Habitat complexity mediates the predator–prey space race

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Abstract. The spatial relationship between predator and prey is often conceptualized as a behavioral response race, in which prey avoid predators while predators track prey. Limiting habitat types can create spatial anchors for prey or predators, influencing the likelihood that the predator or prey response will dominate. Joint spatial anchors emerge when predator and prey occupy similar feeding habitat domains and risk and reward become spatially conflated, confusing predictions of which player will win the space race. These spatial dynamics of risk-foraging trade-offs are often obscured by habitat heterogeneity and community complexity in large vertebrate systems, fueling ambiguity regarding the generality of predictions from predator–prey theory. To test how habitat distribution influences the predator–prey space race, we examine correlation in puma and vicuña habitat selection and space use at two sites, one of which generates a distinct risk–foraging trade-off at a joint spatial anchor. The distribution of vegetation, which serves as both forage for vicuñas and stalking cover for pumas, differs between the sites; the llano contains a single central meadow that acts as a joint spatial anchor, while the canyon is characterized by more heterogeneous vegetation. Puma–vicuña habitat selection correlation was positive in the llano and negative in the canyon, and similarly, utilization distributions were more strongly correlated in the llano than the canyon. Vicuña locations occurred at higher values of puma habitat selection and utilization in the llano than in the canyon. Similarly, puma locations in the llano occurred at higher values of vicuña habitat selection and utilization than in the canyon. Although pumas consistently selected for and utilized vegetative and topographic cover regardless of habitat distribution, vicuñas only selected against vegetation in the heterogeneous canyon site, reducing spatial correlation with pumas. Our work suggests a joint spatial anchor favors pumas in the space race due to the inability for vicuñas to avoid crucial foraging habitat. The outcome of the predator–prey space race appears to be strongly informed by the distribution of habitat, whereby corresponding predictability of predator and prey favors predators in the spatial game.

Key words: antipredator behavior; habitat domain; habitat selection; predator–prey response race; Puma concolor; *spatial anchor; utilization distribution;* Vicugna vicugna.

Introduction

Predators search for their prey; prey avoid their predators. This ecological adage has been conceptualized as a behavioral "response race" in which both prey and predators are mobile and make decisions about space use, resulting in spatially varying and dynamic levels of predation (Sih 1984, 2005). Predators win the race by successfully finding and killing their prey. Prey win by successfully avoiding predators and reducing predator-

induced mortality. The recognition of this dyadic response between prey and predators has led to improved understanding of predator–prey dynamics (Mitchell and Lima 2002, Luttbeg and Sih 2004), including the influence of predators on prey populations (Bastille-Rousseau et al. 2016) and the flexibility of prey behavioral responses to risk (Ferrari and Chivers 2009, Basille et al. 2015).

The response race may be strongly influenced by predator hunting mode and habitat distribution, because these factors can mediate the hunting capacity of the predator and the ability of prey to detect, escape, or avoid predators (Schmitz et al. 2004, 2017). When predators are confined to a narrow habitat domain to hunt successfully, prey can readily avoid them, resulting

in strong spatial antipredator behavior (Hugie and Dill 1994, Heithaus 2001, Schmitz et al. 2017). Any limitation on predator hunting conditions (i.e., required stalking cover) allows prey to mitigate their predation risk by utilizing areas where predator hunting efficacy is diminished (Sih 1984, Cresswell et al. 2010, Schmitz et al. 2017). However, when prey depend on a limited and patchy food resource they may be forced to endure higher spatial overlap with predators, as predators are able to readily predict prey location (Sih 2005). The outcome of the behavioral response race between predator and prey is therefore contingent on which of the two players is more constrained in their shared landscape.

The dynamics and outcomes of predator–prey interactions are of great interest in systems featuring large vertebrates because of the importance of these species for ecosystem function and conservation (Estes et al. 2011). However, large vertebrate systems are often characterized by multiple interacting predators and prey, as well as substantial variation in habitat structure and distribution. This inherent complexity makes it difficult to disentangle behavioral motivations and choices of focal predator and prey species, and has led to persistent questions about how predators affect prey space use and the predictability, generality, and strength of the ensuing antipredator responses in large herbivores (Moll et al. 2017). Much of the existing research has focused on prey behavioral responses in wolf-prey systems of North America (Basille et al. 2013, Courbin et al. 2013, Bastille-Rousseau et al. 2015, DeMars and Boutin 2018) in which prey, such as elk and caribou, adopt spatial avoidance tactics in some cases (Mao et al. 2005, Latombe et al. 2014, DeMars and Boutin 2018) but not in others (Kittle et al. 2008, Middleton et al. 2013, Kohl et al. 2018), fueling the debate regarding the importance of risk effects in other large vertebrate communities. Wolves are habitat generalists and cursorial hunters, which are not expected to stimulate strong spatial antipredator responses in their prey (Preisser et al. 2007, Makin et al. 2017), and wolf hunting mode may explain the ambiguity in studies investigating nonconsumptive effects (Kauffman et al. 2010, Creel et al. 2013, Middleton et al. 2013). In contrast, the hunting domain of ambush carnivores is often limited to habitats with sufficient hiding cover, which might enable prey to assess risks and spatially avoid risky places (Hopcraft et al. 2005, Davidson et al. 2012, Elbroch and Wittmer 2012). Recent studies have called for greater taxonomic and geographic diversity in this research area to test the generality and context-dependency of prey responses to risk (Moll et al. 2017).

Herein, we evaluate the outcome of the spatial response race between the puma (*Puma concolor*) and its primary camelid prey, the vicuña (*Vicugna vicugna*) in a simple landscape in the high Andes. As in many arid landscapes, our study area is characterized by a gradient of habitat complexity; vegetation is either clumped in highly distinct, isolated meadows surrounded by bare plains or diffusely scattered across large complexes of intermixed meadows and shrubland canyons. Plains function as a refuge from predation yet contain very little forage for vicuñas, whereas meadows and canyons are forage-rich but provide stalking cover for predators (Donadio and Buskirk 2016). The isolated meadows in this landscape amount to joint "spatial anchors" (sensu Sih 2005) for both pumas and vicuñas, whereby pumas rely on the cover provided by meadows for stalking prey, and vicuñas rely on the meadows for forage. Risk and reward are therefore entirely conflated in these joint spatial anchors, which allow both predator and prey to better predict the presence of the other, giving neither an information advantage. The prey response could be predicted to dominate because the presence of a refuge allows prey to successfully avoid hunting predators (Sih 1984). Conversely, the predator response could be predicted to dominate as is often the case when patches vary in resource availability and prey are reliant on a fixed distribution of resources (Sih 2005). Joint spatial anchors therefore confuse the dynamics of the predator–prey space race and our ability to predict whether habitat limitation will favor predator or prey.

We test if landscape complexity mediates the predator–prey space race, favoring either predator or prey, by measuring outcomes of the race in sites with and without a joint spatial anchor. We examine evidence for two competing predictions: (1) the prey response will dominate in the presence of a joint spatial anchor or (2) the predator response will dominate in the presence of a joint spatial anchor. To test for both mechanism and outcome of the predator–prey space race, we evaluate correlation in both habitat selection (to assess continuity in spatial decision-making) and space use (to assess the spatial manifestations of habitat selection). The first prediction will be supported if prey select and use unvegetated, open refuge habitat and predator–prey spatial correlation is lower in the site with a joint spatial anchor. The second prediction will be supported if predator–prey spatial correlation is greater where a joint spatial anchor occurs due to selection for vegetation (i.e. forage) by prey. Our comparative approach allows for direct testing of the influence of the habitat distribution and context on response race outcomes in a single-predator, single-prey system characterized by simple and contrasting habitat types. We discuss inferences regarding the dynamics of predator–prey response races in large vertebrate communities and the implications on broader ecological interactions.

METHODS

Study system

We conducted this research between 2014 and 2017 at the 166,000-ha San Guillermo National Park, located in San Juan Province, Argentina (465630 E, 6765029 N; Zone 19J). The park, which is representative of the Andean Puna ecoregion, contains three

primary habitat types: plains, dominated by bare ground interspersed with sparse, short grasses; canyons, characterized by bare ground with diffuse shrubs and patchy grasses; and meadows, defined by dense tall grasses (Donadio and Buskirk 2016). Vegetation is limiting in this semiarid system (Fig. 1a) and provides both hunting cover for pumas and food for vicuñas. Meadow habitat makes up only 1.5% of the park and is the primary food source for vicuñas (Middleton, Donadio, & Smith, *unpublished data*). Thus, risk and reward are intrinsically linked to vegetation, forcing prey into a classic choice between food and safety (Donadio and Buskirk 2016).

The puma, an ambush predator, captures its prey by stalking within cover provided by vegetation, uneven terrain, and rocks (Bank and Franklin 1998, Donadio and Buskirk 2016). The vicuña, a medium-bodied ungulate (~40 kg; Franklin 2011), occupies the same habitats year-round, grazing in groups with high fidelity to foraging sites (Franklin 1974). In the park, vicuñas and guanacos (*Lama guanicoe*) are the largest herbivores, and although both species are prey of pumas (Donadio et al. 2010), vicuñas are 10 times more abundant than guanacos (Puig and Videla 2007; E. Donadio, *unpublished data*). Previous work in this site found that over 90% of adult and at least 50% of juvenile vicuña mortalities resulted from puma predation (Donadio et al. 2012, Perrig et al. 2017), and pumas subsist primarily on vicuñas as prey (Donadio, Middleton, and Smith, *unpublished data*). There are no other predator species capable of killing an adult vicuña at the study site.

We conducted our study in two distinct areas within the park: Llano de los Leones (3,360–4,031 m, 10,200 ha) and San Guillermo Canyon (3,312–3,925 m, 13,900 ha). Llano de los Leones (hereafter, the llano) contains a single, large meadow in the middle of an extensive, open plain. The plain serves as a prey refuge due to lack of stalking cover (Fig. 1b, c). San Guillermo Canyon (hereafter, the canyon) has greater topographic variation and vegetation cover, consisting of a complex array of smaller meadows interspersed with open plains and shrubby canyons (Fig. 1b, d). To quantify the environmental differences between the llano and canyon, we created a grey level co-occurrence matrix for elevation, slope, and normalized difference vegetation index (NDVI) at each site and compared dissimilarity estimates (R package glcm v1.6.1; Zvoleff 2016). To demonstrate the greater availability of forage resources in the canyon, we extracted values of NDVI at 100 random points in each site and compared mean values between the llano and canyon using a Mann-Whitney U test. We used the LANDSAT 8 maximum NDVI for 2015 as our NDVI metric. We chose to use maximum NDVI rather than a time-varying metric because our intention was to locate vegetation. Because vegetation as a whole is very scarce in San Guillermo, foraging areas for vicuñas are constrained to areas with any plant matter (although grasses are preferred to shrubs; Borgnia et al. 2010). Using maximum NDVI facilitated more liberal estimates of vegetation distribution in our study sites. We confirmed that spatial distribution of relative NDVI did not vary across seasons by calculating correlations between NDVI layers from January, April, July, and October of
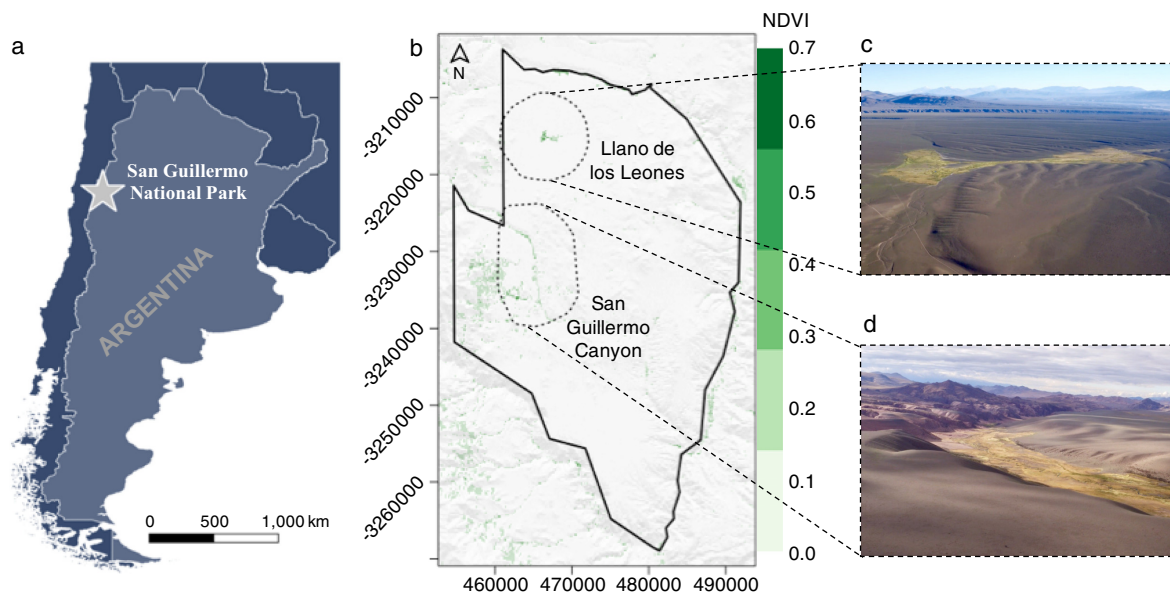

Fig. 1. (a) San Guillermo National Park is located in San Juan Province, Argentina near the Chilean border. (b) Maximum normalized difference vegetation index (NDVI) in 2015 in San Guillermo National Park; NDVI can range from −1 to 1, where values near 0 signify bare ground and approach 1 with increasing greenness. Photos are shown of (c) isolated meadow habitat adjacent to open plains in Llano de los Leones and (d) greater vegetation distribution and topographic variation in San Guillermo Canyon (photos by Joe Riis).

2015 within the sampling extent of both puma and vicuña locations (Appendix S1).

Predator–prey spatial correlation

We fit adult female vicuñas with GPS collars (GPS 6000SD; Lotek, Newmarket, Ontario, Canada) and deployed GPS collars (Iridium Track M2D; Lotek) on pumas in the llano and canyon (PERMIT #DCM 455 and subsequent renewals issued by the Argentine Park Service). We collared a maximum of one vicuña per social group to avoid replication in habitat selection analyses. We determined the borders of the llano and canyon study sites by deriving a 99% minimum convex polygon of all vicuña locations in each site and adding a 1-km buffer to represent available habitat. Vicuña and puma GPS collars were programmed to record a location every three hours. We monitored vicuñas from 29 April 2014 to 16 February 2017 and pumas from 8 April 2014 to 21 February 2017.

We examined correlations in puma and vicuña habitat selection and space use to determine the outcome of the space race. Differences in habitat selection among predator and prey indicate the decision-making mechanisms that explain differences in space use. Space use is the outcome of habitat selection and illustrates the degree of spatial partitioning between predator and prey, providing a direct measure to evaluate the predator–prey space race.

To assess puma and vicuña habitat selection, we developed resource selection functions (RSF) in each study site. To model the RSFs, we simulated random locations for vicuña and puma models within the home ranges of each individual vicuña and puma, whereby each GPS location was matched by one random location. Home ranges were defined as the 95% contour line of individual kernel utilization distributions (KUD) using a bivariate normal kernel, where the ad hoc method was used to estimate the smoothing parameter (R package adehabitatHR; Calenge 2006). We fit mixed-effects logistic regression models to observed and random GPS locations within each site with a random intercept for individual animal. Habitat covariates in each RSF included elevation, NDVI (as described above in *Methods: Study area*), and ruggedness (the mean of the absolute differences between the elevation at the focal cell and the surrounding eight cells; Wilson et al. 2007). All habitat covariates had a 30 m resolution, therefore analysis for selection of microhabitat features was not possible (e.g. shallow depressions in flat plains and differing grass heights) and all habitat selection inferences are best applied at the landscape scale. We scaled and centered all habitat covariates included in RSF models. We determined the best model of all combinations of the three habitat covariates using an information theoretic approach (Burnham and Anderson 2002). We validated habitat selection models using area-adjusted cross-validation following (Boyce et al. 2002), whereby bins were determined by deciles of RSF values for validated

locations. We used a bootstrapping approach, calculating a Spearman rank coefficient between the bin rank and the mean area-adjusted frequency from 100 iterations.

To determine patterns of space use, we calculated KUDs (spatially explicit probability density estimates of space use) for individual pumas and vicuñas within each site. We then scaled the pixels in each individual KUD between zero and one to account for different sample sizes among individuals and derived single site-level species utilization indices by averaging the scaled individual KUDs. We then examined the associations between utilization and habitat covariates by fitting linear models to data extracted from 1000 randomly generated points within the boundary of each site, whereby KUD values were the dependent variable and elevation, ruggedness, and NDVI were the independent variables.

We assessed how a joint spatial anchor affected the ability for vicuñas to spatially avoid pumas by calculating the Pearson correlation coefficient between puma and vicuña site-specific predictive surfaces of habitat selection and utilization distribution. To test for differences in vicuña exposure to habitats selected for and used by pumas, we compared puma RSF and KUD values at vicuña locations using a Mann-Whitney U test. We conducted an analogous test on puma exposure to habitats selected for and used by vicuñas.

RESULTS

We fitted GPS collars on 11 female vicuñas in the llano and 13 in the canyon, and nine pumas total (four males and five females). Individual vicuñas remained in either the llano or canyon, whereas pumas readily moved between the two sites. Seven collared pumas used the llano, while all collared pumas used the canyon at some point during the duration of the study. The minimum distance between the llano and canyon sites, which were defined by 99% kernel utilization distributions from pooled vicuña locations, was 3.1 km. The canyon was characterized by greater dissimilarity in elevation, slope, and NDVI than the llano (Table 1). The canyon also had greater average NDVI.

The model that best predicted vicuña habitat selection included all three tested environmental covariates in the

TABLE 1. Comparison of habitat characteristics between study sites Llano de los Leones and San Guillermo Canyon.

Site	Dissimilarity (GLCM)			NDVI
	Elevation	Slope	NDVI	
Llano de los Leones	0.075	0.953	0.199	0.068 ± 0.017
San Guillermo Canyon	0.188	1.058	0.297	0.107 ± 0.027

Notes: Dissimilarity metrics are derived from grey-level co-occurrence matrices (GLCM) for each habitat layer in Llano de los Leones and San Guillermo Canyon. Mean and standard deviation of NDVI are measured from 100 randomly sampled locations within each site.

llano (Appendix S2: Table S1) and canyon (Appendix S2: Table S2). Vicuñas selected against elevation and ruggedness in both sites but differed in their relationship to NDVI, selecting for NDVI in the llano (single meadow site with a joint spatial anchor) and against NDVI in the canyon (diffuse vegetation site with a more complex habitat distribution; Appendix S2: Table S3; Figs. 2, 3a, b). Vicuña habitat selection models were strongly predictive of use in the llano ($r_s = 0.93$) and the canyon ($r_s = 0.71$). Puma habitat selection was also best predicted by all three habitat covariates in the llano (Appendix S2: Table S4) and canyon (Appendix S2: Table S5). Pumas selected for ruggedness and NDVI, but against elevation (Appendix S2: Table S3; Figs. 2, 3c, d) in both the llano and the canyon (Appendix S2: Table S6). Puma RSFs were strongly predictive of use in the llano ($r_s = 0.99$) and the canyon ($r_s = 1.00$). Vicuña and puma habitat selection was positively correlated in the llano ($r_p = 0.32$) and negatively correlated in the canyon ($r_p = -0.38$). Vicuña locations in the llano (0.459 ± 0.001 [mean $\pm$ SE]) occurred at higher values for puma habitat selection than in the canyon (0.290 ± 0.001; $W = 1,412,600,000$, $P < 0.001$). Similarly, puma locations in the llano (0.560 ± 0.002) occurred at higher values for vicuña habitat selection than in the canyon (0.356 ± 0.002; $W = 48,452,000$, $P < 0.001$).

Vicuña utilization was concentrated in the central meadow in the llano site (Fig. 3e) and in an open plain in the canyon site (Fig. 3f). In the llano, vicuña utilization was most influenced by a positive correlation with NDVI, but was also negatively correlated with elevation and ruggedness (Appendix S2: Table S6). In the canyon, vicuña utilization was similarly negatively correlated with elevation and ruggedness, but showed no relationship to NDVI (Appendix S2: Table S6). Puma utilization was concentrated in the central meadow in the llano site (Fig. 3g) and in rugged and vegetated areas of the canyon site (Fig. 3h). In both the llano and canyon, puma utilization was negatively correlated with elevation and positively correlated with ruggedness and NDVI (Appendix S2: Table S6). Utilization indices for puma and vicuña were more strongly correlated in the llano ($r_p = 0.45$) than in the canyon ($r_p = 0.10$). Vicuña locations in the llano occurred at three times the puma utilization index (0.348 ± 0.001) when compared to the canyon (0.110 ± 0.000; $W = 1,972,000,000$, $P \ll 0.001$; Fig. 4). Puma locations in the llano occurred at nearly seven times the vicuña utilization index (0.093 ± 0.001) when compared to the canyon (0.013 ± 0.000; $W = 45,173,000$, $P < 0.001$; Fig. 4).

DISCUSSION

We evaluated how paired predator and prey limitation of feeding habitat domains shapes the outcome of a space race between pumas and vicuñas, a common predator–prey pair in the high Andes. We examined evidence for two competing predictions; first, we tested whether a joint spatial anchor to meadow vegetation, where vicuñas can predict and avoid attack by using the adjacent plains refuge, would decrease spatial
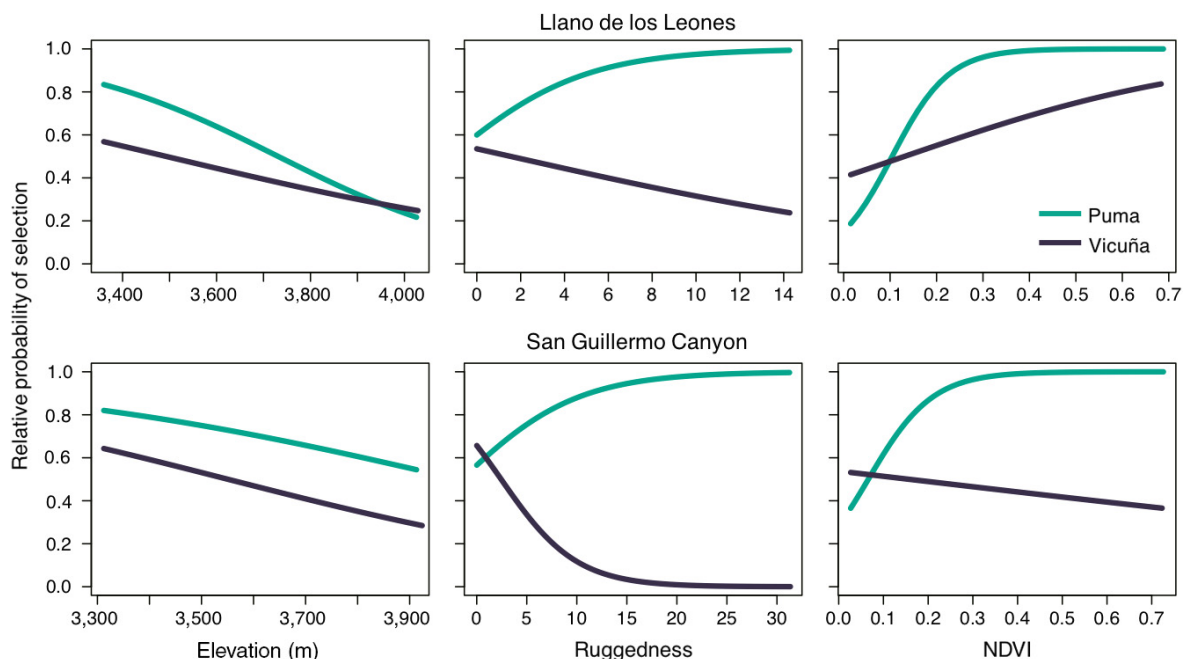

FIG. 2. Coefficient estimate curves for covariates in vicuña and puma resource selection function (RSF) models for Llano de Los Leones (top) and San Guillermo Canyon (bottom). The scales of the x-axes represent the range of values available within a given site for each habitat covariate. Ruggedness is the mean of the absolute differences between the elevation at the focal cell and the surrounding eight cells.
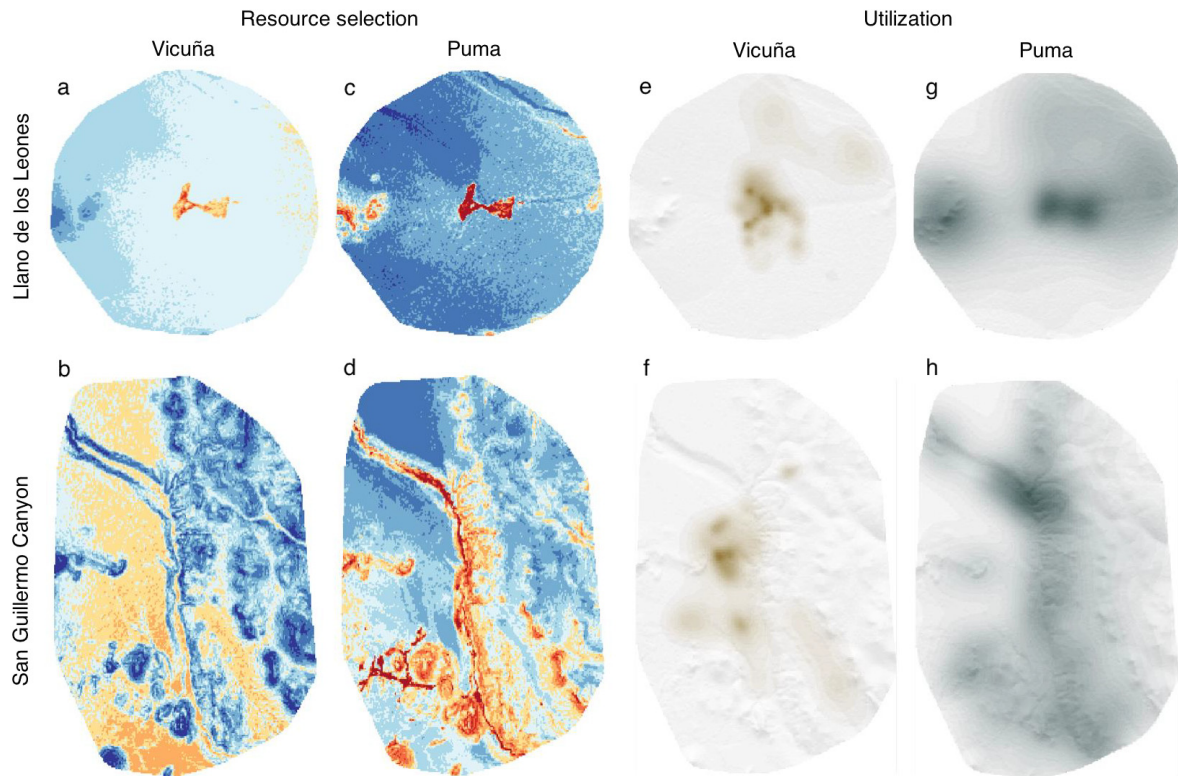
Fig. 3. Habitat selection models and mean utilization distribution for vicuñas and pumas in Llano de los Leones (llano) and San Guillermo Canyon (canyon). Panels a–d show predictive surfaces of habitat selection for vicuñas and pumas in the (a, c) llano and (b, d) canyon, where red represents a higher relative probability of use and blue represents lower relative probability of use. Panels e–h show mean utilization distributions for vicuñas and pumas in the (e, g) llano and (f, h) canyon.

correlation between pumas and vicuñas, allowing the vicuña response to dominate. Alternatively, we tested whether a joint spatial anchor would concentrate foraging vicuñas in areas of good stalking cover for pumas, thus increasing spatial correlation and allowing the puma response to dominate. We found that a joint spatial anchor in the llano site increased correlation in puma and vicuña habitat selection and space use, causing pumas to win the spatial response race. Vicuña locations occurred at higher values of puma habitat selection and utilization in the llano than in the canyon, indicating that vicuñas use habitats preferred and used by their only predator when constrained by a spatial anchor. Similarly, puma locations in the llano were at higher values of vicuña habitat selection and space use than in the canyon, suggesting that pumas have the advantage of increasing encounter rates when they share a spatial anchor with their prey.

Many experimental studies of predator–prey interactions assume clear trade-offs between food and safety. Our findings reveal that when these conditions are met in the wild, predators have the spatial advantage, but that when they are relaxed, prey have the spatial advantage. The observed spatial response race between pumas and vicuñas in San Guillermo diverges from predictions described by Sih (1984), whereby prey should win when they are mobile and have access to a refuge (as in the llano), and neither predator nor prey should dominate if predator and prey are mobile and refuges are limited (as in the canyon). Counter to these predictions, pumas are the clear winner in the llano. One explanation for this disconnect is the scale of our analysis; although vicuñas are forced by nutritional demands to select for vegetation in the llano, they may employ spatiotemporal risk-avoidance behaviors that still allow use of the refuge during risky times (Smith et al. 2019). Vicuñas are more vigilant in vegetated than open areas, indicating that they also mitigate risk through temporal (i.e., activity budget) risk-avoidance strategies (Donadio and Buskirk 2016) and may be able to seek refuge if a predator is detected. Recent evidence also suggests that large herbivores may mitigate risk by altering diel patterns of habitat selection (Kohl et al. 2018). If vicuñas are at greater risk of predation at night, they may take refuge during high-risk periods of the diel cycle. Therefore, high correlation in habitat selection and utilization in the llano may not fully account for fine-scale patterns of refuge use. Our results highlight how rare classic food-safety trade-offs may be in large vertebrates on vast landscapes and the need for further study of the capacity for risk reduction
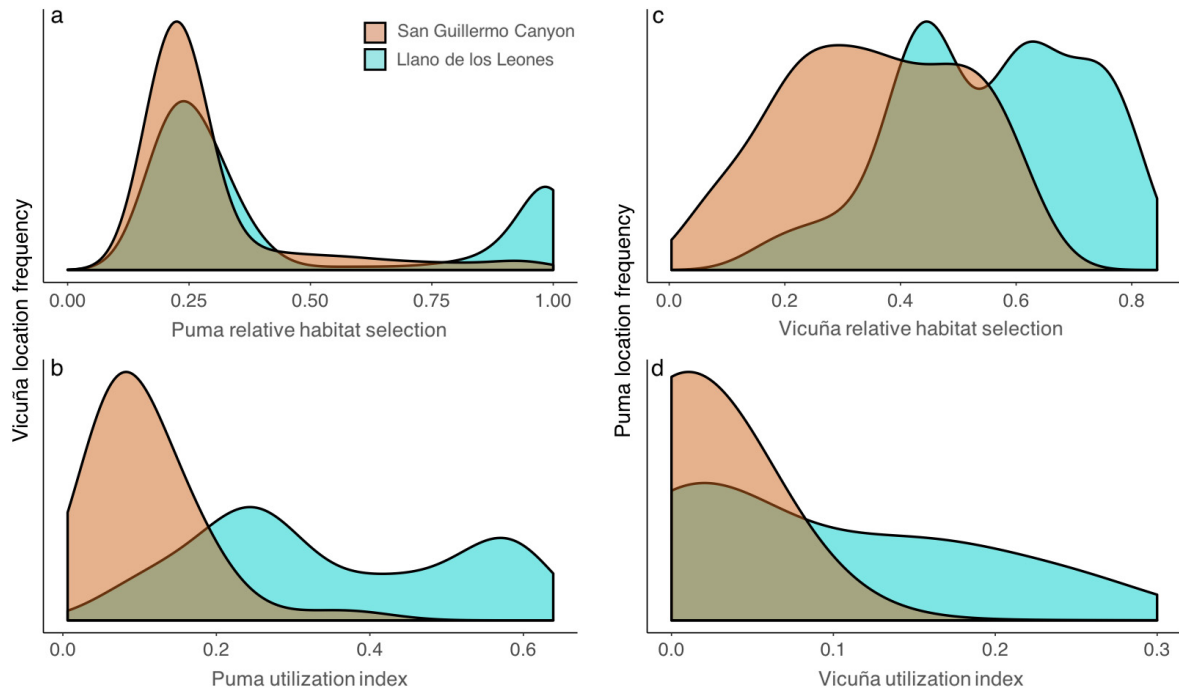
Fig. 4. Density plots for the distribution of puma (a) resource selection function (RSF) and (b) utilization index values at vicuña GPS locations and (c) vicuña resource selection function (RSF) and (d) utilization index values at puma GPS locations. Frequency distributions are shown for Llano de los Leones and San Guillermo Canyon. Vicuña locations in Llano de los Leones occurred at significantly higher puma RSF and utilization index values than in San Guillermo canyon, and puma locations in Llano de los Leones occurred at significantly higher vicuña RSF and utilization index values than in San Guillermo canyon.

through additive effects of prey space use, activity budgets, and diel activity patterns.

Although we documented diversions from theory regarding the predator–prey space race, puma and vicuña habitat selection strategies mirrored expectations for predator and prey. Predators are predicted to select for prey food resources rather than prey themselves (Iwasa 1982, Lima and Dill 1990, Hugie and Dill 1994, Hammond et al. 2007), particularly in resource-limited environments with strong prey competition (Sih 1998). Puma habitat selection in San Guillermo conformed to this prediction. Pumas in San Guillermo exhibited a consistent habitat-selection strategy in which they preferred and used areas with higher stalking cover (and hence increased capture probability), as well as areas with high prey forage availability, irrespective of vicuña habitat selection or vegetation distribution. These findings are consistent with expectations for ambush predators (Hopcraft et al. 2005, Horinouchi et al. 2009). Conversely, vicuñas modified their habitat selection and utilization depending on resource distribution. When tied to a spatial anchor in the llano, vicuñas selected for and utilized areas with vegetation, however when released of this constraint in the canyon, vicuña habitat selection was negatively correlated with vegetation and utilization showed no relationship to vegetation. This outcome substantiates theoretical expectations that prey will avoid their own food resources to mitigate risk when

the environment can accommodate flexible space use (Lima and Dill 1990, Hammond et al. 2007).

Our findings indicate that joint limitation of feeding habitat domain gives predators the spatial advantage, both in regard to mechanism and outcome of space use decisions. Correlation in habitat selection values flipped from positive in the llano to negative in the canyon, illustrating strong spatial antipredator behavior by vicuñas when they are less constrained in their feeding habitat domain. There were also differences in puma and vicuña space use between the sites, but to a lesser magnitude. In both sites correlation in space use was positive, although spatial correlation was weak in the canyon site. While our results suggest that a joint spatial anchor favors predators in comparison with a more heterogeneous landscape, pumas are still able to locate vicuñas effectively in both sites regardless of spatial risk-avoidance behaviors used by vicuñas.

The dynamics of the spatial response race have strong implications for the nonconsumptive effects of predation. Spatial antipredator behavior can cause prey to reduce their use of preferred resources, potentially incurring nutritional costs and reducing fitness (Hernández and Laundré 2005) or activating behaviorally-mediated trophic cascades (Beckerman et al. 1997, Suraci et al. 2016). Consistent with trophic cascades theory, previous work in San Guillermo suggests that vicuñas exert greater herbivory pressure on vegetation communities in

safe habitats due to increased foraging and reduced vigilance, whereas reduced foraging rates in risky habitats lead to release of meadow grasses (Donadio and Buskirk 2016). Here we provide further evidence for the spatial mechanism of these relationships at the landscape scale. Vicuñas in our study selected against vegetation in the canyon, which contains greater topographic variation and thereby increased stalking cover for predators. In contrast, vicunas selected for vegetation in the llano where feeding habitats are adjacent to a refuge. The risk-induced reduction in foraging pressure by vicuñas may therefore contribute to the greater distribution of vegetation in the canyon site.

We report two primary insights regarding habitat influences on the predator–prey space race. First, the nature of predator–prey interactions, and likely their cascading effects, are contingent on the relationship between habitat distribution and similarity of feeding habitat. Joint limitation of feeding habitat domains in predator and prey appears to favor predators in the spatial game due to forced selection for risky habitats by prey. Secondly, prey spatial antipredator behavior might reduce, but not reverse, spatial correlation between predator and prey. Habitat selection analyses may better represent animal decision-making than they do spatial patterns of risk and overlap with predators. Habitat constraints on both predator and prey should be considered in assessments of the landscape of fear and the spatial manifestations of predator–prey interactions. Evaluation of the context-dependency of habitat utilization by both players simultaneously may assist development of holistic conservation approaches that preserve resources required by predator and prey.

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