

# Home sweet home: fitness consequences of site familiarity in female black-tailed deer

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**Abstract** Individual animals strive to maximize fitness by gaining access to food while minimizing predation risk, and spatial knowledge of both forage resources and predation risks has long been presumed to be advantageous. Actual fitness benefits of site familiarity, however, have rarely been demonstrated. We placed GPS collars on 57 female black-tailed deer in coastal California over 4 years to track seasonal movements, determine home ranges, and monitor survival and cause of mortality. We used seasonal home ranges and core areas as measures of site familiarity and modeled how mortality risk varied with use of familiar areas, forage availability, age class, and elevational overlap with simultaneously collared pumas using Cox proportional hazards models. The use of familiar areas was the best predictor of mortality risk, and deer that had a 40 % probability of leaving their home range in a given week were four times more likely to die.

Puma predation was the largest cause of mortality, and deer whose average weekly elevation was farther from the average elevation of pumas were less likely to die. While forage availability was not related to mortality risk, deer with lower forage availability were more likely to leave their home range during both summer and winter. Our results provide a rare example of fitness benefits associated with site familiarity and the use of familiar areas as a refuge from predation. The benefits of site familiarity are likely widespread in ungulates, especially when there are stable home ranges, complex habitats, and few cues of predation risk.

**Keywords** Forage availability · Home range · *Odocoileus hemionus columbianus* · Predation · *Puma concolor* · Private information

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Individuals maximize fitness by optimizing the trade-off between forage intake and the risk of predation (Sih 1980; Kie 1999). Both access to high-quality forage and avoidance of predators are ultimately linked to the physical space or habitat individuals occupy. Individuals with better information should thus be expected to have greater fitness (Dall et al. 2005). This supposition has led to an enduring belief among behavioral ecologists that familiarity with a physical space, or site familiarity, improves individual fitness (Baker 1978; Greenwood and Harvey 1982; Stamps 1995; Harwood et al. 2003). Benefits associated with site familiarity have also been proposed as the mechanism underlying the widespread occurrence of site fidelity in multiple taxa (Switzer 1993; Wolf et al. 2009). Many species expend great effort to return to previously occupied seasonal ranges, often migrating over large distances, and such fidelity to a particular location has been shown to enhance survival and reproductive success (Switzer 1993). Although it is assumed that the mechanisms

of these benefits are related to site familiarity, the actual fitness consequences of site familiarity have rarely been demonstrated (Piper 2011).

The main proximate mechanism underlying site familiarity is the spatial memory of resources and physical habitat features (Piper 2011; Spencer 2012), which can occur across different scales (van Beest et al. 2013). Home ranges (or territories in species defending exclusive access to an area) are the result of decisions made by individuals at multiple scales, ranging from the selection of habitats from those available over larger areas (Johnson 1980) to decisions made during daily movements and foraging bouts (Wolf et al. 2009; van Beest et al. 2013). The home range thus represents an animal's best solution to optimize energy intake while simultaneously minimizing the risk of predation. Within home ranges, familiarity has been linked to advantages such as increased use of high-quality forage patches after an initial learning period (Wolf et al. 2009) and better escape ability from simulated predators (Clarke et al. 1993). Fitness consequences associated with site familiarity should therefore also be detectable at the home range scale.

Much of our current understanding of the advantages associated with site familiarity comes from studies on birds (Piper 2011). Ungulates, however, are a taxonomic group where individuals should also benefit from site familiarity. Many ungulate species show high fidelity to seasonal home ranges (Edge et al. 1985; Purdue et al. 2000; Wittmer et al. 2006) and are long-lived, both important traits for spatial learning (Piper et al. 2008; Spencer 2012). Ungulates also utilize spatial knowledge at several spatial scales, showing plasticity in home range size and seasonal movements (Fryxell and Sinclair 1988). Variation in these behaviors has already been linked to seasonal variation in forage quality (Garrott et al. 1987; Pettorelli et al. 2007) as well as predation risk (Fryxell et al. 1988; Wittmer et al. 2006), highlighting the potential benefits of site familiarity in ungulates (van Beest et al. 2013).

Black-tailed deer (*Odocoileus hemionus columbianus*), a subspecies of mule deer (*Odocoileus hemionus*), occupy complex forested habitats in coastal areas of western North America. Both species are known to move between seasonal ranges, and their fidelity to these ranges is well documented (Geist 1981; Garrott et al. 1987; McCorquodale 1999). Seasonal home ranges are comparatively small given their body size, particularly in black-tailed deer in forested areas with high resource availability (Geist 1981). The small size of seasonal ranges combined with documented among-year fidelity suggests that site familiarity should be an important fitness determinant in these species.

Black-tailed deer, like other ungulates, are also well suited for site familiarity studies since their body size allows researchers to fit them with GPS collars that provide data required to understand potential benefits of familiarity including habitat use and selection, movements, survival probabilities,

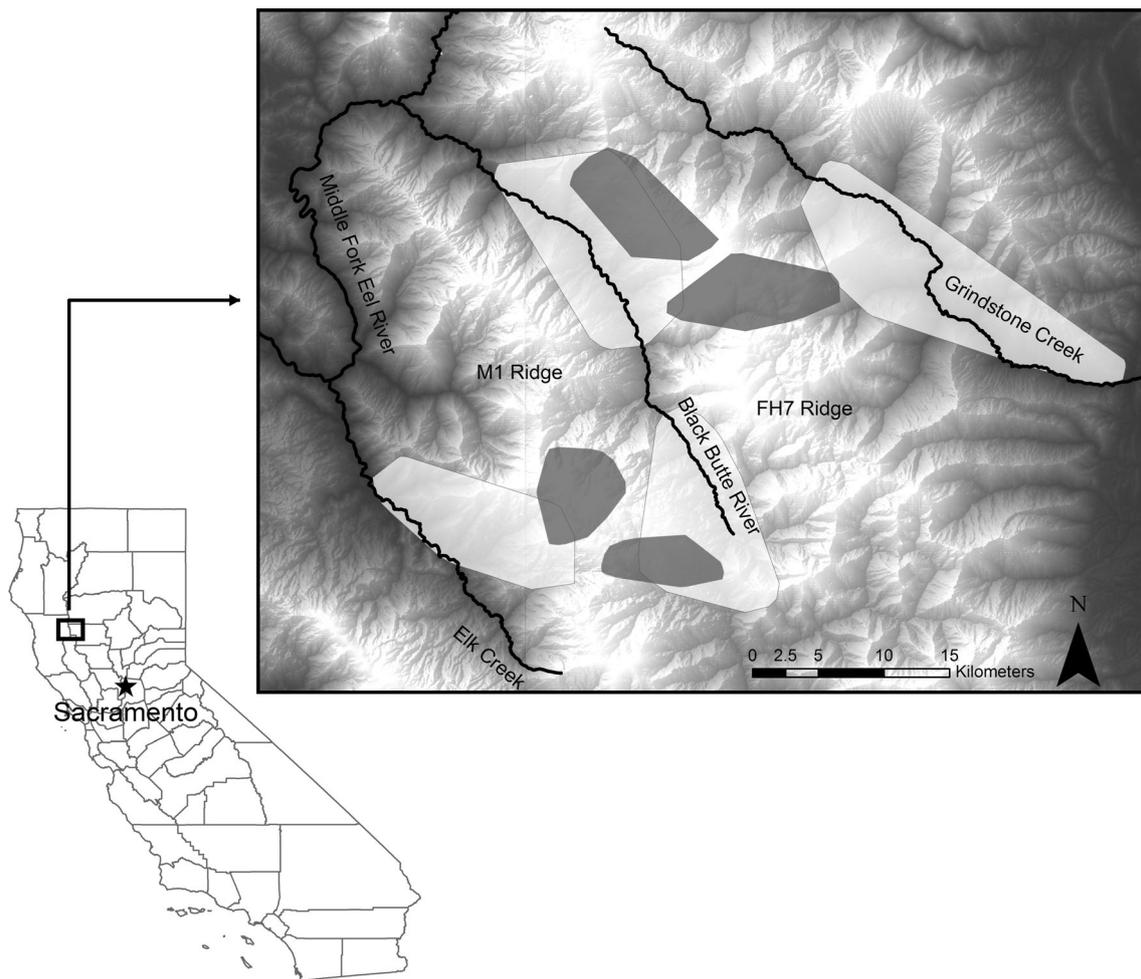
and cause of mortality. Here, we report the fitness consequences of site familiarity determined from a study of black-tailed deer in northern California over 4 years. We placed GPS collars on 57 female deer to (a) track seasonal movements, (b) determine seasonal home ranges and core areas, and (c) monitor survival and cause of mortality. We then used estimates of seasonal home ranges and core areas as measures of site familiarity to examine how predation risk varied in familiar and unfamiliar areas while accounting for the effects of forage availability and age class on survival (Loison et al. 1999; Hopcraft et al. 2010). Specifically, we tested the following predictions of the effects of site familiarity on the use of space by black-tailed deer: (P1) The risk of death will be lower inside compared to outside seasonal home ranges and core areas of individual deer; (P2) If P1 is true, then deer with more forage availability within their home range will be less likely to move outside identified home ranges; (P3) Older deer will be less likely to leave their home range due to improved familiarity with the distribution of forage and predation risk; (P4) Territory size should decrease with adulthood as spatial learning occurs.

## Materials and methods

### Study area

Our ~1,000-km<sup>2</sup> study area spanned three watersheds and two large ridges in the California coastal mountains and was located almost completely within the Mendocino National Forest (Fig. 1). Terrain was rugged and steep except on ridge tops. Vegetation at low elevations included mixed oak woodlands (*Quercus* spp.), dense chaparral, and grasslands, while mid-elevations were comprised mainly of mixed coniferous forests dominated by pine (*Pinus* spp.) and Douglas-fir (*Pseudotsuga menziesii*). High-elevation plant communities were a mix of true fir (*Abies* spp.), shrub species (e.g., *Ceanothus* spp., *Prunus* spp.), and scattered dry and wet meadows. Important deer forage included herbaceous plants, *Ceanothus* shrubs, and oak leaves. Almost all precipitation (mean=1,320 mm) occurred from October through April. Snow was generally limited to elevations >950 m and occurred irregularly during dry winters.

The study area supported a diverse predator community that included pumas (*Puma concolor*), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). Black-tailed deer were the only resident ungulate. Female black-tailed deer spent summer and winter clustered in high-quality habitats (Fig. 1). Summer ranges were located on ridge tops where females also gave birth, and winter ranges were in drainages at lower elevations. Deer usually traveled the short distance (typically 5–10 km) between their seasonal ranges in a single day (unpublished data). Pumas tracked elevational movements of deer, although GPS location



**Fig. 1** The study area in the context of the state of California showing the three watersheds and two main ridges (*M1* and *FH7*). The relief in the map shows elevation with *darker areas* indicating lower elevation. Summer ranges are shown as *dark gray polygons* and winter ranges as *white polygon*

data of simultaneously fitted individuals showed that the mean summer elevation used by collared deer was higher than that of pumas in our study area (Allen et al. 2014).

#### Adult deer capture, monitoring, and mortality assessment

We captured 60 adult female deer on high-elevation summer ranges from 2009 to 2013 and fitted them with GPS collars (Lotek™ or Telonics™) programmed to record locations every 1 to 5 h. Capture methods have been described in Casady and Allen (2013), and all procedures were approved by an Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886). Three individuals died from capture-related mortalities and were censored from all analyses. GPS collars of seven individuals failed prior to retrieval of location data and were thus excluded from our mortality risk analysis (see below). Age of deer was determined based on cementum annuli methods and based on observed differences in survival probabilities were grouped into the following three age categories: yearlings (1–

2 years old), prime-aged adults (2–7 years old), and senescent individuals (>8 years) (Marescot et al. 2014).

We monitored deer status from the ground every 1–4 days from mid-June through mid-September and every 7–14 days from the ground or the air during the rest of the year. Collars were programmed to switch to a mortality signal after 4 h of inactivity to facilitate mortality recovery. Mortalities on summer range were typically recovered within 1 week of first detection (mean=8.2 days, standard error (SE)=1.8), while investigation of mortalities during winter was often delayed due to inclement weather and difficulties accessing winter range (mean=147.5 days, SE=19.5). Cause of mortality was determined during site investigations using systematic criteria including disposition of the carcass, predator sign, evidence of caching, bite marks, and blood (Atkinson and Janz 1994).

#### Home range, forage, and weather

Home ranges and core areas were estimated at the 95 and 50 % isopleth, respectively, using the local convex hull (LoCoH)

method with the “minimum spurious hole covering” rule (Getz and Wilmers 2004; Getz et al. 2007). We estimated individual home ranges and core areas for summer and winter separately based on observed patterns in space use and excluded locations during distinct elevational movements. We then calculated the weekly probability of deer leaving their home range and core area by dividing the number of locations outside the home range/core area by the total number of locations for each week. We chose a weekly interval because of data showing that pumas in our study area on average killed 1.07 deer per week (Allen et al. 2014).

We assigned individuals to distinct summer and winter ranges using spatial gaps in the GPS data greater than twice the size of the average diameter of an adult home range and geographic features that created barriers to movement. The extent of these distinct seasonal ranges was determined using 95 % minimum convex polygons (MCPs) from GPS locations of all collared deer within each seasonal range. Detailed vegetation data were collected on summer and winter ranges using a combination of remote sensing and vegetation surveys. All vegetation types were classified according to the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG), a vegetation classification system developed by the United States Forest Service that uses infrared satellite imagery and field verification to classify multiple vegetation types in terms of overall cover type (e.g., conifers, shrubs) and detailed vegetation classes (e.g., ponderosa pine *Pinus ponderosa*) (Brohman and Bryant 2005). In addition, we quantified the biomass of important deer forage (including forbs, grasses, shrubs, and trees) on summer range using plant surveys (Forrester 2014). We focused on summer vegetation because of the critical need for quality nutrition during late pregnancy and lactation (Parker et al. 2009).

We estimated the amount of summer forage available to each deer by calculating the amount of forage for each CALVEG habitat type within individual home ranges and core areas (forage  $\text{g/m}^2 \times \text{habitat area}$ ), summing these values for all habitat types, and then dividing by the total area. Herbaceous biomass varied among years and was thus calculated separately for each year. Shrub biomass varied little among years, and its availability was calculated for all years combined. We also created a forage availability index for summer and winter home ranges and core areas by calculating the area of high-quality forage CALVEG vegetation types within individual home ranges and core areas using ArcGIS. High-quality CALVEG vegetation types included oak woodland, herbaceous, and shrub species preferred by black-tailed deer (Dasmann and Taber 1956; Wallmo 1981).

We acquired daily precipitation and temperature data from four United States Geological Survey (USGS) weather stations and snowpack depth from two California state snow-monitoring areas located in the study area. We created a winter severity index that was the number of days below freezing ( $0^\circ\text{C}$ ) from arrival on winter range to each week during the year. We accounted for

difference in elevation between deer home ranges and weather stations by adjusting the temperature of the weather station nearest the winter range by the standard environmental lapse rate of  $6.49^\circ\text{C}/1,000\text{-m}$  elevation. Our weather variables included winter severity index, total precipitation to date, previous total winter precipitation, and total April snowpack.

### Statistical analysis

We used Kaplan-Meier procedures (Pollock et al. 1989) based on weekly encounter histories to determine survival rates. We tested for differences in survival among years, age classes, seasons, and between individual summer and winter ranges using log-rank tests (Cleves et al. 2010).

We used cumulative incidence functions (CIFs) to calculate the summer, winter, and annual cause-specific mortality rates of deer and used the delta method to calculate associated standard errors (Coviello and Boggess 2004). Cumulative incidence functions model the risk of death occurring from one of several causes as the probability of the time of death ( $T$ ) from cause  $i$  occurring before time  $t$ :

$$\text{CIF}_i(t) = P(T \leq t \text{ and death from cause } i). \quad (1)$$

We examined how forage availability, proximity to predators, weather, and individual deer characteristics affected the risk of mortality and the probability of a deer spending time outside its home range or core area using an a priori set of models (ESM 1). We used the amount of summer herbaceous and oak forage and the area of herbaceous and oak CALVEG cover types within seasonal home ranges and core areas in the “forage” model. We used the distance between the mean monthly elevation of pumas and deer (Allen et al. 2014) in the “proximity to predators” model. We created a “weather” model with precipitation and the number of freezing days as time varying covariates for each weekly encounter date. The “individual deer” model consisted of age class and the probability a deer was inside or outside the 95 or 50 % isopleth of its seasonal LoCoH home range. We also tested for combinations of each of the variables (e.g., forage + proximity to predators + weather). Prior to our analysis, we ensured covariates were not highly correlated (i.e., correlation coefficients  $<|0.7|$ ).

We modeled the risk of mortality using Cox proportional hazards (Cox 1972; Therneau and Grambsch 2000), following the standard form:

$$h(t|\mathbf{X}_j) = h_0(t)\exp(\mathbf{X}_j\beta_x), \quad (2)$$

where  $h(t|\mathbf{X}_j)$  is the hazard rate for the  $j$ th deer at time  $t$ ,  $h_0(t)$  is the baseline hazard function, and the regression coefficients  $\beta_x$

are estimated from the risk covariates  $X_j$  for the  $j$ th deer. The  $\beta_x$  are used to estimate hazard ratios that are a measure of the relative risk of death, where the hazard ratios are the exponential functions of the  $\beta$ s from Eq. 1, and a hazard ratio (HR) of less than or greater than 1 represents a smaller or greater chance of death, respectively. We considered a hazard ratio significantly different than 1 if the 95 % confidence interval did not overlap 1. We used a delayed entry design with left and right censored data with survival time based on biological years (Fieberg and DelGiudice 2009) beginning on June 1 where deer entered the analysis at capture and exited upon death or dropping their GPS collar (Hosmer et al. 2011).

We modeled the probability of a deer moving outside the 95 or 50 % isopleth of its seasonal home range with a multiple failure Cox proportional hazards model (Therneau and Grambsch 2000). Deer were counted as outside of their range if any locations fell outside the home range/core area on the day selected for the encounter history. We used the same model set described in the survival analysis above.

We tested the assumption of proportional hazards for covariates in Cox hazards and CIF models using graphical methods and Schoenfeld residual plots (Grambsch and Therneau 1994). We assessed model fit by plotting the cumulative hazard function against the Cox-Snell residuals and testing for a 1:1 fit (Therneau and Grambsch 2000).

We selected models using Akaike information criterion adjusted for small sample sizes ( $AIC_c$ ) and presented models within 4  $AIC_c$  units of the best model (Burnham and Anderson 2002). We considered nested models as competitors for best model only if parameters in the model were significant at the 0.1 level or if parameters were not merely a subset of the competing model (Burnham and Anderson 2002; Arnold 2010). If multiple non-nested models were within  $\Delta 4 AIC_c$  of the best model, we report model-averaged parameters (Burnham and Anderson 2002).

We conducted post hoc analyses to test if lower survival probabilities of senescent deer could be attributed to differences in home range composition and habitat selection between age classes. We tested for differences in the amount of forage inside home ranges/core areas of prime-aged and senescent individuals using repeated measures analysis of variance (rANOVA) or Friedman's test for repeated measures if variables could not be transformed to meet normality assumptions, with age class as the independent variable and amount of specific habitats as dependent variables. We tested if the amount of forage within a home range was normally distributed with the Shapiro-Wilk test and used Bartlett's test to determine if variance was homoscedastic.

## Results

### Survival rates

A total of 21 deer died during the study. There were no differences in survival between winter and summer ranges (likelihood ratio (LR) test,  $\chi^2_{df=1} = 0.15, p=0.70$ ) or among the eight identified seasonal ranges (LR test,  $\chi^2_{df=7} = 9.28, p=0.319$ ). There also was no significant difference in annual survival among years (LR test,  $\chi^2_{df=3} = 4.81, p=0.308$ ). Annual survival differed among age classes (LR test,  $\chi^2_{df=2} = 6.15, p=0.046$ ), with prime-aged females experiencing higher survival (0.78, SE=0.06, coefficient of variation (CV)=0.10) than both yearlings (0.64, SE=0.16, CV=0.39) and senescent individuals (0.60, SE=0.15, CV=0.69).

Predation was the primary cause of mortality in all seasons, although delays retrieving winter mortalities resulted in a high number of unknown mortalities on winter range (Table 1). All predation mortalities but one were due to pumas. A 2-year-old nutritionally stressed deer was killed by a black bear.

### Home ranges, core areas, and risk of death (P1)

We pooled data across years since there were no significant differences in survival. All covariates met proportional hazard assumptions. Several competing models were within  $\Delta 4 AIC_c$  of the top model in both the home range and core area analyses, so we averaged model parameters. The probability of leaving an individual home range was the best predictor of mortality risk, and deer with a 40 % probability of moving outside their respective home ranges were four times more likely to die (Table 2). The probability of individuals leaving core areas had a weaker relationship with mortality risk. Individuals with a 40 % probability of leaving their core area in a given week were twice as likely to die as animals that stayed within the core. The top core area models did not explain mortality risk as well as the top home range models ( $>\Delta 7 AIC_c$ , see ESM 1).

Mortality risk was reduced by 3 % for each additional hectare of herbaceous habitat within a home range and by 10 % for every 100-m difference in average monthly elevations of simultaneously collared pumas. Core area models

**Table 1** Cause-specific mortality rates shown as cumulative incidence functions by season and annually for adult female black-tailed deer in Mendocino National Forest from 2009 to 2013

Cause of mortality	Summer	SE	Winter	SE	Annual	SE
Predation	0.12	0.04	0.06	0.02	0.18	0.05
Unknown cause	0.01	0.01	0.08	0.03	0.09	0.03
Poaching	0.01	0.01	0.02	0.01	0.03	0.02

**Table 2** Model averaged results for Cox proportional hazards models within  $\Delta 4$  AIC<sub>c</sub> of the top model

	Covariate	Hazard ratio	Standard error	95 % confidence interval
Home range models	Probability of leaving home range	1.42	0.09	1.19–1.69
	Herbaceous area in home range (ha)	0.97	0.02	0.94–1.00
	Young age class	3.22	0.63	0.94–11.06
	Senescent age class	2.38	0.48	0.93–6.10
	Distance from pumas	0.90	0.04	0.82–0.98
Core area models	Probability of leaving core area	1.17	0.08	0.75–1.00
	Herbaceous area in core area (ha)	0.84	0.09	0.70–1.01
	Young age class	2.24	0.43	0.91–5.49
	Senescent age class	2.13	0.34	1.11–4.11
	Distance from pumas	0.98	0.02	0.95–1.01

Hazard ratios greater or less than 1 indicate an increase or decrease in mortality risk, respectively, and 95 % confidence intervals indicate if the hazard ratio is significantly different than 1. Hazard ratios for the probability of leaving the home range/core area and herbaceous area indicate the change in mortality risk for a 10 % increase in probability of leaving the range/area and a 1-ha increase in herbaceous habitat in the range/area, respectively. Hazard ratios of the young and senescent age classes are in comparison to prime-aged adults. Results for the young age class should be interpreted cautiously since the sample size is small ( $n=4$ ). Distance from pumas is an index of predation risk that indicates the change of risk for every 100-m increase in the difference between the average elevation of deer and pumas in the study area

showed similar relationships (Table 2). Senescent individuals were two times more likely to die than prime-aged deer at either spatial scale. Mortality risk for deer remained constant for most of the year but declined in spring (Fig. 2). Weather, biomass of summer forage, and amount of oak habitat within

individual home ranges or core areas did not predict variation in mortality risk.

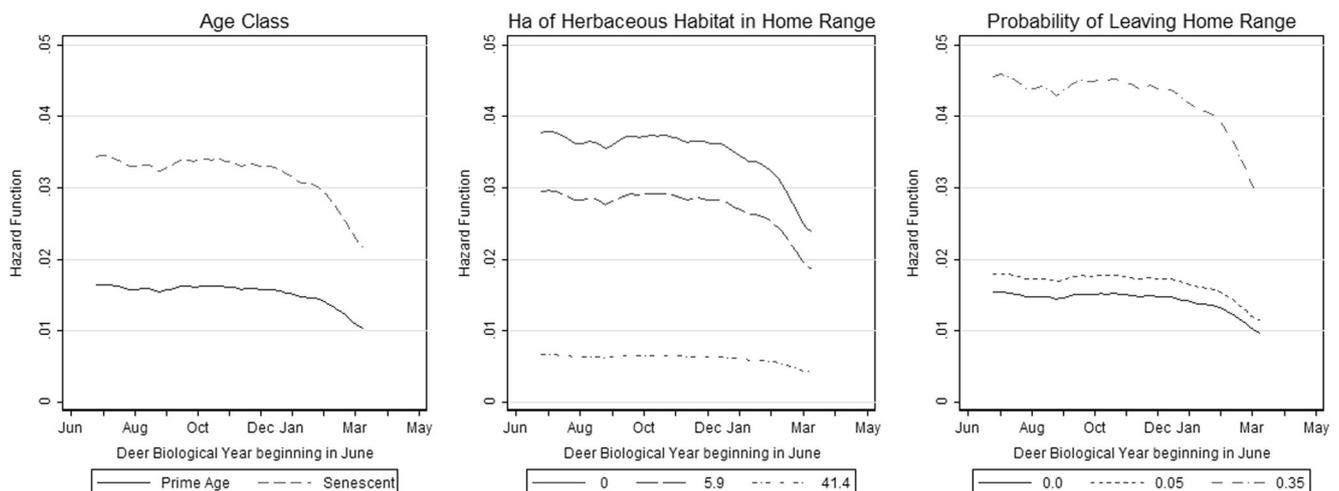
Of 21 observed mortalities, 13 occurred outside respective 95 % home range isopleths, and 18 occurred outside of respective 50 % core area isopleths. Distances of mortalities to nearest home range boundaries averaged 1,171 m (SE=325 m), with eight mortalities >700 m outside identified home ranges.

#### Factors influencing leaving individual home ranges (P2 and P3)

A single model explaining the probability of an individual leaving its home range was strongly supported ( $w_i=0.93$ ). After controlling for the amount of precipitation and freezing days, both of which reduced the probability that deer would leave their home ranges, the amount of herbaceous forage habitat within home ranges and the biomass of herbaceous and oak forage on summer range reduced the probability of stepping outside identified ranges (Table 3). Deer were also 65 % more likely to leave their home range during winter despite the significantly larger range size (ANOVA,  $F_{1, 143} = 11.95$ ,  $p < 0.001$ ). Age class had no impact on the likelihood of leaving home ranges in either summer or winter (Table 3).

#### Effects of age on home range size (P4)

There was no difference in home range sizes of prime-aged and senescent individuals during summer (0.62 vs. 0.60 km<sup>2</sup>, rANOVA,  $F_{2, 46} = 0.02$ ,  $p = 0.98$ ) or winter (0.89 vs. 0.72 km<sup>2</sup>, rANOVA,  $F_{2, 43} = 0.13$ ,  $p = 0.88$ ). There were also no differences in the size of the core areas of prime-aged and senescent individuals during summer (0.07 vs. 0.08 km<sup>2</sup>, rANOVA,  $F_{2, 46} = 0.52$ ,  $p = 0.60$ ) or winter (0.11 vs. 0.08 km<sup>2</sup>, rANOVA,



**Fig. 2** Hazard rates for age class, forage area within home range, and the probability of leaving the home range for adult female black-tailed deer in the Mendocino National Forest from 2009 to 2013. Values for hectares of

herbaceous habitat and probability of leaving the home range are the 10, 50, and 90 % quantiles of covariate values. See Table 2 for the significance of covariates on deer mortality risk

**Table 3** Cox proportional hazards model results for the top model of the probability of leaving the home range for adult female deer in Mendocino National Forest from 2009 to 2013

Covariate	Hazard ratio	<i>p</i> value	95 % confidence interval
Seasonal range	1.65	0.005	1.162–2.349
Herbaceous area in home range	0.99	0.019	0.987–0.998
Summer home range herbaceous biomass	0.95	0.049	0.906–0.999
Summer home range oak browse biomass	0.97	0.024	0.948–0.996
Cumulative precipitation	0.98	0.049	0.957–0.999
Cumulative days below freezing	0.99	<0.001	0.996–0.998

Odds ratios greater or less than 1 indicate an increase or decrease in probability of leaving the home range, respectively, and *p* values indicate if the hazard ratio is significantly different than 1

$F_{2, 43} = 0.23, p = 0.80$ ). The mean seasonal range size for all deer >2 years of age was 0.71 km<sup>2</sup> (SE=0.04), with summer home ranges averaging 0.61 km<sup>2</sup> (SE=0.05 km<sup>2</sup>) and winter home ranges averaging 0.86 km<sup>2</sup> (SE=0.07 km<sup>2</sup>). The mean core area size was 0.08 km<sup>2</sup> (SE=0.004), with summer core areas averaging 0.07 km<sup>2</sup> (SE=0.004) and winter core areas averaging 0.10 km<sup>2</sup> (SE=0.008). Yearlings utilized slightly larger summer (0.82±0.37 km<sup>2</sup>) and winter ranges (1.17±0.27 km<sup>2</sup>) than other age classes but had similar sized core areas (summer mean=0.07 km<sup>2</sup>, SE=0.01; winter mean=0.10, SE=0.03). There was no difference in the amount of forage habitat within home ranges of prime-aged and senescent individuals in either summer (rANOVA,  $F_{2, 46} = 0.01, p = 0.99$ ) or winter (rANOVA,  $F_{2, 43} = 0.24, p = 0.78$ ). There was also no difference in the amount of forage habitat in core areas in summer (rANOVA,  $F_{2, 46} = 0.32, p = 0.73$ ) or winter (rANOVA,  $F_{2, 43} = 1.28, p = 0.29$ ). Senescent deer ( $n = 12, 50 \pm 1.85$  kg) weighed more than prime-aged deer ( $n = 44, 45 \pm 1.04$  kg) in our study area (unequal variance *t* test,  $t_{54} = -2.383, p = 0.02$ ).

## Discussion

The fitness effects of site familiarity have rarely been demonstrated despite the expected widespread relevance of the concept (Piper 2011). We found strong fitness benefits of using familiar areas in a medium-sized ungulate, the black-tailed deer, which is negatively affected by predation across much of its distribution (Forrester and Wittmer 2013). The observed fitness benefits linked to familiarity were lower risks of mortality and predation at two different scales inside identified seasonal home ranges. Furthermore, we found a link between bottom-up effects and the probability of use of familiar spaces.

Specifically, deer with access to greater amounts of forage within seasonal home ranges and access to higher quality summer range were less likely to leave their home range during weekly monitoring intervals and thus venture into risky areas. Given that the home range is one of the most widely used metrics to describe the spatial ecology and habitat requirements of vertebrates (Burt 1943; Kie et al. 2010), these findings have significance for our understanding of the role of site familiarity and private information on space use and survival.

One of the presumed benefits of site familiarity is an improved knowledge of the spatial distribution of both forage quantity and quality. In mid-sized ungulates such as black-tailed deer, the amount of digestible energy (or forage quality) is more important than the overall amount of forage (Kie 1999; Parker et al. 2009; Hopcraft et al. 2010). Selecting and ingesting high-quality forage takes more time than searching for forage patches (Kie 1999), and familiarity with high-quality forage patches thus minimizes the overall time an individual spends foraging in potentially risky habitats. The very small size of seasonal home ranges (mean=0.74 km<sup>2</sup>) and core areas (mean=0.08 km<sup>2</sup>) we observed in our study make it highly likely that deer were familiar with the seasonal distribution of forage and also had sufficient access to high-quality forage to operate at such small scales.

Familiarity with very small home ranges also resulted in lower predation risk for deer within their seasonal home range and inside core areas, and this relationship was consistent among seasons and various habitat types. The consistency of the effect suggests the direct link between familiarity and lower risk of predation, but it is unlikely that deer actively avoided predators. Actively avoiding predation depends on the ability of prey to interpret predator and habitat specific cues of risk (Lima 2002; Creel and Winnie Jr. 2005; Laundre 2010) as well as the characteristics of predators and the space in which they interact with prey (Lima 2002). Pumas are the only predators of adult deer in our study area and are ambush predators that prefer to hunt in structured habitat (Holmes and Laundre 2006). Pumas also operate at much large spatial scales than their ungulate prey (Logan and Sweaner 2010), and in our study area, the documented respective home ranges of female and male pumas were 375 and 490 times larger (Allen 2014) than the average seasonal range of black-tailed deer. Puma activity within any given deer home range would thus likely be sporadic providing few active cues (e.g., scent markings, regular travel paths, etc.) that deer could detect and use to avoid them. Thus, it is unlikely deer actively avoided predation based on private information about pumas they gathered inside their home ranges.

It is more likely that the higher survival rates we observed for deer remaining within their home ranges were simply a consequence of reduced encounter probabilities with pumas. Minimizing the time spent foraging reduces predation risk as

it allows individuals to minimize movement and return to bedding areas to ruminate and digest their food (Kie 1999). Such an interpretation would be consistent with predictions from the theory of predator–prey “shell games” (Mitchell and Lima 2002). Predator–prey shell game theory predicts that the risk of attack from a predator is determined by the predictability of prey occurrence in a given area, prey vigilance, and the killing efficiency of the predator (Mitchell and Lima 2002). The optimal strategy of prey facing predators with a high killing efficiency is to avoid all predator encounters by remaining stationary (Mitchell and Lima 2002), while the prey response to a low killing efficiency predator should be large-scale random movements (Lima 2002). Deer are unlikely to survive an attack by pumas (Hornocker 1970), and if deer perceive the known area of their home range as safer than unknown territory (a de facto refuge), the response of staying within a small home range is adaptive against a predator with high killing efficiency whose location is uncertain (Sih 1992; Mitchell and Lima 2002). An alternate explanation for the observed lower risk of mortality within individual home ranges would be that deer selected for safe home ranges within a common risk landscape and that deer outside these safe areas were more likely to die regardless of site familiarity. We were, however, unable to test for a common vs. individual landscape of risk due to an insufficient sample size of deer with overlapping home ranges. We thus caution that there exist other mechanisms besides site familiarity that may result in the use of the home range area as a de facto refuge.

The concept of a home range as a refuge is, however, also consistent with our results regarding forage availability and the probability of a deer leaving a home range. If some areas are safe and some areas are risky, deer should only forage in risky areas when forced there by hunger (Sinclair and Arcese 1995). Our results showed this exact effect, as lower forage availability increased the chance of a deer leaving their home range and abandoning the advantages of site familiarity for a higher risk area. The role of forage limitation varied seasonally given that deer were more likely to step outside their home ranges in winter. Our results also indicated the possibility of delayed fitness effects of access to summer forage, given that deer with more forage biomass on the summer range were less likely to leave their home range in summer and winter.

We also found physiological constraints to the benefits of site familiarity. Senescent individuals were twice as likely to die than prime-aged adults, even though we did not find evidence of lower weight in senescent individuals as reported elsewhere (Nussey et al. 2011). The increased probability of older deer dying was also not linked to differences in forage availability or to the likelihood of leaving the home range. Senescence may have affected the ability of older deer to detect and avoid pumas in less obvious ways not measured by weight or body condition (Boyd et al. 1994; Réale and Festa-Bianchet 2003).

Given the wide occurrence of site fidelity in ungulates (Switzer 1993; Wolf et al. 2009), the fitness benefits of site familiarity are also likely to be widespread. We predict that site familiarity will be important for ungulates with high site fidelity under three conditions: (1) when there are enough forage resources for stable home ranges, (2) when habitat has structure and biotic complexity, and (3) when the direct cues of predation risk are unclear and do not allow ungulates to determine well-defined spatial refuges. Habitat structure is important because ungulates in complex habitats are more likely to be solitary and rely on individual predator evasion rather than group defense strategies (Jarman 1974). The value of private information gained by an ungulate familiar with a site will also increase in areas with more habitat complexity (Piper 2011). The importance of site familiarity in the fitness of ungulates that fit these criteria remains to be investigated, as well as the role of spatial knowledge in balancing predation risk from multiple predators with different hunting strategies (e.g., social and cursorial carnivores such as wolves (*Canis lupus*) vs. solitary and ambush predators such as pumas in the same community). The importance of site familiarity to reproductive success is also unknown and important. We suggest that benefits of site familiarity within home ranges will be widespread, and inclusion of this concept will improve our understanding of both ungulate behavior and predator–prey interactions (Piper 2011) and help predict how ungulates may react to large-scale habitat changes (Faille et al. 2010).

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