


# Habitat selection when killing primary versus alternative prey species supports prey specialization in an apex predator

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## Keywords

apparent competition; black-tailed deer; migration; *Odocoileus hemionus columbianus*; predation; *Puma concolor*; resource selection function; ungulates.

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## Abstract

Many predators specialize on one or several prey species that they select from the range of potential prey. Predator specialization on primary versus alternative prey is driven in part by encounter rates with prey and a predator's habitat selection. Although habitat selection changes with behavioural state, this has not been well-recognized in the resource selection function (RSF) literature to date, often because auxiliary data on the predator's behavioural states (e.g. hunting) are absent. We monitored habitat selection of pumas *Puma concolor* in a multi-prey system in northern California, where pumas specialized on black-tailed deer *Odocoileus hemionus columbianus*. We employed multiple RSF analyses on different datasets to test the following three hypotheses: (1) Pumas utilize habitats in proportion to their availability; (2) Pumas select specific habitat features when killing black-tailed deer, their primary prey; (3) Pumas do not select distinct habitats from those identified under hypothesis 1 when killing alternative prey. We found that pumas in our study selected for specific habitats and habitat features in general, but that their selection was more pronounced when killing black-tailed deer. In summer, kill sites of deer were associated with rugged terrain, but gentle slopes and northerly aspects. In winter, pumas killed deer at low elevations, on gentle slopes and on northerly and westerly aspects. Overall, evidence suggested that pumas tracked their primary prey across seasonal migrations, which were short in distance but resulted in pronounced changes in elevation. When killing alternative prey, pumas showed little evidence of habitat selection, suggesting they may kill alternative prey opportunistically. Our results hold implications for how data should be partitioned when modelling baseline habitat selection of predators, hunting habitat selection and predation risk for prey species, as well as for how we model ecological processes such as apparent competition.

## Introduction

Many predators specialize on one or several prey species they select from a range of potential prey. When these prey species disproportionally contribute to a predator's numerical response, they are referred to as its primary prey (Holt, 1977). Prey selection for primary versus alternative prey reflects intrinsic predator energetic evolution and predator morphology, as well as extrinsic factors, such as prey availability and vulnerability (Carbone *et al.*, 1999; Hebblewhite, Merrill & McDonald, 2005; Balme, Hunter & Slotow, 2007). Predator selection for primary versus alternative prey affects the stability of ecological communities. For example, when a high abundance of primary prey sustains predators at high abundances, they may

disproportionately impact alternative prey (i.e. apparent competition; Holt, 1977), initiate Allee effects (McLellan *et al.*, 2010) and drive rare, alternative prey towards extinction (Wittmer *et al.*, 2013).

Prey selection and functional responses are driven by predator encounter rates with prey and a predator's temporal and spatial habitat selection (Holling, 1959; Stephens & Krebs, 1986; Hopcraft, Sinclair & Packer, 2005; Fortin *et al.*, 2015). Based on foraging theory, predators should select habitats that increase encounter rates with their primary prey rather than invest in increasing encounters with suboptimal, alternative prey; focusing on primary prey maximizes energy intake and minimizes the costs associated with hunting (Stephens & Krebs, 1986; Carbone *et al.*, 1999). The behaviours of apex

predators generally support the habitat selection predictions of optimal foraging theory. For example, grey wolves *Canis lupus* select habitat that increases encounter rates with their primary prey, and only increase their predation of alternative prey where these prey species co-occur most with primary prey (Treves *et al.*, 2004). Pumas *Puma concolor* exhibit seasonal prey selection for rare bighorn sheep *Ovis canadensis* only when migratory bighorn sheep significantly overlap with the puma's primary prey, mule deer *Odocoileus hemionus*, on winter range (Johnson *et al.*, 2013). African lions *Panthera leo* in the semi-arid Makgadikgadi ecosystem select for habitat that increases encounter probabilities with their primary prey, but change their habitat selection to increase encounters with alternative prey when their primary prey migrates (Valeix *et al.*, 2012).

Many studies use global positioning system (GPS) locations and resource selection functions (RSFs; Manly *et al.*, 2002) to evaluate animal habitat selection (Sawyer *et al.*, 2007; Dellinger *et al.*, 2013; Ranglack & du Toit, 2015; Cristescu *et al.*, 2016). However, habitat selection can vary according to behavioural state (Nathan *et al.*, 2008; Cristescu, Stenhouse & Boyce, 2015; Kusler *et al.*, 2017). Thus, analyses lacking behavioural context may offer generic insights into where animals are likely to occur, but miss the importance of lesser used habitats and their potential fitness benefits (Bose *et al.*, 2018). For carnivores, behavioural states of individuals can be readily identified through interpreting signs found at GPS location clusters of collared individuals (Elbroch, Lowrey & Wittmer, 2018). Field visitation of GPS clusters is thus widely used by researchers to gain insights into an animal's behaviour and to estimate prey selection and kill rates of large carnivores (Tambling *et al.*, 2010; Pitman, Swanepoel & Ramsay 2012; Elbroch *et al.*, 2018). These data are also used to quantify and map hunting habitat for carnivores (Elbroch *et al.*, 2013) and its counterpart, risky habitat for prey species (Hopcraft *et al.*, 2005).

Taking advantage of a combination of GPS telemetry and simultaneous information on behaviour, we investigated whether apex predators (pumas) show specialization in habitat selection when killing different types of prey. We focused on pumas in a multiprey system in northern California, and conducted field investigations of aggregated location data to differentiate hunting behaviour from other behaviours, such as resting and scent marking. Black-tailed deer *O. h. columbianus* were the primary prey of this puma population (Allen *et al.*, 2015), and most deer in the area exhibited seasonal, elevational migrations (Bose *et al.*, 2017) that we expected to affect the seasonal habitat selection of pumas. We tested three hypotheses: (1) Pumas will exhibit habitat generalism across seasons, using habitats in proportion to their availability; (2) When hunting primary prey, puma habitat selection will be more refined than that observed in baseline habitat selection; (3) Pumas hunt alternative prey opportunistically and the habitat features associated with alternative prey kill sites will be the same as those for baseline habitat selection (hypothesis 1). To test our hypotheses, we determined seasonal RSF analyses utilizing different subsets of location data: (1) all location data, which we assumed reflected baseline habitat selection across all behavioural states; (2) kill sites of black-tailed deer; and (3) kill sites of alternative prey.

## Materials and methods

### Study area

We conducted our study in and adjacent to the Mendocino National Forest in northern California, USA (39°42'N, 122°55'W). The study area encompassed approximately 1000 km<sup>2</sup>. Elevation in the study area ranged from 400 to 2450 m. Topography and climate are described in detail in Allen *et al.* (2015). Major vegetation types changed with increasing elevation. At low elevations, plant communities included oak woodlands (*Quercus* spp., *Aesculus californicus*, *Arctostaphylos* spp.), chaparral (*Ceanothus* spp., *Adenostoma fasciculatum*) and grasslands (*Bromus* spp., *Avena* spp.). Pine (*Pinus* spp.) forests occurred at mid-elevations, whereas at higher elevations plant communities were dominated by mixed-coniferous hardwood forests (*Pinus ponderosa*, *P. iambertiana*, *Abies concolor*, *A. magnifica*, *Pseudotsuga menziesii*, *Arbutus menziesii*, *Quercus* spp.). Silviculture and cattle grazing were historically the primary land management activities, which resulted in a mosaic of even-aged forest stands and openings dominated by non-native grasses.

Black-tailed deer were functionally the only ungulate prey available to pumas; domestic cattle grazed in the Mendocino National Forest during summer and non-native pigs *Sus scrofa* occurred at lower elevations but neither were part of the diet of pumas (Allen *et al.*, 2015). A total of 19 alternative prey species, however, contributed to the diet of pumas, including rodents [California ground squirrel (*Otospermophilus beecheyi*), Douglas squirrel (*Tamiasciurus douglasii*), golden-mantled ground squirrel (*Callospermophilus lateralis*), Western grey squirrel (*Sciurus griseus*), dusky-footed wood rat (*Neotoma fuscipes*)], lagomorphs [black-tailed jackrabbit (*Lepus californicus*), brush rabbit (*Sylvilagus bachmani*)], carnivores [black bear (*Ursus americanus*), coyote (*Canis latrans*), fisher (*Martes pennanti*), grey fox (*Urocyon cinereoargenteus*), raccoon (*Procyon lotor*)] and birds [American robin (*Turdus migratorius*), California quail (*Callipepla californica*), California towhee (*Melospiza crissalis*), mountain quail (*Oreortyx pictus*), mourning dove (*Zenaidura macroura*), red-breasted sapsucker (*Sphyrapicus ruber*), wild turkey (*Meleagris gallopavo*)] (Allen *et al.*, 2015).

### Animal captures and field methods

Between June 2010 and November 2012, we captured seven pumas (five females, two males) using trained hounds and box traps. One male and one female were classified as subadult (i.e. <3 years); all other pumas were considered adults. Capture methods were described in detail in Allen *et al.* (2015) and approved by the Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886) and by the Wildlife Investigations Laboratory of the California Department of Fish and Wildlife.

All captured pumas were fitted with ARGOS satellite GPS telemetry collars (Lotek 7000SAW; New Market, Ontario, Canada). We programmed collars to acquire GPS locations at 2-h intervals and downloaded the location data via satellite every 3 days. We displayed location data in ArcGIS 3.2

(ESRI, Redlands, CA, USA) to identify clusters of GPS points indicating potential prey kill sites. We defined GPS clusters as  $\geq 5$  locations (or a minimum of 8 h between first and last locations) within 150 m of each other that contained at least one crepuscular or nocturnal location. This is the same definition of clusters used in previous work (e.g. Elbroch & Wittmer, 2013), except we employed a longer time threshold, as larger clusters are associated with higher probabilities of finding puma kills (Elbroch *et al.*, 2013). Using handheld GPS units (Garmin 60csx), we investigated 598 of the 609 identified clusters to search for possible prey remains on average within one week ( $\bar{x} = 6.78 \pm 8.18$  SD) after the puma left the area. We identified prey species found at clusters (i.e. kill sites) through skeletal features and external characteristics (hair, pelage or feathers) and used carcass state and, whenever possible, locations of bite marks to assess whether the prey had been killed or whether pumas had been scavenging.

### Kill sites and random sites

We employed a use-availability RSF design (Manly *et al.*, 2002) to evaluate habitat selection by pumas in three different ways: (1) based on all puma locations, (2) based on 288 identified kill sites of black-tailed deer and (3) based on 64 identified kill sites of alternative prey. We extracted habitat covariates associated with kill sites for the first GPS location of each cluster.

Our procedure follows the framework of within-home range, third order habitat selection analysis (Johnson, 1980) using telemetry locations as use data. To sample available habitats, we first estimated individual 100% minimum convex polygon home ranges for all seven collared pumas and then performed a sensitivity analysis to inform the choice of the most adequate number of random locations to characterize availability inside puma home ranges (Stabach *et al.*, 2016). Based on sensitivity analysis outputs, we generated 150 random locations per 1 used puma location for habitat selection modelling. The large number of random locations allowed sampling of less common habitat types within the study area (Northrup *et al.*, 2013). Potential bias from 'contamination' or 'false-negatives' (i.e. pixels classified as available that may have been used) due to the large number of random locations was counteracted by sampling at the landscape scale which contained large numbers of available pixels relative to the sample of used pixels. To further reduce false-negatives, we created a buffer with 75-m radius from the centre of each identified prey kill cluster and sampled availability outside these buffers. This buffer radius likely encompassed most kill and feeding sites, the latter being more concealed sites where pumas often drag prey for consumption after making the kill (Allen *et al.*, 2015).

### Habitat covariates

We considered topography (elevation, slope, aspect and ruggedness), vegetation (seven vegetation types), cover (canopy at base height) and edge density as biologically relevant

covariates for puma habitat selection analyses (e.g. Elbroch *et al.*, 2013; Robinson *et al.*, 2015; Kusler *et al.*, 2017).

### Topography

We obtained altitude data (*elevation*; continuous, metre) from the 30-m resolution ASTER (Advanced Spaceborne Thermal Emission and Reflection radiometer) global digital elevation model (GDEM: <https://earthexplorer.usgs.gov>; accessed 06 February 2015). We derived inclination (*slope*; continuous, percentage) and aspect (sine [*aspect(E-W)*; continuous, radians] and cosine [*aspect(N-S)*; continuous, radians] transformed) from the ASTER GDEM layer using the Spatial Analyst surface tools in ArcGIS 10.2. We calculated a vector ruggedness measure (*ruggedness*; continuous, unitless) from the ASTER GDEM in ArcGIS 10.2 following Sappington, Longshore & Thompson (2007).

### Vegetation and edge density

We acquired vegetation layers including vegetation type and vertical cover [canopy at base height (*canopy*; continuous, percentage)] from Landscape Fire and Resource Management Planning databases (LandFire; [www.landfire.gov](http://www.landfire.gov); accessed 19 January 2017). To reduce model parameters, we broadly reclassified vegetation types into seven distinct habitat classes (all categorical, unitless): conifer (*conifer*), hardwood (*hardwood*), grassland (*grassland*), riparian (*riparian*), shrub (*shrub*), barren and sparse vegetation (*open*) and developed upland forests, agricultural land and water (*other*). We used *conifer* as the reference class for comparison among vegetation types, as it was the most abundant form of vegetation in our study area.

To estimate habitat edge density, we obtained a road layer for our study area from USDA Forest Service maps (<https://www.fs.usda.gov/detail/r5/landmanagement>; accessed 25 January 2017) and overlaid it on Google Earth maps. We digitised additional or incomplete tracks and roads within the study area and used this modified layer for the final analysis. We generated a river/stream layer by hydrological modelling of the ASTER DEM layer in ArcGIS 10.2 using the hydrology tool-set. We calculated the density of linear feature edges (river/stream/road edges), defined as the interfaces between these features and any adjacent vegetation type. We also calculated the density of vegetation edges, defined as the interfaces between open (herbaceous vegetation, shrubs and grasslands independent of age as well as regenerating forests < 20 years old) and closed-canopy (all forest successional classes  $\geq 20$  years) vegetation. Calculations were carried out using the Spatial Analyst density tools in ArcGIS 10.2. We combined density of linear feature edges and density of vegetation edges to obtain edge density (*edge*; continuous, km/km<sup>2</sup>) information as a predictor variable in our analyses.

### Resource selection functions

We built a set of 15 *a-priori* candidate models for summer (June–November) and winter (December–May) separately

(Supporting Information Tables S1–S6). To examine whether site characteristics differed between puma locations, black-tailed deer kill sites, other prey kill sites and available locations, we estimated RSFs for each subset separately using mixed-effects logistic regression of the form;

$$g(x_{ij}) = \ln \left[ \frac{\pi(x_{ij})}{1 - \pi(x_{ij})} \right] = \beta_0 + \beta_1 x_{1ij} + \dots + \beta_n x_{nij} + \gamma_{0j}$$

where  $g(x_{ij})$  is the model estimated for puma location or kill site location  $i$  for puma individual  $j$ ;  $\pi(x_{ij})$  is the conditional mean of  $g(x_{ij})$  given  $x_{ij}$ ;  $\beta_n$  is the estimated coefficient for covariate  $x_{nij}$ ;  $\beta_0$  is the mean intercept; and  $\gamma_{0j}$  is the random per-subject intercept, which effectively controls for variation due to unbalanced individual sampling (Gillies *et al.*, 2006).

Before running the RSFs, we tested for multicollinearity among the predictor variables used in each model. Variables with correlation coefficients  $\geq |0.6|$  were not used together in any model. We standardized all continuous variables to allow direct comparisons of parameter estimates. We fit generalized linear mixed models (GLMMs) using the library *lme4* (Bates *et al.*, 2007) in programme R (R Development Core Team, 2014). We used an information-theoretic approach based on Akaike's Information Criterion with a correction for small sample sizes ( $AIC_c$ ; Burnham & Anderson, 2002) to identify the best performing models. We retained for interpretation models with  $\Delta AIC_c < 4$  and  $\Delta AIC_c < \Delta AIC_{cNull}$ . However, in cases where competing models with just one additional variable had  $\Delta AIC_c < 2$ , we maintained for inference only the most parsimonious model, to avoid inclusion of uninformative parameters in our final model set (Arnold, 2010). We estimated relative importance of covariates by ranking independent variables in the final model set based on their summed  $AIC_c$  weights ( $wAIC_c$ ; Symonds & Moussalli, 2011).

We estimated the fit of models in the final set by calculating the marginal coefficient of determination ( $R^2_{GLMM(m)}$ ), which represents the variance explained by fixed factors; and the conditional coefficient of determination ( $R^2_{GLMM(c)}$ ), which represents the variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013). We calculated the marginal and conditional coefficients of determination in programme R (R Development Core Team, 2014) with the function *r2glmm* in the *MuMIn* package (Barton, 2018). Values of  $R^2_{GLMM(m)} < R^2_{GLMM(c)}$  indicate that random effect inclusion outperforms fixed effects alone; whereas  $R^2_{GLMM(m)} = R^2_{GLMM(c)}$  suggests that the clustering within subject is either non-existent or too weak to detect.

We assessed predictive ability of our top models with  $k$ -fold cross-validation (Boyce *et al.*, 2002). We randomly partitioned the data by individual within seasonal models to construct a training set (80% of data) and test set (20% of data). We then used model-averaged estimates from our training models to calculate predicted RSF values for the random locations. Subsequently, we ranked the random locations based on predicted values and binned them into 10 equal groups. We quantified the fit using the Spearman rank correlation coefficient based on the frequency of used points in each of 10 equal bins of predicted values (Boyce *et al.*, 2002).

## Results

### Puma prey

Between June 2010 and November 2012, we obtained 19 988 GPS relocations from our seven collared pumas ( $\bar{x} = 2855 \pm 1595$  SD, range 971–5342) and visited 598 GPS location clusters in the field. Pumas killed black-tailed deer at 288 clusters (mean per puma 41, range 9–65), 203 in summer and 85 in winter. Pumas killed alternative prey at 64 clusters, of which 59 were rodents, lagomorphs and birds and 5 were meso- or large carnivores (Allen *et al.*, 2015). We found more prey clusters of non-deer prey in summer ( $n = 46$ ) than in winter ( $n = 18$ ).

### Baseline habitat selection

Top models that included a random intercept for puma individual had improved fit over fixed effects alone (Supporting Information Tables S1 and S4) and showed that pumas selected for and against a wide variety of habitats (Table 1; Fig. 1).

In summer, pumas selected for rugged terrain, northerly aspects, gentle slopes and areas with high edge density. They also selected shrub and the *other* habitats category while avoiding grassland (Table 2; Supporting Information Table S7; Supporting Information Fig. S1). Based on the  $AIC_c$  ranking, we retained three models (cumulative  $wAIC_c = 1.00$ ) that were complex (range = 10–13 covariates) (Table 1; Supporting Information Table S1). The top models had excellent power of prediction ( $r_s = 0.95$ ; 0.92; 0.90, Fig. 2a).

In winter, pumas selected for low elevations, gentle slopes and northern aspects. They also selected for hardwoods and high edge density, while avoiding open and riparian areas (Table 2; Supporting Information Table S7; Supporting Information Fig. S1). We retained only the full model for winter ( $wAIC_c = 1.00$ ; Table 1; Supporting Information Table S4), which had good predictive ability ( $r_s = 0.88$ , Fig. 2c).

### Habitat selection for black-tailed deer kill sites

Including a random intercept for puma individual in top models did not improve fit over fixed effects only (Supporting Information Tables S2 and S5). Model outputs showed seasonal variability in habitat selection for deer kills (Table 1 and Fig. 1).

In summer, pumas were more likely to kill black-tailed deer in rugged terrain, on gentle slopes and northerly aspects (Table 2; Supporting Information Table S7; Supporting Information Fig. S1). Overall, only one model containing five covariates was retained for summer ( $wAIC_c = 0.94$ ; Table 1; Supporting Information Table S2). The predictive power of this model was excellent ( $r_s = 0.92$ , Fig. 2b).

In winter, pumas selected lower elevations, gentle slopes, northerly and westerly aspects when killing deer (Table 2, Supporting Information Table S7, Supporting Information Fig. S1). Three models for selection of deer kill sites were retained for winter (cumulative  $wAIC_c = 0.98$ ; Supporting



**Table 1** Supported models ( $\Delta AIC_c < 4$  and  $\Delta AIC_c < \Delta AIC_{cNull}$ ) for puma baseline habitat selection, as well as selection of black-tailed deer (primary prey) and alternative prey kill sites

Season	Model set	Model structure	K	LL	AIC <sub>c</sub>	$\Delta AIC_c$	wAIC <sub>c</sub>
Summer	Baseline	Ruggedness + slope + aspect(E-W) + aspect(N-S) + vegetation class + edge	13	-50 067.29	100 160.60	0	0.56
		Full	15	-50 065.83	100 161.70	1.09	0.32
	Deer kill sites	Elevation + ruggedness + slope + vegetation class + edge	12	-50 069.80	100 163.60	3.03	0.12
		Elevation + ruggedness + slope + aspect(E-W) + aspect(N-S)	7	-1209.92	2433.80	0	0.94
Winter	Alternative prey kill sites	Ruggedness + edge + canopy	5	-272.53	555.10	0	0.52
		Full	15	-24 233.21	48 496.40	0	1.00
	Deer kill sites	Elevation + aspect(E-W) + aspect(N-S) + edge	6	-492.06	996.10	0	0.55
		Elevation + ruggedness + aspect(E-W) + aspect(N-S) + edge	7	-491.92	997.80	1.72	0.23
	Alternative prey kill sites	Elevation + ruggedness + slope + aspect(E-W) + aspect(N-S)	7	-492.04	998.10	1.96	0.21
		Elevation + ruggedness + slope + aspect(E-W) + aspect(N-S)	7	-98.14	210.30	0	0.73
		Elevation + ruggedness + aspect(E-W) + aspect(N-S) + edge	7	-99.45	212.90	2.62	0.20

Information Table S5). The models had a relatively small number of covariates (range 4–5) and excellent predictive power ( $r_s = 0.92; 0.95; 0.94; \text{Fig. 2d}$ ).

### Habitat selection for alternative prey kill sites

The addition of a random intercept for puma individual in the top models did not improve fit compared with fixed effects only (Supporting Information Tables S3 and S6). Pumas showed seasonal variation in habitat selection for non-deer kills (Table 1; Fig. 1).

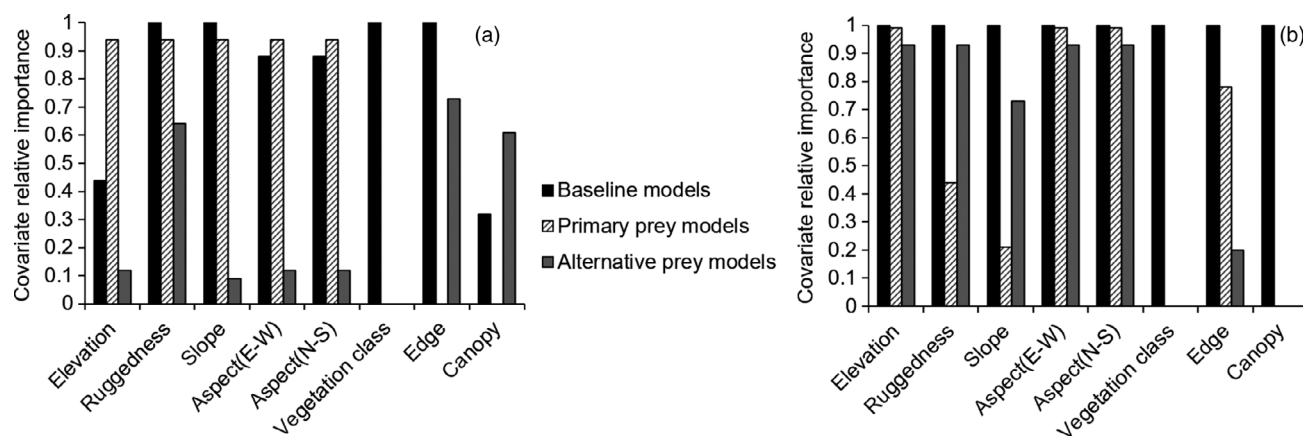
In summer, high ruggedness was significantly associated with selection of kill sites of non-deer prey species (Table 2, Supporting Information Table S7; Supporting Information Fig. S1). However, there was considerable uncertainty in model selection for kill sites of alternative prey species, as illustrated by the null model having lower  $\Delta AIC_c$  than two models with  $\Delta AIC_c < 4$  (Supporting Information Table S3), as well as by wAIC<sub>c</sub> of only 0.52 for the only model with  $\Delta AIC_c < \Delta AIC_{cNull}$ .

In winter, pumas selected for kill sites of alternative prey at lower elevations (Table 2, Supporting Information Table S7; Supporting Information Fig. S1). This output was derived from two models retained for winter (Supporting Information Table S6), each with five covariates and a cumulative wAIC<sub>c</sub> of 0.93.

For both seasons, the results of habitat selection for alternative prey kill sites must be interpreted with caution, because small sample sizes precluded estimation of predictive ability. For the same reason, we do not plot seasonal predictive probability surfaces for non-deer kills by pumas.

### Discussion

Pumas in our study selected specific habitats in general, but their selection was more pronounced (as illustrated by fewer predictors in top models) when killing black-tailed deer, their primary prey, than when baseline habitat selection inclusive of all behavioural states was considered. Selection for some habitats was likely associated with increased encounter rates and successful killing of their primary prey, such as in rugged terrain, on gentle slopes and northerly aspects in summer; and at low elevations, on gentle slopes as well as northerly and westerly aspects in winter. Other aspects of selection may have reflected prey vulnerability rather than abundance, such as small prey group sizes in some habitats resulting in decreased overall vigilance; or availability of microhabitat features enabling stalking cover, as has been shown for other large carnivores (Hebblewhite *et al.*, 2005; Balme *et al.*, 2007). Our results also suggested that pumas hunting alternative prey showed limited selection of habitats beyond topographic features including ruggedness in summer and low elevations in winter. This may indicate that pumas kill alternative prey opportunistically, rather than attempt to increase encounter rates with them by selecting for unique habitat features. In contrast, the more refined habitat selection for primary prey as well as their general selection for certain habitats more than



**Figure 1** Relative importance of covariates associated with summer (a) and winter (b) puma baseline habitat selection, as well as selection of black-tailed deer and alternative prey kill sites in the Mendocino National Forest, California. Importance values were calculated by summing AIC<sub>c</sub> weights of models that included the respective covariate and which received support ( $\Delta\text{AIC}_c < 4$  and  $\Delta\text{AIC}_c < \Delta\text{AIC}_{c_{\text{Null}}}$ ).

**Table 2** Parameter estimates of top models ( $\Delta\text{AIC}_c < 4$  and  $\Delta\text{AIC}_c < \Delta\text{AIC}_{c_{\text{Null}}}$ ) for puma baseline habitat selection, as well as selection of black-tailed deer and alternative prey kill sites

Model covariate	Summer			Winter		
	Baseline	Deer kill sites	Alternative prey kill sites	Baseline	Deer kill sites	Alternative prey kill sites
Elevation	++	+		—*	—* —* —*	—* —*
Ruggedness	+* +* +*	+*	+*	+	+ +	— —
Slope	—* —* —*	—*		—*	—*	
Aspect(E-W)	— —	+		+	+* +* +*	— —
Aspect(N-S)	—* —*	—*		—*	—* —* —*	— —
Grassland	—* —* —*			+		
Hardwood	++ +			+*		
Open	++ +			—*		
Other	+* +* +*			—		
Riparian	++ +			—*		
Shrub	+* +* +*			+		
Edge	+* +* +*		+	+*	+ +	—
Canopy	—		—	—		

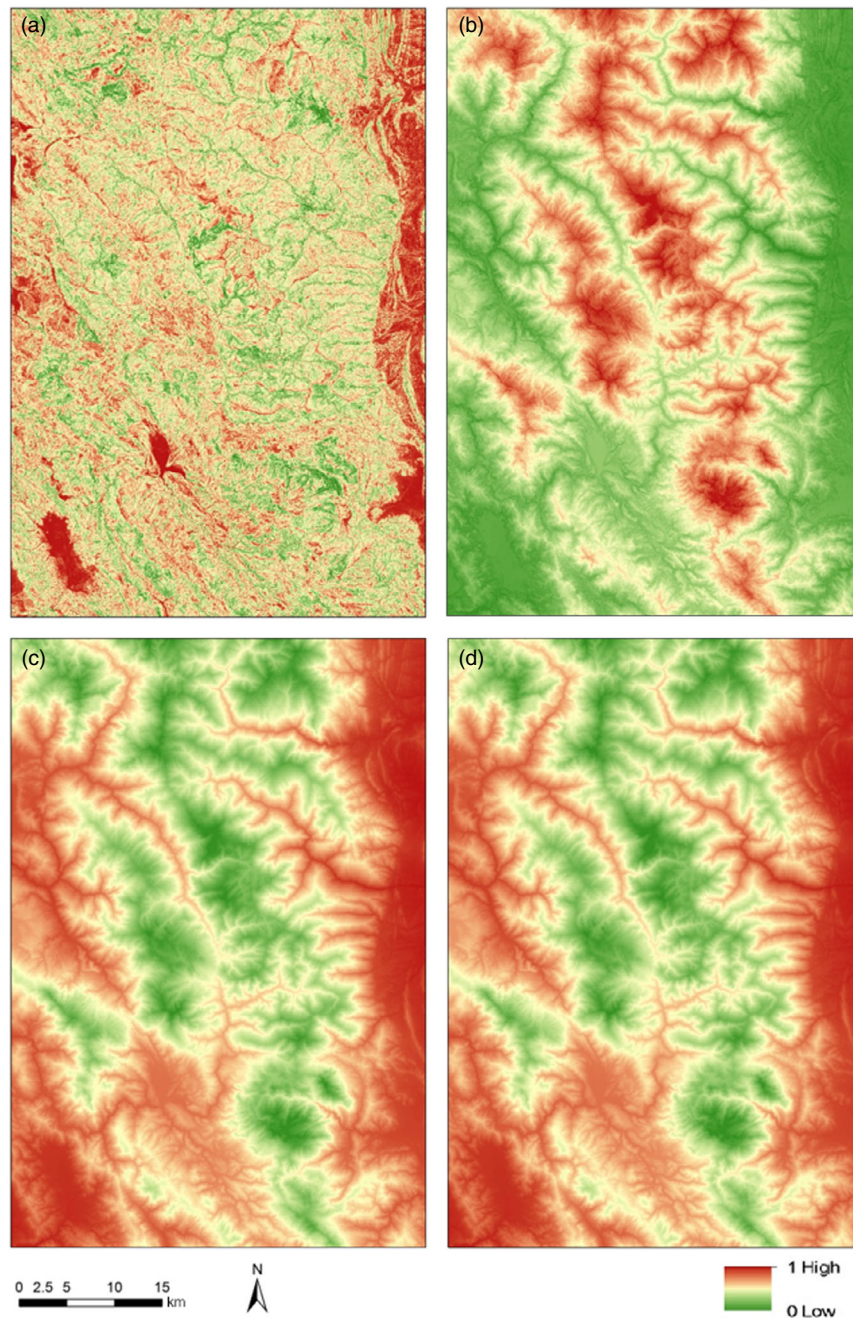
The direction of the parameter estimate (“+” or “—”) is provided. Estimates for which 95% confidence intervals did not overlap zero have an asterisk.

expected given their availability suggested that puma habitat selection might be more specialized than previously thought (Sunquist & Sunquist, 2002; Stoner *et al.*, 2013; Warren *et al.*, 2016). Because habitat selection is influenced by behavioural state, empirical data on animal behaviour such as collected in this study, or behavioural state inference from state-space modelling (Patterson *et al.*, 2008) should be used routinely to improve understanding of habitat selection (and hence animal distribution).

Outputs of baseline habitat selection models lead us to reject our first hypothesis that pumas would exhibit habitat generalism across seasons, using habitats proportionally to their availability. For example, pumas selected lower elevations in winter, likely because most black-tailed deer congregated on distinct ranges at lower elevations during winter (Bose *et al.*, 2017). Pumas also selected for and against several habitats

throughout the year, including selecting for northerly aspects and edge habitats while avoiding steep slopes throughout the year. Edge habitats in particular have previously been identified as important habitats for pumas and have been linked to hunting (Holmes & Laundré, 2006). Shrub and hardwood forest habitats were selected in summer and winter, respectively, whereas grasslands and other open habitats as well as riparian areas were avoided seasonally. Black-tailed deer in our study area mostly selected for these same features (Bose *et al.*, 2018), suggesting pumas may be selecting these areas as hunting habitats with abundant primary prey. Individual pumas varied in their habitat selection, but our sample sizes were too small to determine whether puma age or sex explained this variation.

We found support for our second hypothesis, that puma habitat selection when killing their primary prey would deviate



**Figure 2** Predicted relative probability of puma habitat suitability in the Mendocino National Forest, California. Separate predictions are presented for puma baseline habitat selection in summer (a); selection of black-tailed deer kill sites in summer (b); baseline habitat selection in winter (c); and selection of black-tailed deer kill sites in winter (d).

from baseline selection reflecting more refined choices. Specifically, pumas were more likely to kill black-tailed deer on gentle slopes and northerly aspects irrespective of the time of the year, but rugged terrain was selected in summer, whereas lower elevations and sometimes westerly aspects were selected in winter. The seasonal differences largely matched the habitat use patterns of the local black-tailed deer population (Bose *et al.*, 2018) and suggest that pumas tracked and followed the

short migrations and the resulting changes in the distribution of their primary prey. This observation differed from results described from the Rocky Mountains, where pumas switched prey as a strategy to deal with ungulate migrations and changing prey availability (Elbroch *et al.*, 2013). In California's Southern Sierra Nevada on the other hand, pumas exhibited several strategies in response to mule deer migration. Some performed a slow migration following mule deer while others



exhibited rapid migration patterns resulting in distinct home ranges on ungulate summer and winter ranges (Pierce *et al.*, 1999). The variation in behaviours among puma systems may reflect the different ecological drivers influencing their altitudinal migrations, or may emphasize that individual carnivores in populations exhibit different strategies to contend with varying prey availability. In our study system, 19% of the 64 collared adult female deer remained inside their home ranges year-round (Bose *et al.*, 2017), providing some support that individual pumas may be able to successfully remain in place rather than follow elevational migrations.

Modelling outputs were somewhat supportive of our third hypothesis, that pumas would hunt alternative prey opportunistically, and that habitat selection associated with alternative prey kill sites would be similar to baseline selection. Few regression covariate estimates for alternative prey models exhibited confidence intervals that did not overlap zero, and those covariates in these models aligned with the top models of baseline selection. This suggests that pumas hunt alternative prey that are available or abundant in habitats where they hunt primary prey or opportunistically during non-foraging behaviours, but do not change their habitat selection specifically to hunt alternative prey. We wish to emphasize however that sample sizes of alternative prey kill sites were small and a larger sample might have yielded different outcomes.

Our results support the framework of most large carnivore studies, which choose to ignore non-ungulate prey when modelling hunting habitat. This approach is likely used due to the disproportionately high contribution of ungulates to the diets of large carnivores (Carbone *et al.*, 1999), but the difficulty of locating small prey at GPS clusters of large carnivores may also be a contributing factor (Elbroch *et al.*, 2018).

Our research suggests that pumas track black-tailed deer, their primary prey and that at least in this system, the functional responses for alternative prey exhibited by resident pumas with territories are unlikely driven by habitat selection. Further research, however, is needed to better determine why predators sometimes disproportionately select alternative prey, but kill such prey opportunistically, in other systems. Dispersing pumas disproportionately select small prey (Elbroch, Feltner & Quigley, 2017), for example, and their prey selection may or not be influenced by habitat selection for dispersal corridors. Outcomes from such research have important implications for the management and conservation of species affected by apparent competition (Wittmer *et al.*, 2013) particularly in complex multi-species systems where kill site habitats may also be predator specific (Apps *et al.*, 2013).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Fig. S1.** Predicted relative probabilities for puma habitat selection in the Mendocino National Forest, California.

**Table S1.** Candidate models for puma baseline habitat selection in summer based on GPS location data from seven pumas in the Mendocino National Forest, California

**Table S2.** Candidate models for puma kill site selection of black-tailed deer in summer based on GPS cluster investigations for seven pumas in the Mendocino National Forest, California

**Table S3.** Candidate models for puma kill site selection of alternative prey in summer based on GPS cluster investigations for seven pumas in the Mendocino National Forest, California

**Table S4.** Candidate models for puma baseline habitat selection in winter based on GPS location data from seven pumas in the Mendocino National Forest, California

**Table S5.** Candidate models for puma kill site selection of black-tailed deer in winter based on GPS cluster investigations for seven pumas in the Mendocino National Forest, California

**Table S6.** Candidate models for puma kill site selection of alternative prey in winter based on GPS cluster investigations for seven pumas in the Mendocino National Forest, California

**Table S7.** Parameter estimates of top models ( $\Delta AICc < 4$  and  $\Delta AICc < \Delta AICc_{Null}$ ) for puma baseline habitat selection, as well as selection of black-tailed deer and alternative prey kill sites