and native carnivores (i.e., consuming prey similar to prey of native carnivores but receiving human subsidies) and the fact we have observed dogs in LBNP foraging on puma kills and other carrion, we suspect that dogs are scavenging from puma kills. Because high levels of scavenging can increase puma kill rates (Elbroch and Wittmer 2013; Smith et al. 2017), it is possible that dogs are increasing livestock depredation rates, which in turn is enhancing human-carnivore conflicts. Interestingly, the occurrence of livestock in culpeo fox diet was much higher compared with studies featuring large ungulate prey (i.e., guanacos) in natural systems (Johnson and Franklin 1994a). Thus, finer-scale, spatiotemporal partitioning might explain the high proportion of livestock found in the diet of culpeo foxes, especially if humans, or their dogs, increase prey abandonment by pumas. The feedback loop among livestock, native predators, domestic dogs, and humans on public and private lands warrants further exploration, as it could amount to unintended consequences and a challenging management scenario.

#### Conclusion

Carnivores can avoid aggressive interspecific interactions by partitioning space, time, or resources with their competitors. However, many of the ecological rules derived from natural systems do not explicitly account for how humans, and human-associated species, shape niche partitioning among native carnivores. Notably, we found that native carnivores were active during the times humans were not active, leading to high temporal overlap within the carnivore community. Furthermore, we also observed high dietary overlap within the native carnivores. The high temporal and dietary niche overlap left space as the most critical niche axis for native carnivores to partition. However, shared food resources, especially through carrion subsidies, will very likely bring these species back into spatial overlap and thus interspecific conflict. Our work highlights the need for a mechanistic understanding of all three critical niche axes to predict how carnivore communities, and

communities broadly, will be structured in emerging human landscapes. Because of the constrained temporal niche and diminishing resource partitioning caused by humans, carnivores most importantly require space in human landscapes.

Managing and conserving communities in the Anthropocene present many challenges, and these novel interactions can create challenging problems that require creative management solutions. In many ways, humans acted as an apex carnivore by fundamentally altering the dominance hierarchy within the carnivore community. However, the effects from humans to carnivores are largely unidirectional: humans are largely trophically decoupled from native carnivores, human risk cues are novel compared with what carnivores have historically evolved under, and the efficiency at which humans kill other species is unique and unprecedented. The novelty of human-carnivore interactions reinforces our need to study all three critical niche axes simultaneously to understand the consequences for carnivore communities more broadly.

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#### Statement of Authorship

M.R.C. and J.N.P. designed the study; M.R.C. collected and analyzed the data, with help from J.N.P., A.D.M., and E.D.; and M.R.C. and J.N.P. wrote the manuscript with A.D.M. and E.D.

#### Data and Code Availability

Analyses reported in this article can be reproduced using the data and code provided at the Dryad Digital Repository (<https://doi.org/doi:10.5061/dryad.00000004p>; Rodriguez Curras et al. 2021).

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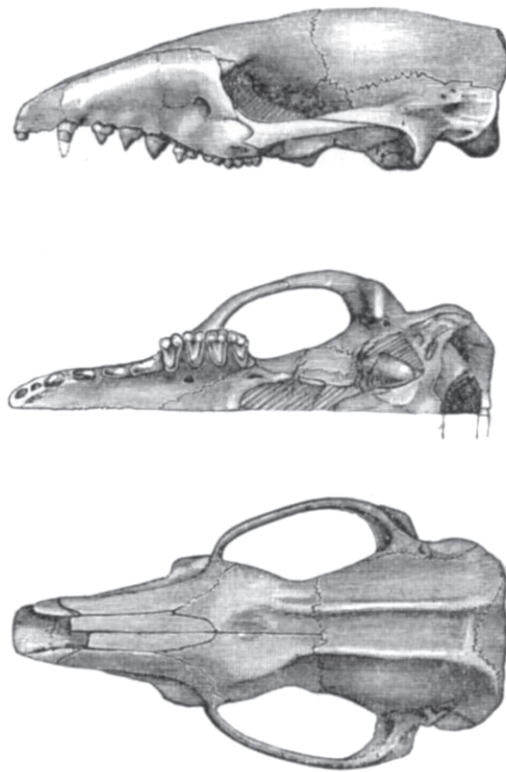
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“As yet but one species of *Leptictis* is known, the *L. haydeni* Leidy [figured]. This animal has been found in the White River beds of Nebraska. . . . It resembles the gray fox of North America in the rib-like temporal ridges of its skull.” From “The Creodonts (continued)” by E. D. Cope (*The American Naturalist*, 1884, 18:478–485).