



ARTICLE

Food limitation reduces risk avoidance by prey, but does not increase kill rates in a simple predator–prey system

Francisco J. Molina¹  | Justine A. Smith²  | Emiliano Donadio³ |
Arthur D. Middleton⁴ | Jonathan N. Pauli⁵ | Jacob R. Goheen¹

¹Program in Ecology and Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA

²Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, Davis, California, USA

³Fundación Rewilding Argentina, Los Antiguos, Argentina

⁴Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, California, USA

⁵Department of Forest and Wildlife Ecology, University of Wisconsin–Madison, Madison, Wisconsin, USA

Correspondence

Francisco J. Molina

Email: franchomolina@gmail.com

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Abstract

Prey often induce antipredator behaviors when balancing food acquisition against safety. The starvation–predation hypothesis (SPH) posits that, during food shortages, the risk of starvation requires prey to forego antipredator behavior to increase feeding rates. Such shifts in antipredator behavior may further increase the risk of predation and therefore kill rates by predators. We tested the SPH and its consequences for kill rates in a single large prey, single large predator system. In the Argentine Andes, we evaluated whether risk avoidance by vicuñas (*Vicugna vicugna*) decreased during periods of food scarcity. From three years of GPS relocations collected simultaneously from vicuñas and pumas (*Puma concolor*), resource selection functions revealed that vicuñas increased their exposure to pumas during nongrowing seasons by reducing the avoidance of canyons and increasing selection for meadows, both of which offer more food of higher quality than relatively safe plains. However, and despite vicuñas becoming more risk-prone during nongrowing seasons, kill rates by pumas did not change between growing and nongrowing seasons. Contrary to evidence from mesocosm experiments, relaxation of antipredator behavior by prey did not translate into increased kill rates by predators. Our results enhance understanding of the interplay between food limitation and predator–prey interactions within ecosystems and may improve ecologists' ability to predict when and where behaviorally mediated trophic cascades are more likely to occur.

KEYWORDS

ambush predator, habitat selection, predation risk, *Puma concolor*, risk effects, seasonality, ungulate, *Vicugna vicugna*

INTRODUCTION

Animals attempt to optimize food acquisition and safety. In doing so, they often reduce rates of energy intake in

exchange for greater safety from predators (Brown & Kotler, 2004; Holbrook & Schmitt, 1988; Lima & Dill, 1990; Sih, 1980). To achieve a food-safety optimum, foragers employ a suite of antipredator behaviors including

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selecting safer habitats (e.g., Creel et al., 2005; Ford et al., 2014; Holbrook & Schmitt, 1988; Sih, 1982), reducing movement rates (e.g., Anholt & Werner, 1995; Sih, 1982), altering daily patterns of activity (e.g., Bakker et al., 2005; Schmitz et al., 1997), and spending more time vigilant (e.g., Brown et al., 1999; Creel et al., 2014). Such behaviors often come at the expense of foraging which, in some cases, could reduce fitness (i.e., risk effects sensu Creel & Christianson, 2008; Gaynor et al., 2019; Peckarsky et al., 1993; Zanette et al., 2011). Therefore, quantifying the factors that drive variation in antipredator behavior—as well as any costs and benefits associated with such behavior—has implications that extend from individual physiology to the impacts of species in ecosystems (Schmitz et al., 2008).

Resource limitation can be a key factor driving when, where, and how strongly animals exhibit antipredator behavior by inducing state-dependent decision-making (Luttbeg et al., 2003; Oates et al., 2019). The starvation–predation hypothesis (SPH, McNamara & Houston, 1987; analogous to the predation-sensitive foraging hypothesis of Sinclair & Arcese, 1995) predicts that during food shortages (i.e., during winters or droughts), and assuming a trade-off between food abundance and safety (Lima, 1998; Lima & Dill, 1990; Sih, 1980), animals must forego antipredator behavior and increase foraging in areas where predation risk is high to cover energetic needs. Conversely, during periods of food abundance, individuals should seek to minimize predation risk by foraging in safer, food-limited areas (see also Anholt & Werner, 1995; Schmitz et al., 2008).

For mammalian herbivores living in seasonal environments, the extent to which individuals conform to the central prediction of the SPH might hinge on local patterns of productivity (food abundance). Specifically, support for the SPH might be dampened at sites with extreme productivity levels and boosted at sites of intermediate productivity. At the low extreme of productivity, herbivores living in environments where food is continuously limiting should have minimal energetic opportunity to forego the greater energetic returns within risky areas, regardless of seasonal variations in food abundance. Conversely, and at the high extreme of productivity, herbivores exposed to high food abundance year-round could maintain risk avoidance regardless of season, as safe areas would continuously provide sufficient food to meet energetic demands. Thus, support for the SPH should be strongest at intermediate levels of productivity, where food in safe areas is abundant in periods of peak productivity and insufficient when productivity declines, thereby creating the conditions necessary to uphold the SPH.

Traditionally, the SPH has focused on the prey's perspective, with ecologists evaluating how changes in

food abundance interact with predation risk to affect the antipredator behavior, vital rates, and population size of prey (Clark, 1994; Karels et al., 2000; Krebs et al., 1995; McNamara & Houston, 1987). However, if the SPH is supported, shifts in antipredator behavior could have knock-on consequences for predators (Lima, 2002). Specifically, increased antipredator behavior during periods of food abundance should make killing prey more challenging for predators, while dampened antipredator behavior during food scarcity should render prey more vulnerable to predation (Sinclair & Arcese, 1995). Although these predictions have some support from controlled mesocosm experiments (e.g., Anholt & Werner, 1995; Sih, 1986), the application of theory to unmanipulated, free-ranging populations is an essential goal of ecology (Sagarin & Pauchard, 2010). Understanding whether and how predators increase their kill rates to capitalize on food-limited, risk-prone prey should inform predictions of predator–prey dynamics in novel conditions, particularly if global alterations in productivity and seasonality via climate change affect the antipredator behavior of prey (Grimm et al., 2013).

Herein, we tested the SPH and its extension to kill rates of predators in an ecosystem in which large mammals drive spatial patterns of vegetation growth. In a high Andean desert of western Argentina, vicuñas (*Vicugna vicugna*) are the most abundant large (>5 kg) herbivores and pumas (*Puma concolor*) are their main cause of mortality (Donadio et al., 2012). Food limitation at the end of the nongrowing season reduces body condition by depleting their fat reserves (Donadio et al., 2012). Such an altered state could affect decision-making by vicuñas, prompting them to trade safely in open plains (where food is scarce and of poor quality), for more abundant, high-quality food in meadows and canyons (where the risk of predation by pumas is high; Donadio & Buskirk, 2016). Indeed, Donadio et al. (2012) found that vicuñas killed in meadows and canyons tend to have lower fat content than those killed in plains, and this pattern was more pronounced by the end of the nongrowing season.

We addressed two primary questions: (1) Do vicuñas conform to the SPH, foraging in areas perceived as risky more frequently during the nongrowing season relative to the growing season? And (2) if this central prediction is supported, and to extend the SPH to predator behavior, do kill rates of pumas track risk proneness of vicuñas? To answer these questions, we used three years of GPS data collected simultaneously from collared pumas and vicuñas inside a protected area. We combined GPS data from collars with satellite-derived proxies of habitat types to evaluate habitat selection of pumas and vicuñas in the growing and nongrowing seasons. We quantified kill rates by visiting GPS clusters from collared pumas in the

field and building a model to predict vicuña kills. Through these efforts, we sought to better understand the role of food limitation in predicting the extent of antipredator behavior in large herbivores, its consequences for kill rates by predators, and its potential impact on the indirect effects of predator–prey interactions on the ecosystem.

Under the SPH, we expected that vicuñas would accept more risk during the nongrowing season relative to the growing season by increasing selection for habitats selected by pumas. Our study system encompassed vicuñas living under two levels of food limitation (Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). We expected vicuñas at the site with lower food abundance (low productivity) to meet predictions by the SPH to a lower extent than vicuñas in the site with higher food abundance (intermediate productivity). We expected seasonal shifts in vicuña risk proneness to be coupled with kill rates, such that increased risk proneness in the nongrowing season would correspond to higher kill rates by pumas.

METHODS

Study system

We conducted our work between April 2014 and February 2017 in San Guillermo National Park (SGNP), located in San Juan Province, Argentina (29°25′0.12″ S, 69°15′0″ W, Zone 19J). The park encompasses 166,000 ha of high-altitude desert, with scant vegetation cover (<10%; Donadio & Buskirk, 2016). In SGNP, pumas are the only large (>10 kg) carnivore and the main predator of adult vicuñas, the most abundant ungulate (7.6–13.7 individuals/km² during our study; Monk et al., 2022). Pumas are responsible for over 90% of adult and 50% of juvenile vicuña mortalities (Donadio et al., 2012; Perrig et al., 2017), and vicuñas are the primary food of pumas (Donadio et al., 2010). Pumas are ambush predators that hunt using cover provided by vegetation, uneven terrain, and rocks (Bank & Franklin, 1998). In SGNP, vicuñas occupy the same areas year-round and graze in groups typically composed of a single male, three females (range 1–6), and two calves (range 1–4) (Karandikar et al., 2023).

SGNP consists of three distinct habitats—plains, canyons, and meadows—each of which differs in the abundance and quality of forage for vicuñas and in the availability of stalking cover for pumas (Donadio & Buskirk, 2016). Plains are open and primarily comprise bare ground with sparsely distributed, short grasses and shrubs, thereby offering limited forage of low quality for

vicuñas; however, these features also create a refuge from predation as they result in minimal stalking cover for pumas. Canyons are characterized by a complex topographic relief and moderate vegetation cover consisting of tall shrubs and grasses, thereby providing stalking cover for pumas and modest forage availability of intermediate quality for vicuñas. Meadows contain tall, dense grasses that provide both abundant, high-quality forage for vicuñas and stalking cover for pumas. Throughout the diel cycle, pumas consistently select for meadows and canyons and avoid plains (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019), yet they select only for meadows when killing (Smith et al., 2020). Vicuñas avoid plains and select meadows for feeding during daytime, but they select for plains and avoid meadows at night (Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). Vicuñas avoid canyons, regardless of the time of day (Smith, Donadio, Pauli, Sheriff, & Middleton, 2019).

We conducted our study in two adjacent sites within SGNP differing in the amount and distribution of food available to vicuñas, as described by Smith, Donadio, Pauli, Sheriff, Bidder, et al. (2019): Llano de los Leones and San Guillermo Canyon. In the Llano de los Leones (3360–4031 m; 10,200 ha; 88.8% plains, 9.7% canyons, 1.5% meadows), food for vicuñas is concentrated in a 118-ha meadow in the middle of an extensive, open plain. In contrast, the San Guillermo Canyon (3312–3925 m; 13,900 ha; 26.7% plains, 64.9% canyons, 8.4% meadows) contains an array of smaller meadows interspersed with plains and canyons. In addition, and relative to the Llano de los Leones, the San Guillermo Canyon offers greater forage availability in plains from higher overall productivity (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). Such differences between the Llano de los Leones and the San Guillermo Canyon drive trade-offs between foraging and risk avoidance by vicuñas (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). Within the Llano de los Leones, vicuñas rely year-round on the single large meadow for food and are therefore limited in their ability to avoid risk (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). Conversely, the greater overall productivity in the plains of the San Guillermo Canyon relative to the Llano de los Leones allows vicuñas to minimize risk by avoiding both meadows and canyons (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). Also, the more numerous and dispersed meadows in the San Guillermo Canyon may result in a less predictable distribution of vicuñas, from the perspective of pumas (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). Despite these differences, both sites provide access to both high-quality forage and refugia. Therefore, we expected vicuñas at each site to increase their

exposure to pumas by foraging more frequently in meadows, canyons, or both during the nongrowing season.

Animal capture

We captured 24 adult female vicuñas, 11 in the Llano de los Leones and 13 in the San Guillermo Canyon, from April through June in 2014 and 2015. Prior to captures, we made observations on vicuñas to identify and target individuals from distinct family groups. Vicuñas were immobilized by administering Carfentanil (0.03–0.06 mg/kg vicuña) or Thiafentanil oxalate (0.06–0.1 mg/kg vicuña) at 15–42 m from a parked truck or by slowly approaching them on foot. Immobilized individuals were fitted with GPS collars (GPS 6000SD; Lotek, Newmarket, Ontario, Canada) before reversal with Naltrexone (100 mg/1 mg Carfentanil; 10 mg/1 mg Thiafentanil). Family groups were cohesive and moved together when approached for darting. We also captured nine pumas (four females and five males) between April 2014 and January 2016 using leg-hold snares. Pumas were darted with a combination of Ketamine (2 mg/kg) and Xylazine (2 mg/kg) and fitted with GPS collars (Iridium Track M2D; Lotek) before reversal with Yohimbine (0.125 mg/kg). Established mammal handling guidelines (Sikes et al., 2016) were followed during animal capture and handling.

At both sites, the area occupied by collared pumas wholly encompassed and exceeded that of collared vicuñas (Appendix S1: Figure S1). Thus, while individual vicuñas did not move between sites, all collared vicuñas were exposed to predation risk from the same collared pumas. Both vicuña and puma GPS collars recorded locations at 3-h intervals. We monitored pumas and vicuñas, including kill sites (see below), from 8 April 2014 through 21 February 2017. Fieldwork was conducted under permit number DCM 455 and subsequent renewals issued by the Argentine Park Service.

Determination of growing and nongrowing seasons

We identified periods of food abundance and food scarcity for vicuñas by defining growing and nongrowing seasons based on time series of the normalized difference vegetation index (NDVI) for our study sites and period (Merkle et al., 2016; Pettorelli et al., 2005; Appendix S1: Figure S2). NDVI has a positive relationship with plant biomass and quality in SGNP, as shown by comparisons among habitats between NDVI and plant height, cover,

and N content (Appendix S2: Table S1). NDVI has been previously used to quantify seasonal variation in primary productivity in SGNP (Donadio et al., 2012). For the purposes of our study, we focused on the end of each season as this was more relevant to our predictions on the risk-prone behavior of vicuñas under the SPH. Thus, we operationally defined the growing season as the last three months of plant green-up (i.e., those with a positive NDVI slope; January through March) before plants began to senesce (Esmaili et al., 2021; Garel et al., 2006; Merkle et al., 2016), and the nongrowing season as the last three months before plant green-up recommenced (July through September). As vegetation growth peaks, vicuñas accumulate body reserves (Donadio et al., 2012) and should become increasingly risk-averse, according to the SPH. Conversely, as the nongrowing season progresses, vicuñas deplete their body reserves (Donadio et al., 2012). Therefore, we expected vicuñas to become increasingly risk-prone with the progression of the nongrowing season.

Determination of kill sites

We visited GPS “clusters” of puma locations to identify kill sites (sensu Knopff et al., 2009; Ng’weno et al., 2019). Clusters were defined by ≥ 2 GPS locations occurring within 36 h and 20 m from one another. We visited clusters within 30 days of their formation. At each cluster site, we searched for carcass remains and, if present, clear signs that a puma killed the animal (e.g., puma tracks, carcass remains covered with gravel or grass, canine punctures in hide or skull, dragging marks, and broken and chewed large bones and ribs). We exhaustively searched for puma GPS clusters in the field over a series of one- to two-month periods in 2014 (23 September–24 October), 2015 (10 January–1 March, 13 May–21 June, 28 September–19 November), and 2016 (13 January–27 February, 9 May–17 June, 24 September–12 October), which together comprised ~25% of the span over which we monitored pumas. We investigated 1174 out of 1209 (97%) clusters identified within the field search periods and found 349 kills. Despite the presence of scavengers such as Andean condors (*Vultur gryphus*), mountain caracaras (*Phalcoboenus megalopterus*), and culpeo (*Lycalopex culpaeus*) and gray foxes (*L. gymnocercus*), extensive field observations by the authors in this system indicate that carcasses in SGNP remain visible for many years after pumas kill vicuñas. Bones, hide, stomachs, and wool are typically preserved due to the cold and dry conditions of this environment (Monk, 2022). Thus, the spatiotemporal window used to investigate clusters allowed us to reliably quantify all kill remains.

To identify kill sites from GPS clusters occurring outside of our field search periods, we used data on the occurrence of vicuña kills from field-investigated clusters to determine the probability that a cluster was a kill site by fitting a mixed-effects binomial logistic regression model (Smith et al., 2020). We ranked models based on Akaike information criterion (AIC) and selected the simplest model within 2.0 ΔAIC_c units of all possible models with the following characteristics as potential predictors: (1) number of locations in a cluster, (2) total duration that the cluster was active (time from first to last location), (3) proportion of locations that occurred at night, (4) total number of locations at night, (5) fidelity to the cluster over the cluster duration (time spent at the cluster divided by the total time between the first and last points in the cluster), and (6) the mean distance of each location to the cluster center (Anderson & Lindzey, 2003; Smith et al., 2015). We included a random intercept for individual puma to control for differences in sample size and nonindependence of locations within individuals. The best model retained variables 1 (number of locations in a cluster) and 6 (fidelity to the cluster), whereby kill clusters had more locations and lower fidelity than nonkill clusters. We cross-validated the model using bootstrap resampling for 1000 iterations by fitting the model with 80% of the cluster data and testing the model performance on the withheld 20% of cluster data. Our model showed a high mean accuracy in correctly classifying clusters as kill sites (79%; positive predictive value: 0.87, negative predictive value: 0.63). The cutoff to assign a cluster as a kill or a nonkill was determined by finding the optimal cutoff that maximized sensitivity and specificity using receiver operating characteristic (ROC) curves (Smith et al., 2015, 2020). We assigned the time of the first location in the cluster to be the time of kill. The application of our model to all clusters generated over the entire life of pumas' GPS collars (April 2014–February 2017) produced a data set of 660 kill sites for subsequent analyses (Appendix S2: Table S2).

Seasonal resource selection functions

To evaluate whether vicuñas took more risks during periods of food scarcity (as predicted by the SPH), we developed resource selection functions (RSF) for vicuña, puma, and kill site GPS data, distinguishing between growing and nongrowing seasons. We considered vicuñas to be engaged in risk-prone habitat selection if they selected for the same habitats that were selected by pumas in general (all locations; Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019) or specifically when killing

(kill sites; Smith et al., 2020). We built separate vicuña RSFs for individuals inhabiting the Llano de los Leones and the San Guillermo Canyon. For puma and kill site RSFs, we did not conduct site-specific analyses because individual pumas readily move between the Llano de los Leones and the San Guillermo Canyon (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). In the San Guillermo Canyon, we expected vicuñas to show a pronounced increase toward risk proneness in the nongrowing season because greater productivity allows vicuñas to avoid risky areas by foraging in safe plains (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). In the Llano de los Leones, we also expected to observe an increase toward risk proneness in the nongrowing season, but we expected this increase to be dampened relative to the San Guillermo Canyon (if low productivity in the dominant safe plains of the Llano de los Leones forced vicuñas to seek food in the scarce risky areas year-round; Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). We expected puma habitat selection and kill site selection to remain stable across seasons, because pumas in SGNP are strongly anchored to habitats with stalking cover (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019; Smith et al., 2020).

To model RSFs, we fitted mixed-effects logistic regression models to used and available GPS locations with a random intercept for individuals. We randomly generated a single “available” location for every GPS (used) location within the annual home ranges of each individual vicuña and puma. Home ranges were defined as the 95% contour line of individual kernel utilization distributions (KUDs) built using the R package *adehabitatHR* (Calenge, 2006). Because vicuñas rarely venture into (risky) meadows or canyons at night (Smith, Donadio, Pauli, Sheriff, & Middleton, 2019), we built vicuña RSFs using only diurnal relocations (ranging between 0900 and 1800 h). For puma and kill site RSFs, we used data from the whole diel cycle. Predictor variables included vegetation (NDVI), ruggedness (terrain ruggedness index, TRI), and elevation. All three predictor variables had a 30-m resolution. We chose predictor variables based on their association with the aforementioned habitat classes (Smith et al., 2020; Appendix S1: Figure S3) and previous knowledge of their selection or avoidance by both pumas and vicuñas (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). We used the LANDSAT 8 maximum NDVI for 2015 as a proxy for the location of vegetation (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). NDVI is strongly predictive of meadow habitat and TRI is positively associated with canyon habitat (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli,

Sheriff, & Middleton, 2019). Plains are associated with both low TRI and low NDVI. Elevation is not strongly predictive of any given habitat type in SGNP, but we included it as a covariate because it influences habitat selection by both pumas and vicuñas (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). All covariates were scaled and centered and exhibited low correlation among themselves ($r < 0.5$ for all pairwise combinations of covariates).

Seasonal kill rates by pumas

To evaluate whether increased risk-prone behavior by vicuñas was followed by an increase in lethality by pumas, we calculated kill rates by GPS-collared pumas for the growing and nongrowing seasons. For each specific season-year, we calculated weekly kill rates by dividing the number of kills that each collared puma made over the total number of weeks its collar was active. To compare seasonal kill rates separately for the Llano de los Leones and the San Guillermo Canyon, we used only kills located within the annual 99% minimum convex polygon derived from all relocations by collared vicuñas at each site and adding a 1-km buffer (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019). We compared kill rates between the growing and nongrowing seasons at each site and within the entire extent of GPS relocations for collared pumas using a mixed-effects linear model with a random intercept for individual pumas. We log-transformed kill rates to meet normality assumptions.

RESULTS

From April 2014 through February 2017, we collected 14,811 GPS points from 15 vicuñas and 9 pumas during the growing seasons (mean relocations \pm SE: vicuñas = 597.00 ± 45.49 , pumas = 324.67 ± 78.60) and 21,508 GPS data from 23 vicuñas and 8 pumas during the nongrowing seasons (mean relocations \pm SE: vicuñas = 565.61 ± 63.28 , pumas = 535.13 ± 114.42).

Seasonal RSFs

During both the growing and nongrowing seasons, pumas consistently selected for NDVI and TRI (Figure 1; Appendix S1: Figures S4, S6B, and S7B; Appendix S2: Table S3). When killing, pumas consistently selected for NDVI but neither avoided nor selected for TRI, regardless of season (Figure 1; Appendix S1: Figures S4, S6C, and S7C; Appendix S2: Table S3).

At the Llano de los Leones, vicuñas selected for NDVI and avoided TRI during the growing season. Vicuñas also selected for NDVI but neither avoided nor selected for TRI during the nongrowing season (Figure 2; Appendix S1: Figures S5 and S6A; Appendix S2: Table S3). At the San Guillermo Canyon, vicuñas avoided both NDVI and TRI during the growing season; vicuñas shifted to selection for NDVI and decreased the avoidance of TRI during the nongrowing season (Figure 2; Appendix S1: Figures S5 and S6A; Appendix S2: Table S3).

Seasonal kill rates

Kill rates by pumas (mean vicuña kills per week) in the Llano de los Leones were 0.98 ± 0.31 SE in the growing season and 1.14 ± 0.35 SE in the nongrowing season. Kill rates by pumas in the San Guillermo Canyon were 0.82 ± 0.23 SE in the growing season and 0.83 ± 0.92 SE in the nongrowing season. Within the entire extent of GPS relocations for collared pumas, kill rates were 1.80 ± 0.13 SE in the growing season and 1.99 ± 0.11 SE in the nongrowing season.

Kill rates did not change significantly between the growing and nongrowing seasons (Figure 3) within the Llano de los Leones ($t = 0.52$, $df = 9.95$, $p = 0.62$) and the San Guillermo Canyon ($t = 0.138$, $df = 14.65$, $p = 0.89$), nor within the entire extent of GPS relocations for collared pumas ($t = 1.26$, $df = 26.01$, $p = 0.22$).

DISCUSSION

We found support for the SPH, which posits that risk avoidance by animals should attenuate during periods of food limitation (McNamara & Houston, 1987). Vicuñas in the high Andes became increasingly risk-prone in the nongrowing season by increasing selection for meadows and decreasing avoidance of canyons. These habitats offered more abundant, higher quality food, but were strongly selected by pumas or, in the case of meadows, entailed greater risk of predation. Our results provide support for the SPH complementary to that from mesocosm experiments (e.g., Anholt & Werner, 1995; Holbrook & Schmitt, 1988), while adding to a growing body of evidence for the SPH in systems featuring large carnivores and their ungulate prey (Oates et al., 2019; Sinclair & Arcese, 1995).

Local environments might impose constraints that influence risk avoidance. Animals in areas where risk avoidance is limited by a strong food-safety trade-off may be less likely to meet the predictions of the SPH, if they

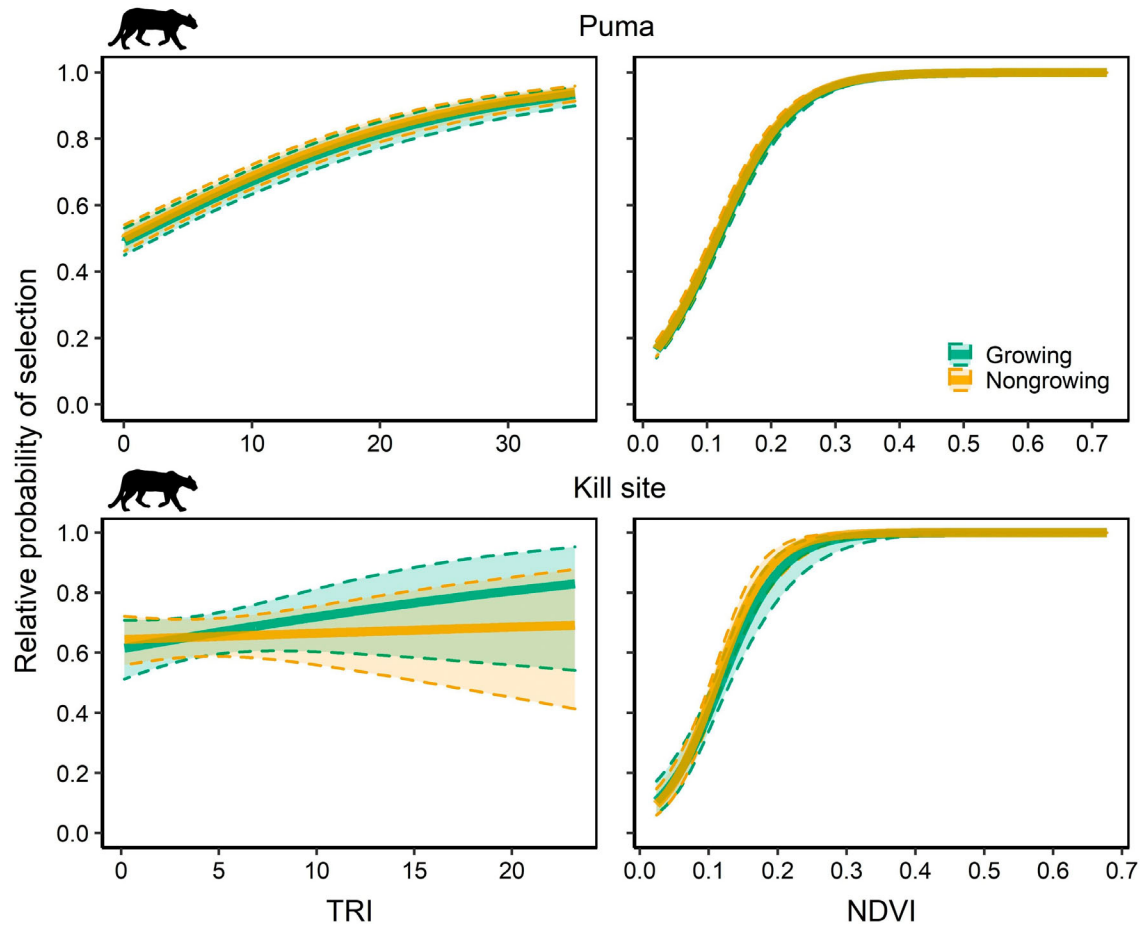


FIGURE 1 Relative probability of selection and 95% CIs from puma and kill site resource selection function (RSF) models during the growing and nongrowing seasons, San Guillermo National Park 2014–2017. Pumas consistently selected for normalized difference vegetation index (NDVI) and terrain ruggedness index (TRI), regardless of season. The scales of the x -axes represent the range of available values within 95% kernel density surface isopleths derived from puma or kill site locations used in the RSFs. High NDVI is a proxy for meadow habitat, high TRI is a proxy for canyon habitat, and both low NDVI and low TRI in combination represent open plain habitat.

are continuously constrained by food limitation to forage in risky areas. In the Llano de los Leones, vicuñas foraged as expected by the SPH. However, seasonal shifts in risk avoidance were not as pronounced as in the San Guillermo Canyon, with individuals increasingly using canyons but not meadows as the nongrowing season progressed. Instead, vicuñas consistently selected for meadows, which we attribute to food scarcity in the plains of the Llano de los Leones, forcing vicuñas to select food-rich, risky meadows throughout the year. In the San Guillermo Canyon, vicuñas avoided both risky meadows and canyons by feeding in safe plains during the growing season, but they increased their exposure to risk both by shifting to selection for meadows and decreasing avoidance of canyons during the nongrowing season, presumably because they no longer could sustain body condition exclusively from the plains due to depletion of fat reserves as plant productivity decreased (Donadio et al., 2012; Appendix S2: Figure S1). Hence,

overall productivity at the San Guillermo Canyon seemed sufficiently high to permit vicuñas to avoid food-rich (but risky) areas during the growing season but not during the nongrowing season, thereby prompting them to forage as expected under the SPH (Anholt & Werner, 1995; McNamara & Houston, 1987; Schmitz et al., 2008). In sum, vicuñas in the Llano de los Leones met the predictions of the SPH, albeit to a lesser degree than those in the San Guillermo Canyon, presumably due to limited forage availability in safe plains year-round (Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019).

In addition to testing the predictions of the SPH for prey foraging throughout the year, we extended the SPH to evaluate whether the seasonal relaxation of risk avoidance by prey increased the kill rates of predators. Despite the increased risk-prone behavior of vicuñas in the nongrowing season, kill rates by pumas did not change appreciably between seasons at either site. This is contrary to evidence from mesocosm experiments, in which

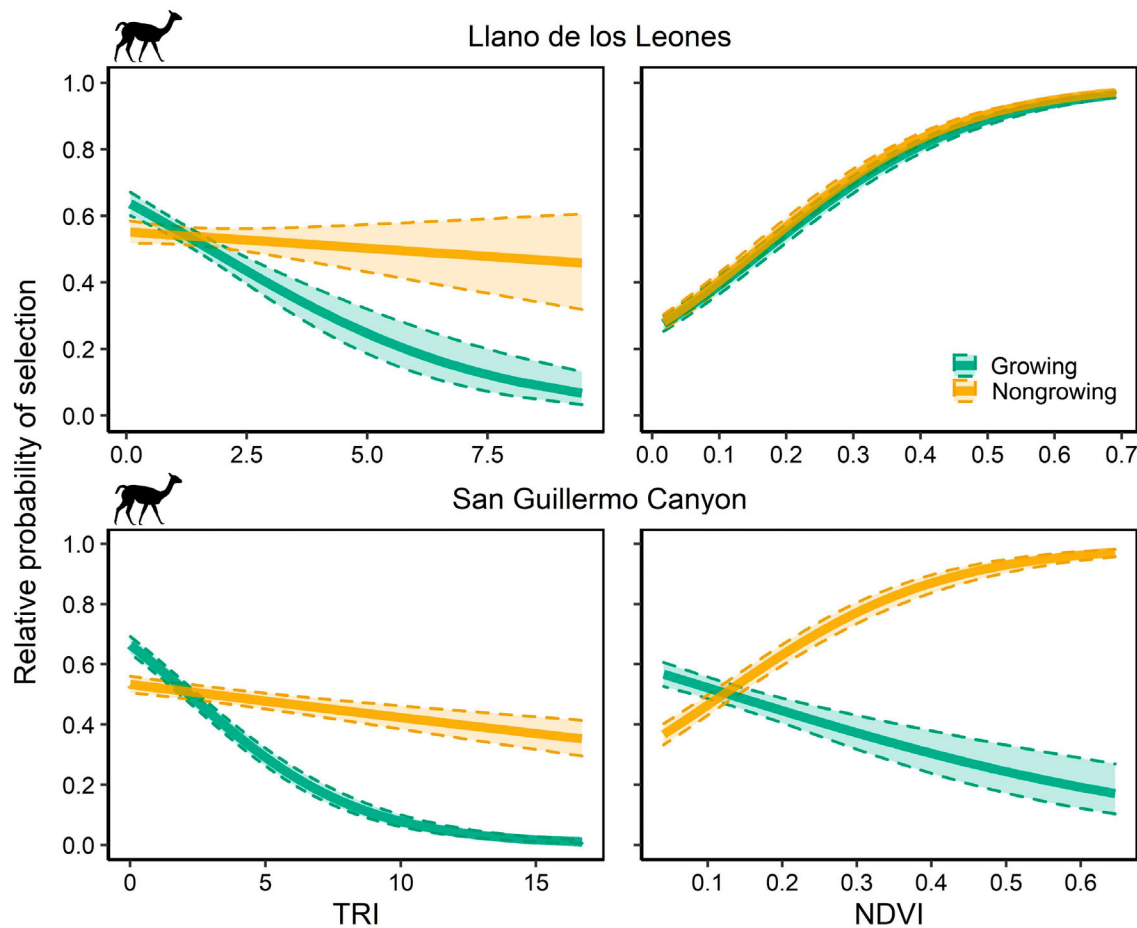


FIGURE 2 Relative probability of selection and 95% CIs from vicuña resource selection function (RSF) models for the Llano de los Leones and the San Guillermo Canyon, during the growing and nongrowing seasons, San Guillermo National Park 2014–2017. Avoidance of terrain ruggedness index (TRI) was strongest in the growing season within both sites; avoidance of normalized difference vegetation index (NDVI) was strongest in the growing season within the San Guillermo Canyon. The scales of the x-axes represent the range of available values within 95% kernel density surface isopleths derived from vicuña relocations used in the RSFs. High NDVI is a proxy for meadow habitat, high TRI is a proxy for canyon habitat, and both low NDVI and low TRI in combination represent open plain habitat.

higher kill rates of predators were positively correlated with more risk-prone prey (Anholt & Werner, 1995; Sih, 1986). We propose two explanations for our results. First, because the consequences of underestimating risk are severe (i.e., being killed), vicuñas could be overestimating risk (Abrams, 1994; Bouskila & Blumstein, 1992; Gaynor et al., 2019). In other words, there could be a mismatch between vicuñas' perceived risk and the actual risk of predation, leading to an exaggerated risk avoidance. Error management theory suggests that overestimation of risk has an evolutionary basis, because such individuals should exhibit reduced mortality relative to those that underestimate risk (Bouskila & Blumstein, 1992; Johnson et al., 2013). To both estimate and respond to predation risk, prey must be able to perceive it predictably, thereby creating a mental risk map, that is, a landscape of fear (Gaynor et al., 2019; Laundré et al., 2001). Pumas are ambush predators that rely on topographic or vegetative

cover provided by canyons and meadows to hunt, and such cover likely is a reliable cue of predation risk for vicuñas (Donadio & Buskirk, 2016; Smith, Donadio, Pauli, Sheriff, Bidder, et al., 2019; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019; Smith et al., 2020). Similar to previous research, and regardless of season, our results indicate that both canyons and meadows are risky in terms of probability of encountering pumas, and meadows are particularly risky in terms of lethality: the probability of pumas killing vicuñas, given an encounter (Moll et al., 2017). Vicuñas use diel refuges by only feeding in meadows during daytime and spending nighttime in safe plains (Smith, Donadio, Pauli, Sheriff, & Middleton, 2019; see also Kohl et al., 2018), and they increase vigilance and reduce foraging rates in meadows and canyons relative to plains (Donadio & Buskirk, 2016). From a seasonal perspective, our work further demonstrates that, when food availability affords them the ability

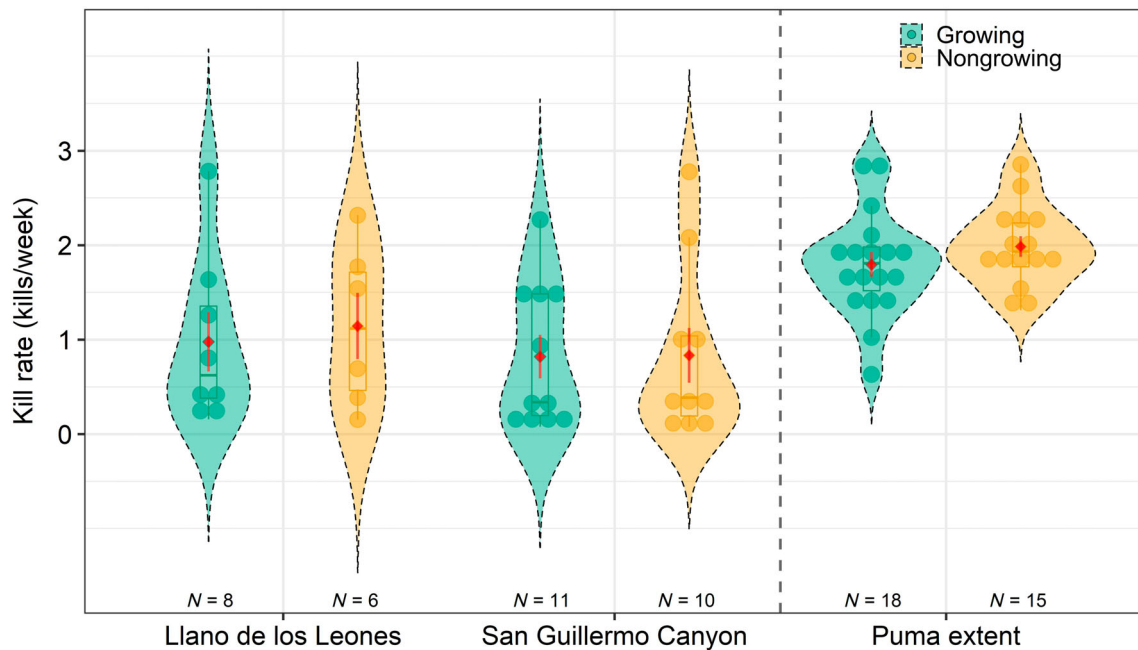


FIGURE 3 Weekly kill rates by GPS-collared pumas during the growing and nongrowing seasons, San Guillermo National Park 2014–2017. Despite vicuñas becoming more risk-prone in the nongrowing season, the kill rates of pumas were not statistically distinguishable between seasons at neither the Llano de los Leones and the San Guillermo Canyon, nor within the entire extent of collared pumas, which encompassed and exceeded both study sites occupied by GPS-collared vicuñas. Data points represent kill rates derived from unique puma–year–season combinations. Red diamonds and vertical lines indicate mean \pm SE.

to do so, vicuñas accurately perceive and avoid risky places (meadows and canyons). Therefore, the hypothesis that vicuñas overestimate risk seems unlikely to explain why kill rates of pumas do not track the increased use of “risky” habitats by vicuñas in the nongrowing season.

An alternative explanation to explain the negligible impact of relaxation of risk avoidance by prey on kill rates is predator satiation (Sweeney & Vannote, 1982; Williams et al., 1993). Pumas in SGNP could be satiated if they are able to kill enough vicuñas to meet their energetic needs, regardless of vicuñas’ shifting risk aversion. Vicuña densities in San Guillermo are high (7.6–13.7 individuals/km² between 2014 and 2017; Donadio & Buskirk, 2016; Monk et al., 2022). Pumas in San Guillermo kill ca. two vicuñas per week, both during the growing and nongrowing seasons (Figure 3), amounting to an estimated biomass consumption rate of 11.43 kg vicuña day⁻¹ puma⁻¹ (given average adult vicuña weight ~40 kg; Franklin, 2011). This figure falls near the upper end of the average range of ungulate biomass consumption rates for North American pumas (8.28–12.04 kg/day; Cristescu et al., 2022), suggesting that pumas in San Guillermo might be satiated. However, vicuña births are pulsed during the growing season (Donadio et al., 2012), which might increase kill rates and decrease the size of vicuñas killed, because pumas

from temperate latitudes typically select for young animals (fawns) following birth pulses of their ungulate prey (Allen et al., 2014; Knopff et al., 2010). Therefore, a reduction in kill rates caused by more risk-averse vicuñas during the growing season could have been offset by an increase in kill rates of newborns. Because our field search periods marginally encompass nongrowing seasons, our data did not allow us to test for season-specific kill patterns with our kill site model, thus leaving this hypothesis as an open question for future work. Further research could disentangle the relative contributions of each of these hypotheses on the effect of relaxed risk avoidance by vicuñas on both kill and biomass consumption rates by pumas.

Our results also have implications at the ecosystem level, particularly through effects on behaviorally mediated trophic cascades (BMTCS; Ripple et al., 2016; Schmitz et al., 2004, 2008). The BMTC concept typically refers to the indirect, positive effects that predators have on vegetation by inducing antipredator behavior of herbivores, such that vegetation is released from herbivory in areas perceived as risky (Atkins et al., 2019; Ford et al., 2014; Schmitz et al., 1997). BMTCS are of great interest to ecologists, especially for their potential relative to large carnivore ecology and conservation (Alston et al., 2019; Ripple et al., 2014; Suraci et al., 2016). However, it remains unclear what environmental factors trigger

BMTCs (Jia et al., 2018; Peacor et al., 2022; Schmitz et al., 2004; Shurin et al., 2002). Our results supporting the SPH suggest that BMTCs are more likely to occur during periods of relative food abundance, when herbivores can afford to avoid areas perceived as risky by feeding in areas perceived as safe. A corollary of this prediction is that BMTCs should attenuate during periods of food shortages, when increased risk of starvation forces herbivores to relax antipredator behavior and feed more frequently in risky areas. Similarly, systems where herbivores can afford to display antipredator behavior throughout the year should sustain BMTCs irrespective of seasonal fluctuations in productivity, whereas systems where herbivores cannot meet energetic requirements exclusively in safe areas during any season are unlikely to sustain BMTCs. In sum, integrating predictions of the SPH into BMTC theory will likely provide insights into the environmental contexts that promote BMTCs.

Using a three-year data set from a single large prey, single large predator system, we tested the SPH and its predator-centric extension. Our results support the SPH, indicating that prey dampen antipredator behavior during seasonal shortages of food abundance. Our work also points toward a potential refinement of the SPH, suggesting that chronic food limitation may limit the extent to which prey conform to predictions by the SPH by constraining the ability of prey to avoid risk. Further, we show that the relaxed antipredator behavior of prey does not necessarily affect predator kill rates. Further integration of the SPH and its contingencies might illuminate when, where, and how interactions between large carnivores and their prey are likely to reverberate across some ecosystems and attenuate in others.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Molina et al., 2023) are available from Figshare: <https://doi.org/10.6084/m9.figshare.21343359.v1>.

ORCID

Francisco J. Molina  <https://orcid.org/0000-0001-9529-3974>

Justine A. Smith  <https://orcid.org/0000-0001-8753-4061>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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