Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places

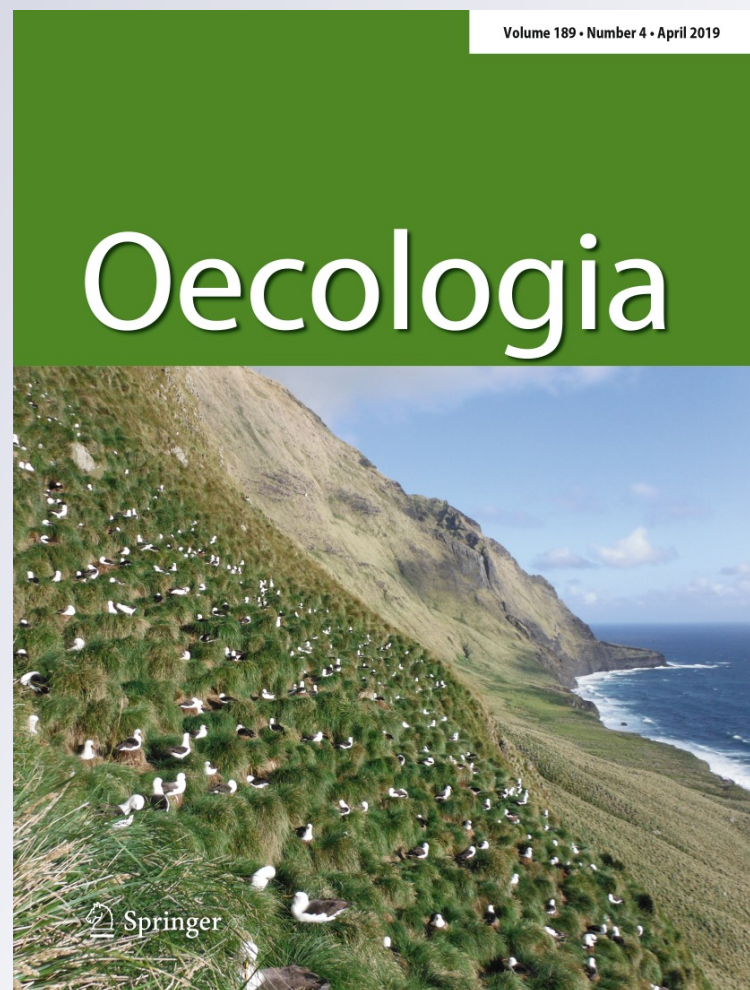## Justine A. Smith, Emiliano Donadio, Jonathan N. Pauli, Michael J. Sheriff & Arthur D. Middleton

Springer

Springer

BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places

Justine A. Smith[1] · Emiliano Donadio[2] · Jonathan N. Pauli[3] · Michael J. Sheriff[4] · Arthur D. Middleton[1]

Abstract

The landscape of fear is an important driver of prey space use. However, prey can navigate the landscape of fear by exploiting temporal refuges from predation risk. We hypothesized that diel patterns of predator and prey movement and space use would be inversely correlated due to temporal constraints on predator habitat domain. Specifically, we evaluated habitat selection and activity of the vicuña and its only predator, the puma, during three diel periods: day, dawn/dusk, and night. Pumas selected the same habitats regardless of diel period—vegetated and rugged areas that feature stalking cover for pumas—but increased their activity levels during dawn/dusk and night when they benefit from reduced detection by prey. Vicuñas avoided areas selected by pumas and reduced activity at night, but selected vegetated areas and increased activity by day and dawn/dusk. Vicuña habitat selection and movement strategies appeared to reduce the risk of encountering pumas; movement rates of pumas and vicuñas were negatively correlated across the diel cycle, and habitat selection was negatively correlated during dawn/dusk and night. Our study shows that an ambush predator's temporal activity and space use patterns interact to create diel refugia and shape the antipredator behaviors of its prey. Importantly, it is likely the very nature of ambush predators' static habitat specificity that makes predator activity important to temporally varying perceptions of risk. Prey which depend on risky habitats for foraging appear to mitigate risk by feeding when they can more easily detect predators and when predators are least active.

Keywords Activity · Diel migration · *Puma concolor* · Predation risk · Resource selection · Temporal partitioning · *Vicugna vicugna*

✉ Justine A. Smith
jsmith5@berkeley.edu

1 Department of Environmental Science, Policy, and Management, University of California - Berkeley, Berkeley, CA 94720, USA

2 INIBIOMA, CONICET-Universidad Nacional Comahue, 8400 Bariloche, Argentina

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

4 Department of Ecosystem Science and Management, Huck Institute of the Life Sciences, Pennsylvania State University, University Park, PA 16802, USA

Introduction

Prey rely on a host of behavioral risk-avoidance strategies to reduce interactions with predators and avoid the ultimate consequence of poor decision-making—being killed. Predators that have narrow and predictable habitat domains (i.e., habitat required for hunting) should stimulate specific risk-avoidance behaviors that allow prey to exploit spatial refugia from predation risk (Schmitz 2005; Preisser et al. 2007; Schmitz et al. 2017). While the concept of the habitat domain has been applied widely in a spatial context, it has also been recognized that prey respond to temporal variation in predation risk across scales including seasons (Griffin et al. 2005), lunar cycles (Kotler et al. 2010; Palmer et al. 2017), diel cycles (Courbin et al. 2019), and immediate predator cues (Creel et al. 2008; Dröge et al. 2017). Temporal variation in predation risk can arise from constraints that dictate when a predator can effectively exploit its habitat domain. The interaction of spatial and temporal factors,

therefore, further limits predator habitat domains and may create temporal refugia for prey in risky habitats.

Temporal refugia can become available on a diel cycle if predators are nocturnal and the opportunity for temporal partitioning is therefore predictable (Dodson 1990). The emergence of temporal refugia during the day may be particularly strong for prey with ambush carnivore predators that employ a sit-and-pursue hunting strategy. Because they rely on stealth, many ambush carnivores exploit the cover of darkness to hunt and therefore experience a temporally varying habitat domain, where hunting "habitat" is constrained by the availability of effective cover in both space and time. As a result, ambush carnivores are generally more active crepuscularly or nocturnally (Harmsen et al. 2011; Soria-Díaz et al. 2016) or select habitats on a diel cycle, choosing areas where they have a high probability of successful prey capture at night (Loarie et al. 2013). Although ambush carnivores do not regularly chase prey, they travel to seek prey or preferred hunting areas (e.g., Williams et al. 2014), possibly explaining why activity is often higher for ambush carnivores during dawn/dusk and night periods. In turn, prey can mitigate the spatial landscape of fear by tracking "predator downtimes" and exploiting temporal refugia (Kohl et al. 2018). Ungulate prey species respond to higher predation risk at night by reducing their activity to decrease encounters with predators (Makin et al. 2017; Wu et al. 2018) or by modifying their space use at night (Lone et al. 2017; Kohl et al. 2018; Courbin et al. 2019) to avoid features like waterholes (Valeix et al. 2009; Crosmary et al. 2012) or areas with high cover (Leblond et al. 2010). Much of this existing work has either examined only predator or prey, or has only measured a single behavioral metric (e.g., predator presence, predator habitat selection, or habitat characteristics; Moll et al. 2017), limiting our understanding of how temporal habitat domain constraints influence predator–prey interactions.

Here we use a simple large mammal system to examine diel patterns of prey refuge use in response to both temporal habitat selection and activity patterns of predators. San Guillermo National Park, Argentina, is home to a single ambush carnivore, the puma (*Puma concolor*) and a dominant herbivore prey species, the vicuña (*Vicugna vicugna*), and is therefore not complicated by diverse predator and prey assemblages. Vicuñas also maintain relatively static home ranges (Franklin 1974), reducing complexity associated with migration in other large herbivore species (Hebblewhite and Merrill 2007, 2009, 2011). Risk and reward are conflated in rare, isolated patches of vegetation where available forage for vicuñas is concentrated and provides stalking cover for pumas. Areas with topographic variability also provide stalking cover for pumas but offer little forage for vicuñas. Risky habitats are interspersed in a safe but less rewarding matrix of extensive open plains (Donadio and

Buskirk 2016). This unique habitat distribution allows for intuitive understanding of the landscape of fear and spatial patterns of risk-foraging trade-offs, as risk is concentrated in limited areas with topographic and/or vegetative cover.

Our objective was to elucidate two pathways—activity patterns and habitat selection—by which a predator–prey response race manifests on a diel cycle due to the creation of temporal refugia. We hypothesized that diel patterns of puma activity and habitat selection would show inverse relationships with vicuña activity and habitat selection, providing evidence for vicuña exploitation of temporal refugia during the day. We first predicted that pumas would vary both activity and habitat selection by time of day, as is the case in other large ambush carnivores, by moving more and selecting for habitat with greater stalking cover at night (Harmsen et al. 2011; Loarie et al. 2013). Subsequently, we predicted that at night vicuñas would reduce activity to minimize detection by pumas and select habitats with less stalking cover for pumas. Finally, we tested the efficacy of vicuña antipredator behaviors by examining correlations in movement rates and habitat selection among pumas and vicuñas on a diel cycle. We discuss the role of multiple interacting behaviors employed by predator and prey in determining the outcome of a temporally varying predator–prey response race.

Materials and methods

Study system and animal capture

We conducted this research in San Guillermo National Park, San Juan Province, Argentina (19J 471233mE 6771981mN). Due to limited access, San Guillermo National Park experiences very low human disturbance (< 70 visitors annually; only one permanent structure), and therefore animal space use and movement is likely driven by ecological and environmental conditions only. The park protects 166,000 ha of high-altitude deserts, where vegetation cover is scarce and forage availability limited (Donadio and Buskirk 2016). In this simple system, pumas are the only large carnivore and are responsible for over 90% of adult vicuña mortality (Donadio et al. 2012; Perrig et al. 2017). Vicuñas perceive and experience greater risk in habitats with high vegetative cover and topographic variability than in open habitats, as evidenced by decreased feeding rates and increased individual and group vigilance (Donadio and Buskirk 2016).

We captured 24 adult female vicuñas, each in a different family group to avoid pseudoreplication, and fitted them with GPS collars (GPS 6000SD, Lotek). We focused on adult females because they are more consistent members of social groups (Franklin 1974) and are generally the most important demographic group in driving large herbivore population dynamics (Gaillard et al. 2000). We

monitored vicuñas from 4/29/2014 to 2/16/2017. We fitted nine pumas (4 females, 5 males) with GPS collars (Iridium Track M2D, Lotek) and monitored them from 4/8/2014 to 2/21/2017. All vicuña and puma GPS collars were programmed to record locations on a 3-h fix rate. Fieldwork was conducted under permit #DCM 455 and subsequent renewals issued by the Argentine Park Service.

Puma and vicuña GPS locations were assigned as occurring during the day, dawn/dusk, or night. Diel period assignments varied on a daily basis according to local sunrise and sunset times, with locations within 1 h of sunrise or sunset categorized as dawn/dusk.

Central to the idea that daylight creates a temporal refuge is the assumption that visibility can reduce capture rates of vicuñas. Prey in other systems have been found to respond to temporal variation in visibility and their subsequent ability to detect predators (Prugh and Golden 2014; Lynch et al. 2015; Palmer et al. 2017). Camelids in South America, including vicuñas, appear to rely on visual cues to detect predators, and visual detection is hindered during night hours (Sarno et al. 2008).
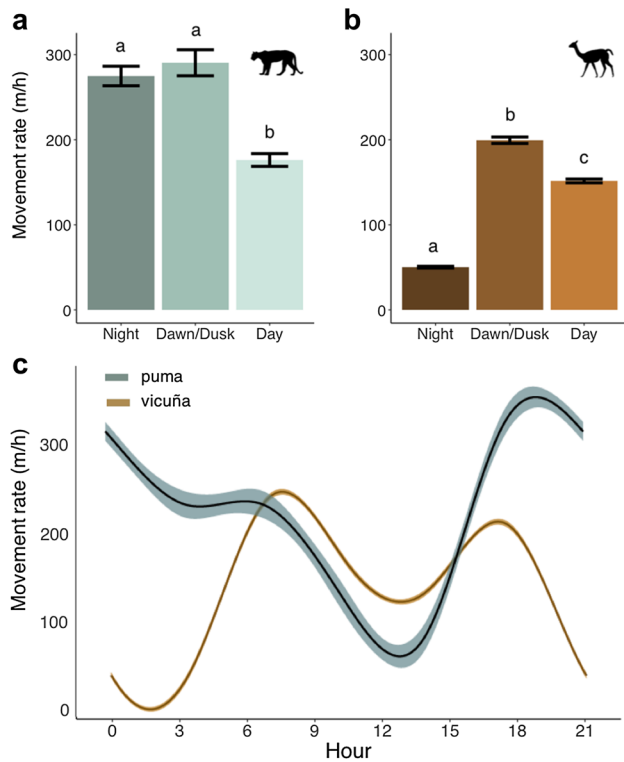
Movement rates

To quantify diel activity patterns for pumas and vicuñas, we first calculated distance between each pair of successive GPS locations and divided the distance by the time difference to obtain a measure of meters traveled per hour. We then calculated the mean movement rate of individuals for each diel period of each day monitored. We ran mixed-effects analysis of variance (ANOVA) tests using R package *nlme* for pumas and vicuñas with a variable for diel period as the predictor, distance traveled as the response variable, and a random intercept for individual, where the sampling unit was average movement rate in a diel period within a single 24-h cycle. We tested for the association between puma and vicuña activity by calculating the Pearson correlation coefficient between the two species' movement rates. We calculated the population mean of individual mean distance traveled per hour between GPS locations at 3-h intervals, yielding eight movement rate estimates within a diel cycle. We examined diel patterns of movement rates by fitting generalized additive mixed models (GAMM) with a cyclic regression spline and a random intercept for individual animal using the mgcv package in R (Kohl et al. 2018). For pumas, we initially examined males and females separately to test for differences in diel movement patterns; because we found no differences (although males moved overall approximately 24% father than females), we pooled sexes for subsequent analyses.

Habitat selection

To model habitat selection by pumas and vicuñas during the day, dusk/dawn, and night, we fitted resource selection functions (RSF) using GPS location data. To ensure independence between GPS locations, we systematically rarified puma and vicuña location data, reducing the sample rate to one location every 9 h by keeping every third location (Northrup et al. 2013). We generated one random location for every included GPS location by individual. Random locations were sampled from within the home range of each individual. We defined home ranges as the 95% contour line of individual kernel utilization distributions (using a bivariate normal kernel). The smoothing parameter was estimated using the ad hoc method (R package *adehabitatHR*; Calenge 2006).

We used mixed-effects logistic regression to fit puma and vicuña RSFs for day, dusk/dawn, and night. Each of the four global models contained scaled and centered covariates for elevation, maximum NDVI from the year 2015, ruggedness (the mean of the absolute differences between the elevation at the focal cell and the surrounding eight cells; Wilson et al. 2007), and an interaction between NDVI and ruggedness. We included the interaction term to account for potential vicuña risk-foraging trade-offs. None of the covariates were correlated above $r = 0.5$. We chose to use maximum NDVI rather than a time-varying metric because it facilitated a more liberal approximation of the location of vegetation throughout the study area. We evaluated temporal consistency of relative NDVI values and found high correlation of NDVI across seasons (Smith et al. 2019). All three covariates had a 30-m resolution. NDVI and ruggedness are both indicators of risk due to stalking cover, whereby cells with higher NDVI contain greater vegetative cover (also indicative of forage availability for vicuñas) and cells with higher ruggedness contain greater topographic cover. To control for differences in sample sizes among individuals, we included a random intercept for individual animals. We ran models using all combinations of the covariates and determined the best models using Akaike's information criterion (AIC; Burnham and Anderson 2002). To validate the best models, we employed an area-adjusted cross-validation approach with 100 iterations of bootstrap sampling (Boyce et al. 2002).

We examined puma and vicuña diel differences in habitat selection by calculating the Pearson correlation coefficient between the spatial estimates of habitat selection for day and night. Spatial estimates were cropped to the 98% kernel density surface isopleths derived from all puma and vicuña locations.

Fig. 1 Mean movement rates of **a** pumas and **b** vicuñas during the day, dawn/dusk, and night; 95% confidence intervals shown. Letters above the bars represent significant differences at $p < 0.05$ identified by a Tukey's HSD test. **c** Movement rates with standard errors by hour for pumas and vicuñas, fit with a generalized additive mixed model

Results

Pumas moved less during the day (176.2 ± 3.8 SE m/h) than during dawn/dusk (290.5 ± 5.9 SE m/h) and night (274.9 ± 7.8 SE m/h; $F = 126$, $df = 2$, $p < 0.001$; Fig. 1a). Conversely, vicuñas moved $3\times$ as far during the day (151.6 ± 1.1 SE m/h) and $4\times$ as far during dawn/dusk (199.4 ± 1.9 SE m/h) than at night (50.2 ± 0.5 SE m/h; $F = 4088$, $df = 2$, $p < 0.001$; Fig. 1b). Mean puma and vicuña movement rates across the diel cycle were negatively correlated due to high nocturnal puma activity and high diurnal vicuña activity ($R = -0.188$; Fig. 1c); however, both species exhibited a dip in movement rates in the middle of the day (Fig. 1c) and had the highest activity during the dawn/dusk period (Fig. 1a).

The best models for puma day, dawn/dusk, and night habitat selection included elevation, ruggedness, and NDVI (Tables S1, S2, S3; Fig. 2). During all periods, pumas selected for ruggedness and NDVI and against elevation (Table S4). Spatial predictions of puma habitat selection in day and night were very strongly correlated ($R = 0.956$, Fig. 3). The best models for vicuña day, dawn/dusk, and night habitat selection included elevation, ruggedness, NDVI, and an interaction between ruggedness and NDVI (Tables S5, S6, S7). Vicuñas consistently selected against ruggedness (Fig. 2) and had a negative interaction between ruggedness and NDVI at all times of day (Table S3). Elevation was selected by vicuñas at night and dawn/dusk but avoided during the day (Table S3; Fig. 2). Vicuñas selected for NDVI during the day and dawn/dusk but selected against NDVI at night (Table S3; Fig. 2).
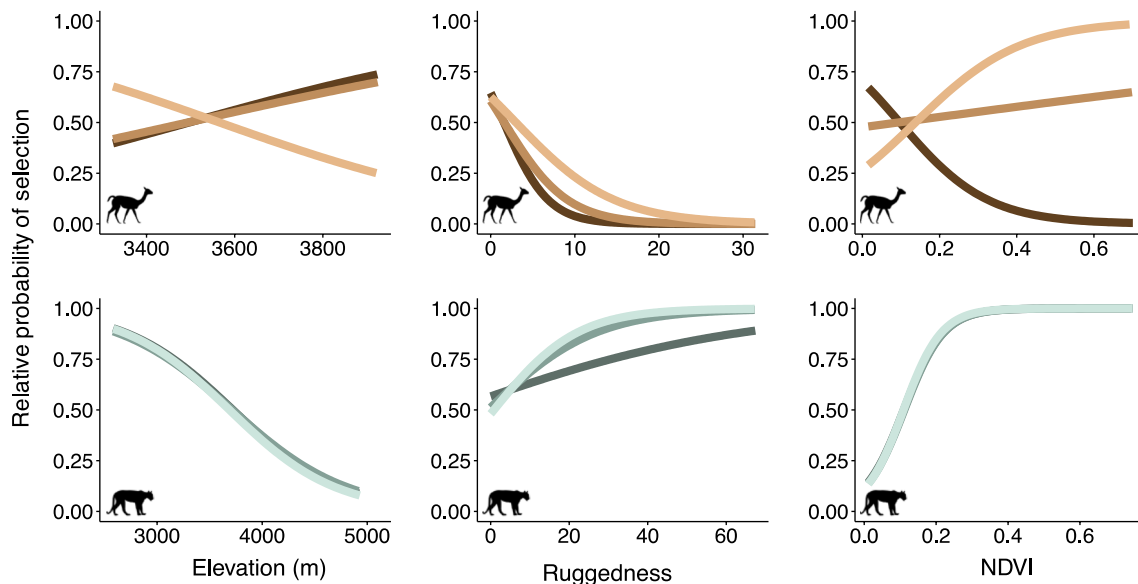
Fig. 2 Relative probability of selection of environmental covariates from vicuña (brown) and puma (teal) habitat selection models using day (light), night (dark), and dawn/dusk (intermediate) locations. The shown range of each covariate is representative of the range of values within a 98% kernel density surface isopleth derived from all vicuña or puma locations (color figure online)
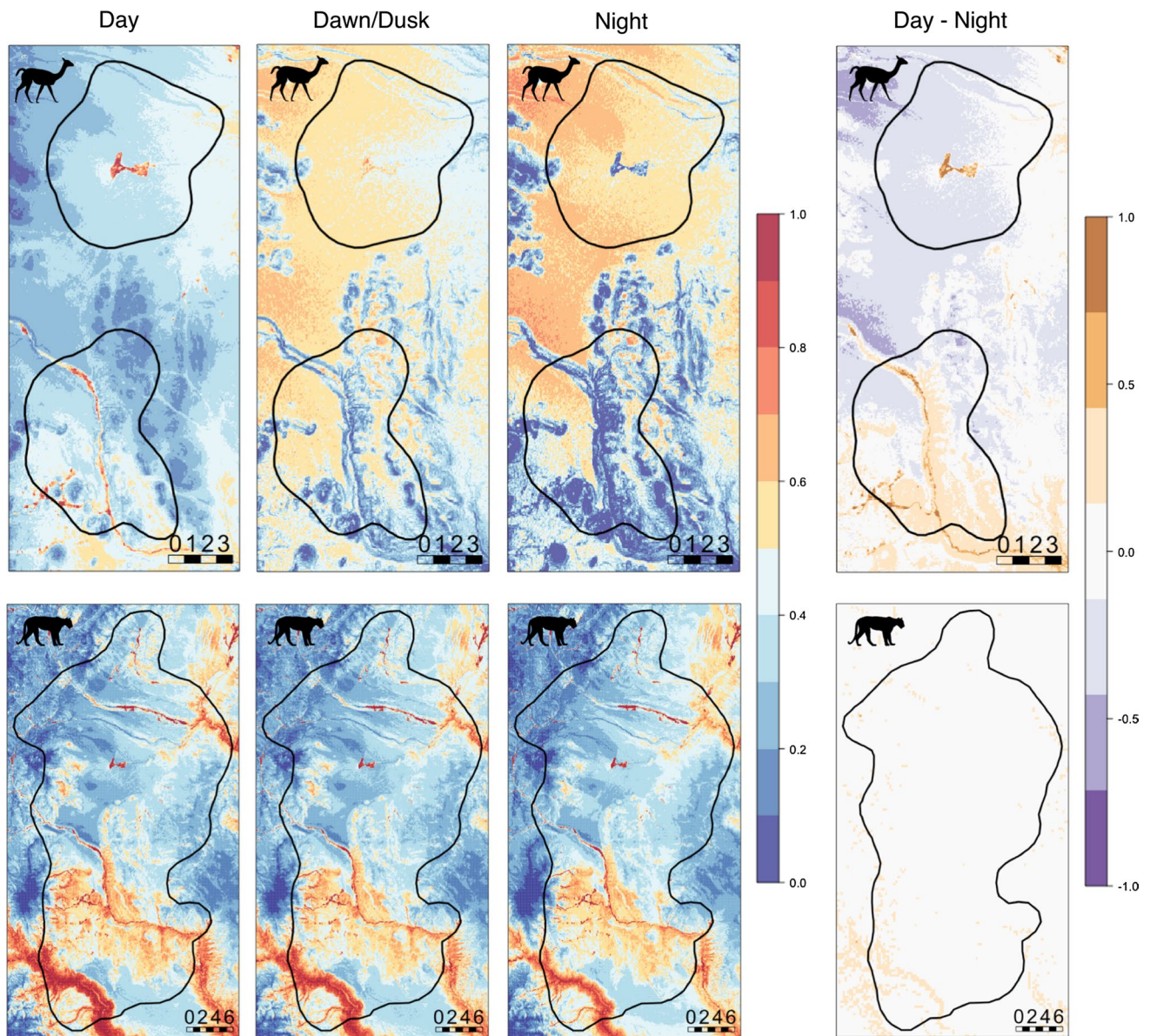
Fig. 3 Spatial predictions of habitat selection using day, dawn/dusk, and night vicuña and puma GPS locations (red = selection; blue = avoidance), and the difference between day and night habitat selection predictions (orange = greater comparative daytime prefer-ence; purple = greater comparative nighttime preference). Polygons represent the 98% kernel density surface isopleths derived from all vicuña and puma locations. Scale bars are shown in kilometers (color figure online)

Spatial predictions of vicuña habitat selection in day and night were not positively correlated ($R = -0.008$, Fig. 3). Puma and vicuña spatial predictions of habitat selection were positively correlated during the day ($R = 0.377$) and negatively correlated at dawn/dusk ($R = -0.564$) and at night ($R = -0.897$).

Discussion

In this system, prey exploit predator downtimes to take advantage of feeding habitats required by both predator

and prey. Our results suggest that puma habitat domains are constrained by conditions that change through time, creating temporal refugia in habitats that would be considered "risky" from a purely spatial assessment. We found that vicuñas exploit these temporal refugia by altering both their habitat selection and movement rates on a diel cycle in response to perceived predation risk. Vicuñas exhibited strong temporal risk avoidance by both moving less and selecting habitats characterized by reduced stalking cover (i.e., lower ruggedness and vegetation) or habitats avoided by pumas (i.e., higher elevation) at night, when pumas were most active. Importantly, an interaction between ruggedness and vegetation was observed in all vicuña habitat selection models regardless of time of day, indicating the significance of a risk-foraging trade-off in foraging habitat that has topographic attributes which favor the ambush strategy of pumas. Therefore, topographically variable foraging habitats may always be risky due to reduced capacity to detect predators.

Our finding that vicuñas responded to puma activity patterns was substantiated by negatively correlated puma and vicuña movement rates throughout the diel cycle, although both species moved most during dawn/dusk periods. Vicuñas avoided areas selected by pumas at night and dawn/dusk, indicating that vicuñas perceive spatial overlap with pumas to be riskier when visibility is low and puma activity is high. Our results indicate that the interaction between activity and habitat selection temporally constrains puma habitat domain and creates a temporal refuge for vicuñas in "risky" but profitable foraging areas during the day.

Our result that high nocturnal predator activity contributes to temporal patterns of prey antipredator behaviors is consistent with other studies on diel patterns of ungulate risk avoidance (Fischhoff et al. 2007; Burkepile et al. 2013; Bogdan et al. 2016; Kohl et al. 2018). However, unlike other studies of diel patterns of ambush predator habitat selection (Loarie et al. 2013), pumas in our study did not exhibit any temporal changes in habitat preference; pumas instead selected for vegetation and ruggedness (both of which provide stalking cover) regardless of time of day. Consistent puma selection for cover may prevent vicuñas from being able to entirely avoid habitats preferred by pumas, because it is in those habitats where vicuñas find abundant and high-quality forage (Donadio and Buskirk 2016). Puma selection for habitats with forage throughout the diel period is likely what drives the strong vicuña diel migration toward vegetated areas during the day and away from them at night. Vicuña diel migration to feeding grounds is responsible for the highest vicuña movement rates occurring at dawn/dusk and may also explain increased puma activity during dawn and dusk periods. More work is needed to substantiate whether predation risk is greatest for vicuñas during times of shared high crepuscular activity rates in predator and prey.

It is worth noting that pumas were present throughout our study area, therefore we are unable to assess vicuña behavior in the absence of predators. In addition, because we were only able to track nine individual pumas for this work, our sample may not represent space use and activity patterns at the population level. However, high overlap in utilization of habitat patches by both males and females in this system indicates that there is low variation in the habitat types and distributions experienced by individual pumas (Smith, Donadio, and Middleton unpubl. data).

Evidence for diel patterns of risk-avoidance behaviors by vicuñas suggests that prey use multiple strategies to mitigate predation risk. In addition to the spatial and activity patterns we describe, vicuñas in this study area exhibit greater vigilance behavior in risky habitats that contain stalking cover for predators (both topographic and vegetative; Donadio and Buskirk 2016). Research on the non-consumptive effects of predation risk, including trait-mediated indirect effects, may overestimate risk effects if only one risk-avoidance behavior is measured (Geraldi and Macreadie 2013). In this case, temporal constraints on puma hunting domain may allow for greater utilization of high-quality forage by vicuñas than would be predicted by habitat domain theory alone. However, the presence of predators appears to reduce pressure on vegetation by stimulating prey avoidance of vegetative cover at night and increased movement during the day (whereby a single patch is less likely to be depleted). We suggest that temporal refugia may facilitate the stability of similar systems, whereby prey can access but not overexploit their forage resources. Investigation of other temporal scales of environmental variation including lunar cycles and seasons might further illustrate the consequences of behavioral decisions made by predator and prey. We encourage future research that explores the effects of temporal predator habitat domain constraints on prey behavior, demography, and trophic cascades.

Author contribution statement JAS, ED, and ADM conceived of the study. ED, JNP, MJS, and ADM provided materials. ED, JNP, and ADM collected the data. JAS analyzed the data. JAS and ADM wrote the manuscript, and ED, JNP, and MJS contributed to revisions.

References

Bogdan V, Jůnek T, Vymyslická P (2016) Temporal overlaps of feral cats with prey and competitors in primary and human-altered habitats on Bohol Island, Philippines. PeerJ 4:e2288. https://doi.org/10.7717/peerj.2288

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow F (2002) Evaluating resource selection functions. Ecol Model 157:281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Burkepile D, Burns C, Tambling C, Amendola E, Buis G, Govender N, Nelson V, Thompson D, Zinn A, Smith M (2013) Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. Ecosphere 4:1–19. https://doi.org/10.1890/ES13-00078.1

Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Courbin N, Loveridge A, Fritz H, Macdonald D, Patin R, Valeix M, Chamaillé-Jammes S (2019) Zebra diel migrations reduce encounter risk with lions at night. J Anim Ecol 88:92–101. https://doi.org/10.1111/1365-2656.12910

Creel S, Winnie J, Christianson D, Liley S (2008) Time and space in general models of antipredator response: tests with wolves and elk. Anim Behav 76:1139–1146. https://doi.org/10.1016/j.anbehav.2008.07.006

Crosmary W-G, Valeix M, Fritz H, Madzikanda H, Côté S (2012) African ungulates and their drinking problems: hunting and predation risks constrain access to water. Anim Behav 83:145–153. https://doi.org/10.1016/j.anbehav.2011.10.019

Dodson S (1990) Predicting diel vertical migration of zooplankton. Limnol Oceanogr 35:1195–1200. https://doi.org/10.4319/lo.1990.35.5.1195

Donadio E, Buskirk S (2016) Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. J Mammal 97:966–977. https://doi.org/10.1093/jmammal/gyw020

Donadio E, Buskirk SW, Novaro AJ (2012) Juvenile and adult mortality patterns in a vicuña (*Vicugna vicugna*) population. J Mammal 95:1536–1544

Dröge E, Creel S, Becker M, M'soka J (2017) Risky times and risky places interact to affect prey behaviour. Nat Ecol Evol 1:1123–1128. https://doi.org/10.1038/s41559-017-0220-9

Fischhoff I, Sundaresan S, Cordingley J, Rubenstein DI (2007) Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. Behav Ecol 18:725–729. https://doi.org/10.1093/beheco/arm036

Franklin WL (1974) The social behavior of the vicuña. In: Geist V, Walther F (eds) The behaviour of ungulates and its relation to management. IUCN Publications, Morges, Switzerland, pp 477–487

Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temproral variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31:367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Geraldi NR, Macreadie PI (2013) Restricting prey dispersal can overestimate the importance of predation in trophic cascades. PLoS One 8:e55100. https://doi.org/10.1371/journal.pone.0055100

Griffin P, Griffin S, Waroquiers C, Mills S (2005) Mortality by moonlight: predation risk and the snowshoe hare. Behav Ecol 16:938–944. https://doi.org/10.1093/beheco/ari074

Harmsen B, Foster R, Silver S, Ostro L, Doncaster CP (2011) Jaguar and puma activity patterns in relation to their main prey. Mamm Biol Z Säugetierkd 76:320–324. https://doi.org/10.1016/j.mambio.2010.08.007

Hebblewhite M, Merrill E (2007) Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377–387. https://doi.org/10.1007/s00442-007-0661-y

Hebblewhite M, Merrill EH (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454. https://doi.org/10.1890/08-2090.1

Hebblewhite M, Merrill E (2011) Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120:1860–1870. https://doi.org/10.1111/j.1600-0706.2011.19436.x

Kohl MT, Stahler DR, Metz MC, Forester JD, Kauffman MJ, Varley N, White PJ, Smith DW, MacNulty DR (2018) Diel predator activity drives a dynamic landscape of fear. Ecol Monogr. https://doi.org/10.1002/ecm.1313

Kotler BP, Brown J, Mukherjee S, Berger-Tal O, Bouskila A (2010) Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. Proc R Soc Biol Sci 277:1469–1474

Leblond M, Dussault C, Ouellet J (2010) What drives fine-scale movements of large herbivores? A case study using moose. Ecography 33:1102–1112. https://doi.org/10.1111/j.1600-0587.2009.06104.x

Loarie S, Tambling C, Asner G (2013) Lion hunting behaviour and vegetation structure in an African savanna. Anim Behav 85:899–906. https://doi.org/10.1016/j.anbehav.2013.01.018

Lone K, Mysterud A, Gobakken T, Odden J, Linnell J, Loe L (2017) Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. Oikos 126:624–632. https://doi.org/10.1111/oik.03486

Lynch E, Northrup J, McKenna M, Anderson C, Angeloni L, Wittemyer G (2015) Landscape and anthropogenic features influence the use of auditory vigilance by mule deer. Behav Ecol 26:75–82. https://doi.org/10.1093/beheco/aru158

Makin D, Chamaillé-Jammes S, Shrader A (2017) Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. Anim Behav 127:225–231. https://doi.org/10.1016/j.anbehav.2017.03.024

Moll R, Redilla K, Mudumba T, Muneza A, Gray S, Abade L, Hayward M, Millspaugh J, Montgomery R (2017) The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. J Anim Ecol 86:749–765. https://doi.org/10.1111/1365-2656.12680

Northrup JM, Hooten MB, Anderson CR Jr, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecology 94:1456–1463. https://doi.org/10.1890/12-1688.1

Palmer MA, Fieberg J, Swanson A, Kosmala M, Packer C (2017) A "dynamic" landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. Ecol Lett 20:1364–1373. https://doi.org/10.1111/ele.12832

Perrig PL, Donadio E, Middleton AD, Pauli JN (2017) Puma predation subsidizes an obligate scavenger in the high Andes. J Appl Ecol 54:846–853. https://doi.org/10.1111/1365-2664.12802

Preisser EL, Orrock JL, Schmitz OJ (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator–prey interactions. Ecology 88:2744–2751. https://doi.org/10.1890/07-0260.1

Prugh L, Golden C (2014) Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. J Anim Ecol 83:504–514. https://doi.org/10.1111/1365-2656.12148

Sarno RJ, Grigione MM, Arvidson LD (2008) Lack of response of an open-habitat ungulate to the presence of predator urine. Rev Chil Hist Nat 81:179–183. https://doi.org/10.4067/S0716-078X2008000200003

Schmitz OJ (2005) Behavior of predators and prey and links with population-level processes. Oxford University Press, New York

Schmitz O, Miller J, Trainor A, Abrahms B (2017) Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. Ecology 98:2281–2292. https://doi.org/10.1002/ecy.1916

Smith JA, Donadio E, Pauli JN, Sheriff MJ, Bidder OR, Middleton AD (2019) Habitat complexity mediates the predator-prey space race. Ecology

Soria-Díaz L, Monroy-Vilchis O, Zarco-González Z, Soria-Díaz L, Monroy-Vilchis O, Zarco-González Z (2016) Activity pattern of puma (*Puma concolor*) and its main prey in central Mexico. Anim Biol 66:13–20. https://doi.org/10.1163/15707563-00002487

Valeix M, Loveridge AJ, Ecology S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW (2009) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30. https://doi.org/10.1890/08-0606.1

Williams TM, Wolfe L, Davis T, Kendall T, Richter B, Wang Y, Bryce C, Elkhaim GH, Wilmers CC (2014) Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. Science 346:81–85. https://doi.org/10.1126/science.1254885

Wilson M, O'Connell B, Brown C, Guinan J, Grehan A (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar Geod 30:3–35. https://doi.org/10.1080/01490410701295962

Wu Y, Wang H, Wang H, Feng J (2018) Arms race of temporal partitioning between carnivorous and herbivorous mammals. Sci Rep 8:1713. https://doi.org/10.1038/s41598-018-20098-6