

EVIDENCE FOR A NEW SEARCH BEHAVIOR: PORCUPINES “SCOUT” FOR
WINTER HABITAT DURING SUMMER IN A COASTAL DUNE SYSTEM

By

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ABSTRACT

EVIDENCE FOR A NEW SEARCH BEHAVIOR: PORCUPINES “SCOUT” FOR WINTER HABITAT DURING SUMMER IN A COASTAL DUNE SYSTEM

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Species are often challenged by periodic changes in food availability and habitat quality. These environmental conditions may provide strong selective pressure for animals to strategically "scout" for important resources during periods of abundance, when exploratory movements are less costly. North American porcupines experience a drastic shift in forage quality from summer - a time of abundant, high quality forage - to winter, a nutritional bottleneck. I evaluated potential scouting behaviors of porcupines in Tolowa Dunes State Park, California using movement and habitat-use data. I compared summer and winter space use of porcupines using GPS data and monitored seasonal use of winter habitat with the use of trail cameras. I also measured nutritional and structural variables of these habitats and used these data to model potential drivers of scouting behavior. Results provided evidence for scouting, suggesting that structural characteristics of winter habitat were driving summer movements. Specifically, it appears porcupines sampled winter habitat randomly during summer, then selected a subsample of those areas to use during winter using information about habitat structure, rather than winter forage quality. Porcupines in Tolowa may be limited by potential areas to seek refuge from winter rainfall and cold temperatures. More broadly, these results provide

evidence of a previously undescribed search behavior that other species may be utilizing to inform selection of resources and habitat. More research is needed to improve our understanding of the way scouting is exhibited across taxonomic groups and habitat types.

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INTRODUCTION

Movement offers animals a number of evolutionary advantages – via movement, individuals can seek out food, shelter, and mates, which ultimately result in increased energy consumption, protection, and reproduction (Nathan et al. 2008). In addition to directly perceiving information about their environment through movement, animals may also remember spatial, environmental, and experiential details to increase travel efficiency and inform resource acquisition in the future (Fagan et al. 2013). This cognitive capacity allows animals to maximize the quality of selected habitat, inform navigation at the landscape scale, and revisit sites with periodically available resources. However, memory also comes with energetic and behavioral costs: long-term memory storage generally requires larger brains and more sleep (Stickgold 2005). Furthermore, gathering information about the spatial distribution of resources might come with a dangerous learning period, which may require exploratory movements that increase energy costs and risks of predation (Fagan et al. 2013).

The costs and benefits of enhanced spatial memory exist as a series of adaptive trade-offs that determine the capacity for an animal to process, encode, and retrieve memories over time (Fagan et al. 2013). Relying too heavily on memory when moving through a landscape can reduce an animal's ability to update its cognitive map with new information (Boyer and Walsh 2010). Further, the older the memory, the more likely it is to degrade or mismatch remembered environmental conditions (Avgar et al. 2015). Considering these trade-offs and limitations, reliance on memory should be most

beneficial to animals in areas of moderate spatiotemporal habitat complexity (Fagan et al. 2013). Thus, an animal that resides in an area with patchy or predictable periodic shifts in habitat quality will benefit most from knowing where and when to meet its needs outside of its immediate perceptual range.

During movement, animals use attribute memory in concert with spatial memory to update their cognitive map with information about resource quality and abundance, and temporal factors related to both (Fagan et al. 2013). A number of examples (e.g., wild mangabeys [*Saguinus sp.*] returning to known fruiting trees [Janmaat et al. 2006], or black bears [*Ursus americanus*] visiting foraging areas outside of their home range when resources are limited [Powell 2012]) illustrate the capacity for animals to rely on long-held memories gathered from direct experience. In most cases, information gathering is considered a secondary consequence of other behaviors. For example, animals may learn about the quality of food resources while foraging, or discover a novel resting site while hunting. However, there is evidence that animals may deliberately move solely for the purpose of gathering information. For example, brush mice (*Peromyscus boylii*) will exhibit search movements to gather information during pre-dispersal (Mabry and Stamps 2008). Additionally, some bird species have been shown to engage in “prospecting” (Boulinier and Danchin 1997, Pärt and Doligez 2003, Calabuig et al. 2010, Delgado et al. 2014), a behavior to gather attribute information regarding the success of nearby nest sites in the current breeding season to inform selection during future breeding seasons. This behavior has most commonly been demonstrated in long-distance migrants

(Boulinier and Danchin 1997, Betts et al. 2008), where information gathering for future seasons can only take place in the same season in prior years.

Many non-migratory animals subsist in environments that change drastically between seasons, both in resource availability and weather conditions. Animals faced with this challenge should benefit from gathering information during the abundant season about pertinent resources for the limiting season, a search behavior I will hereafter refer to as “scouting.” However, scouting should only be beneficial if the resources needed during the limiting season are available for evaluation in the abundant season.

Across its range, the North American porcupine (*Erethizon dorsatum*) has adapted physiologically (Roze 2009, Felicetti et al. 2000, Coltrane and Barboza 2010, Coltrane et al. 2011) and behaviorally (Sweitzer and Berger 1992, Sweitzer 1996, Snyder and Linhart 1997, Somers and Thiel 2008, Coltrane 2012, Mabile and Berteaux 2014, Pokallus and Pauli 2016) to increase the likelihood of surviving winter, a period of time with reduced forage quality and often frigid weather conditions (Coltrane and Barboza 2010). During non-winter months, porcupines forage as generalists (Roze 2009), switching between broad-leaved foliage, annual forbs, and fruits such as apples and acorns to meet nutritional needs (e.g., nitrogen and sodium [Coltrane and Barboza 2010]) and accumulate fat stores needed to survive the winter months (Roze 2009). However, with the arrival of winter, most of these high-quality resources are no longer available. During this nutritional bottleneck (Coltrane and Barboza 2010), porcupines forage as facultative specialists by reducing their diets to a more digestively challenging and poor-quality diet of evergreen leaves, needles, and bark (Coltrane 2012). In addition to maximizing

accumulation of fat stores during non-winter months, porcupines must carefully select winter forage to minimize consumption of plant defense chemicals (Diner et al. 2009) and maximize acquisition of important nutrients such as nitrogen to increase energy acquisition and retention (Roze 2009).

Winter also challenges porcupines with extreme cold, rain and snow, leading to weight loss (Sweitzer and Berger 1993) and increased contraction of pneumonia (Hooven 1971). For this reason, porcupines will occupy dens during winter or rest in other structures that offer cover and thermal protection, foraging as closely as possible to the den during this time (Roze 2009). The availability of den structures may itself be a limiting resource, and in many places, rock dens may not be available at all. In coastal Northern California, female porcupines were observed using hollow logs or short tunnels in sand dunes as den spaces during winter (Appel 2016). Many porcupines also occupied short, dense, windswept conifer trees on the dunes, despite the abundant availability of taller, more linearly standing trees of the same species nearby (pers. obs.). The unique shrub-like morphology of these conifers may offer similar thermal benefits to a den space and protection from rainfall while also being a primary food resource.

The Northern California population of porcupines in Tolowa Dunes State Park (hereafter “Tolowa”) faces a compressed set of environmental conditions compared to other areas of their range (Appel et al. 2018): winters are mild and wet, but summers are not as nutritionally beneficial as other places across their range. Specifically, porcupines in Tolowa have a lower diversity of broad-leaved and mast-producing trees available to them during summer and experience high winter rainfall. Despite these conditions,

porcupines appear to employ the same resource acquisition strategies as elsewhere in their range. Like most porcupines, the Tolowa population relies on higher-quality forage during summer, switching in winter to the needles and bark of a few coniferous and evergreen species (Appel et al. 2018). Unlike most landscapes within the porcupine's distribution, seasonal resources in Tolowa are spatially segregated: winter food and den resources (coastal scrub) occupy the foredunes and summer food resources (shrub swale) are available in the troughs and backdunes (Figure 1).



Figure 1. Distribution of ecotypes across Tolowa Dunes State Park, Del Norte County, CA.

Given (1) the spatial separation of winter resources relative to summer resources, and (2) the availability of winter resources for evaluation during summer, it is possible that porcupines in Tolowa scout for winter resources during summer, when they are more energetically able to afford exploratory movements. The patchy spatial distribution of summer and winter habitat should enable detection of scouting movements. Furthermore, porcupines are known to have impressive spatial memories, with the ability to remember complex mazes up to 100 days after the initial learning period (Sackett 1913). Because precision and accuracy of spatial memories decay over time, adult porcupines may experience pressure to scout every year for the purpose of reinforcing and updating their cognitive maps with spatial and attribute information about critical winter resources. This combination of environmental and cognitive factors makes porcupines in Tolowa an ideal case for study scouting behavior of this species in a natural system.

I hypothesize that porcupines in Tolowa are scouting for winter habitat during summer to inform future selection of winter food and cover resources. Detection of scouting may be difficult compared to other behaviors, such as food acquisition or searching for mates. For this reason, I conducted several analyses and generated 4 predictions based on the movement and space use of porcupines in this system that would fit the scouting hypothesis. (1) Winter home range overlap: winter home ranges should be smaller than, and mostly contained within, summer home ranges. Additionally, the overlapping area should contain high winter utilization and low summer utilization. (2) Seasonal visitation: visits to winter habitat during summer should be short and infrequent, creating a negative relationship between summer visitation and winter space use. (3)

Random summer sampling: porcupines should be detected at fewer trees during winter, for longer periods of time, when compared to summer. Visited trees during winter should be a subset of trees scouted during summer. (4) Winter habitat selection: areas revisited during winter should differ in structure or nutrition when compared to areas only visited during summer.

To test this hypothesis and its predictions, I evaluated scouting with movement and habitat-use data. Movement data were gathered from a combination of global positioning system (GPS) and very high frequency (VHF) collars, used to evaluate the relationship between summer and winter space use of individual porcupines for predictions 1 and 2. To test prediction 4 with these data, I also quantified and compared the structural and nutritional qualities of winter areas visited by porcupines during summer to areas revisited during winter. To test predictions 3 and 4, I monitored the seasonal use of specific evergreen trees by porcupines in winter habitat by deploying 30 trail cameras and manipulating their perceived nutritional and structural qualities by baiting some with an apple and salt and/or a 19 liter bucket. The inherent structural and nutritional qualities of each tree with a camera were also quantified and included in models using camera data to test prediction 4.

STUDY AREA

The study was conducted in Tolowa Dunes State Park of Del Norte County, California (400215.74 E, 4638200.81 N, 10 T), one of the state's largest undeveloped coastal areas (California Department of Parks and Recreation 2009). While porcupines have been detected throughout Tolowa, time and resource limitations restricted the study area to only the northern section of the park (9.2 km²; Figure 2). The study area is bordered to the south by a major road (speed limit = 50 mph), the east by private properties and ranchland, the north by the Smith River, and to the west by the Pacific Ocean.

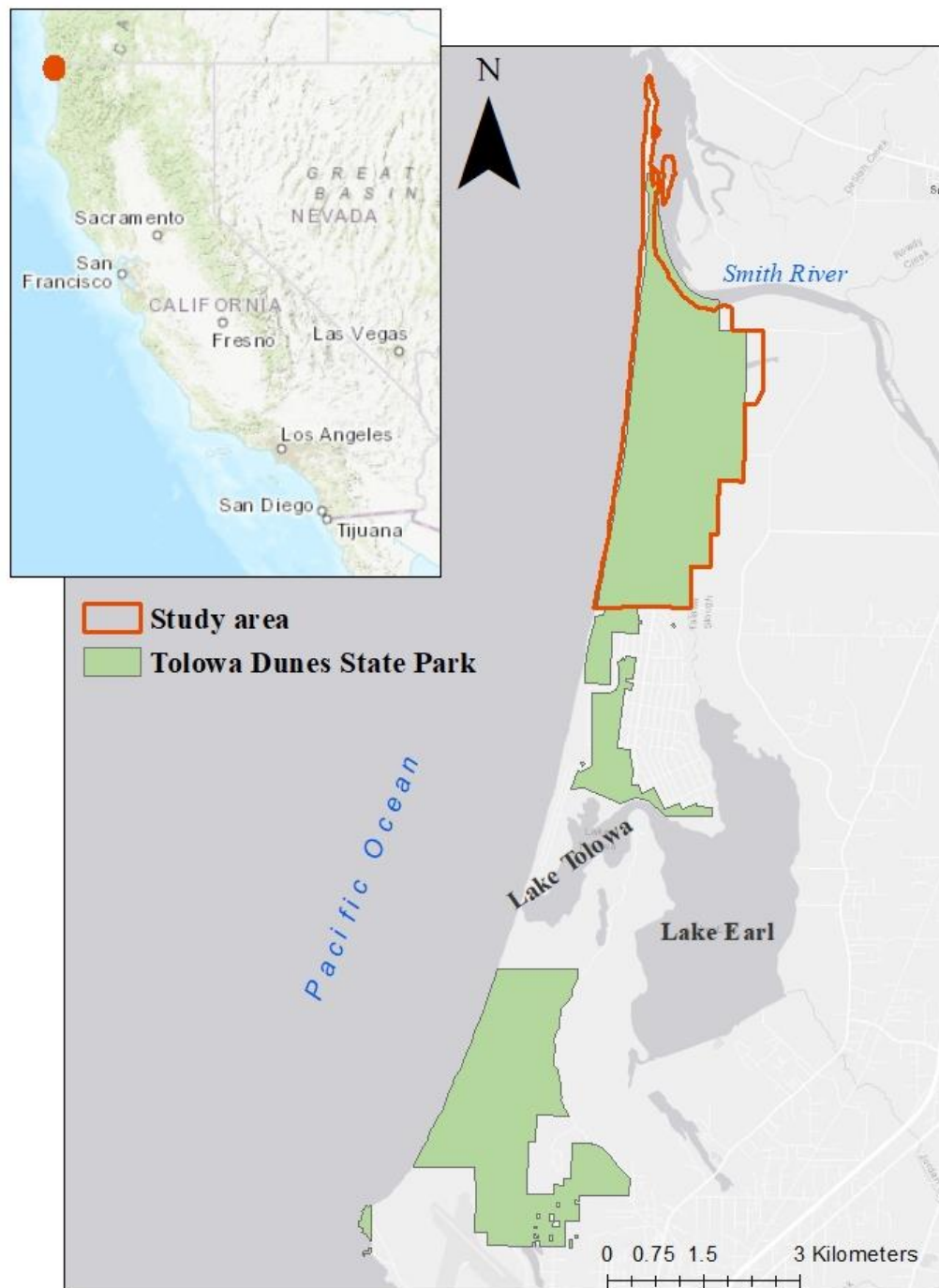


Figure 2. Boundaries of Tolowa Dunes State Park in Del Norte County, CA, USA. Area where the porcupine captures and camera study took place are outlined in orange.

Tolowa is characterized by a warm-summer Mediterranean or oceanic climate, with winters of above-freezing temperatures and high precipitation (Appel et al. 2018). The area supports a coastal dune forest community, with many ecotypes patchily distributed across the park (Figure 1). Open dunes and coastal scrub contain species such as coyote brush (*Baccharis pilularis*), California wax myrtle (*Morella californica*), dune mat forbs, and non-native European beachgrass (*Ammophila arenaria*). Forested backdunes are populated with tree species such as shore pine (*Pinus contorta contorta*) and Sitka spruce (*Picea sitchensis*; Mad River Biologists 2009). Many species of willow (*Salix sp.*) dominate the wooded and shrub swales, along with more sparsely represented species like red alder (*Alnus rubra*), Oregon crabapple (*Malus fusca*), twinberry honeysuckle (*Lonicera involucrata*), cascara buckthorn (*Frangula purshiana*), Douglas' spirea (*Spiraea douglasii*), and other native shrubs and forbs. In addition to woody species, swales and meadows contain native and non-native sedges (*Carex sp.*), rushes (*Juncus sp.*), and grasses (family *Poaceae*). The eastern edges of Tolowa and bordering fields were previously managed for cattle grazing and Aleutian cackling goose (*Branta hutchinsii leucopareia*) spring foraging habitat (Mad River Biologists 2009). While Tolowa is no longer grazed by cattle, high densities of invasive reed canary grass (*Phalaris arundinaceae*) and other non-native species introduced for grazing still persist in many areas of the park. Areas surrounding Yontocket Slough, a remnant channel of the Smith River, contain especially high densities of reed canary grass as well as native water pepper (*Persicaria hydropiperoides*) and yellow pond lily (*Nuphar lutea*) in areas regularly inundated with water.

In Tolowa, porcupines do not appear to experience heavy risk of predation. Coyotes (*Canis latrans*) are common in the region of coastal Del Norte County and often heard vocalizing in Tolowa (pers. obs.), however it is expected they only prey on porcupines when availability of more desirable prey sources are limited (Thurber et al. 1992, Prugh 2005). Rarely, mountain lions (*Puma concolor*) are seen in the park, a species known to occasionally prey on porcupines (Sweitzer et al. 1997). The primary predator of porcupines, the fisher (*Pekania pennanti*), is not known to occur within the boundaries of Tolowa. We found no evidence of predation on porcupines in Tolowa during the course of this 4-year study.

METHODS

For this study, I defined winter as 1 November – 29 February and summer as 1 March – 31 October, as these divisions relate to the timing of falling and reemerging leaves on deciduous trees (Appel 2016). All animal handling and tracking procedures were approved by the Humboldt State University Institutional Animal Care and Use Committee (IACUC; 14/15.W.73-A and 15/16.W.32-A).

Movement Analyses

I collected movement and habitat-use data from individual porcupines using GPS trackers and VHF telemetry units. To investigate the relationship between seasonal movements, I first assessed the spatial overlap of seasonal home ranges for each porcupine. Then, on a finer scale, I examined the relationship between summer and winter movement for each individual. Finally, to investigate the potential drivers of scouting behavior, I used model selection to determine which combination of nutritional and structural variables could predict if summer areas would be revisited during winter.

Data collection

To initially locate and capture porcupines, a field crew and I conducted searches of the study area from nightfall to dawn during June and July of 2015, 2016, and 2017. Flashlights and thermal cameras were used to increase detection probability. If an un-collared porcupine was seen in an open area, under vegetation, or on a low branch

during a search period, we strategically surrounded the animal and gently coaxed it into a 75 liter trashcan. Once captured, each porcupine was weighed with a hanging scale with a 0.01-kg precision (UltraSport V2-30; Jennings Scale, Phoenix, Arizona). To acquire the animal's mass, I subtracted the predetermined weight of the trash can from the total weight. If the porcupine was less than 4 kg, it was considered juvenile and too small to be collared (Dodge 1982). Adult porcupines were immobilized for collar deployment with Ketamine (5 mg/kg) and Xylazine (2 mg/kg), injected intramuscularly at the base of the tail (Morin and Berteaux 2013). Once immobilized, porcupines underwent a physical examination, which included determination of sex and several morphometric measurements, including body length, body circumference, length of hind foot, and presence of ectoparasites. For long-term identification of each individual, a passive integrated transponder (PIT) tag (Biomark, Boise, Idaho) was inserted subcutaneously between the shoulder blades. Finally, a VHF radio transmitter (model RI-2D; Holohil Systems Ltd., Carp, Ontario) and GPS tracker (i-gotU model GT-600 or GT-120; Mobile Action Technologies, New Taipei City, Taiwan) were placed on the adult animal with a handmade nylon collar, fitted and secured to the neck using a small zip tie (Appendix A). The total mass of the collar, with VHF and GPS, was less than 3% of the average porcupine's body mass at capture. A total of 25 porcupines were captured and collared, 14 in 2015, 6 in 2016, and 6 in 2017 (one of which was recaptured from 2016).

Visual relocations occurred irregularly, but always more than 24 hours apart for each porcupine. Additional locations for porcupines were obtained from GPS units, set to record 1 point per hour, with a maximum battery life of approximately 6 weeks. I

excluded points taken within the first 8 hrs after release of the animal to ensure data were not affected by handling or recovery from immobilization (Appel 2016). To increase accuracy of remaining GPS data, points for each porcupine were cleaned using an algorithm (I. Axsom, unpubl. data) to remove outliers. The algorithm compared nearest neighbor distances between each point and its previous and next point in time. If both distances were greater than the distance between the past and future point, then that central point was removed, unless neither of those distances was greater than 20 m, to prevent over-thinning of point clusters (Appel 2016).

Units were charged and replaced for each porcupine throughout each season, with the goal of attaining an equal abundance of movement data from each porcupine for summer and winter. However, acquisition of GPS locations for porcupines was ultimately limited by weather and convenience of capture, as units were not weather-proof and frequently failed prior to battery death due to water exposure. This was an especially prevalent problem during the winter months. Additionally, porcupines were often seen in trees at heights that were unsafe for capture, preventing the replacement of their GPS units at regular intervals. Thus, some porcupines were excluded from analyses due to a lack of summer or winter GPS data.

Prediction 1: Winter home range overlap

To explore the spatial patterning expected of the winter home range overlap prediction, I used GPS and VHF data from 11 porcupines to construct summer and winter kernel density estimates (KDEs) at the 95% isopleth using the `adehabitatHR` package

(Calenge 2006) in Program R (R Core Team 2019). For each porcupine, the degree of overlap and probability of use in the overlapping region for each season were calculated using two methods (

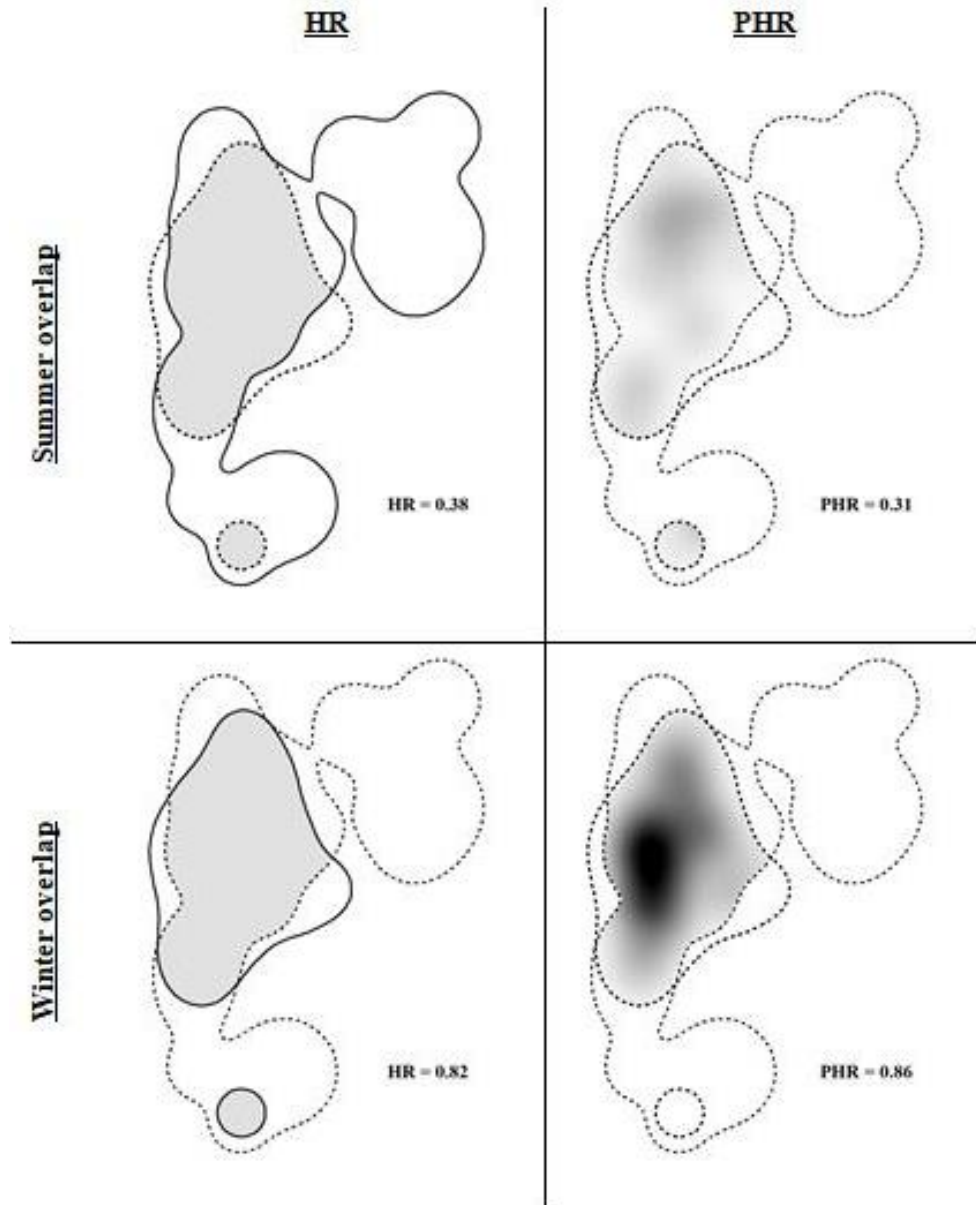


Figure 3). First, I calculated the proportional overlap of seasonal home ranges using the following equation from Kernohan et al. (2001):

$$HR_{i,j} = \frac{A_{i,j}}{A_i}$$

where A_i is the area of season i 's home range, and $A_{i,j}$ is the area overlapping both seasonal home ranges. Next, I calculated the probability of a porcupine in season j being located in its season i home range (Feiberg and Kochanny 2006), $PHR_{i,j}$:

$$PHR_{i,j} = \iint_{A_i} \hat{UD}_j(x,y) dx dy$$

where \hat{UD}_i is the estimated utilization distribution for season i and \hat{UD}_j the estimated UD for season j . This method assumes that \hat{UD}_i is >0 only in A_i and \hat{UD}_j is >0 only in A_j . In other words, A_i and A_j represent the extents of spatial use for seasons i and j . These metrics were used to calculate the overlap of winter home range over summer home range ($j = \text{winter}$), and the reciprocal ($j = \text{summer}$).

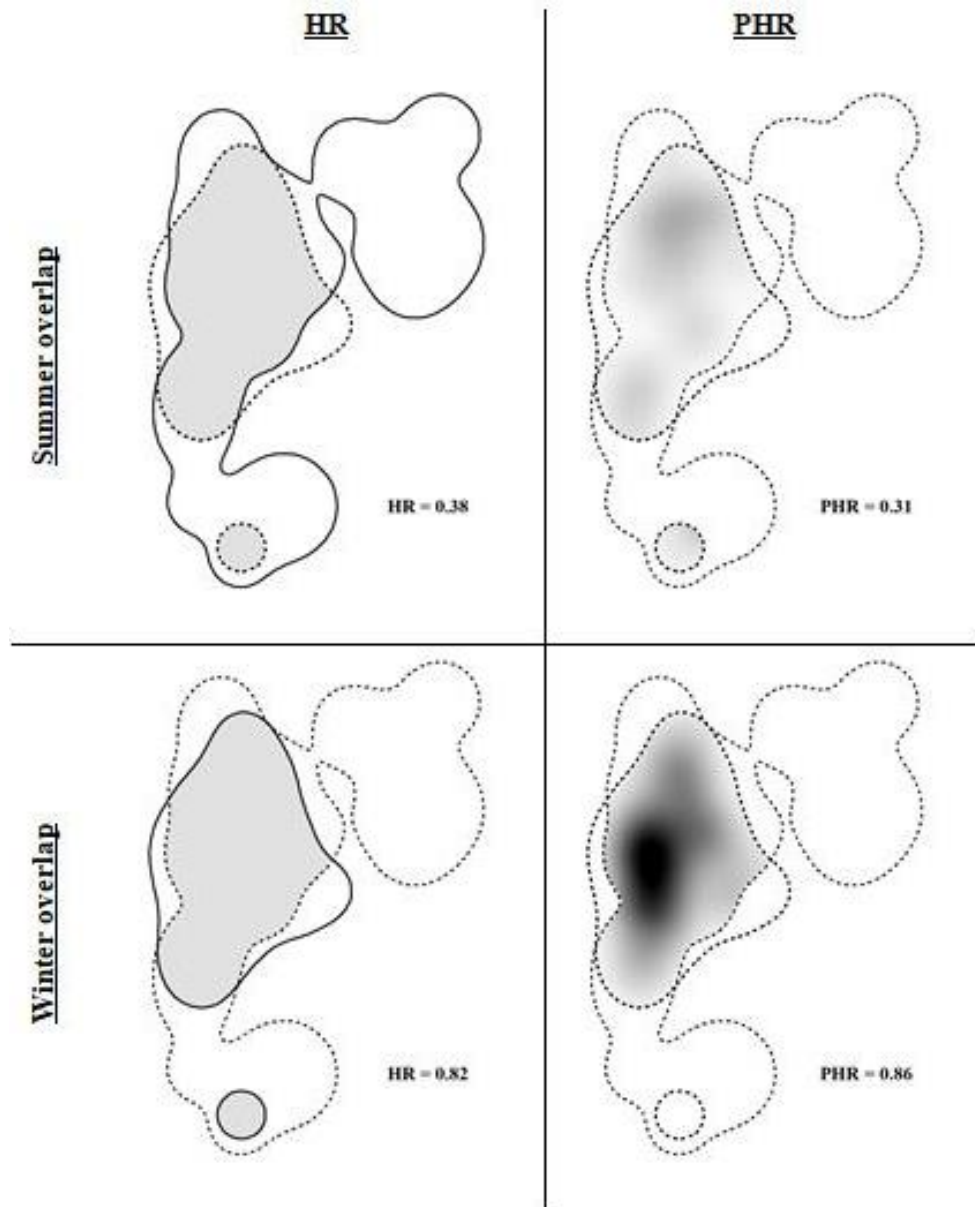


Figure 3. A conceptual diagram showing the difference between two methods of quantifying home range overlap for each direction of seasonal overlap: the proportional area of intersection (HR), and the volume of utilization distribution within the intersecting area (PHR) for each season. PHR can be interpreted as the probability of using the overlapping area during the overlapping season. Home range boundaries are the 95% isopleths for summer and winter KDEs for a female porcupine in Tolowa Dunes State Park, Del Norte County, CA. Overlapping seasonal home range is depicted as a solid line in the HR panels.

For each overlap metric, I compiled a candidate model set of 13 multiple linear regressions, representing all combinations of the following predictor variables: number of relocations (within season), direction of overlap (summer on winter or winter on summer), and sex. Using AICc, each candidate set underwent model selection to determine which combination of predictor variables best explained the HR and PHR overlap values among porcupines.

Prediction 2: Seasonal visitation

The seasonal visitation prediction assumes that winter porcupine locations should fall disproportionately in areas visited only once or twice in their summer home range. Therefore, if porcupines were exhibiting a scouting behavior, areas with low, but not zero, numbers of summer visits should contain more winter points when compared to randomized data. To test this prediction, I first reduced the sample of porcupines to include only individuals with GPS data for summer and a consecutive winter. This eliminated 8 individuals, leaving a remainder of 3 porcupines for this analysis.

I constructed annual 100% minimum convex polygons (MCPs) by combining locations from GPS units and visual locations from telemetry (VHF locations) for each porcupine. These MCPs were filled with hexagonal cells, each 20 m in diameter. Within each cell, I tallied the number of winter GPS points and used the T-LoCoH package (Lyons et al. 2019) in program R to determine the number of separate summer visits (NSV) from summer GPS data. NSVs can be interpreted as the number of times an animal returned to an area during summer, given a defined inter-visit gap period. These calculations used an inter-visit gap period of at least 24 hrs.

To determine if winter space use was a product of summer space use, I randomized summer visitation and evaluated the relationship of this randomized summer space use to observed winter locations. To do this, each cell's NSV value was randomly sampled without replacement 100 times (Figure 4). The mean number of winter points found in cells of each NSV value for all iterations and their 95% confidence intervals were reported and compared to the observed data (Figure 4). The seasonal visitation prediction was considered supported if areas with 0 NSV had fewer winter locations than random.

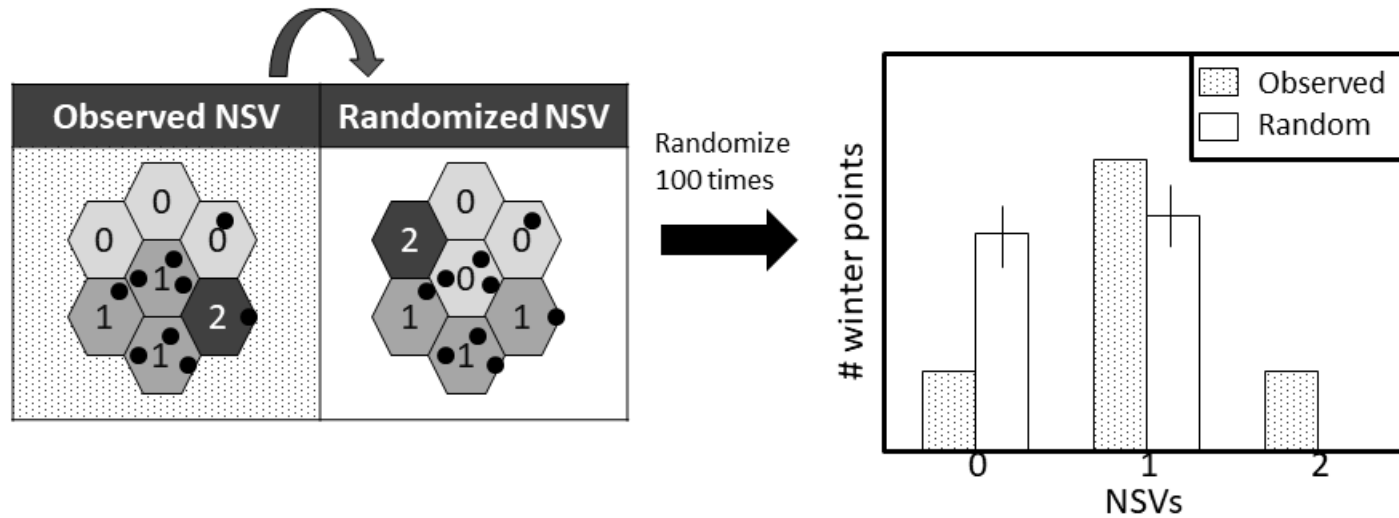


Figure 4. Conceptual diagram depicting how summer space use was randomized for each porcupine, then compared to the observed relationship between summer and winter visitation. Shaded hexagonal cells correspond to the number of separate visits (NSV) during summer; where cells are shaded darker as NSV values increase. Solid points represent winter locations.

Prediction 4: Winter habitat selection – Area use

Data from porcupines whose movement analysis supported the seasonal visitation prediction were combined and used in an analysis to test prediction 4 on winter habitat selection. Because porcupines throughout their range experience considerable nutritional and physiological stress during winter, scouting individuals are likely searching for future shelter, dietary resources, or a combination of these factors. Therefore, I collected information on the nutritional quality of available forage and described the structure of specific winter habitat areas that porcupines visited during summer.

I determined sampling locations from the combined summer GPS and VHF data for all porcupines included in this analysis. Using GPS data, I created a set of sampling locations by visually estimating centroid locations within clusters of 5 or more points that fell over conifer patches in dune habitat. VHF locations that overlapped conifer patches and were greater than 20 m from any GPS centroid were also added to the set of sampling locations. Collection of foliage samples occurred from May 7-11 2018. At each sampling location, at least 12 g of leaf tissue were taken from the nearest shore pine and/or wax myrtle tree with evidence of foraging or porcupine scat in the immediate area. Samples were collected in small, sealed plastic bags and stored in a freezer at -18°C until undergoing chemical analysis. In cases where more than one tree met sampling conditions, samples were collected from all trees with evidence of porcupine activity. If there was no evidence of porcupine activity, the nearest shore pine and/or wax myrtle were sampled regardless; making note that no sign was evident. Finally, if a sampling

point fell in an area without either species of tree, nothing was sampled. In total, only 4 points were omitted from sampling.

To obtain metrics of forage quality, I measured a number of nutritional variables shown or thought to be influential in porcupine foraging selection: acidity, nitrogen, potassium, sodium, magnesium, and calcium (Roze 2009). Prior to analysis, samples were dried using a Preservator 220 freeze dryer (VirTis, Gardiner, NY), turned to fine powder in a coffee grinder, stored in re-sealable plastic bags, and placed in a desiccator between analyses. Acidity was determined by taking 0.375 g of tissue per sample and mixing with 3 ml of nanopure water in a 15 ml centrifuge tube. Tubes were placed on a Maxi-Rocker shake table (Labline, Kalbadevi, Mumbai) for at least 1 hr, then centrifuged at 13,000 RPMs for 10 min. Supernatant was reserved in 10 ml glass tubes, then measured with an Orion Star A111 pH meter (Thermoscientific, Waltham, Massachusetts) for values of acidity. Percent dry weight of nitrogen was quantified using a modified Kjeldahl analysis. To conduct this analysis, freeze dried tissue was digested in sulfuric acid, then diluted with nanopure water and measured in a TNM-L Total Nitrogen unit (Shimadzu Scientific Instruments, Kyoto, Japan). To measure the remaining nutrients, I incinerated plant tissue in a muffle furnace (Thermoscientific, Waltham, Massachusetts), then digested the ash in 20% HCl until all liquid was evaporated. Samples were then reconstituted with 20% HCl, diluted with nanopure water, then measured using an atomic absorption spectrophotometer (Thermoscientific, Waltham, Massachusetts). For each variable, outlier samples were re-measured to minimize the probability that machine or human error caused false high or low values. Since certain

sampling locations had more than one associated tree, the minimum pH and maximum nutrient value at each location were used to represent the quality of forage for that area in models.

I also measured several variables related to habitat structure at each centroid location, including: canopy height, canopy density, and area of available forest habitat. These measurements were created using LiDAR data acquired in 2016 (Office for Coastal Management 2016). I created a canopy height model (CHM) for the study area by converting tiles to a digital terrain model, then normalizing each tile to isolate the height of vegetation. These normalized tiles were then rasterized into a CHM. To create a canopy density model (CDM), I used the normalized tiles to create 2 new rasters: (1) a canopy raster and (2) a total raster. The canopy raster reported the number of LiDAR points within each 2 m² cell that were more than 0.25 m high ($Z > 0.25$), while the total raster contained all points. I then divided the canopy by the total raster to create a map of canopy density, in which all cells contained values between 0 and 1, where values closer to 1 represented denser canopies. To attribute these values to each summer centroid, I buffered each point by 20 m, preserved only the canopy area within each buffer, and extracted the mean, maximum, and standard deviation of both models. I also calculated the total area of canopy within each buffer, which represents the area of immediately surrounding forest habitat.

Each sampling location represented an area that was visited by a porcupine during summer only, or re-visited again during winter. Factors determining which areas were re-visited could be related to quality of winter forage, structure of winter habitat, or a

combination of these two factors. To determine which set of variables best explained the visitation status of each sampled area, I used logistic regression and a candidate set of 19 models: 11 using forage quality variables and 8 using structural variables, and then selected the best performing model from each group using AICc. The response variable was coded “0” for summer visit only and “1” for sites visited in summer and re-visited in winter. All variables from these top models were used to create a combined model of nutrition and structure, then included in a final selection with all 21 models (**Error! Reference source not found.**), including a null with no predictors, to determine which model performed best.

Table 1. List of 21 logistic regression candidate models explaining the effect of structure and nutrition on the log-odds of a summer-visited area being revisited by a porcupine during winter in Tolowa Dunes State Park, Del Norte County, CA. Variables in nutritional models include presence/absence of a shore pine (SP) or wax myrtle (WM), acidity of foliage (pH), and percent dry weight of nutrients in foliage: nitrogen (N), sodium to potassium ratio (Na/K), magnesium (Mg), and calcium (Ca). Structural variables include area of surrounding tree habitat (Area), maximum canopy height (MaxHeight), standard deviation of canopy density (SD_Dens), and mean canopy density (Mean_Dens) within a 20 m buffer of each location. A combined model was created by including all variables from the best performing models of the nutrient and structural groups. Interactions between terms were denoted with (*).

Model Type	Predictors
Null	~ 1
Nutrients	~ pH + N + Na/K + Mg + Ca
Nutrients	~ pH + N + Mg + Ca
Nutrients	~ pH + N
Nutrients	~ pH + N + Na/K
Nutrients	~ Mg + Ca
Nutrients	~ SP + WM + pH + N + Mg + Ca + WM*pH + WM*N
Nutrients	~ SP + WM + pH + N + Mg + Ca + SP*pH + SP*N
Nutrients	~ SP + WM + pH + N + Na/K + WM*pH + WM*N
Nutrients	~ SP + WM + pH + N + Na/K + SP*pH + SP*N
Nutrients	~ SP + WM + pH + N + WM*pH + WM*N
Nutrients	~ SP + WM + pH + N + SP*pH + SP*N
Structure	~ Area + MaxHeight + SD_Dens
Structure	~ MaxHeight
Structure	~ SD_Dens + Mean_Dens
Structure	~ MaxHeight + SD_Dens
Structure	~ Area
Structure	~ MaxHeight + SD_Dens + MaxHeight*SD_Dens
Structure	~ Area + MaxHeight + SD_Dens + MaxHeight*SD_Dens
Structure	~ Area + SD_Dens + Area*SD_Dens
Combined	~ Mg + Ca + MaxHeight

Camera Analyses

I collected habitat-use data using trail cameras placed under shore pine and wax myrtle trees in winter habitat on the western half of Tolowa. Cameras were used to monitor and compare seasonal use of winter habitat, to test prediction 3 (random summer sampling). Furthermore, the nutritional and structural values of some camera trees were experimentally manipulated by baiting with an apple, salt, and/or a 19 liter bucket. The actual nutritional and structural characteristics of these trees were also quantified. To test prediction 4, I compared visitation at cameras during each season to determine which combination of structural and nutritional variables best explain visitation.

Data collection

To monitor the use of winter habitat by porcupines in Tolowa between seasons, I deployed 30 trail cameras (10 Stealthcam G34s [Stealthcam, Grand Prairie, Texas] and 20 Bushnell HDs [Bushnell, Overland Park, Kansas]) under evergreen trees in the dunes from June 2017 to March 2018 (Figure 5). Locations were selected by stratifying the western half of Tolowa into 10 areas of roughly equal size. For each stratum, 3 points were randomly distributed. If a point did not fall in a forested area, then the point was manually reassigned to the nearest tree or patch within a 50 m radius. All cameras were deployed under shore pine or wax myrtle trees, because the bark and foliage of these two species are prevalent winter dietary items for porcupines in Tolowa (Appel et al. 2018).



Figure 5. Distribution of trail cameras in Tolowa Dunes State Park, Del Norte County, CA. Timing of baiting buckets in front of cameras with apples and salt are noted by colors and symbols, where buckets were baited year round (Both), during summer only (Summer), winter only (Winter), or neither season (Neither). Control cameras were never baited nor supplied with a bucket. Cameras that were excluded from the study due to mechanical failure are also noted.

The points within each stratum were assigned one of 3 general treatment groups: baited bucket, un-baited bucket, or control, where baited buckets were treated once a month with a handful of salt and a whole red delicious apple. Apples were used as bait to increase the desirability of a tree, as porcupines in Tolowa are known to go out of their way to consume the fruits of apple trees (Appel et al. 2018). Sodium was used in case porcupines in Tolowa experience a strong annual sodium drive, as they do in inland regions of their range (Felicetti et al. 2000, Roze 2009, Coltrane and Barboza 2010). Baited and un-baited cameras were propped on homemade rebar posts, pointed toward the center of a tree where a 19 liter bucket lay on its side. The buckets were used as shelters for the bait as well as an attractive structural contribution to the tree. Control cameras received no bucket or bait. Additionally, with the change of season from summer to winter, 5 strata were randomly selected to have their baited and un-baited buckets switch treatments. Thus, a total of 5 treatment groups existed in regards to baiting schedule: both seasons, summer only, winter only, never baited, or control (Figure 5).

Cameras were set to take 3 consecutive photos per trigger, with a minimum gap period of 15 seconds between triggers. Baited cameras were checked once every month to replace bait, while the rest were checked at least once every 2 months, to replace batteries and memory cards. A group of 14 volunteers assisted in the collection of data from camera images. To minimize observer bias during the data collection process, volunteers were required to complete a training process and pass a calibration test. Data were recorded for each image by identifying species, number of individuals, presence or absence of a collar (for porcupines), and if the animal was interacting with the bucket,

bait, or camera (e.g., rubbing, sniffing, climbing, chewing, or inspecting closely). The calibration test compared data I collected to that of each individual volunteer, determining the level of similarity for each data collection category by calculating a Kappa statistic (Viera and Garrett 2005). If the average Kappa value was greater than 0.8, datasets were considered a close to perfect match (Viera and Garrett 2005) and volunteers were then allowed to independently collect data on images. If not, volunteers underwent additional training and were asked to revise their data recording until they passed evaluation. While every effort was made to check cameras at a frequency that minimized disruption in the sampling period, some cameras experienced unexpected technical failures that reduced the amount of time they were recording data each season.

Prediction 3: Random summer sampling

Many porcupines in Tolowa were observed in the GPS data occupying specific, small areas of dune forest for 4-12 hours at a time. Because these cameras were placed under dense tree canopies, the area of detection was narrow. Therefore, the number of porcupines detected at each camera may not directly correlate to intensity of use. For this reason, I measured porcupine “visitation” (V_s), a unit-less measure of porcupine use for each camera and season, with the following equation:

$$V_s = \left(\frac{x * i}{t} \right) * 100$$

where each day within the sampling period of each season (s) was divided into intervals of a defined length (i). The total number of time intervals with porcupine detection (x) was multiplied by the length of the interval (i), and then divided by the total time the

camera was on for the season (t). Finally, values were multiplied by 100 to increase interpretability of the visitation values (V_s). I quantified visitation using a small and large interval (0.5 and 4 hours) to test the sensitivity of this approach.

To test prediction 3, the number of cameras visited by porcupines was compared between summer and winter, as were the mean visitation times at cameras.

Prediction 4: Winter habitat selection – Tree use

In addition to manipulating the nutritional and structural characteristics of certain trees with the placement of apples and buckets, I also measured their inherent nutritional and structural qualities. From May 7-11 2018, I collected foliage samples from all camera trees, and processed them in the lab to quantify pH, nitrogen, potassium, sodium, magnesium, and calcium, using previously described methods. I also summarized the standard deviation, maximum, and mean canopy height and density within 20 m of each camera location. However, the spatial extent of the previously constructed canopy height and density models excluded 6 camera locations. To include these cameras, I created canopy height and density models using LiDAR data acquired during 2009 (Office for Coastal Management 2019), then conducted a simple linear regression to predict more current canopy height and density values for each outlier camera.

To evaluate the potential drivers of scouting at the population level, I created a candidate set of 18 linear regression models to explain summer visitation at cameras: 10 with forage quality variables and 8 with habitat structure variables. Using AICc to evaluate model performance, I used all variables from top forage and structure models to create a combined model. A null model, containing no predictors, was also included for

comparison. Finally, to determine which set of variables best explained summer visitation to cameras, I conducted a final selection with all 20 of these models (**Error! Reference source not found.**). The same set of initial candidate models (Table 2) were created with winter visitation as a response variable, and underwent the same selection process to determine which set of variables best explained winter visitation to cameras.

Table 2. Logistic regressions comprising candidate model sets, explaining the effects of structure and nutrition on porcupine visitation to trail cameras during summer and winter, separately, in Tolowa Dunes State Park, Del Norte County, CA. All models were included in each seasonal candidate set, except for those with an “S” or “W”, which were exclusively included in either the summer or winter model sets, respectively. Variables in nutritional models include total time an apple was present in front of each camera during summer (AppleTime.S) and winter (AppleTime.W), presence/absence of a wax myrtle (WM) at camera location, acidity of foliage (pH), as well as percent dry weight of the following nutrients in foliage: nitrogen (N), sodium to potassium ratio (Na/K), magnesium (Mg), and calcium (Ca). Structural variables include presence/absence of a bucket (Bucket), area of surrounding tree habitat (Area), maximum canopy height (MaxHeight), standard deviation of canopy density (SD_Dens), and mean canopy density (Mean_Dens) within a 20 m buffer of each location. Combined model was created by including all variables from the best performing models of the nutrient and structural groups. Interactions between terms were denoted with (*).

Model Type	Predictors
Null	~ 1
Nutrients (S)	~ AppleTime.S
Nutrients (W)	~ AppleTime.S + AppleTime.W
Nutrients	~ pH + N + Na/K + Mg + Ca
Nutrients	~ pH + N + Mg + Ca
Nutrients	~ pH + N
Nutrients	~ pH + N + Na/K
Nutrients	~ Mg + Ca
Nutrients	~ SP + WM + pH + N + Na/K + Mg + Ca + WM*pH + WM*N
Nutrients	~ SP + WM + pH + N + Na/K + WM*pH + WM*N
Nutrients	~ SP + WM + pH + N + WM*pH + WM*N
Nutrients	~ SP + WM + pH + N + Mg + Ca + WM*pH + WM*N
Structure	~ Bucket
Structure	~ Area + MaxHeight + SD_Dens + Mean_Dens
Structure	~ MaxHeight
Structure	~ SD_Dens + Mean_Dens
Structure	~ MaxHeight + SD_Dens
Structure	~ Area
Structure	~ MaxHeight + SD_Dens + MaxHeight*SD_Dens
Structure	~ Area + SD_Dens + Area*SD_Dens
Combined (S)	~ AppleTime.S + Area
Combined (W)	~ AppleTime.S + AppleTime.W + Area + STD_DENS + Area*STD_DENS

RESULTS

Movement Analyses

Summer and winter KDEs were constructed for 11 porcupines (5 male and 6 female; Table 3) to assess the spatial overlap of use. The best performing model explaining total area of overlap (HR; Table 4) between summer and winter home ranges included sex (estimate = -0.15; 95% confidence intervals = -0.3046 - -0.0115) and season of overlap assessed (estimate = 0.20; 95% confidence intervals = 0.0596 – 0.3514). Specifically, male home ranges had lower overlap between seasons than females, and winter home ranges overlapped with summer more than summer home ranges overlapped with winter. The top model for probability of use in the overlapping home range area included only season of overlap assessed (Table 5). Specifically, overlap values were greater when winter home ranges were compared to summer (estimate = 0.22; 95% confidence intervals = 0.0127 – 0.4391). The next best model for probability of use in the area of overlap was within 2 Δ AICc scores of the top model (Table 5). This model also included season, as well as the number of points used to create summer home ranges. However, number of summer points had confidence intervals that overlapped zero.

Table 3. Summary of available porcupine location data attained from visual and triangulated locations using radio telemetry (VHF) and GPS locations randomly sampled at minimum 24 hr intervals (GPS). Initial capture year is denoted for each porcupine, along with sex (F=female, M=male). Animals were collared and tracked in Tolowa Dunes State Park, Del Norte County, CA.

PorcID	Capture year	Sex	Summer			Winter		
			GPS	VHF	Total	GPS	VHF	Total
15.01	2015	F	0	38	38	2	15	17
15.02	2015	F	0	44	44	4	7	11
15.03	2015	M	0	36	36	39	16	55
15.07	2015	F	0	34	34	0	12	12
15.11	2015	M	0	28	28	1	5	6
15.12	2015	F	19	36	55	32	12	44
15.13	2015	F	0	29	29	2	7	9
15.14	2015	M	1	26	27	3	16	19
16.19	2016	M	93	18	111	26	8	34
17.23	2017	F	58	15	73	39	4	43
17.25	2017	M	48	14	62	0	9	9

Table 4. Top 5 models from a candidate set of 13 linear regression models, evaluated using AICc to determine which combination of variables best explained the area of seasonal home range overlap (HR) among porcupines: sex, number of locations used to build each seasonal home range, and direction of overlap (summer on winter or winter on summer). Points used to construct summer and winter KDEs were derived from visual and GPS locations of 11 porcupines in Tolowa Dunes State Park, Del Norte County, CA for at least two seasons, from summer of 2015 to winter of 2018.

Models	df	w	AICc	Δ AICc
~ Sex + Season	4	0.51	-10.11	0
~ Season	3	0.17	-7.90	2.21
~ SummerPts + Season	4	0.13	-7.38	2.73
~ Sex + SummerPts + WinterPts	6	0.04	-5.23	4.87
~ WinterPts + Season	4	0.04	-4.89	5.21

Table 5. Top 5 models from a candidate set of 13 linear regressions, evaluated using AICc to determine which combination of variables best explained the probability of use in overlapping seasonal home range area (PHR) among porcupines: sex, number of locations used to build each seasonal home range, and direction of overlap (summer on winter or winter on summer). Points used to construct summer and winter KDEs were derived from visual and GPS locations of 11 porcupines in Tolowa Dunes State Park, Del Norte County, CA for at least two seasons, from summer of 2015 to winter of 2018.

Models	df	w	AICc	Δ AICc
~ Season	3	0.33	4.82	0
~ SummerPts + Season	4	0.22	5.62	0.80
~ Sex + Season	4	0.12	6.89	2.06
~ WinterPts + Season	4	0.08	7.75	2.93
~ SummerPts	3	0.07	7.87	3.04

Of the 3 porcupines included in individual movement analyses (**Error! Reference source not found.**), 2 of them, both female, revisited areas of low, but not zero, summer visitation more often during winter than would be expected assuming no relationship between summer and winter space use (Figure 6). The third porcupine, a male, used new areas more often than random during winter, and used cells with less than expected visitation (Figure 6; NSV = 1; number of winter points = 35), assuming no relationship between seasonal space use (estimate = 42.3; 95% confidence intervals = 35.84 – 48.75).

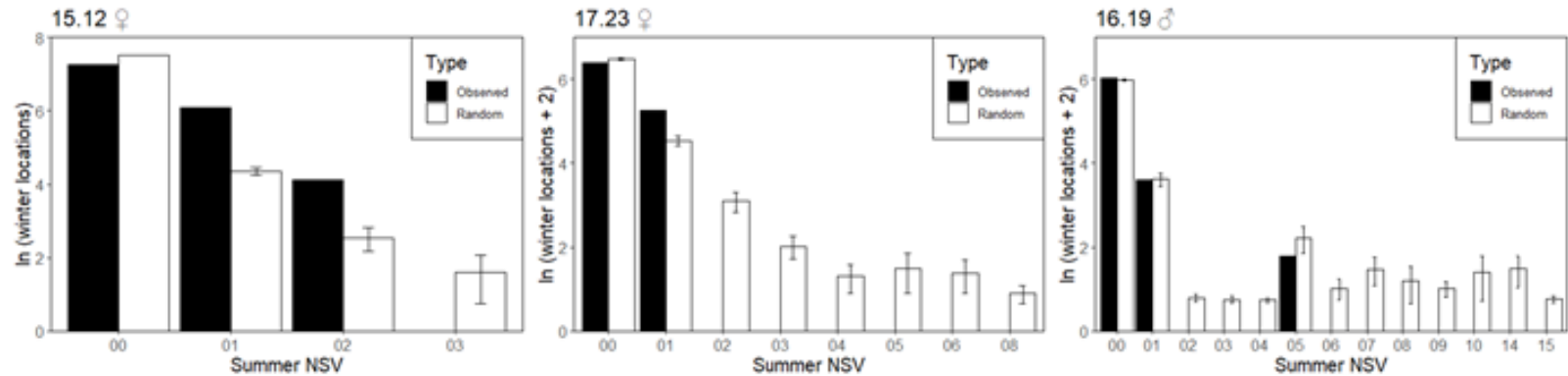


Figure 6. Number of winter porcupine locations captured within hexagonal cells (diameter = 20 m) that received a number of separate visits (NSV) during summer (inter-visit gap period = 24 hrs), compared to the number of winter points captured in these same cells when NSV values were randomized. Winter and summer locations for 3 porcupines derived from GPS data, collected in Tolowa Dune State Park, Del Norte County, CA.

Of the models explaining the probability of re-visitation during winter to summer use areas, the null, containing no predictors, was the top model (Table 6). However, the next two best models occurred within 2 Δ AICc values from the best model (Table 6). Predictors in these models included maximum canopy height (estimate = -0.25; 95% confidence intervals = -0.68 – 0.08), and area of surrounding forest habitat (estimate = -0.01; 95% confidence intervals = -0.02 – 0.00), both of which had CIs that overlapped 0.

Table 6. Top 5 models from a candidate set of 21 logistic regressions, explaining the effect of structure and nutrition on the log-odds of a summer visited area being revisited by a porcupine during winter. Summer visited areas were derived from GPS data of 2 female porcupines (one during 2015-2016, the other 2017-2018) in Tolowa Dunes State Park, Del Norte County, CA.

Model type	Models	df	w	AICc	Δ AICc
Null	~ 1	1	0.29	47.09	0
Structure	~ MaxHeight	2	0.22	47.21	0.12
Structure	~ Area	2	0.20	47.59	0.50
Structure	~ MaxHeight + SD_Dens	3	0.07	49.53	2.44
Nutrients	~ Mg + Ca	3	0.05	50.91	3.82

Camera Analyses

Out of 30 cameras, 3 were removed from analyses due to theft or frequent mechanical failure during one or both seasons. Of the 27 remaining cameras, porcupines were detected at 15 cameras during summer and 19 cameras during winter. In addition to being detected at more cameras during winter, total visitation (V_s) to cameras during winter was 1.17 times greater than summer when intervals were defined as 0.5 hours, and 1.08 times greater when intervals were set as 4 hours. Porcupines visited cameras of all

treatment groups during both seasons. During summer, the trees that were never baited were visited most often, and trees baited during both seasons were visited least often (Table 7). However, during winter, trees baited during both seasons were visited most often, and trees baited during summer were visited least often (Table 7).

Table 7. Summary of mean porcupine visitation (V_s) to each treatment group, when visitation is calculated using one of 2 interval lengths, from a total of 27 cameras deployed under evergreen trees in Tolowa Dunes State Park, Del Norte County, CA.

Interval (hr)	Bait schedule	# Cameras	Mean summer (V_s)	Mean winter (V_s)
0.5	Both	5	0.04	0.12
	Summer	5	0.07	0.02
	Winter	5	0.03	0.11
	Neither	4	0.15	0.06
	Control	8	0.04	0.05
4	Both	5	0.24	0.44
	Summer	5	0.43	0.18
	Winter	5	0.22	0.75
	Neither	4	1.05	0.48
	Control	8	0.26	0.35

Top models for visitation during summer differed between interval lengths (

Table 8). When intervals were defined at 0.5 hours, visitation to camera trees during summer was best explained by a null model with no predictors (

Table 8). However, the next best model was within $2 \Delta AICc$ of the top model and contained area of surrounding forest habitat as a predictor (estimate = -0.0004, 95% confidence intervals = -0.0009 – 0.0001). When the interval was defined as 4 hours, visitation to camera trees during summer was best explained by a model with area of forest (estimate = -0.002, 95% confidence intervals = -0.006 – 0.0008), while the next best model within $2 \Delta AICc$ was the null.

Table 8. Top 5 models from a candidate set of 20 multiple linear regression models, explaining the effect of structure and nutrition on porcupine visitation to trail-cameras during summer at trees in their winter habitat. Cameras were placed in dune conifer habitat in Tolowa Dunes State Park, Del Norte County, CA from June 2017 to March 2018. Apples and/or buckets were present at a portion of cameras each season (S=Summer) as a treatment to manipulate the nutritional and structural features of each tree. Visitation was calculated using interval lengths of 0.5 and 4 hours.

Interval length (hr)	Model type	Model	df	w	AICc	Δ AICc
0.5	Null	~ 1	2	0.26	-31.00	0
	Structure	~ Area	3	0.25	-30.89	0.10
	Structure	~ Max_HGT	3	0.10	-28.99	2.00
	Structure	~ Bucket	3	0.08	-28.69	2.31
	Nutrition	~ AppleTime.S	3	0.07	-28.45	2.55
4	Structure	~ Area	3	0.26	64.05	0
	Null	~ 1	2	0.26	64.10	0.05
	Structure	~ Max_HGT	3	0.09	66.16	2.11
	Structure	~ Bucket	3	0.08	66.38	2.32
	Nutrition	~ AppleTime.S	3	0.07	66.66	2.61

Top models for visitation during winter also differed between interval lengths (

Table 9). When intervals were defined at 0.5 hours, visitation to trees in winter was best explained by a model containing 3 variables: total surrounding forest area, standard deviation of canopy density, and an interaction between the two (

Table 9). Both forest area (estimate = -0.004; 95% confidence intervals = -0.007 - -0.001) and standard deviation of canopy density (estimate = -2.98; 95% confidence intervals = -5.13 - -0.82) were negatively related to time spent at trees during winter. However, their interaction indicated that, for trees with more surrounding forest habitat, there was a positive relationship between visitation and standard deviation of canopy density (estimate = 0.013, 95% confidence intervals = 0.003 – 0.023; Figure 7). However, when intervals were defined at 4 hours, visitation to trees in winter was best explained by area of surrounding forest (estimate = -0.002, 95% confidence intervals = -0.005 – 0.0007). While the next best model within $2 \Delta AICc$ was the null.

Nutritional models did not perform well in movement (Table 6) and camera (Table 8) analyses, despite there being variability among samples for most nutrients (Appendix C).

Table 9. Top 5 models from a candidate set of 20 multiple linear regression models, explaining the effect of structure and nutrition on porcupine visitation to trail-cameras during winter at trees in their winter habitat. Cameras were placed in dune conifer habitat in Tolowa Dunes State Park, Crescent City, CA from June 2017 to March 2018. Apples and/or buckets were present at a portion of cameras each season (S=Summer and W=Winter) as a treatment to manipulate the nutritional and structural features of each tree. Visitation was calculated using interval lengths of 0.5 and 4 hours.

Interval (hr)	Model type	Models	df	w	AICc	Δ AICc
0.5	Structure	~ Area + SD_Dens + Area*SD_Dens	5	0.57	-27.47	0
	Structure	~ Area	3	0.15	-24.85	2.61
	Null	~ 1	2	0.08	-23.62	3.84
	Structure	~ Max_HGT	3	0.03	-21.88	5.58
	Combined	~ Area + SD_Dens + Area*SD_Dens + AppleTime.S + AppleTime.W	7	0.03	-21.39	6.07
4	Structure	~ Area	3	0.29	58.77	0
	Null	~ 1	2	0.27	58.89	0.12
	Structure	~ Max_HGT	3	0.09	61.10	2.33
	Structure	~ Bucket	3	0.08	61.39	2.61
	Structure	~ Area + SD_Dens + Area*SD_Dens	5	0.05	62.17	3.40

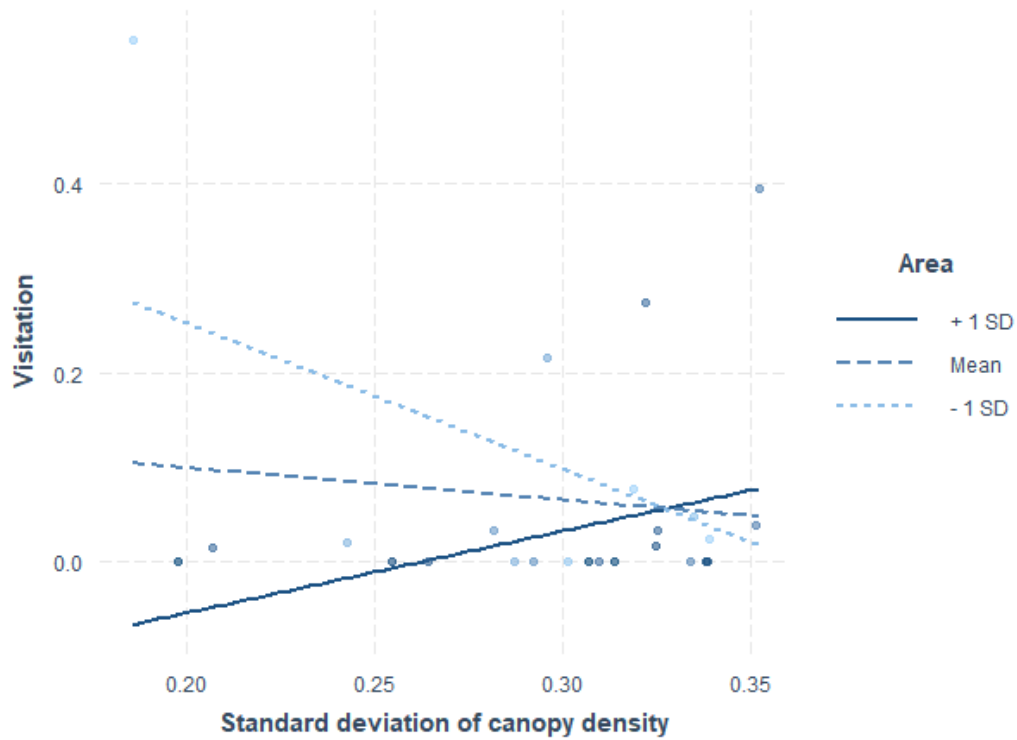


Figure 7. Interaction between the standard deviation of canopy density and the area of surrounding forest habitat, and their relationship to winter porcupine visitation to cameras placed under evergreen trees in Tolowa Dunes State Park, Crescent City, CA.

DISCUSSION

My analyses provide evidence that porcupines in Tolowa were scouting for winter resources during summer to optimize use and selection of winter habitat. Specifically, results from this study support predictions 1 and 2 (winter home range overlap and seasonal visitation), while predictions 3 and 4 (random summer sampling and winter habitat selection) were partially supported. Overall, I found strong support across these complementary analyses for scouting behavior in porcupines, particularly females. Porcupines appeared to move in summer for the purpose of gathering information related to winter habitat selection.

Overall, porcupines had winter home ranges nested within their summer home ranges in areas of low utilization. Females tended to have greater area of overlap (HR) of their winter home ranges within their summer home ranges compared to males. By contrast, the probability of use (PHR) of the summer home range during winter did not differ between sexes. These results supported the “winter home range overlap” prediction, but with stronger evidence for female-only scouting. Results from the movement analysis also supported this potential sex bias. Of 3 porcupines included in the movement analysis, data from 2 females supported the seasonal visitation prediction – they both used areas of low, but non-zero, visitation in summer more frequently than random. The third porcupine, a male, tended to use places never visited in summer. Based

on these individual analyses, I concluded that male porcupines either do not scout, or they scout for resources not quantified in this study.

In addition to winter being a nutritional bottleneck and period of challenging weather, it is also a gestational period for pregnant female porcupines (Roze 2009). Gestation may provide an additional energetic cost to females during winter, incentivizing them to scout for winter resources during summer. While I did not find visual evidence of offspring accompanying porcupines during summer movements to winter habitat areas, a female porcupine was once seen with a porcupette days prior to making a long movement to the dunes in July 2015 (pers. obs.). Porcupettes start separating from their mothers in late August (Roze 2009), suggesting this porcupine was likely accompanied by her offspring during this scouting movement. Considering this assumption, scouting may doubly serve to inform the mother and offspring of what areas offer the best winter habitat. Alternatively, the presence of a porcupette may elevate the risk of these movements for both animals. Scouting may, therefore, be more likely utilized by females without a porcupette, or during early summer, prior to birthing.

Male porcupines, however, could be more concerned with gathering information about potential mates than suitable winter locations. Males hone in on receptive females via scent marking throughout summer before mating in fall (Roze 2009). Therefore, males may be scouting for access to females during early spring and summer, using scent to determine availability of potential mates. If this were the case, every male summer home range should partially overlap with several core areas of different female summer home ranges. Given the small sample size of this study, we were unable to evaluate

spatial relationships between male and female home ranges in Tolowa. However, Roze (2009) found that male home ranges were likely to vary drastically in size and overlap one or more female home ranges, but not male home ranges – consistent with the findings in this study.

Porcupine visitation to cameras during summer and winter varied depending on the interval length selected for defining visitation. The shorter length of 0.5 hours most closely matched the observed period of time porcupines were seen in front of cameras. The null model predicting summer visitation was within 2 Δ AICc of the top model in both cases. However, winter top models differed between intervals. While each interval resulted in a structural top model, the best model for the 4 hour interval was within 2 Δ AICc of the null. Thus, the winter habitat selection prediction was better supported with a shorter visitation interval. However, the top 5 models for both interval lengths primarily contained structural models, suggesting that the ability to detect this signal decreases with increased interval length. Because porcupine activity may vary depending on season, time of day, and availability of surrounding habitat, a single interval length may not accurately represent porcupine visitation to these cameras.

With an interval length of 0.5 hours, summer visitation to cameras was best explained by the null model and winter visitation by a structural model, containing area of forest habitat, standard deviation of canopy density, and an interaction between these 2 predictors. These results provide support consistent with the winter habitat selection prediction. Porcupines appeared to randomly sample winter habitat during summer, consistent with the idea that they were gathering information about the structural

composition of winter habitat available to them. Then, in winter, they selected a subset of the trees visited in summer, with selection apparently driven by structural rather than nutritional characteristics. Specifically, cameras with high winter visitation appeared to be surrounded by less forest habitat with reduced variability in canopy density. Forest patches in the western dunes experience coastal wind stress and therefore typically grow in very short and dense habits (Mad River Biologists 2009). This is especially true for small patches, because there is less refuge from the wind for these trees to grow taller. Thus, if standard deviation of canopy height is low in a small patch, canopy density is likely high within that patch as well. Therefore, small patches may provide a thermal advantage for porcupines during winter while also minimizing exposure to rain with less variability in canopy density. However, within this model, the standard deviation of canopy density and area of surrounding forest also interacted to explain winter visitation to trees. Winter visitation became positively correlated with standard deviation of canopy density when areas of surrounding forest habitat were large. Within larger patches, some trees find refuge from the wind and are able to grow taller, producing structural heterogeneity within the patch (Mad River Biologists 2009). Porcupines preferred large patches with more variable canopy density; presumably because these patches offered ample fine-scale pockets of high-density canopy to select from to seek cover from rain and provide insulation from cold weather. Additionally, larger forest areas also provide more area to forage, without requiring porcupines to leave the patch and expose themselves to adverse weather conditions or perceived risks of predation.

The scouting hypothesis assumes that porcupines move through winter habitat randomly during summer, visiting random patches to gain information about winter habitat quality. However, movement and fine-scale habitat use is rarely random (Fronhofer et al. 2013). Animals use sensory cues to perceive their surroundings and therefore interpret habitat quality and inform habitat use. For example, a ‘Bayesian forager’ may use information gained from these cues to determine how long to stay, or if it should move to the next location (Klaassen et al. 2006). Similarly, animals may infer the current state of an unvisited patch by using information gained from adjacent patches or similar habitat (Fronhofer et al. 2013). Thus, it may be that porcupine movements during summer were not entirely random. Rather, porcupines may have utilized memory in concert with visual and/or olfactory cues to bias their summer visits to include only areas that they inferred to be of high quality. For example, if porcupines prefer areas with short canopies during winter, they might avoid visiting patches with tall trees during summer. Similarly, because porcupines are generally regarded as a solitary species (Roze 2009), they may use olfactory cues from conspecific fecal material or bark foraging to avoid overlapping search areas with other porcupines. Or, conversely, they may use olfactory cues from conspecifics to determine where high-quality patches are, similar to prospecting birds that use conspecific cues to locate high-quality nesting areas. If porcupines were using inference to bias their summer movements in Tolowa, then the difference between visited and unvisited areas would be smaller than if summer visits were random. This potentially small signal coupled with the small sample size of

porcupines in this study may explain the weak support I received for prediction 4 (winter habitat selection).

An alternative hypothesis to scouting is that porcupines are instead searching for concentrated sources of sodium by traveling closer to the ocean during summer. Animals typically require a 1:1 ratio of sodium to potassium in their diets to maintain basic bodily functions (Roze 2009). However, most plant tissues contain significantly less sodium than potassium, driving herbivores to search for alternative sodium sources (Roze 2009). During late spring through summer, porcupines generally experience a strong sodium drive in response to depleted cecal stores of sodium that were used to survive during winter (Roze 2009). However, results from this study and Appel et al. (2018) suggest that this alternative explanation to scouting movements is unlikely. In this study, 10 camera traps were baited with apple and salt in a bucket every month during summer and winter. Images from those cameras revealed only rare instances where porcupines quickly investigated the bait by entering the bucket, which would be required to access the sodium source. Porcupines were far more likely to sniff the buckets briefly, or ignore them entirely. Furthermore, a study using camera traps to test the use of sodium-impregnated salt boards as a non-invasive porcupine detection method found that porcupines in Tolowa were not likely to gnaw on or investigate these sodium sources (C. L. Appel, Humboldt State University, unpublished data). This evidence collectively suggests that porcupines do not actively seek sodium during spring and summer in Tolowa, as they are known to do elsewhere. Furthermore, ratios of sodium to potassium in this study generally meet or exceeded a 1:1 ratio, due to salt deposits from ocean spray

or fog. Thus, sodium is likely not a limiting nutrient for porcupines along the coastal regions of their range.

Nitrogen is an additional critical nutrient for porcupines to attain year-round (Roze 2019). All plants are relatively low in protein, driving herbivores to make foraging decisions which maximize their nitrogen intake. For example, elk will time their migrations to coincide with the emergence of new-growth vegetation, which is richer in nitrogen and energy when compared to older grass blades (Hamel et al. 2009). During the growing season, porcupines are also known to selectively forage on new-growth leaves of deciduous trees (Roze 2009). However, during winter, foraging options and plant growth are drastically diminished. The primary winter dietary resource for porcupines is tree cambium, which is known to be particularly depleted of nitrogen, as well as high in secondary compounds and fiber, which can hinder the absorption of nitrogen in the gut (Felicetti et al. 2000). Results of this study indicate that nitrogen content of leaf tissue is not a significant driver of winter habitat selection by porcupines in Tolowa. However, this conclusion may be attributed to the absence of bark data for measured trees, or the lack of data describing the defense chemistry and fiber concentration of measured tissues.

In addition to providing evidence for scouting behavior, this study also offers insight into porcupine fourth-order winter habitat selection. It is generally accepted that, across their range, porcupines evaluate winter habitat based on 2 primary factors: forage quality (Stricklan et al. 1995, Roze 2009, Appel et al. 2018) and availability of shelter (Stricklan et al. 1995, Zimmerling 2005, Somers and Thiel 2008). The results presented here suggest that porcupines considered the structural composition of winter habitat

rather than nutritional factors when deciding which areas to use. However, this could be due to an incomplete understanding of the nutritional landscape from a porcupine's perspective. For instance, I was not able to quantify bark nutrition, which is a primary winter dietary resource for porcupines. Alternatively, it may be that in the tradeoff between acquiring high-quality forage and shelter, porcupines are settling for suboptimal forage by choosing to occupy areas of refuge during the winter. Thus, nutrition may not drive fine-scale selection of winter habitat in porcupines occupying coastal regions.

While studies have implied that fine-scale foraging decisions by porcupines are at least partially driven by nutritive factors – given the importance of summer fat stores on surviving winter's nutritional bottleneck – very little evidence has been found to support this claim. Instead, it seems that porcupines make selective decisions to meet nutritional needs at a slightly broader scale. Rather than selecting certain trees within a species, porcupines appear to select at the species level to maximize consumption of appropriate nutrients. For instance, during summer and fall in the Catskill Mountains, porcupines switched between different species of maple (*Acer sp.*), ash (*Fraxinus sp.*), and beech (*Fagus sp.*) to time feeding during periods of peak forage quality and to avoid waves of inducible plant defenses (Roze 2009). These porcupines also did not select linden trees (*Tilia sp.*) based on nutritional or biochemical factors measured in leaves from used and available trees (Roze 2009). Similarly, porcupines in Utah did not discriminate between trees of the same species based on nutrition; however, consumed plant species had differing nutritional and chemical compositions (Stricklan et al. 1995). Further evidence suggests that porcupines may discriminate between genetic and biochemical features of

individuals of the same species while making foraging decisions in the winter (Diner et al. 2009). Because plant defense chemistry was not measured from trees in this study, I am unable to infer its potential role as an attribute driver in scouting.

While porcupines appear to employ scouting as a strategy to inform the use and selection of winter habitat in Tolowa, it remains unclear if they exhibit this behavior in other areas of their range. In most places, porcupines are annually challenged by weather conditions and reduced diet during winter (Sweitzer and Berger 1992, Sweitzer 1996, Roze 2009, Coltrane and Barboza 2010, Mabile et al. 2010), and would seem to benefit from this search behavior. However, the ability to remotely detect scouting through movement is easiest when resources used during the limiting season are spatially segregated from those used during the abundant season. Therefore, the ability to study scouting by porcupines in different plant communities would likely depend on the spatial distribution of summer and winter resources.

When interpreting these results, it is important to consider the relationship between memory and time. Some memories degrade over time (Fagan et al. 2013), providing incentive for adult porcupines to continue visiting winter areas during summer to maintain and update their cognitive maps. However, if an area has been visited several times over many years, this increases the likelihood that spatial and attribute memories are well established, lessening the need for a summer visit. More specifically, winter visitation to cameras was best explained by structural variables, but this relationship was driven by high visitation to 2 trees. This may be explained by a few individuals in the population that maintained previous knowledge of specific trees, bolstering their winter

visitation without needing a summer visit. Or, perhaps, high visitation rates were a result of inferred tree quality, using cues from information gathered during summer about other high-quality trees, but not spatial memory.

The movement analysis also provided weak evidence for the winter habitat selection prediction. A null model containing no predictors outperformed all other models explaining the probability of returning to an area during winter. However, the next two models contained structural variables, and both occurred within 1 Δ AICc value of the null. The weak signal supporting the winter habitat selection prediction is likely a result of data availability and sample size. With a more collared individuals and comprehensive sets of GPS data for each season, I would be better able to evaluate the relationship between summer and winter space use for porcupines in Tolowa.

Movement is a product of the relationship between an animal's internal state and its environment (Nathan et al. 2008). That is, an animal will move to meet its needs, and the duration of that movement will depend on where resources exist on the landscape (e.g., foraging locations, water sources, den sites, and refuge from predators). Many long-held models of resource selection, such as the "ideal free" and "ideal despotic" distribution, assume that animals have perfect knowledge of the habitat they're selecting (Fretwell 1972). While perfect knowledge is rarely attained, it greatly benefits an animal to have information regarding the quality and distribution habitat available to them. Information gathering as a method to optimize selection of critical resources occurs in different ways across a variety of taxa. Information about the location and quality of resources can be gained incidentally, while those resources are being actively used (e.g.,

mangabeys selecting previously used fruit trees; Janmaat et al. 2006), or intentionally, through information sharing (e.g., honey bees [*Apis sp.*; Janson et al. 2007], elephants [Family Elephantidae; Hart et al. 2008], and bighorn sheep [*Ovis canadensis*; Jesmer et al. 2018]) and deliberate search movements (e.g., “prospecting” [Reed et al. 1999]). This study on scouting in porcupines adds to the growing literature on animal movement primarily conducted for the purpose of gathering information.

The benefit of scouting should increase with the number of limiting seasons an animal experiences over the expected course of its lifetime. Because seasonal cycles of resource availability typically occur on an annual scale, the number of limiting seasons in an animal’s life should be positively correlated to its expected lifespan. Despite the cognitive abilities of some short lived animals to store and retrieve spatial memories (e.g., small rodents [Martin and Clark 2007], food caching songbirds [Sherry and Hoshooley 2009], reptiles, and fish [Rodríguez et al. 2002]), it would be minimally beneficial for such an animal to expend energy scouting if it is only projected to experience a few limiting seasons over the course of its life. In contrast, animals with long lifespans may experience several limiting seasons. Many long-lived animals species have demonstrated their ability to learn and share spatial information and the critical importance of doing so (Hart et al. 2008, Jesmer et al. 2018). Thus, animals with increased lifespans are better equipped to store and communicate spatial knowledge, and should receive greater return from investing energy in scouting movements to prepare for several limiting seasons. However, age would be a bad predictor of scouting in rare cases when seasonal cycles of abundance occur on shorter temporal scales. Desert rodents, for example, have relatively

short lifespans, but may experience hundreds of days that exceed their maximum temperature thresholds (limiting/challenging seasons). In such cases, it is better to consider the number of limiting seasons the species is projected to experience over the course of a lifetime as a predictor of probable scouting behavior.

Temporal patterns of habitat availability and quality will also determine if scouting is likely to occur. For scouting to be advantageous, bouts of information gathering must be exhibited in preparation for a period of hardship; otherwise it would be more efficient to gather information during relevant seasons or as a secondary consequence of some other behavior (i.e., searching for the best fruit tree while foraging, or gathering information about a productive nest site during the breeding season). Furthermore, resources available during the abundant season must also be of a high enough quality to support exploratory movements during the abundant season. Considering these assumptions, species with a facultative specialist foraging strategy (e.g., porcupines [Coltrane 2012] and pygmy rabbits (*Brachylagus idahoensis*) [Shipley et al. 2009]) may be ideal candidates for expanding research on this new exploratory behavior. Additionally, other species that rely on habitat structures, such as dens (e.g., bears [Family Ursidae; Tietje and Ruff 1980], foxes [*Vulpes sp.*; Cook and Cook 2016], squirrels [Family Sciuridae], and raccoons [*Procyon sp.*; Robb et al. 2006]), to survive winter months may experience strong selective pressure to explore and gather information before winter arrives.

For scouting to occur, resources must be available to evaluate during the abundant season. Considering this, migrating animals may not be likely candidates to consider

when studying scouting behavior. While these individuals experience drastic shifts in seasonal resources and are certainly capable of storing long-term spatial memories, winter ranges may be too far away to explore during the abundant season. Similarly, while carnivores may experience a reliable fluctuation in available dietary resources throughout the year, their food resources are mobile. Thus, information gathered during the abundant season may not reflect resource availability during the limiting season. However, many carnivores are also dependent on the structural quality of stationary habitat features, such as areas for denning, hunting, or caching prey (Althoff 1980, Akenson et al. 2003, Weir et al. 2012). It would be beneficial for such animals to passively scout for such areas while moving through their territory, and use those spatial memories when seasonally relevant. Similarly, while conspecifics are not stationary, carnivores may conduct scouting movements before the mating season to locate olfactory cues that provide information on the location and quantity of eventual potential mates.

Risk of predation likely also determines the degree to which an animal is able to scout. When food resources are reduced in abundance and/or quality, animals often choose to increase their risk of predation to decrease their risk of starvation. For instance, in the Great Basin, porcupines were observed grazing in open habitat to reduce their likelihood of starvation in late-winter, however consequentially experienced increased instances of predator-caused mortality (Sweitzer 1996). Similarly, when stressed with low temperatures, redshanks (*Tringa totanu*) will choose areas to forage with high reward and high predation risk (Hilton et al. 1999). Scouting may diminish the degree of food stress in limiting seasons and therefore reduce the likelihood of individuals needing to

move through high-risk environments to attain food resources. Though, the probability of animals scouting may depend on the risk of predation during the abundant season. If predation risk during the abundant season presents a greater threat to survival than a lack of knowledge during the limiting season, then scouting may not occur at all. In this case, predation risk should be lower during the limiting season, to allow for exploratory movements to happen then. Otherwise, if predation risk is consistently high or low across both seasons, it would be more advantageous for animals to scout during the abundant season than to enter the limiting season without spatial information of critical resources.

Spatial patterning of habitat may also drive the evolution or movement patterns of scouting behaviors across taxa. Scouting is easiest to study when spatial partitioning of resources during the challenging season are clumped and segregated from resources used in the abundant season. With this partitioning, it is relatively easy to detect movements between the two areas of resources and identify movements that seem otherwise inexplicable. That is not to say, however, that scouting only occurs in areas with this particular spatial arrangement of habitat. If the distribution of seasonal patches is intermixed, animals may conduct scouting behaviors while traveling between two high quality patches during the abundant season. If an animal briefly stops to explore areas and resources for future use, this would also be considered scouting, but may be more difficult for researchers to detect in GPS or telemetry data. Scouting is not expected to occur, however, in areas with highly mixed heterogeneity of habitat, because memory is not beneficial at high levels of spatiotemporal habitat complexity (Fagan et al. 2013).

In summary, researchers should consider scouting as a probable behavioral mechanism for species that are (1) non-migratory and long-lived, (2) capable of storing and using spatial memory, (3) challenged by periodic shifts in resource availability and quality, and (4) living in areas where seasonal resources are spatially segregated but adjacent. Expanding this research to a variety of taxa is a critical first step toward understanding how scouting may occur under a variety of different habitats and conditions.

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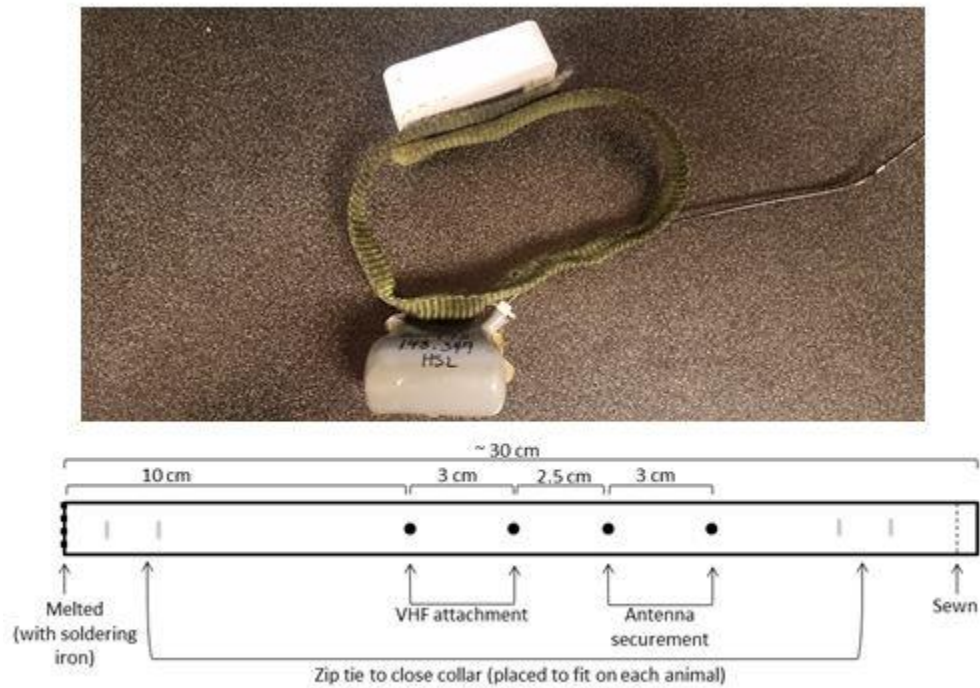
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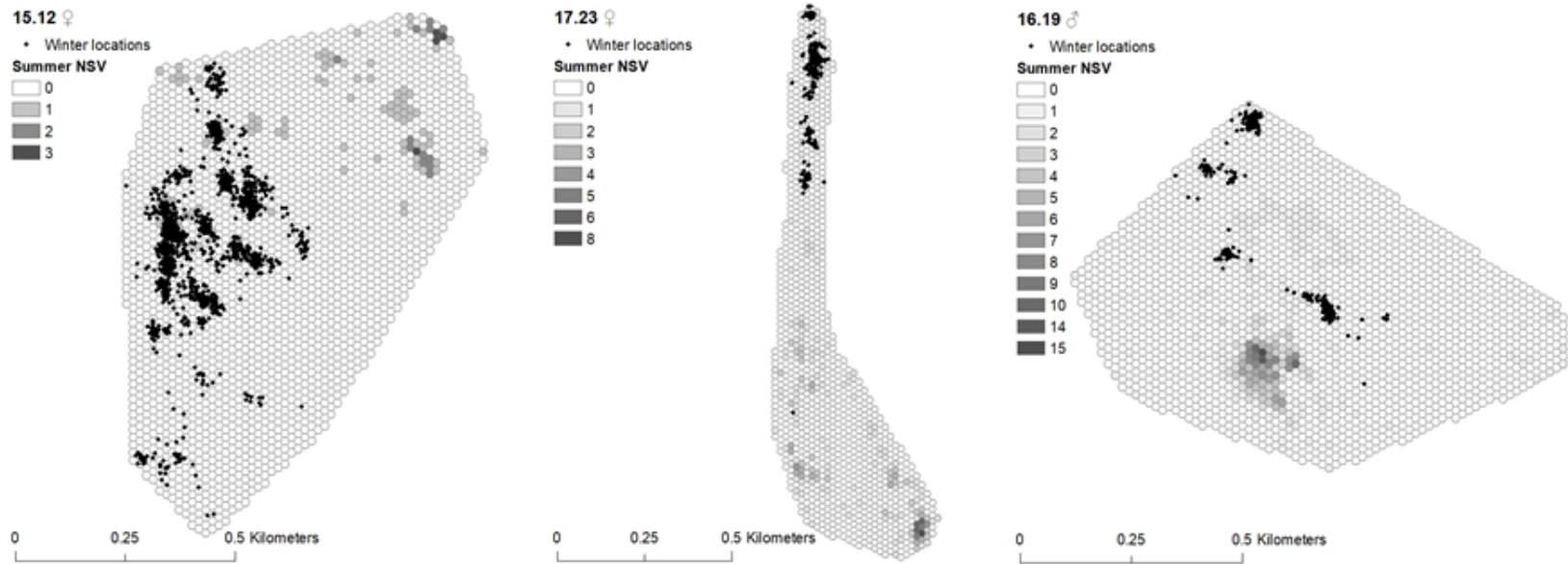
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APPENDIX A



Appendix A: Collar design for attaching VHF and GPS units to porcupines. A single zip tie was used to attach the VHF unit and another was used affix the ends of the collar together during animal processing. The GPS unit was placed on the dorsal side of the neck with Velcro and tightly secured using industrial tape.

APPENDIX B



Appendix B: The relationship between summer and winter space-use of 3 porcupines in Tolowa Dunes State park, Del Norte County, CA, in 2015, shown with winter locations overlaid on hexagonal grids clipped to each animal's 100% annual minimum convex polygon, depicting number of separate visits (NSVs) during summer.

APPENDIX C

Species	Variable	Min	Mean	Max
Shore pine	pH	3.52	3.81	4.03
	N	0.66	1.06	1.38
	Na	0.05	0.22	0.64
	K	0.02	0.24	0.49
	Ca	0.11	0.21	0.36
	Mg	0.28	0.46	3.09
Wax myrtle	pH	5.06	5.18	5.34
	N	1.28	1.46	1.85
	Na	0.19	0.45	0.68
	K	0.05	0.14	0.48
	Ca	0.25	1.02	3.66
	Mg	0.28	0.52	0.71

Appendix C. Summary of values attained from nutritional variables across all samples, for two tree species. Sample collection occurred May 7-11 2018 in Tolowa Dunes State park, Del Norte County, CA. All variables, except for pH, are reported in percent dry weight.