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Original Article

Perceived risk structures the space use of competing carnivores

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Competition structures ecological communities. In carnivores, competitive interactions are disproportionately costly to subordinate carnivores who must account for the risk of interspecific killing when foraging. Accordingly, missed opportunity costs for meso-carnivores imposed by risk can benefit the smallest-bodied competitors. However, the extent to which the risk perpetuates into spatial partitioning in hierarchically structured communities remains unknown. To determine how risk-avoidance behaviors shape the space-use of carnivore communities, we studied a simple community of carnivores in northern Patagonia, Argentina: pumas (*Puma concolor*, an apex carnivore), culpeo foxes (*Lycalopex culpaeus*; a meso-carnivore), and chilla foxes (*Lycalopex griseus*; a small carnivore). We used multi-species occupancy models to quantify the space use within the carnivore community and giving-up densities to understand the behaviors that structure space use. Notably, we applied an analytical framework that tests whether the actual or perceived risk of predation most strongly influences the space use of subordinate carnivores although accounting for their foraging and vigilance behaviors. We found that there was a dominance hierarchy from the apex carnivore through the meso-carnivore to the subordinate small carnivore, which was reflected in space. Although both meso- and small carnivores exhibited similar predator avoidance behavioral responses to apex carnivores, the habitat associations of apex carnivores only altered meso-carnivore space use. The biases in risk management we observed for meso-carnivores likely translates into stable co-existence of this community of competing carnivores. We believe our analytical framework can be extended to other communities to quantify the spatial-behavioral tradeoffs of risk.

Key words: competition, giving-up density, perceived risk, risk management, spatial-behavioral tradeoffs.

INTRODUCTION

The exploitation of a limited resource by two or more species can strongly structure ecological communities (Gause 1934; Hardin 1960; Holt 1977). Within the carnivore guild, competition is especially apparent because carnivores have evolved to become highly effective killers (Gittleman 1989). For carnivores, interspecific competition is often manifested as interference, whereby dominant guild members display aggression or even kill subordinate species (Case and Gilpin 1974; Holt and Polis 1997). These interactions are disproportionately costly to smaller bodied species (Palomares and Caro 1999; Donadio and Buskirk 2006; de Oliveira and Pereira 2014), though subordinate species can benefit from large carnivore provisioning (i.e., facultative scavenging; Prugh et al. 2009; Elbroch and Wittmer 2012). Consequently, subordinate carnivores

must navigate risky landscapes to avoid interspecific killing whereas maximizing foraging opportunities (Suraci et al. 2016).

Much of what we know about risk perception and avoidance comes from predator–prey interactions (Lima and Dill 1990). Prey simultaneously balances energetic demands and anti-predator behaviors, though the quality of prey information about predation risk and the costs and benefits of refuge use predominantly influence behavioral adaptations (Sih 1992). Intuitively, prey is expected to overestimate risk and be more cautious—despite ambiguity in the signal—because the fitness cost of underestimating risk (i.e., death) is higher than missed opportunity costs (Abrams 1994; Brown et al. 1999). Direct cues of risk, like smelling, hearing, or seeing a predator, relate immediate information and can be informative for escaping predation when being targeted (Lima and Dill 1990). Such direct cues are often extrapolated beyond the given encounter by tying them to indirect cues like habitat type or horizontal cover, which can reveal generally risky areas to be avoided (Preisser et al. 2005; Preisser et al. 2007). These indirect cues of predation risk culminate in the “landscape of fear” (Laundre et al.

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2010) and often influence space-use more broadly (Janssen et al. 2007; Laundre et al. 2010). Predators that exhibit a narrow habitat domain, with a preference for specific habitat characteristics, have been found to influence space-use more strongly (Schmitz 2008), causing the prey to spatially or temporally avoid those areas (Schmitz et al. 2017; Smith et al. 2019). Because indirect cues of risk provide less accurate information on the identity and state of potential risk, the costs of false-positive (missed opportunity costs) and false-negative errors (potential death) will generally lead species to become more wary (i.e., cause species to perceive a higher level of risk than is actually present; Sih 1992; Lima and Bednekoff 1999). The way species cope with predation risk is an important component of community structure because the fear of death has at least as strong of an effect on prey distribution and abundances as direct predation (Preisser et al. 2005, 2007; Guiden et al. 2019).

Much like prey, subordinate carnivores navigate potentially deadly encounters with dominant carnivores (Berger et al. 2008) and so our understanding of risk avoidance interactions are largely transferable between predator–prey and predator–predator systems (Mukherjee et al. 2009); indeed, predator–prey interactions shape how we think about carnivore intraguild interactions and competition (Polis et al. 1989; Holt and Polis 1997). Carnivore communities, however, are further structured by facilitation (i.e., resource provisioning); these two opposing forces (suppression and facilitation) create a “fatal attraction” for meso- and small carnivores (Sivy et al. 2017). The lower resource availability found at higher trophic levels, compounded by the difficulty in acquiring or subduing profitable prey, tends to aggregate carnivores over shared and limited resources like carrion (Sivy et al. 2017). Consequently, risk avoidance in carnivore communities is an especially important driver of community structure (Ritchie and Johnson 2009), particularly because prey can more easily move to different resource patches to avoid predation (Smith et al. 2019). In multi-carnivore communities featuring a hierarchy of three or more levels (*sensu* Prugh and Sivy 2020), the missed opportunity costs of being overly cautious has the added cost that these tradeoffs for safety can be beneficial for smaller bodied competitors.

To minimize the risk of fatal interactions, the best strategy for subordinate carnivores is to partition space (Fedriani et al. 2000), especially in environments where resources are limited (Robinson et al. 2014) and where species exhibit constrained diel patterns (Balme et al. 2017). Understanding the ecological consequences of behaviorally mediated space-use provides insight into the structure of communities (Schmitz et al. 1997). Indeed, the “landscape of fear” for meso-predators may be especially steep, with little safety offered (Ritchie and Johnson 2009). Much of the focus on risk avoidance in carnivores have come from dyadic interactions attempting to untangle how predation risk affects foraging (Hunter and Caro 2008; Leo et al. 2015) or from systems where multiple dominant carnivores affect a single subordinate species (Durant 2000; Creel et al. 2001). The combination of behavioral interactions and interspecific killing have been shown to cause continental scale trophic cascades (i.e., meso-predator release; Soule et al. 1988; Crooks and Soule 1999) from dominant apex carnivores through small, subordinate species (Newsome and Ripple 2014). However, the extent to which the risk of predation perpetuates into spatial partitioning in a multi-level, hierarchical community of carnivores remains unknown and a framework for understanding these effects has not been established.

To assess how risk avoidance shapes the space-use of carnivore communities, we studied a simple community of carnivores in northern Patagonia, Argentina. Pumas (*Puma concolor*) are dominant, apex carnivores that select areas to maximize hunting success (Smith

et al. 2019), kill large ungulates that provision smaller carnivores (Elbroch and Wittmer 2013), and potentially mediate the structure of carnivore communities (Novaro et al. 2005). Culpeo foxes (*Lycalopex culpaeus*) exhibit dietary and temporal niche overlap with pumas (Rodríguez Curras et al. *in Review*) and are also killed by pumas (Donadio and Buskirk 2006). The smaller chilla foxes (*Lycalopex griseus*) overlap somewhat in niche space with pumas and culpeo foxes (Rodríguez Curras et al. *in Review*) and are occasionally killed by both (see de Oliveira and Pereira 2014). We hypothesized that the fear of interspecific conflict with dominant carnivores would alter the behavior of subordinate species. Specifically, we predicted that culpeo and chilla foxes would exhibit heightened levels of anti-predator behaviors (i.e., vigilance and exploratory behavior) in areas of high puma occupancy, and, therefore, will trade food consumption for safety. Furthermore, we predicted that culpeo foxes would alter their space-use in response to indirect cues of predation risk from pumas (i.e., habitat characteristics) to a higher degree than chilla foxes. To test our predictions, we used multi-species occupancy models to address the space-use within the carnivore community and giving-up densities (GUDs) at foraging stations to understand the behaviors that structures space-use. We then integrated these two approaches into an analytical framework to disentangle how subordinate species spatially respond to perceived and actual risk.

METHODS

Fieldwork was conducted in and around Laguna Blanca National Park (LBNP; -39.05°W , -70.03°S ; Figure 1a), located in the Patagonian steppe of northern Patagonia (Figure 1b). The southeast portion of the park is dominated by the Mellizo Sur Volcano, with sharp volcanic rocks scattered throughout its foothills. Cerro Laguna Volcano shapes the central landscape of the park, providing sharp slag gulches to the west of the peak. The northern portion of the park is a basaltic plateau that surrounds the Laguna Blanca wetlands and meadows. The lake is fed by two ephemeral streams, the Llano Blanco and the Pichi-Ñireco that have carved gorges in the plateaus in the northwestern extent of the park. The climate is arid (150–200 mm precipitation annually) with precipitation mostly in the winter and spring. The average maximum temperature during summer is 23 °C, and the average low temperature during winter is 0 °C.

LBNP and the surrounding area is home to a community of six native carnivores: Pumas, Geoffroy’s cat (*Leopardus geoffroyi*), pampas cats (*Leopardus colocolo*), and three facultative scavengers, culpeo foxes, chilla foxes, hog-nosed skunks (*Conepatus chinga*). Although designated a national park, ranching of goats, sheep, cows, and horses is prominent in the park and surrounding area, and due to these practices, there are two exotic carnivores within our study site: dogs (*Canis lupus familiaris*) and domestic cats (*Felis catus*). All native carnivores are strictly nocturnal and exhibit high diel overlap ($\geq 75\%$ overlap; Rodríguez Curras et al. *in Review*). Pumas in our study area predominantly consumed livestock, which was found in the diets of both culpeo and chilla foxes (Rodríguez Curras et al. *in Review*).

Field sampling

To study the space use of chilla foxes, culpeo foxes, and pumas, we deployed 46 camera traps (Bushnell Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS, USA) within and around LBNP in a random design but buffered 300 m from dirt roads, highways, and peaks, and 500 m from ranchers’ houses (Figure 1a). Camera traps were spaced an average of 2.00 km (± 0.17) apart,

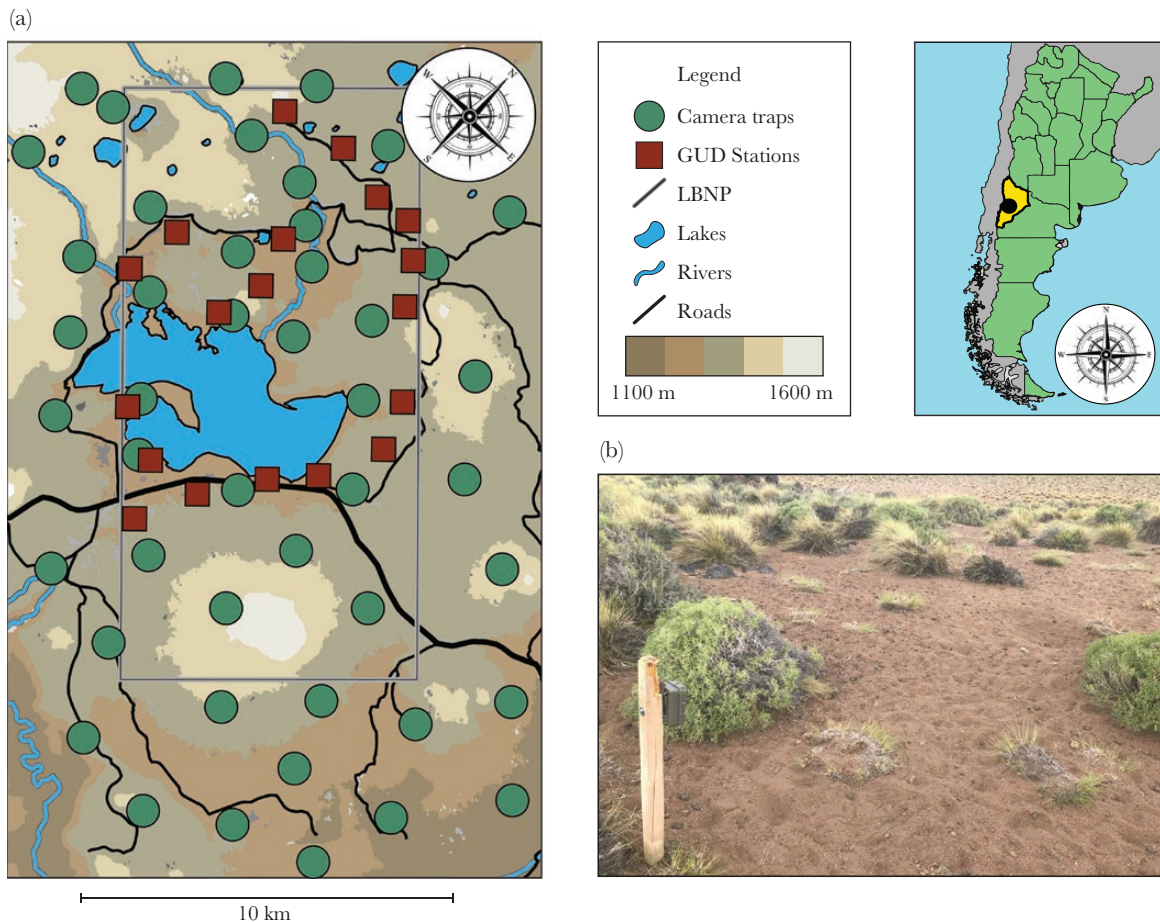


Figure 1

(a) Map of our study area at Laguna Blanca National Park, Neuquén, Argentina, and the surrounding area including the locations of camera traps and giving-up density (GUD) stations. The insert shows our study site (black dot) in relation to Argentina (green). (b) An image of our simplified GUD stations, showing a camera trap pointing at the staged foraging area which blends with the surrounding area.

staked 0.75 m above the ground, and angled toward a 0.5 m reference stake ~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 maintained a relatively brief sampling period, including a two-week burn-in period, during winter (i.e., July 10–October 10), to help ensure closure for our occupancy modeling. We checked camera traps two or three times a month. Photos were processed and tagged (Adobe Bridge, Adobe Systems, San Jose, CA, USA), and metadata created using the R package *camtrapR* (Niedballa et al. 2016).

To study how pumas influence the space use of chilla and culpeo foxes, we experimentally manipulated foraging stations across a gradient of puma occupancy. We set a total of twenty-five GUD stations (see below) stations within LBNP at least 1 km apart. Within 50 m of these locations, we selected a small patch of open, sandy habitat ≥ 300 m from roads (Figure 1a). GUD stations were set up independently of the camera stations used for our occupancy models (Figure 1) and all baited stations were set up after our camera trap study ended (October 15–December 10). Each station comprised of a natural, excavated foraging area (30 cm³) filled with 15 chicken necks cut to equal sizes (~60 g of food offered in total mixed in with excavated dirt to produce diminishing returns) and a single camera trap (Bushnell Trophy Cam HD) supported by a wooden stake 0.75 m above the ground (Figure 1b). Cameras were

set to take a video recording for 60 s every trigger, with 0 s between triggers. GUD stations were activated in the late afternoon (between 1600 and 2100) and alternated which stations were set up first daily. GUD stations were checked in the morning (between 0700 and 1100) and, again, alternated which stations were checked first. We alternated which GUD stations were active at any one time so that the minimum distance between active GUD stations was 2 km. Each GUD station was operational for a maximum of five days, until the station was used by avian scavengers, or until a fox used the station, at which point the station was not reactivated. A GUD station was considered used when a fox searched within the GUD station. After a use event, GUD data was collected from each station and videos were scored to quantify behavior at the feeding stations.

At each camera trap site and GUD station, we measured habitat characteristics at four sampling plots; these plots were established by generating one random angle within each compass quadrant and a random distance between 5–25 m from the camera location. For the GUD stations only, we chose the central location for sampling as 25 m from the GUD station itself because of our selection of open patches for our GUD locations. To test the effects of the horizontal cover and visibility on the occupancy and behavior of foxes, we measured horizontal cover by photographing a 1 × 1 m plain white sheet and estimating the

percent obscured by vegetation and rocks (e.g., low horizontal cover values are sites with less obstructions and clearer sightlines; Collins and Becker 2001). We took the average horizontal cover of the four measurements to represent the site level cover. We also estimated the minimum distance to lakes and streams for each camera trap and quantified the proportion of cliffs and landscape heterogeneity within a 500 m buffer using a digital elevation model and Landsat 8 satellite imagery data. For cliffs, we created a roughness layer (i.e., the difference in slope between adjacent cells) from our digital elevation model and used the upper 90% values (i.e., the values of the greatest difference between adjoining cells) buffered by 50 m. For landscape heterogeneity, we created a 500 m buffer around each camera trap and GUD station and used the standard deviation of the visual spectral band of the Landsat imagery data within each buffered area. These covariates capture a variety of habitat features that pumas, culpeo foxes, and chilla foxes may partition (Johnson and Franklin 1994a; Jiménez et al. 1996; Laundré and Hernández 2003; Novaro et al. 2004), furthermore, they capture the heterogeneity of habitat within LBNP and can they can also mediate the behavioral interactions between these carnivores.

Occupancy models

We used multi-species occupancy to estimate the probability of occupancy of subordinate carnivores conditional on the probability of occupancy of the dominant member of the guild. As many as twenty-one combined occupancy and detection parameters could be estimated in a single model and lead to unfeasibly large number of models. Consequently, we used three sequential stages of model fitting in the R package *unmarked* (Fiske and Chandler 2011) to simplify the structure of nuisance parameters (detection) and reduce the final, inferential model set to a reasonable number (Richmond et al. 2010; Doherty et al. 2012; Robinson et al. 2014): (1) single-species detection, (2) single-species occupancy, and (3) multi-species occupancy. For each step, we used the same site- and survey-specific covariates for chilla foxes, culpeo foxes, and pumas. The top detection and occupancy model from each sequential step were carried forward to the multi-species occupancy model. For the single-species models, we identified the covariates to be used in the multi-species model via Akaike Information Criterion (AICc; Burnham and Anderson 2002), and the likelihood function (Richmond et al. 2010; Rota et al. 2016). We tested for multi-collinearity within the predictor variables and standardized our covariates before model fitting.

We split camera trap surveys into ten 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. Survey periods were used to generate site-specific detection histories for each species (MacKenzie et al. 2002). We assumed sites were closed to changes in occupancy state over the entire period. Because individuals did not have to be continually present at a site for it to be classified as occupied, occupancy in our study can be interpreted as use (MacKenzie et al. 2006). To determine survey specific heterogeneity in detection probability we used survey period, snow cover, moon phase, horizontal cover, and their additive effects as possible covariates.

In our single-species single-season occupancy model (MacKenzie et al. 2002), we identified the best survey specific model covariates for each species. We held occupancy constant [$\psi(\cdot)$] and fit 23 models to explore the influence of the survey

period, moon phase, snow cover, horizontal cover, and their additive combinations on the probability of detecting each species. Only for estimating detection probability did we consider additive effects of covariates. We then carried best detection covariates forward into a set of single-species single-season models, from which we determined the important occupancy covariates for each species. We developed six single-covariate models of occupancy, considering the distance to streams and lakes, cliff habitat, landscape heterogeneity, horizontal cover, and $\psi(\cdot)$. Finally, we created a set of conditional three-species occupancy models from which inferences regarding carnivore co-occurrence were drawn. We used the best detection and occupancy covariates (Supplementary Table 1) from the single-species models to compose the individual species components in the multi-species model. For each species pair (chilla:culpeo, chilla:puma, and culpeo:puma), and the co-occurrence of all three species (chilla:culpeo:puma), we used the top performing model of each species and $\psi(\cdot)$ as possible covariates for the co-occurrence of each group of species. Our final multi-species model suite included a total of 144 models from the different combinations of each covariate for the co-occurrence of each species (chilla:puma, chilla:culpeo, culpeo:puma, and chilla:culpeo:puma). We limited all multi-species occupancy models to a single covariate because of the increased complexity of modeling multi-species interactions. All our results and inference are from the top performing multi-species occupancy model as measured by the AICc.

The effects of spatial autocorrelation for species pairs have been thoroughly investigated (Rota et al. 2016), but fewer studies have described the effects for more species. Accordingly, we attempted to limit spatial autocorrelation with our trap placement. However, the larger carnivores in our study have home ranges that covered the extent of several camera traps ($HR_{Puma} \approx 10\,000$ ha, $HR_{Culpeo\ Fox} \approx 1250$ ha, $HR_{Chilla\ Fox} \approx 150$ ha), which could potentially lead to pseudo-replication. However, because we are interpreting our model results as use, rather than occupancy per se, we contend this is not an issue for our analysis. We nevertheless tested for spatial autocorrelation between the detections of each species and the distance between cameras using a correlogram, variogram, and spline-correlogram.

To draw inference about the spatial association of the carnivore community, and how the occupancy of a dominant guild member affects a subordinate (in a species pair), we used the conditional occupancy probabilities of chilla and culpeo foxes, given the presence or absence of their intra-guild predators (i.e., $\psi[\text{chilla fox} \mid \text{culpeo fox and puma}]$, and $\psi[\text{culpeo fox} \mid \text{puma}]$). Furthermore, we used our top model estimates of occupancy to calculate the species interaction factor (SIF) between chilla foxes, culpeo foxes, and pumas (Richmond et al. 2010). The SIF represents a likelihood ratio of co-occurrence for each pairwise comparison. Because we used a three species model, for each species pair we considered the co-occurrence between species across the occupancy state (i.e., present or absent) of the third species (see Supplementary Material). A SIF value of 1 indicates that the two species occur independently; a value >1 suggests that the two species are more likely to co-occur than would be expected by chance, whereas a value <1 indicates spatial avoidance. For a group of three species, the probability of occurrence for species 1 is conditional on the presence or absence of species 2 and 3 (i.e., four possible outcomes $\psi_{1|11}$, $\psi_{1|10}$, $\psi_{1|01}$, and $\psi_{1|00}$). We used our top multi-species occupancy model estimates of occupancy to calculate the SIF between chilla foxes, culpeos, and pumas (Richmond et al. 2010).

Foraging behaviors and giving-up density (GUD)

We quantified GUDs as the number of offered chicken pieces remaining in the staged foraging area after foraging. From the recorded videos of foxes at the GUD stations, we constructed an ethogram of six simplified behaviors (Table 1) based on previous literature of fox behavioral studies (Leo et al. 2015). Behaviors were represented as the total proportion of time in sight devoted to each behavior. We used a non-parametric Mann-Whitney-Wilcoxon Test to compare GUDs and behavior between culpeo and chilla foxes. Furthermore, we tested the effect of vigilance on GUD (Figure 3b) with a simple linear model and if there was a difference in vigilance between species using an ANOVA.

We tested an a priori set of habitat drivers to explain the GUD of chilla and culpeo foxes. Specifically, we constructed generalized linear models (GLMs; with a binomial error distribution) for each species testing the individual and additive effects of distance to streams and lakes, cliff habitat, landscape heterogeneity, horizontal cover, puma space-use, and a null model; for chilla foxes, we also included the occupancy of culpeo foxes as a potential effect on foraging and vigilance behaviors. At each GUD station, we derived puma and culpeo space-use from our multi-species occupancy model by predicting the occupancy of each species using the measured habitat covariates; we used the expected occupancy at each GUD site. Any variables with a correlation ≥ 0.70 were not included in candidate models. To assess the relationship between habitat covariates and GUDs, we tested a series of 40 models for chilla foxes and 20 models for culpeo foxes (top candidate models are shown in Table 2). We used AICc for model comparison within each species.

Testing perceived versus actual risk

To test how culpeo and chilla foxes spatially responded to predation risk on the landscape, we used a partial regression framework (i.e., a path analysis) using the observed covariance between puma habitat and space-use with culpeo and chilla fox risk-avoidance behavior and space-use. Using this framework, we explored the relative effects of risk perception from habitat characteristics and the actual risk of predation on subordinate carnivore space-use. To test the effect of perceived predation risk from pumas on the occupancy of culpeo and chilla foxes, we used the covariate that was most influential for puma space-use, based on the single- and multi-species occupancy model (i.e., cliff habitat). The association between pumas and rugged terrain (like cliffs) offers an honest signal for species making a decision of habitat use (Laundré and Hernández 2003; Smith et al. 2019). Indeed, prey, in similar systems have been found to avoid more rugged terrain (i.e., what we classified as cliff habitat) because they are less likely to detect and escape from pumas in these areas (Donadio and Buskirk 2016). We used the predicted occupancy of pumas at GUD sites as a measure of actual predation risk because occupancy probabilities capture the variation in the encounter rate between species (Trainor and Schmitz 2014). We formulated the following to calculate the perceived and actual risk effects separately:

$$\gamma_{x_1 \rightarrow y_2} = \frac{cov_{x_1 \rightarrow y_2} \times (cov_{x_1 \rightarrow y_1} \times cov_{y_1 \rightarrow y_2})}{1 - cov_{x_1 \rightarrow y_1}^2}; \quad (1)$$

where, γ is the effect of x_1 on y_2 while accounting for the shared covariance with y_1 , cov is the standardized covariance shared

between the variables in the sub-script, x_1 is either the preferred habitat or the estimated occupancy probability (ψ) of Species 1 (the dominant species), y_1 is the anti-predator behavior (GUDs) measured of Species 2 (the subordinate species; and y_2 is the ψ [Species 2]). The resulting coefficient (γ) quantifies how the subordinate species spatially responds to (1) the habitat associations of their dominant competitor (which we interpreted as perceived risk) or (2) the risk of encounter with their dominant competitor (which we interpreted as actual risk). This value is standardized by the behavioral response (i.e., GUD) of the subordinate species. Throughout the modeling process, we used standardized values (i.e., how a change in one standard deviation of the predictor variable affects the standard deviation of the response) to compare the effects across species.

To test whether the effect of habitat or the occupancy probability of pumas was more influential to the space use of chilla and culpeo foxes, we defined the perceived risk coefficient (i.e., effect of habitat relative to ψ [Species 1]) as:

$$\text{Perceived Risk Coefficient (PRC)} = \frac{\gamma_{\text{Habitat} - \psi(\text{Sp}p.2)}}{\gamma_{\psi(\text{Sp}p.1) - \psi(\text{Sp}p.2)}}; \quad (2)$$

The perceived risk coefficient provides an estimate of the spatial response to perceived risk (the effect of habitat standardized by the behavioral response to habitat) relative to the spatial response to actual risk (the effect of puma occupancy standardized by the behavioral response to puma occupancy). A value of 1.0 indicates that the occupancy of the subordinate species is equally influenced by the perception of risk and the actual risk of predation, based on the space use of the dominant species. A value < 1.0 indicates that the perception of risk is less influential than actual risk, whereas a value > 1.0 indicates that the perception of risk is more influential than actual risk. We used a bootstrapping routine ($N = 10\,000$) to generate a robust estimate of the spatial responses to perceived and actual risk, and the PRC by incorporating the sampling error of each term in the equation from the partial regression (Equation 1). For each modeled parameter, we tested the differences in responses between species using a bootstrapped Z-Test.

RESULTS

We conducted a total of 3116 total camera trap nights from July 10–October 10, 2018. Chilla foxes were the most detected carnivore throughout the study area, being detected in 0.61 of our camera traps, followed by culpeo foxes (0.27) and pumas (0.20). We did not detect spatial autocorrelation between the residuals of our models for any of the species, though we detected autocorrelation between the predicted occupancy probabilities of chilla foxes between camera traps (Supplementary Figure 1). This was likely because chilla foxes occurred at relatively high abundances within our study area.

Multi-species occupancy model

In our single species analysis of chilla foxes, we found that their detection (0.28 ± 0.02 ; ± 1 SE) was relatively low and decreased throughout the survey period ($\beta = -0.18 \pm 0.05$, $P > 0.01$) and with lunar luminosity ($\beta = -0.33 \pm 0.14$, $P = 0.02$). For culpeo foxes, we choose the simpler detection model including only horizontal cover for subsequent modeling because of near-equal support and the minimal effect on the likelihood of the top model which included horizontal cover and survey period. Culpeo fox detection

probability (0.23 ± 0.01) was intermediate between the species and increased with horizontal cover ($\beta = 0.07 \pm 0.03$, $P = 0.06$). Lastly, puma detection probability (0.13 ± 0.01) was lowest and increased throughout the survey period ($\beta = 0.27 \pm 0.13$, $P = 0.03$; for single-species detection models see [Supplementary Table 1](#)).

In our top single-species occupancy model, chilla foxes were the most widespread carnivore species (occupying 0.65 ± 0.04 of the study area) and their predicted occupancy increased further from streams ($\beta = 0.51 \pm 0.23$). Pumas (0.43 ± 0.06) were estimated to be more widespread than culpeo foxes (0.28 ± 0.03 ; [Figure 2a](#)). Puma predicted occupancy decreased further from cliff habitat ($\beta = -2.41 \pm 1.31$) whereas culpeo fox predicted occupancy decreased further from lakes ($\beta = -0.69 \pm 0.33$; for the top single-species occupancy models [Supplementary Table 2](#) and [Supplementary Figure 2](#)).

In our top multi-species occupancy model, chilla and culpeo foxes exhibited a constant relationship in space-use, whereas the co-occurrence of chilla foxes and pumas was highest closer to lakes ($\beta = 1.94 \pm 1.05$) and the co-occurrence of culpeos and pumas was lowest closer to lakes ($\beta = -6.37 \pm 4.00$; for the top multi-species occupancy models see [Supplementary Table 3](#)). Compared with the single-species occupancy estimates, chilla fox predicted occupancy probability decreased by an average of 31% in the presence of culpeo foxes and in the absence of pumas (0.45 ± 0.03). Meanwhile, in the presence of pumas and in the absence of culpeo foxes, chilla occupancy decreased by an average of 19% (0.52 ± 0.06). As expected, in the absence of both potential competitors,

chilla occupancy increased by an average of 16% (0.74 ± 0.02 ; [Figure 2b](#)). Likewise, the occupancy probability of culpeo foxes, compared with the single-species occupancy estimates, decreased by an average of 43% (0.16 ± 0.04) in the presence of pumas, and increased to by an average of 42% (0.40 ± 0.03) in their absence ([Figure 2c](#)).

The probability of co-occurrence of culpeo foxes and pumas was lowest (0.05 ± 0.02), followed by chilla foxes and culpeo foxes (0.15 ± 0.03), and finally chilla foxes and pumas (0.22 ± 0.06 ; [Table 3](#)). These results were also corroborated from the SIFs of each pairwise species comparison. The SIF of pumas and culpeo foxes was also the lowest (0.21 ± 0.05), followed by culpeo and chilla foxes (0.73 ± 0.03) and then pumas and chilla foxes (0.76 ± 0.04 ; [Table 3](#)).

Foraging behaviors and GUD

There was no difference between the GUD of chilla (7.0 ± 2.0 g) and culpeo (8.0 ± 3.0 g) foxes ($z = -0.37$, $P = 0.71$). The consumption of food at the GUD stations by foxes of both species ranged from the entire consumption of food to foxes being present but only investigating the station. The proportion of time that chilla foxes were vigilant (0.18 ± 0.02) was not significantly higher than that of culpeo foxes (0.12 ± 0.04 ; $z = 1.14$, $P = 0.26$). Alternatively, culpeo foxes spent $>2\times$ more time exploring the area surrounding the foraging stations compared with chilla foxes (0.51 ± 0.08 and 0.19 ± 0.05 , respectively; $z = -2.72$, $P < 0.001$, [Figure 3a](#)). Chilla foxes spent more time moving in the area surrounding the foraging

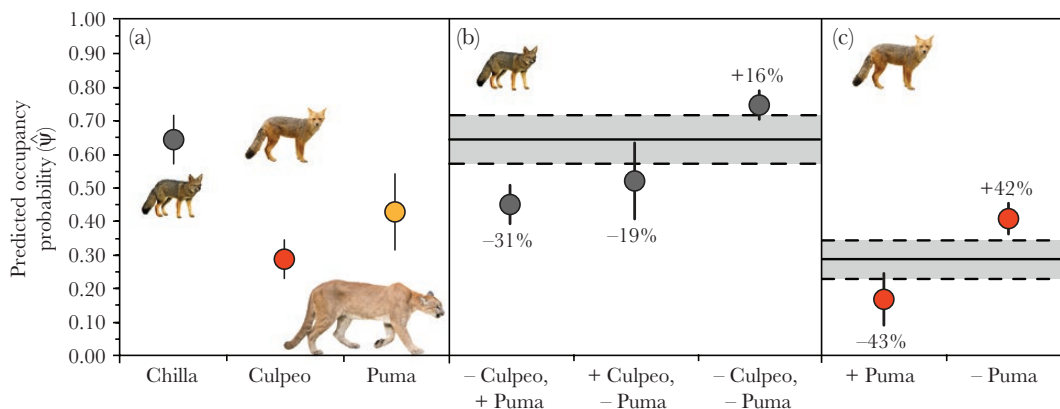


Figure 2

(a) The estimated occupancy probability (circles) of South American chilla foxes (*Lycalopex griseus*), culpeo foxes (*Lycalopex culpaeus*), and pumas (*Puma concolor*), based on the top performing single-species, single-season occupancy model of each species at Laguna Blanca National Park, Argentina, 2018. B and C. The conditional occupancy probability (circles) of South American chilla foxes (b) and culpeo foxes (c) given the presence or absence of their dominant interspecific competitors. The black bars around the circles represent the 95% confidence intervals of the estimated occupancy probability, the solid lines are the single species models, and the dashed lines are the 95% confidence intervals of the estimated occupancy probability of the single-species model.

Table 1

Ethogram of the behaviors that we quantified from fox videos

Behavior	Definition
Vigilance	Head up above body level, ears pricked, sniffing/looking/listening, not doing anything else.
Exploration	Smelling the ground, shrubs, air, or anything outside of the staged foraging area.
Searching	Actively digging or sniffing within the staged foraging area.
Eating	Chewing, tearing, or otherwise consuming the bait.
Moving	Moving on all four legs (regardless of speed).
Other	Jumps backward, startled. Dig around or near tray but not inside the tray. Laying down or sitting, but not foraging or vigilant.

Table 2

Top five GLM for chilla and culpeo foxes of standardized values, including the R^2 , log-Likelihood (logLik), and the Δ AICc. For chilla foxes, the null model is included for reference

	R^2	logLik	Δ AICc	AICwt
Chilla GUD Functions				
$\beta_{\text{Puma}} = 0.89 (\pm 0.15)$	0.79	-6.61	0.00	0.69
$\beta_{\text{Cliff}} = 0.82 (\pm 0.19)$	0.67	-8.98	4.75	0.06
$\beta_{\text{Puma}} = 0.84 (\pm 0.19) + \beta_{\text{Stream}} = -0.10 (\pm 0.19)$	0.79	-6.43	4.87	0.06
$\beta_{\text{Puma}} = 0.89 (\pm 0.16) + \beta_{\text{Lake}} = 0.07 (\pm 0.16)$	0.79	-6.49	4.99	0.06
$\beta_{\text{Puma}} = 0.89 (\pm 0.20) + \beta_{\text{Culpeo}} = 0.01 (\pm 0.19)$	0.79	-6.61	5.24	0.05
Average GUD = 7.09 (± 1.86)	0.00	-15.08	13.02	0.00
Culpeo GUD Formulas				
$\beta_{\text{Puma}} = 0.95 (\pm 0.13)$	0.91	-0.95	0.00	0.78
$\beta_{\text{Cliff}} = 0.93 (\pm 0.17)$	0.86	-2.45	3.00	0.17
$\beta_{\text{Cover}} = 0.89 (\pm 0.21)$	0.77	-4.23	6.56	0.03
Average GUD = 7.57 (± 2.78)	0.00	-9.39	9.88	0.01
$\beta_{\text{Land}} = 0.70 (\pm 0.31)$	0.49	-7.04	12.17	0.00

station compared with culpeo foxes (0.14 ± 0.05 and 0.05 ± 0.02 , respectively; $z = 2.32$, $P = 0.02$, Figure 3a). Interestingly, both species spent similar times foraging and searching within the foraging station (Figure 3a). There was no difference in the amount of time chilla and culpeo foxes spent searching for food ($z = 1.18$, $P = 0.24$) or consuming food ($z = 1.47$, $P = 0.14$; Figure 3a).

The GUD for both species of foxes was positively and strongly related to the amount of time foxes remained vigilant (Figure 3b), and the response of each species was similar ($\beta_{\text{Chilla}} = 0.74[\pm 0.22]$ and $\beta_{\text{Culpeo}} = 0.89[\pm 0.26]$). For both foxes, the most best model of GUDs was the predicted occupancy of pumas (Figure 3c); similarly, the response of each species was similar ($\beta_{\text{Chilla}} = 0.89 \pm 0.15$ and $\beta_{\text{Culpeo}} = 0.95 \pm 0.13$). Interestingly, the predicted occupancy of pumas influenced the vigilance of both culpeo and chilla foxes, but it only influenced exploratory behavior in culpeo foxes (Figure 3d and e). The predicted occupancy of culpeo foxes influenced the GUD of chilla foxes in the absence of pumas but not in their presence {GUD_{Chilla} = $0.73[\psi(\text{Culpeo} | \text{Pumas Absent})]$; Supplementary Figure 3}.

Perceived and actual risk

We combined the occupancy probabilities of pumas, culpeos, and chillas from our multi-species occupancy models with the spatial associations of pumas and the GUDs of meso- and small carnivores to determine how culpeo and chilla foxes responded to puma risk. We found that the perception of risk (i.e., the habitat features most closely associated with pumas) had a lesser effect on the space use of chilla foxes than that of culpeo foxes ($z = 15.98$, $P < 0.01$). Indeed, chilla fox occupancy decreased by 0.44 ± 0.01 and culpeo fox occupancy decreased by 0.91 ± 0.02 with increasing cliff habitat. Meanwhile, the effect of puma occupancy (actual risk) was higher for chilla foxes and lower for culpeo foxes ($z = -5.35$, $P < 0.01$); chilla fox space-use decreased by 0.83 ± 0.01 and culpeo space-use decreased by 0.69 ± 0.04 as puma occupancy increased. Together, this translated into a perceived risk coefficient for chilla foxes which was lower than that of culpeo foxes, 0.53 ± 0.02 and 1.38 ± 0.06 , respectively ($z = 8.13$, $P < 0.01$; Figure 4).

DISCUSSION

Our results indicate that the dominance hierarchy from pumas through culpeo foxes to chilla foxes was reflected in space. Although both meso- and small-carnivores responded similarly to the

predicted space-use of apex carnivores, the indirect cues associated with risk led to a heightened spatial response for meso-carnivores, but not small-carnivores. This resulted in pumas altering the space-use of culpeo foxes to the benefit of chilla foxes. Our results suggest that the landscape of fear for meso-carnivores can create a “landscape of opportunity” for subordinate, small carnivores. Our research aligns with meso-predator suppression found at continental scales (Newsome and Ripple 2014) but highlights the underlying behavioral mechanisms that likely drive these relationships at local scales.

Behavior, especially in the context of risk avoidance, operates across multiple niche axes. Indeed, carnivores can modify their space use (Fedriani et al. 2000; Berger and Gese 2007), diel activity (Hayward and Slotow 2009; Di Bitetti et al. 2010), and resource use (Crooks and Van Vuren 1995; Karanth and Sunquist 1995; Bolnick et al. 2003) in response to competition. Although temporal partitioning has been proposed as a mechanism promoting carnivore coexistence in southern South America (Johnson and Franklin 1994b; Di Bitetti et al. 2010), pumas, culpeos, and chilla foxes in our study area were strictly nocturnal and exhibited high diel overlap (Rodríguez Curras et al. *in Review*). Additionally, whereas culpeo and chilla foxes in our study system exhibit some resource partitioning, they both likely scavenged from puma kills (Rodríguez Curras et al. *in Review*). Space, then, appears to be the singular most important niche axis that these carnivores partition to avoid risk. However, we did not have the data to explicitly test the importance of spatio-temporal partitioning (Amarasekare 2008; Vanak et al. 2013). Future research should focus on the interaction between behavior and spatio-temporal partitioning, which can be an important mechanism for facilitating sympatry among carnivores (Ullas Karanth et al. 2017).

The observed differences in habitat use between competing carnivores might be attributed to hunting strategies (Broekhuis et al. 2013) or resource availability (Rosenheim 2004). However, subordinate carnivores can minimize negative encounters by avoiding the habitat features associated with their predators (Heithaus 2001; Schmitz 2008), especially if the predators have a narrow habitat domain (Schmitz et al. 2017). Although culpeo and chilla fox co-occurrence was mediated by open habitat, pumas strongly influenced the space-use of both species. Importantly, culpeo and chilla foxes mitigated risk as part of their habitat selection, and although both species avoided the habitat associated with pumas (i.e., cliffs), culpeo foxes more strongly avoided these areas. This fear of puma

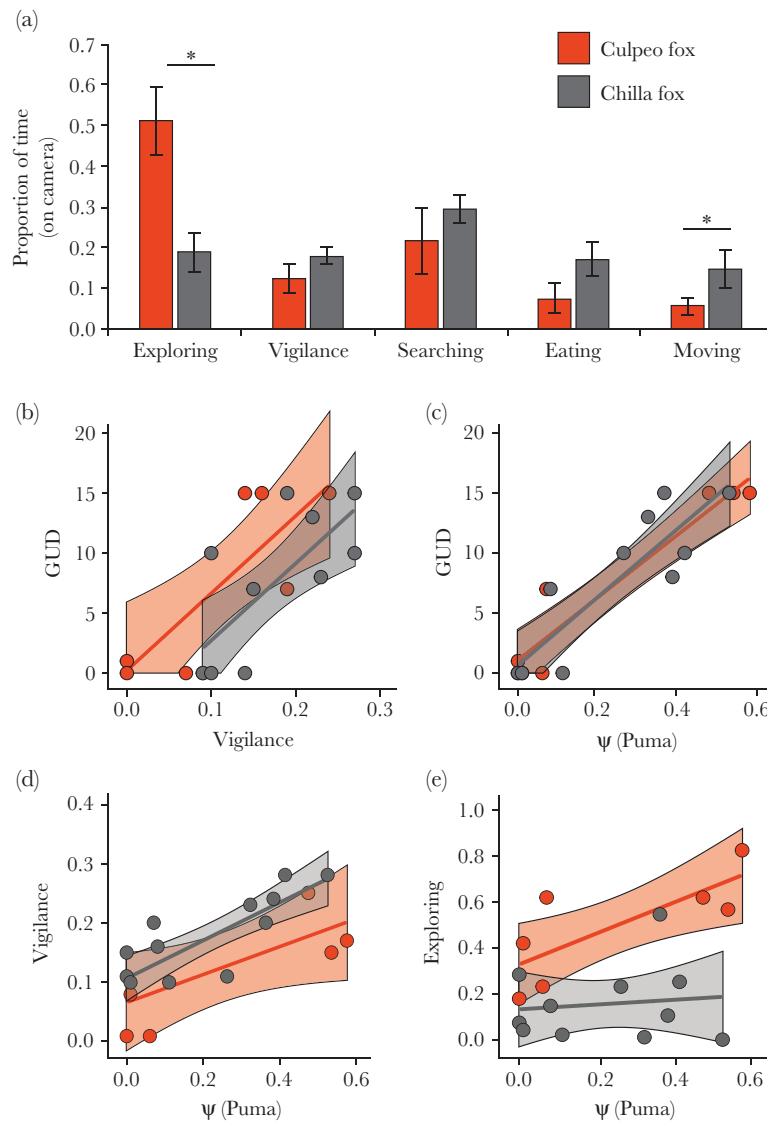


Figure 3

(a) The average proportion (\pm SE) of time spent engaged in Exploration, Vigilance, Searching, Eating, and Moving behaviors for chilla (*Lycalopex griseus*) and culpeo foxes (*Lycalopex culpaeus*; see Table 1 for our detailed Ethogram). Bars with a star (*) represent a significant difference between species ($P \leq 0.05$). (b) The response of GUDs to the amount of time chilla (gray, $r^2 = 0.55$, $F_{1,9} = 10.88$, $P < 0.01$) and culpeo foxes (red, $r^2 = 0.67$, $F_{1,5} = 10.2$, $P = 0.02$) remained vigilant, and (c) the response of GUDs to the expected occupancy of pumas (Ψ (Puma)) at each GUD station (chilla: $r^2 = 0.76$, $F_{1,9} = 33.02$, $P < 0.01$ and culpeo: $r^2 = 0.89$, $F_{1,5} = 50.75$, $P < 0.01$). (d) The response of Vigilance to the expected occupancy of pumas (Ψ (Puma)) at each GUD station (chilla: $r^2 = 0.50$, $F_{1,9} = 10.88$, $P < 0.01$ and culpeo: $r^2 = 0.67$, $F_{1,5} = 10.20$, $P = 0.02$). (e) The response of Exploring to the expected occupancy of pumas (Ψ (Puma)) at each GUD station (chilla: $r^2 = 0.08$, $F_{1,9} = 0.80$, $P = 0.39$ and culpeo: $r^2 = 0.69$, $F_{1,5} = 11.29$, $P = 0.02$).

presence had a greater effect on culpeo fox space-use and was expected given the body size difference and degree of niche overlap between these species (Donadio and Buskirk 2006; Rodriguez Curras *et al.* in Review). Ultimately, the stronger avoidance of pumas by culpeo foxes created a refuge for chilla foxes near cliff habitat; indeed, culpeo foxes had a greater effect on the space use of chilla foxes. This relationship, too, was predicted by the more similar body size, hunting strategy, and taxonomic relationship between culpeo and chilla foxes, which theoretically have a higher likelihood of competition and aggressive interactions (Donadio and Buskirk 2006; de Oliveira and Pereira 2014). These findings expand the previous literature on the cascading effects of a hierarchically structured community of carnivores in which risk aversion of

meso-carnivores benefits the total space available for subordinate small carnivores.

Research on the non-consumptive effects of predation risk may incorrectly estimate risk effects by measuring only one risk-avoidance behavior (Gerald and Macreadie 2013). Indeed, subordinate carnivores in our study used multiple strategies to mitigate risk. Vigilance can be useful for perceiving direct cues of predation risk and escaping predation once targeted (Lima and Dill 1990). Other strategies, such as olfactory cues (i.e., exploratory behavior) can be more influential in perceiving indirect cues of predation risk (Bytheway *et al.* 2013; Leo *et al.* 2015). Although both species were more vigilant at foraging stations associated with greater puma presence, culpeo foxes explored the staged foraging area

roughly two-times more than chilla foxes. Furthermore, we detected a strong correlation between puma space-use and exploratory behaviors for culpeo foxes, but not chilla foxes. GUDs are the culmination of direct and indirect cues of risk because they capture predator avoidance strategies (i.e., vigilance and exploring) relative to resource acquisition (i.e., searching and eating; Brown et al. 1999; Gaynor et al. 2019). Although we found a strong relationship between vigilance and GUDs for both culpeo and chilla foxes, exploratory behavior only influenced the GUD of culpeo foxes. Interestingly, although we found no difference in the average GUD or the GUD response to predation risk between culpeo and chilla foxes, risk avoidance behaviors strongly mediated space-use but the underlying driver was different for each species.

Direct and indirect cues of predation risk are often subtle and difficult to detect by prey (Guiden et al. 2019). Indirect cues like habitat type are particularly important if they offer an honest signal of space use, which is the case for species with a narrow habitat domain (Schmitz et al. 2017). However, the coupling between perceived and actual risk can break down due to the large fitness cost of predation, leading to some species showing a tendency to perceive a higher probability of predation than is actually present, and to “play it safe” (Abrams 1994). For species avoiding predation or interspecific killing, perceived risk does not necessarily match the actual risk of predation. Although accounting for the behavioral responses of meso- and small-carnivores to the actual (i.e., encounter probability) and perceived (i.e., risky habitat) risk of predation, meso-carnivores responded more strongly to the perception of risk and subordinate small carnivores responded more strongly to actual risk on the landscape. The higher perception of time by meso-carnivores aligned with the higher proportion of time exploring, indicating that meso-carnivores used indirect cues of predation risk to assess their foraging decisions, and ultimately their space-use. Alternatively, small carnivores were more vigilant relative to the proportion of time they spent exploring, indicating they

look for direct cues of predation risk to avoid potentially aggressive interactions.

The push-pull of suppression and facilitation has recently been highlighted as a key hypothesis of carnivore community structure (Sivy et al. 2017; Prugh and Sivy 2020). Behavior certainly mediates suppression and facilitation between mammalian carnivores because these interactions take place between cognitive species (Clinchy et al. 2011). Using our described Perceived-Actual Risk framework, we found that meso-carnivores more strongly avoided the habitat features associated with apex carnivores (perceived risk), whereas small carnivores avoided conflict with apex carnivores by avoiding their actual space use (actual risk). The differences we observed in meso- and small carnivore strategies to avoid risk translated into community level effects that structured the space-use of the carnivore community, and can lead to the co-existence of competing carnivores. We believe that this analytical approach is applicable to other systems, including predator-prey, where dominant carnivores (or predators) have strong habitat associations and influence the space use of subordinate carnivores (or prey). The data needs include (1) risk avoidance behaviors (e.g., as GUDs, vigilance or feeding rates, flight initiation distances) that captures missed opportunity costs between risk and foraging; (2) space use

Table 3
Estimates (95% CI) of the probability of co-occurrence and the Species Interaction Factor (SIF) of each pairwise group of carnivores using the output of our top performing multi-species occupancy model

Species pair	P (co-occurrence)	SIF
Puma–Culpeo Fox	0.05 (0.02–0.08)	0.21 (0.11–0.30)
Puma–Chilla Fox	0.28 (0.15–0.41)	0.76 (0.68–0.84)
Culpeo Fox–Chilla Fox	0.14 (0.09–0.20)	0.73 (0.66–0.79)

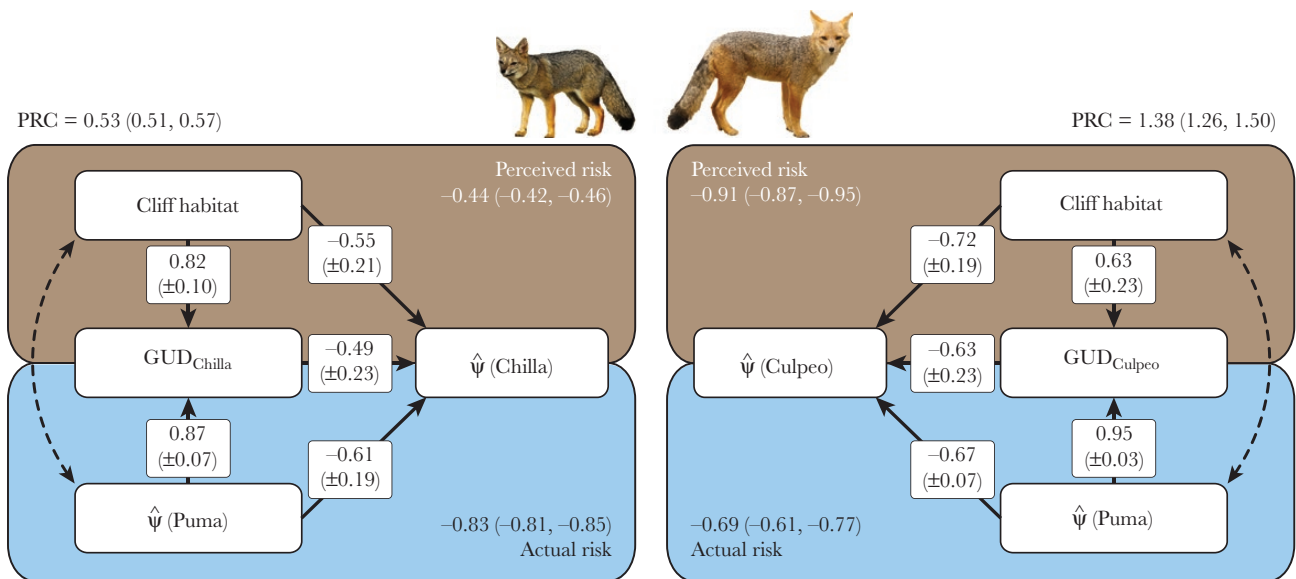


Figure 4
 The spatial responses to perceived (brown shading) versus actual (blue shading) risk model for chilla foxes (*Lycalopex griseus*; left) and culpeo foxes (*L. culpaeus*; right) using the effect of cliff habitat (i.e., because pumas [*Puma concolor*] were strongly associated with cliff habitat). The coefficients show the values (\pm SE) of the shared covariance of the two variables linked by the arrows. “Perceived Risk” (brown shading) is the estimate (95% CI) of Equation 1 using cliff habitat, “Actual Risk” (blue shading) is the estimate (95% CI) of Equation 1 using (Puma), and the Perceived Risk Coefficient (PRC) is Perceived/Actual Risk (Equation 2).

of the dominant carnivore (or predator) and subordinate carnivore (or prey); and (3) site level habitat characteristics associated with the dominant carnivore (or predator). We encourage future research to combine behavioral and spatial utilizing this analytical framework across risk gradients to better understand the drivers of risk avoidance for species.

Patterns of species distributions or occurrences often lack the nuanced behavioral understanding needed to explain the mechanisms that drive space-use (Paine 2010). Unifying the space-use of dominant species with the fear responses of subordinates is important for understanding how carnivore communities are structured. Overall, carnivores can be flexible in their risk avoidance strategies, reacting to direct cues of predation risk or avoiding the habitat associations of their competitors. Understanding the strategies that carnivores use to avoid aggressive interactions and gain access to resources can advance our understanding of carnivore community structure and better predict how these interactions will change in the future.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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AUTHOR CONTRIBUTIONS

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.; M.R.C. and J.N.P. wrote the manuscript with A.D.M. and E.D.

Conflict of interest: The authors declare no conflict of interest.

Data availability: Analyses reported in this article can be reproduced using the data provided by the authors (Rodríguez Curras et al. 2021).

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