






Where and when to hunt? Decomposing predation success of an ambush carnivore

JUSTINE A. SMITH ^{1,6} EMILIANO DONADIO,² OWEN R. BIDDER ³ JONATHAN N. PAULI,⁴ MICHAEL J. SHERIFF,⁵
PAULA L. PERRIG ⁴ AND ARTHUR D. MIDDLETON³

¹Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, California 95616 USA

²Rewilding Argentina, Estancia La Ascensión, Los Antiguos, Santa Cruz 9041 Argentina

³Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720 USA

⁴Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin 53705 USA

⁵Biology Department, University of Massachusetts Dartmouth, Dartmouth, Massachusetts 02747 USA

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Abstract. Predator–prey games emerge when predators and prey dynamically respond to the behavior of one another, driving the outcomes of predator–prey interactions. Predation success is a function of the combined probabilities of encountering and capturing prey, which are influenced by both prey behavior and environmental features. While the relative importance of encounter and capture probabilities have been evaluated in a spatial framework, temporal variation in prey behavior and intrinsic catchability are likely to also affect the distribution of predation events. Using a single-predator-single-prey (puma–vicuña) system, we evaluated which factors predict predation events across both temporal and spatial dimensions of the components of predation by testing the *prey-abundance hypothesis* (predators select for high encounter probability) and the *prey-catchability hypothesis* (predators select for high relative capture probability) in time and space. We found that for both temporal and spatial analyses, neither the prey-abundance hypothesis nor the prey-catchability hypothesis alone predicted kill frequency or distribution; puma kill frequency was static throughout the diel cycle and pumas consistently selected a single habitat type when hunting, despite temporal and spatial variation in encounter rates and intrinsic catchability. Our integrated spatiotemporal analysis revealed that an interaction between time of day and habitat influences kill probability, suggesting that trade-offs in the temporal and spatial components of predation drive the probability of predation events. These findings reinforce the importance of examining both the temporal and spatial patterns of the components of predation, rather than unidimensional measures of predator or prey behavior, to comprehensively describe the feedbacks between predator and prey in the predator–prey game.

Key words: ambush predator; encounter rate; habitat selection; hunting behavior; predation risk; prey vulnerability; Puma concolor; Vicugna vicugna.

INTRODUCTION

In predator–prey games, predators are faced with tracking and killing prey that can use diverse antipredator strategies to reduce the risk of being killed, including spatiotemporal avoidance, vigilance, grouping behavior, and physical defenses (Lima and Dill 1990, Brown et al. 1999, Makin et al. 2017). Both predator and prey are limited in their ability to respond to the strategy of the other: prey by their sensory modalities (Hermann and Thaler 2014), habitat quality and distribution (Crosmarty et al. 2012), and predator lethality (Brown et al. 1999); predators by their hunting mode (Miller et al. 2014), predictability of prey (Sih 2005), and the energetic cost of

hunting (Williams et al. 2014), among other constraints. The diversity and context dependence of prey risk avoidance and antipredator strategies have been well documented across systems, yet rarely is the predator response evaluated as a dynamic strategy in the predator–prey game (Blomberg and Shine 2000, Lima 2002, Lind and Cresswell 2005; but see Quinn and Cresswell 2004, Roth and Lima 2007, Mitchell 2009, Cresswell and Quinn 2010). To better understand outcomes of predator–prey interactions, it is necessary to explore predator strategies and hunting success as a response to prey risk avoidance behaviors (Lima 2002).

Predator hunting success is a function of the probability of encountering prey and the conditional probability that, given an encounter, prey are captured (Lima and Dill 1990, Lima 2002, Hebblewhite et al. 2005). Two hypotheses, the *prey-abundance hypothesis* and the *prey-catchability hypothesis*, have been advanced to

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⁶E-mail: justinesmith@ucdavis.edu

explain spatial variation in predation events. The *prey-abundance hypothesis* (Hopcraft et al. 2005, Balme et al. 2007) posits that spatial patterns of predation will map onto local prey distribution because predators will capture prey where they have higher prey encounter rates (which are largely, although not necessarily linearly, a function of prey density; Ruxton 2005, Ioannou et al. 2008). This hypothesis presumes that prey should respond by avoiding predators in space and time to reduce predation risk. The *prey-catchability hypothesis* (Davidson et al. 2012; analogous to the *ambush habitat hypothesis* in Hopcraft et al. 2005 and the *landscape hypothesis* in Balme et al. 2007) posits that spatial patterns of predation will match those of the probability of capture given an encounter (i.e., intrinsic capture probability, due the reduced ability for prey to detect, through vigilance, or escape predators). Under this hypothesis, prey should respond by utilizing habitats in which they may encounter predators, but where predators have low lethality.

The likelihood that either one of these hypotheses will be supported in a particular system can be influenced by the hunting strategy of the focal predator. Some actively hunting or coursing predators hunt widely across many habitat types, and patterns of predation in these systems may therefore match prey distribution or the probability of encounter. However, ambush predators often hunt in specific habitats that provide hiding and stalking cover (Savino and Stein 1989, Balme et al. 2007, Davidson et al. 2012), limiting predation to areas where prey are easiest to capture. For ambush predators, the spatial pattern of the trade-off between encounter and capture often favors the strategy of maximizing catchability over encounter probability, supporting the *prey-catchability hypothesis* (Hopcraft et al. 2005, Balme et al. 2007, Davidson et al. 2012). However, since prey can readily perceive these areas to be risky due to their reduced ability to detect or escape predators (Laundré et al. 2001, Hopcraft et al. 2005, Hochman and Kotler 2006, Embar et al. 2011), they may avoid foraging nearby (Schmitz and Suttle 2001, Hamel and Côté 2007) or increase vigilance when there (Donadio and Buskirk 2016), potentially reducing the probability that predators will encounter prey in the first place (Smith et al. 2019a). As a result, ambush predators may face pressure to adopt flexible hunting strategies that allow them to balance encounter and capture probability if and when they are opposing.

Predator hunting success may vary not only in space but on a diel cycle, and as such temporal variation in encounter and capture probabilities has long been appreciated as a significant component of predation risk patterns and predator-prey interactions across taxa (Hampton 2004, Hrabik et al. 2006, Ory et al. 2014), and more recently in large vertebrates (Palmer et al. 2017, Kohl et al. 2018, 2019, Courbin et al. 2019, Smith et al. 2019a). Temporal patterns of wolf predation on moose, for example, are not constant throughout the

day but are better predicted by wolf movement rates than light availability (Vander Vennen et al. 2016). Among large terrestrial ambush hunters, hunting is often concentrated at night to decrease the likelihood of detection by prey and optimize the probability of a successful capture if prey are encountered (Valeix et al. 2009, Loarie et al. 2013, Ford and Goheen 2015). These diel patterns mirror spatial trends toward ambush predator selection of habitats with stalking cover over areas of high prey density (Hopcraft et al. 2005, Balme et al. 2007, Davidson et al. 2012). Prey may respond by altering their activity or diel patterns of habitat selection (Hampton 2004, Hrabik et al. 2006, Ory et al. 2014); high nocturnal predation risk typically results in predictable diel antipredator behaviors in prey, including reduced nocturnal activity (Tambling et al. 2015) and selection for safe habitats at night (Moreno et al. 1996, Crosmay et al. 2012, Kohl et al. 2018, Courbin et al. 2019). Given the expected relationship between temporal patterns of kill success and encounter and capture probabilities, the prey-abundance and prey-catchability hypotheses can be expanded to encompass temporal variation in kill probability. The temporal manifestation of the prey-abundance hypothesis would predict that kills will be concentrated during times of peak encounter rates, whereas the temporal prey-catchability hypothesis would predict that kills will be concentrated at times of day when predators are most effective at capturing prey given an encounter (i.e., when vigilance or escape behaviors are least effective; Fig. 1).

Spatiotemporally consistent patterns of predation risk are central to current models of predator-induced non-consumptive effects and trait-mediated indirect effects in ecology. However, assessments of risk regularly rely on a single spatial metric or ignore predator behavior altogether (Moll et al. 2017, Gaynor et al. 2019). As such, understanding the integration and comparison of both spatial and temporal components of predator kill success, and their relationship to prey antipredator strategies, is likely necessary to evaluate the efficacy of risk avoidance behavior in prey (e.g., Kohl et al. 2019). For example, if prey are effective at avoiding risky habitats at night (e.g., Smith et al. 2019a), the particularly narrow spatiotemporal distribution of predator-prey encounter probability may result in a departure from the typical temporal patterns of predation expected for ambush carnivores. Here, we test for the relative importance of the spatiotemporal components of predator kill frequency by examining support for the *temporal prey-abundance hypothesis*, *temporal prey-catchability hypothesis*, *spatial prey-abundance hypothesis*, and *spatial prey-catchability hypothesis* (Fig. 1) in a resource-limited, high Andean system dominated by a single predator (puma, *Puma concolor*) and single prey species (vicuña, *Vicugna vicugna*). We first test the temporal and spatial hypotheses separately, followed by an integrated analysis to determine the relative importance of spatial and temporal variation in encounter and capture probability on kill

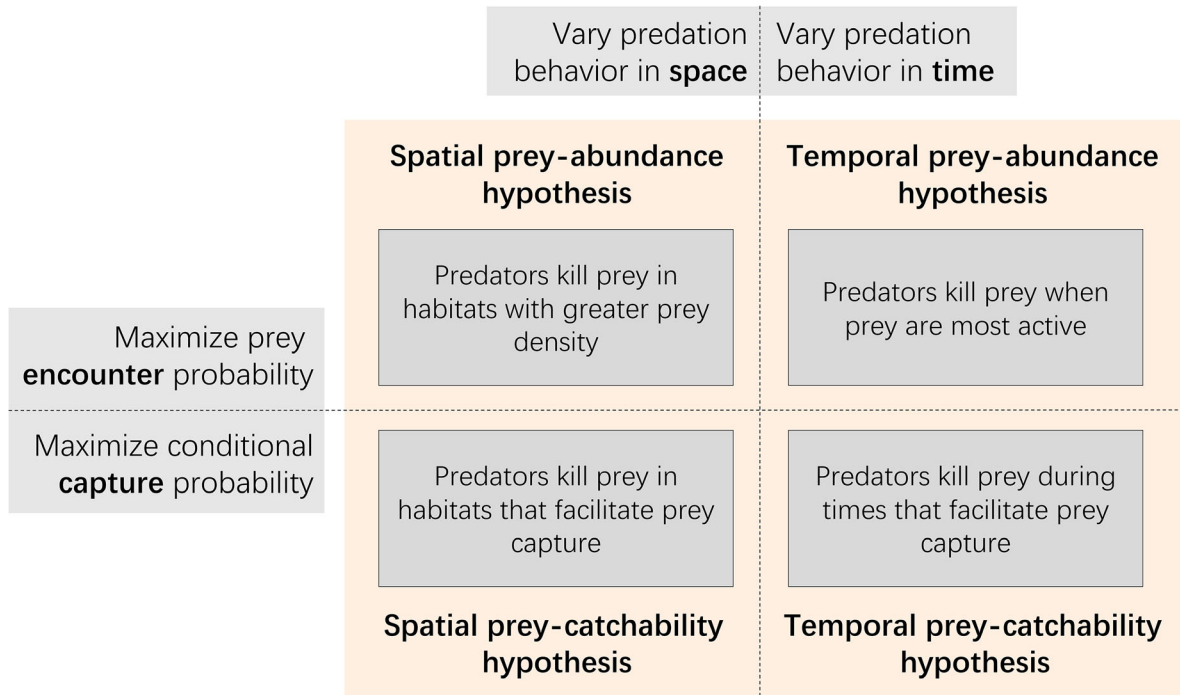


FIG. 1. Four alternative hypotheses to explain patterns in predator hunting behavior along two axes: component of predation risk and type of variation in hunting response. Predators may either attempt to maximize encounter or conditional capture probability, and they may do so by altering their hunting behavior in space or in time.

frequency, distribution, and probability. Specifically, we address the following questions: (1) Are temporal patterns of encounter rates vs. catchability predictive of patterns of kill frequency? (2) Are spatial patterns of encounter distribution vs. catchability consistent with patterns of kill distribution? (3) Is the relative probability of a kill best predicted by the temporal or spatial manifestations of the *prey-abundance hypothesis* (encounter probability) or the *prey-catchability hypothesis* (conditional capture probability)?

Our approach examines the interaction between temporal and spatial patterns of encounter and capture probability to understand how predation events are influenced by the extrinsic (e.g., habitat distribution) and intrinsic (e.g., sensory modality) conditions experienced by prey. Under the temporal prey-catchability hypothesis, we predict that the frequency of puma kills will be concentrated at night (when prey vulnerability is highest due to reduced detection capacity, resulting in high conditional capture probability) as in other puma populations (Beier et al. 1995, Smith et al. 2015), whereas the temporal prey-abundance hypothesis predicts that kill frequency will follow temporal patterns of encounter rates with vicuñas (predicted to be higher during the day; Smith et al. 2019a). Similarly, the spatial prey-catchability hypothesis predicts that puma kills will be concentrated in habitats with stalking cover (where vicuñas have the highest vigilance rates due to greater predation risk; Donadio and Buskirk 2016), whereas the

spatial prey-abundance hypothesis predicts that pumas will disproportionately kill vicuñas where encounter rates are highest (predicted to be in habitats that contain both stalking cover and high-quality forage; Smith et al. 2019a,b). We hypothesize that kill probability is best predicted by an interaction between spatial and temporal patterns of encounter and catchability that are related to the dynamic nature of vicuña antipredator behavior (Smith et al. 2019a), and that there may be a trade-off between encounter and capture probability that results in equalization of captures (Michel and Adams 2009). Our work expands on existing understandings of spatial risk distribution (e.g., Hopcraft et al. 2005, Balme et al. 2007, Davidson et al. 2012) by considering how similar mechanisms shape and interact with temporal predation patterns.

METHODS

Study system and animal capture

We conducted field research from April 2014 to April 2017 at San Guillermo National Park in San Juan Province, Argentina (29° 25' 0.12" S, 69° 15' 0" W, Zone 19J; park area 1,660 km²), a puma–vicuña system in the high Andes. Presumably to increase capture probability, the puma, like many large felid ambush predators, typically exhibits nocturnal or crepuscular activity patterns (Azevedo et al. 2017, Wang et al. 2017) and

feeds and hunts at night (Beier et al. 1995, Smith et al. 2015). Pumas are the only large carnivore in the region and the sole predator of adult vicuñas, the dominant large vertebrate prey in the park (9.5–12.7 individuals/km²; Donadio et al. 2012) and the primary food source for pumas (Donadio et al. 2010). Pumas only have to kill about one vicuña-sized prey item (e.g., mule deer; *Odocoileus hemionus*) every two weeks (Laundré 2005), yet they regularly kill at approximately double that rate, as found across North American systems (Ruth and Murphy 2010). The risk of puma-caused mortality is high for vicuñas; 90–95% of adult vicuña mortality is attributed to puma predation (Donadio et al. 2012, Perri et al. 2017).

San Guillermo National Park has strong delineation between its three dominant habitat types: plains, canyons, and meadows (Donadio and Buskirk 2016). Plains are open habitats made up of primarily bare ground with very sparse, short vegetation and minimal stalking cover. Canyons are characterized by moderate vegetation availability and high topographic stalking cover. Meadows are sparsely distributed habitats that contain tall, dense grasses that provide forage for vicuñas and vegetative stalking cover. In meadow and canyon habitats, reduced sightlines increase vicuña physical encounters with pumas but reduce perceived encounters, giving this stalking predator a catchability advantage. Vicuñas avoid meadows (i.e., use them less than expected given their availability) at night, but return to feed in them during the day (Smith et al. 2019a). Although vicuñas do use individual and group vigilance to mitigate predation risk in meadows (Donadio and Buskirk 2016), they are ultimately anchored to these predictable feeding sites where detection and evasion of stalking predators are low (Smith et al. 2019b). At night, vicuñas select for open plains habitats, which have lower intrinsic risk than meadow and canyon habitats due to higher detectability of stalking predators (Smith et al. 2019a). Pumas are more active at night but do not alter their habitat selection between day and night; instead, pumas always select for meadow and canyon habitats and avoid open plains (Smith et al. 2019a). Vicuña diel patterns of habitat use might therefore stimulate a trade-off for pumas, whereby encounter and capture probabilities are opposing and vary across the diel cycle.

We captured nine pumas (four females and five males) between April 2014 and January 2016 and fit them with GPS collars (Iridium Track M2D, Lotek, Newmarket, Ontario, Canada). We captured adult female vicuñas in April, May, and June of 2014 and 2015 and fit 24 individuals with GPS collars (GPS 6000SD, Lotek). Both vicuña and puma GPS collars were set to record a location at 3-h intervals. We monitored pumas and vicuñas, including documentation of predation and mortality, from early April 2014 through mid-February 2017. This work was conducted under permit #DCM 455 and subsequent renewals issued by the Argentine Park Service.

Determination of encounters and kill sites

We defined an encounter as a physical encounter (puma and vicuña are within a specified distance of one another) rather than a perceived encounter (puma or vicuña is aware of the presence of the other, regardless of their distance apart). An encounter was considered an event in which a vicuña and puma were simultaneously within 350 m of one another. Our encounter distance is more conservative than other studies examining encounters between large herbivores and cursorial predators like wolves (which often use a 1-km threshold; Middleton et al. 2013, Cusack et al. 2019), but is similar to studies assessing encounters with ambush carnivores (500 m; Courbin et al. 2016). Because pumas are ambush predators, they are dangerous only at short encounter distances. Therefore, we selected an encounter distance threshold that reflected the movement speed of vicuñas (mean distance traveled between 3-h fixes) as an approximation of the distance likely to be traveled to avoid an encounter at our scale of data collection. Our collars were set to a 3-h fix rate (whereby locations were recorded simultaneously pumas and vicuñas), therefore we calculated total number of encounters at eight independent times of day.

We visited clusters of puma GPS locations to identify those that were associated with a kill. Clusters were defined by groups of GPS locations (two or more locations) in which each location was within 36 h and 20 m of another location in the cluster. We chose a narrow spatiotemporal window to define clusters to distinguish hunting locations from kill locations, allowing us to more confidently determine the time of a kill. We exhaustively searched puma GPS clusters over one- to two-month periods in spring 2014, 2015, and 2016, summer 2015 and 2016, and fall 2015 and 2016 (Appendix S1: Table S1). We successfully investigated 1,174 out of 1,209 clusters (97%) generated within the field investigation periods combined. Our field investigation spanned approximately 25% of our total puma and vicuña monitoring time (April 2014–February 2017). To predict kill sites from puma location data collected outside of field investigation periods, we fit a model to investigated clusters to determine the probability that a cluster was a kill site and applied it to all clusters generated from the GPS data (approach described in detail in Appendix S1: Table S2).

Diel patterns of encounter rates, catchability, and kill frequency

To examine support for the temporal manifestations of the prey-abundance and prey-catchability hypotheses, we compared the frequency distribution of encounter and kill events across the diel cycle. Possible encounter and kill times were divided into eight periods corresponding with our GPS fix interval. To measure encounter and kill frequency over the diel cycle, we quantified

the proportion of encounters and kills by individual vicuña and puma, respectively, within each of the eight time intervals. Because vicuñas are reliant on visual cues to detect predators (and visual detection is reduced at night, limiting the efficacy of vigilance behaviors; Sarno et al. 2008), we assumed that intrinsic catchability given an encounter was a function of darkness, which we calculated as the inverse sun angle by time of day (package *oce*; Kelley and Richards 2018). Although moon illumination can also influence intrinsic risk as a function of darkness (Kotler et al. 2010, Packer et al. 2011, Prugh and Golden 2014, Palmer et al. 2017), we were primarily interested in broader diel patterns of predation behavior, whereby the night is always darker than the day regardless of lunar period.

We evaluated temporal variation in encounter and kill frequency by fitting a Von Mises kernel distribution to the proportions of encounters and kills by time of day (command *fitlincirc* in package *activity* v1.1 for R software; Xu et al. 2011, Rowcliffe et al. 2014). Specifically, we tested if the linear-circular regression model of proportion of encounters experienced by individual vicuñas and proportion of kills made by individual pumas varied from the null distribution for each of the eight time intervals. We used a running correlation test (15-h moving window) across a diel time series to test for correlations between mean darkness (inverse sun angle), encounter rate, and kill rate across our eight 3-h intervals.

Habitat selection of encounter and kill locations

To examine support for the spatial manifestations of the prey-abundance and prey-catchability hypotheses across the diel cycle, we compared the disproportionate use of habitat classes at encounter locations and kill sites that vary in their intrinsic catchability. We first modeled the distribution of the three distinct habitat types (plains, canyons, and meadows; see *Methods: Study system and animal capture*) in order to assess habitat selection at encounters and kills. We used a random forest modeling approach to determine the distribution and abundance of these three habitat types (Appendix S1: Table S3).

We examined the disproportionate spatial distribution of encounter and kill events by calculating the selection ratios (SR) for encounters and kills in each habitat type by time of day. Selection ratios are greater than 1 when a habitat is used proportionally more than would be expected according to its availability. We calculated selection ratios as the ratio of the proportion of encounters or kills to the proportion of that habitat type available in the study area (Manly et al. 2004, Bergman et al. 2006). We restricted the area of available habitat to a 99% kernel density surface isopleth (ad hoc method to estimate the smoothing parameter; R package *adehabitatHR*; Calenge 2006) derived from vicuña GPS locations as the lowest common denominator of shared habitat (vicuña locations were concentrated within the

distribution of puma kill locations). We only included kill locations that fell within the available habitat area in SR analyses. We tested for differences in habitat selection throughout the day by calculating 95% SR confidence intervals that account for variation in sample sizes among individuals (Manly et al. 2004). We assumed relative catchability to be a static feature of space, whereby habitats that provide stalking cover (i.e., meadows and canyons) allow for greater catchability.

Temporal and spatial contributors to relative kill probability

To examine the relative importance of the temporal and spatial dimensions of encounter and capture probabilities on predation success, we tested support for the prey-abundance and prey-catchability hypotheses as they vary in time and space within one modeling framework. If kill success is more constrained by temporal factors, the temporal prey-abundance hypothesis predicts that the relationship between temporal intrinsic catchability and kill probability will be negative (due to low puma-vicuña overlap at night; Smith et al. 2019a), whereas the temporal prey-catchability hypothesis predicts that this relationship will be positive. If kill success is more constrained by spatial factors, the spatial prey-abundance hypothesis predicts that there will be a positive relationship between kill probability and habitat covariates selected by prey, whereas spatial prey-catchability hypothesis predicts a positive association between kill probability and habitat covariates associated with stalking cover.

To test these four competing hypotheses, we ran a mixed-effects logistic regression model with used vs. available kill site locations as the response variable and predictor variables that included sun angle (i.e., temporal variation) and two habitat covariates (i.e., spatial variation), vegetation (normalized difference vegetation index; NDVI) and ruggedness (terrain ruggedness index, TRI). We chose habitat covariates based on association with the habitat classes and previous knowledge of their available stalking cover and selection by vicuñas. TRI is a proxy for topographic stalking cover, avoided by vicuñas (Smith et al. 2019a,b), and positively associated with canyon habitat. NDVI is a proxy for vegetative stalking cover, selected by vicuñas (Smith et al. 2019a,b), and strongly predictive of meadow habitat. Plains are associated with both low TRI and low NDVI. All covariates were scaled and centered. We used a 10:1 ratio to simulate available kill sites, which were sampled randomly from within each puma's 95% home range. Home ranges were estimated from individual kernel utilization distributions (ad hoc method to estimate the smoothing parameter; R package *adehabitatHR*; Calenge 2006). In addition to sampling available kills in space, we also did so in time by assigning a random sun angle to each available kill site, which we drew from an empirical distribution of sun angles at our site over the course of our

study. To test for relative importance of temporal and spatial covariates and potential spatiotemporal trade-offs in encounter and capture probability, we examined support for all models that included at least one of our three covariates (TRI, NDVI, and sun angle) and interactions between sun angle and each of the two habitat covariates. The model with the lowest AIC score was assumed to be the best performing model.

RESULTS

Diel patterns of encounter rates, intrinsic catchability, and kill frequency

We identified 1,064 encounter events between collared pumas and vicuñas and 1,405 kill events among collared pumas, 676 of which were in the vicuña monitoring area (Appendix S1: Table S4). The remainder of kills were made outside the area occupied by collared vicuñas; although pumas and vicuñas were captured in the same vicinity, pumas have much larger home ranges and therefore their movements extended beyond the area used by our tracked vicuñas. Encounters between pumas and vicuñas were significantly more likely to occur during midday hours of 12:00 and 15:00 and significantly less likely to occur during nighttime hours of 21:00, 00:00, 03:00, and 06:00 (Fig. 2a). Proportion of kills did not vary across the diel cycle; at no time of day was kill frequency higher or lower than expected from the null linear-circular regression model (Fig. 2b). Hourly frequency of encounters was inversely related to darkness (i.e., catchability; $r = -0.87$), but neither catchability ($r = 0.03$) nor encounter frequency ($r = -0.09$) were strongly correlated with kill frequency (Fig. 2c).

Habitat selection of encounter and kill locations

The study area comprised majority plains (59.1%), followed by canyons (35.8%) and meadows (5.1%). The locations of encounters were highly variable by time of day (Fig. 3a, Appendix S1: Table S4). In plains, the dominant habitat type, encounters occurred more often than expected (based on the proportion of plains habitat occurring in the study area) during nighttime hours and less often than expected during daytime hours. Fewer encounters than expected occurred in canyons during all times of day due to avoidance by vicuñas. Approximately the same number of encounters in meadows occurred as expected at night, but there were many more kills in meadows than expected during the crepuscular and day periods (06:00–18:00, Fig. 3a).

Diel patterns of kill site selection ratios were much less variable than those of encounter locations (Fig. 3b, Appendix S1: Table S4). Kill frequency in plains was consistently lower than expected based on the availability of this habitat type. Pumas killed vicuñas in canyons in proportion to their availability during daytime hours,

but less than expected at night. More kills were made than expected in meadows during all times of day.

Temporal and spatial contributors to relative kill probability

The best model predicting relative probability of a kill included NDVI and an interaction between NDVI and sun angle (Fig. 4, Appendix S1: Table S5). Relative kill probability increased with NDVI, but this effect was mediated by sun angle, whereby NDVI must be higher to be associated with high kill probability during the day (i.e., when temporal intrinsic catchability is lower). Neither TRI nor sun angle alone remained in the best model.

DISCUSSION

We provide evidence that the interaction between prey behavior and habitat distribution appears to drive spatiotemporal patterns of kill frequency and predator hunting strategies. High encounter rates during the day and higher catchability at night were associated with stable kill frequency across the diel cycle. Pumas consistently selected only for meadow habitats when killing, although these habitats were avoided by vicuñas at night (reducing encounter probability) and did not include other high-cover canyon habitats (which have high capture probability). Therefore, although puma habitat selection did not change over the diel cycle, disproportionate numbers of kill sites in meadows suggest that pumas are optimizing a spatial trade-off between temporal encounter and capture probabilities. While ambush carnivores are often assumed to be fairly inflexible in the times and places they can hunt successfully, our work highlights that an ambush predator faced with trade-offs in encounter and capture probability is flexible in time but not in space. The outcome of the foraging game between pumas and vicuñas is therefore a result of each player playing their best cards while limited by their unique constraints; pumas are constrained by where they can hunt and thus maximize their success by hunting at all times of the day and night, whereas vicuñas are constrained by where they can forage and thus maximize their success (i.e., reduce their likelihood of death) by only foraging when catchability by pumas is lowest (during the day).

We first asked if temporal patterns of kill frequency were better predicted by the prey-abundance or prey-catchability hypothesis. We found that neither hypothesis was a clear predictor of kill frequency. Kill frequency was uniform across the diel cycle, rather than being concentrated during the day (temporal prey-abundance hypothesis) or at night (temporal prey-catchability hypothesis). Although encounter rate and catchability were negatively correlated and exhibited strong diel patterns, pumas demonstrated temporal flexibility by killing prey at all times of day, possibly representing a trade-off

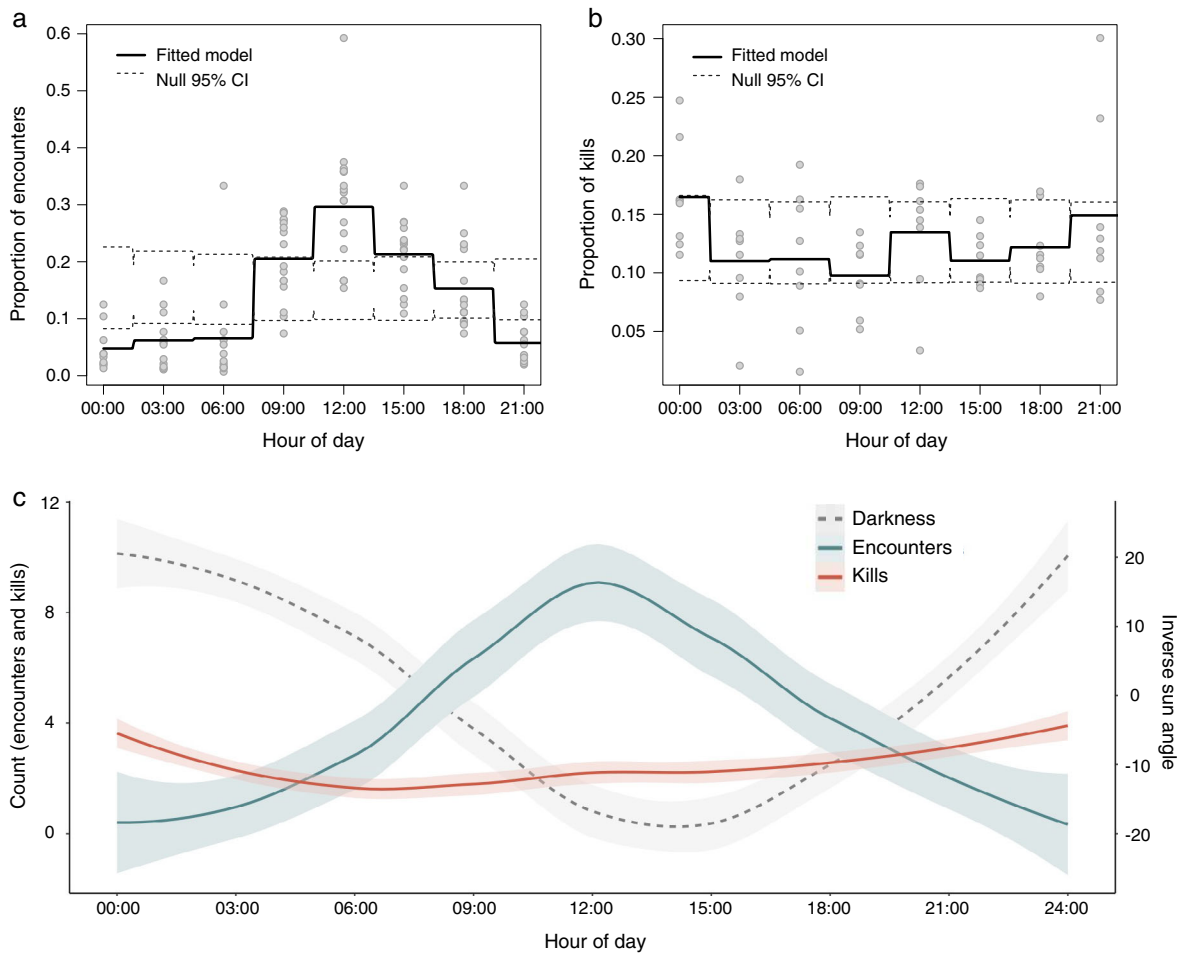


FIG. 2. Patterns of risk across the diel cycle. Proportion of (a) encounters with pumas for each collared vicuña and (b) kills made by each collared puma at 3-h intervals throughout the day. The solid black line represents the fitted linear-circular regression of proportion of encounters/kills by time of day. Dashed lines denote the 95% confidence intervals (CI) of each model, whereby the proportion of encounters or kills made by time of day does not differ from a null model if the solid black line remains inside the CIs. (c) Total individual frequency of puma-vicuña encounters and kills per month at 3-h intervals throughout the day, averaged across individuals. Frequency of encounters is inversely related to catchability (i.e., darkness, measured as the inverse sun angle) across the diel cycle, whereas frequency of kills is not correlated with either encounter rate or inverse sun angle, but rather approximates a uniform distribution by time of day. Darkness trajectory is shown with a broken line to indicate that catchability is estimated by proxy rather than measured.

in the dynamics of encounter and capture probabilities. This result is counter to the dominant understanding of pumas as crepuscular or nocturnal hunters (Harmsen et al. 2011, Soria-Díaz et al. 2016, Zanón-Martínez et al. 2016).

Our second question whether spatial patterns of kill frequency were better predicted by the prey-abundance or prey-catchability hypothesis was similarly inconclusive. The spatial distribution of kill sites did not mirror the distribution of encounters, which were more likely to occur in meadows during the day and in plains at night, nor were high-cover habitats consistently selected at kill sites; although meadows with vegetation cover were consistently selected, canyons with topographic cover were avoided or used only in proportion to their availability.

Finally, we sought to examine the relative importance of temporal and spatial variation in the components of predation risk in determining the relative probability of a kill event. We did not find conclusive support for any individual hypothesis alone. Puma kills were more likely to occur with increasing vegetation, which contains cover and is selected by vicuñas, but not ruggedness, which contains cover but is avoided by vicuñas (consistent with the spatial prey-abundance hypothesis), yet this effect was mediated by sun angle (consistent with temporal prey-catchability hypothesis). Interestingly, the relative probability of a kill was higher in high-vegetation habitats at night than during the day, although vegetation is strongly avoided by vicuñas at night (Smith et al. 2019a) and 99% of our observed encounters in meadow

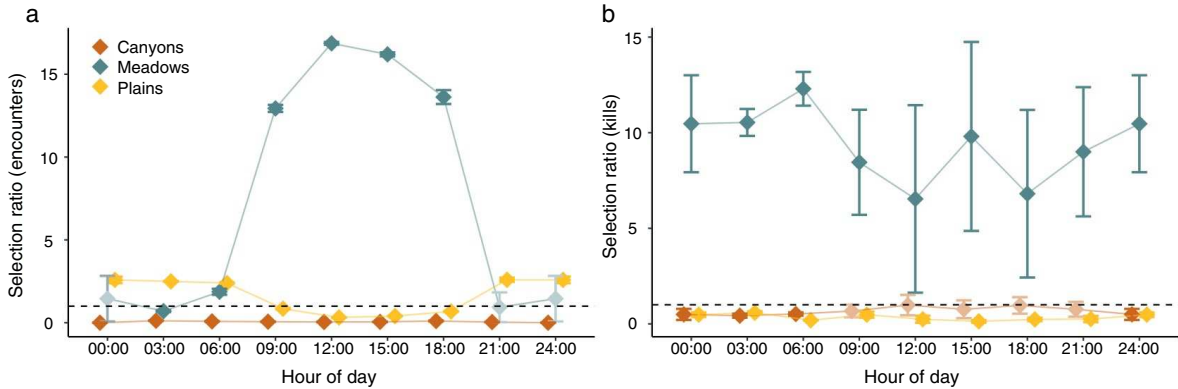


FIG. 3. Selection ratios for (a) puma–vicuña encounters and (b) puma kill sites by habitat type across the diel cycle. Darker shades of each habitat color represent selection ratios that differ from 1 (evidence for statistically significant selection or avoidance). Selection ratios above the dashed line at 1 indicate selection and below the dashed line indicate avoidance. Error bars show sample-size-adjusted 95% confidence intervals.

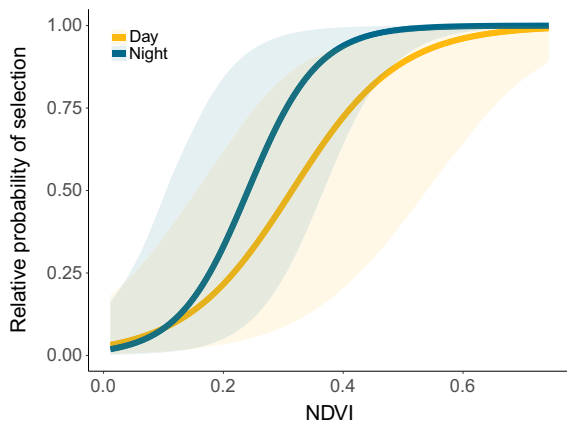


FIG. 4. Relative probability for selection for vegetation (measured by the normalized difference vegetation index, NDVI) and its interaction with sun angle at kill sites. The blue line shows selection for NDVI at the minimum recorded sun angle (i.e., night), and the yellow line shows selection for NDVI at the maximum recorded sun angle (i.e., day). The shaded area represents bootstrapped 95% confidence intervals estimated from 100 simulations (bootpredictlme4 package in R; Duursma 2017).

habitats occurred between 9:00 and 18:00 (Appendix S1: Table S4). These results suggest that kill success is influenced by the interaction between encounter and capture probabilities in both time and space, none of which explain patterns of predation events alone.

We suggest that the spatiotemporal patterns of kill frequency and distribution reflect a trade-off between encounter and capture probabilities across the diel cycle. In meadows, the consistently preferred hunting habitat, pumas capitalize on high encounter rates during the day and high intrinsic catchability at night, creating a uniform temporal distribution of kill frequency but strong selection in regard to kill spatial distribution. This result is supported by our integrated analysis, which revealed

that temporal catchability mediates the effect of spatial encounter probability on puma kill success.

Puma hunting behavior in this system appears to be strongly determined by the dynamics of vicuña food-safety trade-offs that result in a markedly uneven distribution of prey availability in time and space. The propensity for pumas to manifest a cathemeral pattern of kill frequency is facilitated by vicuñas’ need to forage in meadow habitats but ability to escape into the plains during dangerous nighttime hours. Vicuña diel migration therefore is a major contributor to the spatiotemporal distribution of puma kill events. Plains (a refuge for vicuñas with little forage; low-risk, low-reward) and canyons (a habitat preferred by pumas containing only moderate forage; high-risk, moderate-reward) both had fewer kills than expected based on their abundance. Meadows (high-risk, high-reward) had a greater proportion of kills than expected at all times of day, and interestingly, only in meadows did high encounter rates counteract intrinsically lower catchability during the day. In essence, the nature of meadows to serve as a joint spatial anchor for pumas and vicuñas (Smith et al. 2019b) promotes the trade-off between encounter and capture probabilities by stimulating vicuñas to select for this habitat when they have greater detection capacity during the day but avoid it at night (Smith et al. 2019a).

Our results illustrate the flexibility of ambush carnivores to exhibit unexpected temporal patterns of hunting behavior as a response to the interaction between habitat distribution and prey behavior. Spatiotemporal patterns of vicuña behavior contributed to deviations in puma hunting behavior from (1) nocturnal hunting as a dominant strategy and (2) selection for high-cover habitats when hunting (i.e., canyons, although pumas did select for high-cover meadows). Pumas are generally inactive during the day and are primarily nocturnal or crepuscular hunters, even in comparable arid landscapes

(McCain 2008) and protected areas (Harmsen et al. 2011, Soria-Díaz et al. 2016, Zanón-Martínez et al. 2016). Due to the extreme variation in intrinsic vulnerability (i.e., catchability) among highly delineated habitat types in our system, vicuñas select for safe refuge habitats at night (Smith et al. 2019a), forcing pumas in San Guillermo National Park (which are dependent on vicuñas as their primary food source) to hunt during the day more often than other puma populations. Vicuñas also avoid canyons (Smith et al. 2019b), reducing encounter probability in what would otherwise be preferred hunting habitat. Vicuña diel migration therefore limits when and where pumas can encounter prey in habitats with sufficient stalking cover for hunting.

Our results suggest that high-cover habitats will be utilized by ambush predators when hunting, but only if those habitats also provide food resources for prey (as predicted by the leapfrog effect; Iwasa 1982, Hugia and Dill 1994, Hammond et al. 2007). We suggest that although ambush predators are often described as being driven by spatial capture probability (e.g., Hopcraft et al. 2005, Balme et al. 2007, Miller et al. 2015), patchy encounter probabilities with prey in resource-limited landscapes also constrain hunting patterns and strategies (Davidson et al. 2012), particularly when encounter probability varies by time of day in high-cover habitats. Even for ambush carnivores, which rely on stalking cover (from either habitat or darkness) for hunting, the relationship between spatiotemporal distribution of catchability and hunting success appears to be mediated by dynamic and habitat-specific local prey densities. We anticipate that additional spatiotemporal interactions may also be at play that we did not measure; for example, temporal changes in catchability might also vary among habitat types.

We report findings from a predator–prey system dominated by a single predator and single prey species and strongly delineated habitat types. This naturally simple system provides a powerful framework to scale predictions made in controlled experiments up to landscape-level processes in wild populations. We anticipate that our work can provide context to disentangle patterns seen in more complex communities, particularly for those in which prey are similarly constrained in their habitat domains and regular encounters with predators are unavoidable. Although many arid lands of South America are dominated by a simple, dyadic puma–camelid interaction, strong predator–prey dyads are observed even in more complex systems when prey are primarily killed by a single predator (e.g., Carstensen et al. 2016) or one prey is the primary resource for a predator (e.g., Tambling et al. 2014). Studying strongly interacting species is also increasing in relevance as humans continue to simplify predator–prey systems through defaunation. However, some findings from simple systems may not be scalable to more complex systems, and we recognize that the very strong relationship between pumas and vicuñas in our study may amplify the behavioral interplay we

observed when compared to dynamics in more complex systems.

Static spatial assessments of predation risk have been used widely, and yet may poorly approximate predation patterns when temporal differences in encounter and capture probabilities are ignored. We found that prey decision-making altered spatiotemporal patterns of predator behavior by creating trade-offs between dynamic encounter and capture probabilities. In short, the foraging game is dynamic and complex, necessitating quantification of predator and prey behavior in space and time. Importantly, ambush predators in our system did not maximize either capture or encounter probability, but rather mixed the two strategies by killing in high-encounter places at low-catchability times, or low-encounter places at high-catchability times. Our work suggests that habitat context can strongly influence the ability for prey to temporally respond to predation risk and influence the distribution of predation events. It is precisely the feedbacks between predator and prey behavior that create this dynamic; prey attempt to avoid circumstances that are risky in both space and time, and therefore predator encounters with prey are limited to either risky habitats during safe times or safe habitats during risky times. Although single descriptors are commonly used to estimate the distribution of predation risk (Moll et al. 2017), they may not accurately represent the rich and dynamic risk landscape experienced by prey animals. Further complexities are likely to arise when one considers the variability in lethality among predators or vulnerability in prey among individuals, across other scales of variation in risk (e.g., the lunar cycle), and collectively with other risk avoidance strategies (e.g., time allocation). More comprehensive analyses of predation patterns are likely to improve inferences made about the strength of non-consumptive effects of predation risk on prey populations. Future assessments of predation risk should be informed by both the temporal and spatial dynamics of predator–prey games.

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