

SEASONAL HABITAT SELECTION OF THE NORTH AMERICAN PORCUPINE
(*ERETHIZON DORSATUM*) IN A COASTAL DUNE FOREST

By

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ABSTRACT

SEASONAL HABITAT SELECTION OF THE NORTH AMERICAN PORCUPINE (*ERETHIZON DORSATUM*) IN A COASTAL DUNE FOREST

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Wildlife-habitat relationship studies are important for understanding the factors that determine where species occur in space and time. Habitat selection by generalist species should be studied on fine spatial and temporal scales to avoid masking important differences between seasons, localities, or orders of selection. I conducted the first study of habitat use and general ecology of North American porcupines (*Erethizon dorsatum*) in a coastal dune environment. Specifically, I assessed changes in body mass, home range size, and habitat selection in relation to the potential for seasonal nutritional and survival bottlenecks as reported elsewhere. Although they are considered generalists, porcupines have adapted specialized feeding strategies allowing them to survive periods of harsh weather and low food availability. In this study, porcupines were selective in their habitat use at the home-range and within-home-range scales during both summer and winter. In summer, porcupines selected willow-dominated swales, marshes, and fruit trees, and during the winter they selected coastal scrub, dunes, and conifer forests. These changes were most likely driven by forage availability, leading to

dramatic body mass loss between summer and winter. On average, females lost 7.5% of their body mass and males lost 17.8%. Further, four out of five mortalities occurred during the winter, which is consistent with nutritional decline.

Porcupines had larger home ranges during the summer than the winter by approximately 31%. These spatiotemporal changes are similar to those reported elsewhere, indicating that similar strategies are used by this habitat generalist across its range.

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INTRODUCTION

Understanding the relationships between animals and their environments is a fundamental component of ecology and an important step for developing effective conservation and management practices. Researchers are increasingly interested in identifying the critical ecological relationships that determine where species occur in space and time (Scott et al. 2002). This knowledge is useful for building distribution models that can predict how species may respond under future climate scenarios or to identify priority areas for conservation. Although many factors limit species' geographic ranges (Gaston 2003), habitat relationships provide the most fundamental, and often simplest, understanding of how animals interact with their environment. As such, the term habitat has been defined many different ways, but herein I will use the definition by Morrison et al. (2012) as "...an area with a combination of resources (like food, cover, water) and environmental conditions...that promotes occupancy by individuals of a given species (or population) and allows those individuals to survive and reproduce."

For habitat associations to be useful predictors in species distribution models, they must be generalizable to novel times and places (Van Horne 2002). However, many studies fail to consider whether animals use habitats differently across spatial and temporal scales, thus creating models that may not provide biologically meaningful predictions (Morrison 2001, O'Connor 2002, Van Horne 2002). Because animals' use of habitats is inherently dynamic, the critical factors limiting a species at one spatial scale are often different from those operating at other scales (Boyce et al. 2003, Gaston 2003).

Therefore, broad-scale studies tend to be poor descriptors of local conditions, while fine-scale habitat associations may not be generalizable to novel times and places (Van Horne 2002). Despite this limitation, fine-scale studies are the best way to uncover the mechanisms through which animals interact with their habitats and acquire resources, but they should be conducted across the entire gradient of environmental conditions experienced by those animals in order to be most informative (Wiens and Rotenberry 1981, Morrison 2001, Van Horne 2002). In this way, fine-scale habitat studies can inform accurate distribution models and help us understand limiting factors across a species' range (Gaston 2003). For many species, it may not be possible to conduct a single study examining fine-scale habitat selection across the entire range of environments where the species occurs. In that case, a collection of case studies distributed across that variation may be required to understand these relationships.

Habitat selection is a useful framework for studying relationships between animals and their environment at multiple spatial and temporal scales. The selection of habitats refers to an animal's use of certain habitat types disproportionate to their availability within the environment (Johnson 1980), with the assumption that animals will select habitats that confer greater survival and reproduction. Johnson (1980) suggested a hierarchical structure in which selection can be studied at multiple levels: the geographic range of a species (first order), individuals' selection of home ranges within a study area (second order), selection of habitats within home ranges (third order), and selection of food items or other resources for specific life history events (fourth order). Habitat selection studies should be specific to both spatial and temporal scales to avoid masking

important biological differences by pooling data across seasons or localities (Schooley 1994, Boyce et al. 2002, Huston 2002)—for example, differential use of habitats between seasons may reflect important ecological changes with consequences for the timing of critical life history events. In practice, the differentiation between seasons is often chosen in a way that maximizes sample size (e.g., Lenarz et al. 2011) or is not explained at all. However, when biological differences between seasons are suspected, seasonal cutoffs should be chosen meaningfully, by considering factors such as the study species' life history, local climate, and plant phenology.

Many studies of habitat selection have focused on the narrow restrictions faced by specialist species because the factors limiting their survival and reproduction are often more straightforward (Boyce et al. 2002). On the other hand, understanding how habitat generalists are able to cope with a wide range of resources and environmental conditions may provide important insights into adaptive potential, phenotypic plasticity, and the variation in strategies that animals utilize across their ranges. For generalists, the use and relative importance of certain resources changes across spatial scales, locations, and seasons (Boyce et al. 2003, Gaston 2003, Shipley et al. 2009). As a result, the mechanisms behind range limits for generalists are more difficult to discern. For these species, habitat selection studies should be conducted at fine spatial and temporal scales and replicated across a range of geographic and environmental conditions.

The North American porcupine (*Erethizon dorsatum*), a widely distributed herbivore, is considered to be a habitat generalist at the range-wide level (Woods 1973, Roze 2009). Porcupines inhabit many different climates and vegetation communities

across their range, from the deserts of the Southwest (e.g., Sweitzer and Berger 1992, List et al. 1999, Ilse and Hellgren 2001) to the hardwood forests of the Northeast (e.g., Roze 2009 and others) and the timberline in Alaska (e.g., Coltrane and Sinnott 2013). Their broad distribution is made possible by physiological and behavioral adaptations to harsh climates and low-quality diets—in particular, their ability to subsist on bark, needles, and other plant materials indigestible for many herbivores because of their high fiber content and concentrations of toxic plant defense compounds (Coltrane and Barboza 2010). The porcupine's physiological tolerance for cold is remarkable given its evolutionary origin in South America and the fact that its closest extant relatives inhabit tropical climates (Vilela et al. 2009).

Predicting limiting factors for porcupines in terms of habitat requirements is therefore not straightforward, but more specific limitations may exist with respect to their diet. Porcupines feed selectively on trees based on their species, biochemical content, and genetic characteristics (Snyder and Linhart 1997) and may thus be more appropriately referred to as facultative specialists than as feeding generalists (Coltrane 2012). That is, they can utilize highly defended or “difficult” foods at certain times and places but switch to consuming a general diet when available, in contrast with obligatory specialists, whose ability to process specific difficult foods precludes them from exploiting a wider variety of plants (Shipley et al. 2009, Coltrane 2012). This flexibility allows porcupines to take advantage of seasonal plant availability, building up fat stores in summer to survive harsh winters, when they can lose up to 40% of their body mass (Sweitzer and Berger 1993, Berteaux et al. 2005, Roze 2009, Coltrane and Barboza 2010). Because porcupines

remain active during physiologically demanding conditions while consuming a low-quality diet, winter has been described as a nutritional bottleneck for them, when body condition declines and mortality risk is high (Coltrane and Barboza 2010). Further, the gut microbes allowing porcupines to metabolize highly defended and nutrient-deficient plant materials may be specialized to certain populations (Roze 2009). This relationship between seasonal physiological demands and potentially area-specific dietary specialization makes it necessary to study porcupine habitat use at fine spatial and temporal scales and at a variety of geographic locations.

Porcupines have been found to be selective in their habitat use at multiple spatial scales (Tenneson and Oring 1985, Morin et al. 2005, Mally 2008, Coltrane and Sinnott 2013). Their habitat selection is primarily driven by seasonal foraging patterns, which reflect the need to maintain sodium-to-potassium ratios, balance toxin load, and acquire nitrogen and carbohydrates necessary for building fat stores prior to winter (Roze 2009, Coltrane and Barboza 2010, Coltrane et al. 2011). Porcupines generally cope with these demands by foraging on broadleaf trees, fruits, and shrubs during the spring and summer when new growth is abundant and switching to conifer bark and needles in the winter (Woods 1973, Roze and Ilse 2003, Roze 2009). But porcupines often face tradeoffs in trying to satisfy these needs. For example, apples provide a source of carbohydrates during late summer when building fat stores is especially critical, but their acidity inhibits the retention of sodium (Roze 2009). Therefore, Roze (2009) predicted that in coastal habitats, where sodium is not limiting, porcupines should be less restricted in their selection of acidic fruits like apples. Similarly, porcupines are often forced to incorporate

a diversity of plants into their diets to avoid saturating the detoxification pathways through which difficult foods are metabolized (Freeland and Janzen 1974, Shipley et al. 2009, Coltrane 2012)—even when alternatives provide fewer critical nutrients. As is evident in these foraging patterns, porcupine natural history is very strongly tied to their performance in two seasons—specifically, their ability to acquire enough resources during summer to build up adequate fat stores, and their ability to survive harsh winters while losing body mass and subsisting on a low-quality diet.

Resource acquisition also influences porcupine home range sizes, as do harsh winter conditions, predator avoidance, and breeding movements. In the Northeast, porcupines generally have larger home ranges during summer than winter, when movement is difficult in deep snow and their foraging is restricted to areas around den sites (Roze 1987, Griesemer et al. 1998). However, porcupines in Alaska maintain relatively large winter home ranges despite the snow, because forage trees and den sites are patchily distributed and predation risk is low (Coltrane and Sinnott 2013). In the Great Basin, where predation risk is high for porcupines (Sweitzer et al. 1997), they restrict their foraging movements and have smaller home ranges (Sweitzer and Berger 1992). Finally, male porcupines increase their home ranges during the breeding season to seek out potential mates, with dominant males maintaining the largest home ranges (Sweitzer 2003, Roze 2009).

The study of porcupine habitat selection and home ranges with regard to seasonal nutritional bottlenecks has not been extended to mild, coastal climates. Because they are able to exploit a broad diet when available, porcupines should do well in an area like

coastal northern California, where green vegetation is available year-round. However, this region is not believed to have supported high densities of porcupines historically (Yocom 1971)—although data are scarce—and current populations appear restricted to coastal and riparian areas (Appel et al. *In Review*). Porcupines likely experience very different seasonal restrictions at this edge of their range, where temperatures are mild but precipitation can reach 250 cm annually (NOAA 2016a). Further, although both coniferous and deciduous trees are present, they lack the diversity of mixed hardwood forests where porcupines continually switch between foraging on emerging buds, leaves, and fruits which may be necessary to maximize nutrients, maintain requisite sodium-to-potassium ratios, and balance toxin load (Roze 2009). Broadleaf trees in this region, primarily red alders (*Alnus rubra*), bigleaf maples (*Acer macrophyllum*), and willows (*Salix sp.*), are most common in riparian areas. Coastal forests are hardly devoid of year-round vegetation, however. The lack of extensive porcupine damage to conifer trees in coastal northern California (Appel, pers. obs.)—a highly distinctive sign in other areas with porcupines—suggests that where present, they may rely on alternate food sources during the winter. Damage to conifer trees may be less extensive, and therefore less noticeable, in mesic forest types which have alternative foods available year-round, unlike in drier climates (Hooven 1971). Lastly, although snow can inhibit porcupine winter movement (Roze 1987), it is not a factor in coastal northern California, and while the climate is mild, porcupines here may still rely on dens for shelter due to their smaller body size and higher threshold for lower critical temperature compared to northern populations (Coltrane 2012). The combination of low tree diversity, productive

understory vegetation, and relatively mild climate in coastal areas may lead to different patterns of porcupine habitat use, diet, home range sizes, and body mass changes than have been observed elsewhere. Seasonal comparisons of these patterns are needed to provide insight into porcupine ecology at this previously unstudied edge of their range.

The objective of this study was to provide information on porcupine ecology and habitat use in a coastal dune forest ecosystem. Specifically, I sought to (1) describe porcupine body mass changes and survival in relation to possible seasonal nutritional bottlenecks; (2) quantify porcupine home range sizes and overlap between summer and winter; and (3) quantify porcupine habitat selection during summer and winter at the second and third orders, with respect to vegetation classes. I hypothesized that (1) porcupines would not undergo as strong of a seasonal decline in body mass and survival as reported elsewhere, due to mild climate and greater food availability; (2) porcupine home ranges would not change drastically between summer and winter, due to few seasonal restrictions; and (3) porcupines would select vegetation classes dominated by broadleaf trees and shrubs at all times of the year when leaves and fruits were available, select herbaceous vegetation otherwise, and avoid conifer-dominated forests at all times because of the availability of higher-quality foods. This case study uses fine-scale, temporally specific data on habitat relationships for a generalist species to understand how survival strategies change across its range.

STUDY AREA

This study took place in Tolowa Dunes State Park (TDSP) in coastal Del Norte County, California (41.90 °N, 124.20 °W). I captured and tracked porcupines in the northern section of the park, a 9.2-km² area bounded to the north by the Smith River and to the south and east by private land and the Lake Earl Wildlife Area (LEWA; Figure 1). I defined the study area as the northern management unit boundary of TDSP, plus additional patches bordering the eastern edge of the park. Because these patches were connected to TDSP and could be considered biologically available to porcupines, it did not make sense to divide them according to the management unit boundary only. I considered the northern and western borders of TDSP to represent biologically meaningful boundaries, as the Smith River and Pacific Ocean, respectively. The southern border is a major road (speed limit = 50 mph) separating the northern section of TDSP from a patchwork of private and public land.

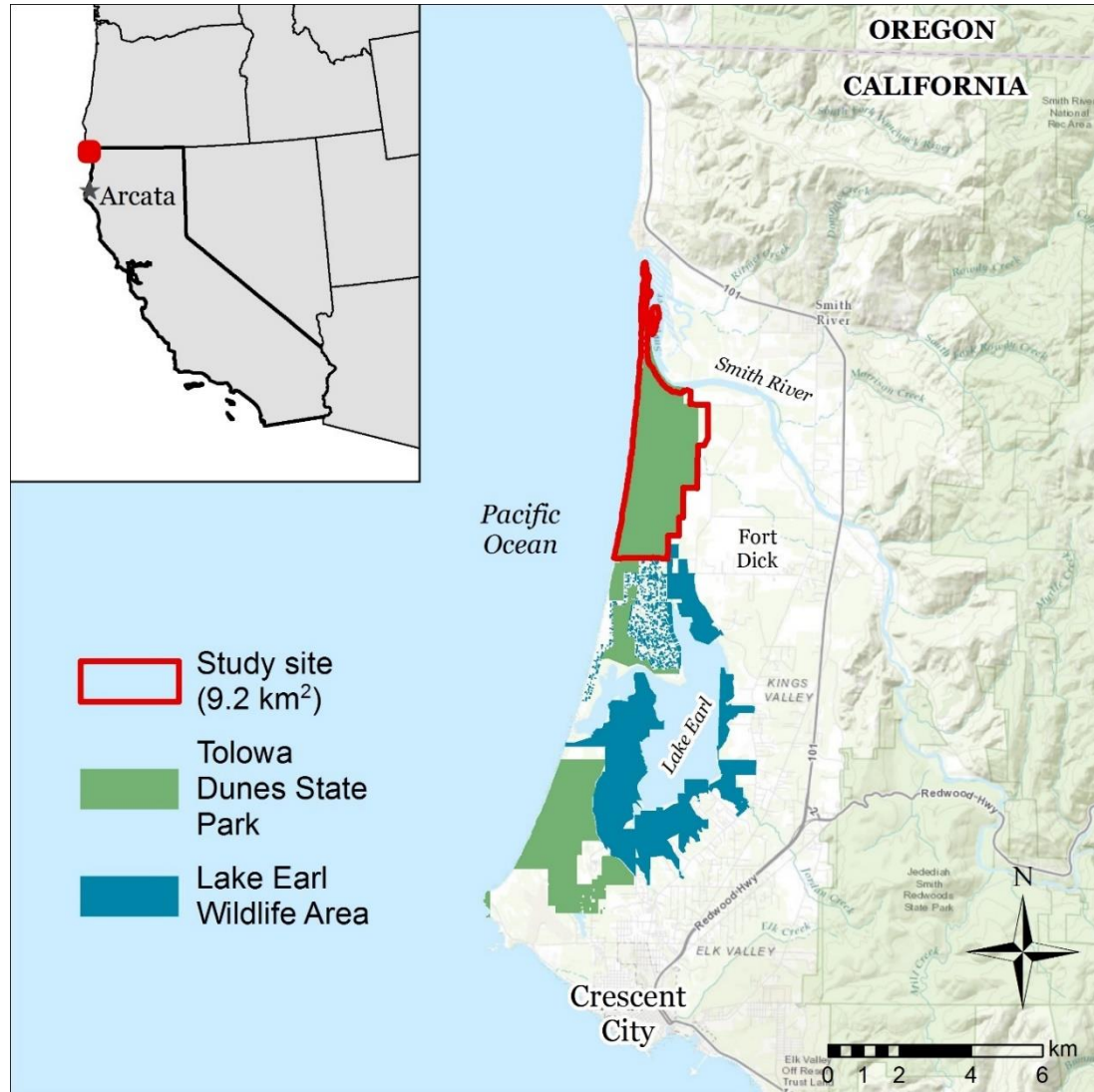


Figure 1. Study site for porcupine captures and radio telemetry in Del Norte County, California.

Vegetation types in TDSP range from open beach strand to nearshore stabilized dunes, coastal dune scrub, conifer forests, wooded and shrub swales, meadows, freshwater marshes and ponds, and agricultural fields (Mad River Biologists [MRB] 2009). Open dunes and coastal scrub contain both native species such as coyote brush (*Baccharis pilularis*), California wax myrtle (*Morella californica*), and dune mat forbs, as

well as non-native European beachgrass (*Ammophila arenaria*). The forested backdunes are dominated by shore pine (*Pinus contorta contorta*) and Sitka spruce (*Picea sitchensis*)—forest types which are considered rare and declining by the California Natural Diversity Database (MRB 2009). Several species of willow dominate the wooded and shrub swales in addition to lower densities of red alder, Oregon crabapple (*Malus fusca*), twinberry honeysuckle (*Lonicera involucrata*), cascara buckthorn (*Frangula purshiana*), Douglas’ spirea (*Spiraea douglasii*), and other native shrubs and forbs. Sedges (*Carex sp.*), rushes (*Juncus sp.*), and grasses (family *Poaceae*)—both native and non-native—are also common in swales and meadows. Much of the eastern part of TDSP and bordering fields were previously managed for cattle grazing and Aleutian cackling goose (*Branta hutchinsii leucopareia*) spring foraging habitat (MRB 2009). Grazing by cows no longer occurs within TDSP, but former pastures now contain high densities of reed canary grass (*Phalaris arundinaceae*) and other non-native species. In addition to native water pepper (*Persicaria hydropiperoides*) and yellow pond lily (*Nuphar lutea*), reed canary grass is especially prevalent around Yontocket Slough, a remnant channel of the Smith River that historically supported populations of juvenile coho salmon (*Oncorhynchus kisutch*; Parish and Garwood 2015).

Historically, TDSP has undergone mixed ownership and land use. The park falls within the ancestral lands of the Tolowa Dee-ni’ people, who maintained significant settlements at Yontocket and several nearby locations prior to the twentieth century. Since then, much of the northern part of TDSP belonged to a private homestead until the State of California took over ownership in the 1970s (Love and Associates 2006).

Historical photos show significantly less forest cover in TDSP prior to state ownership, suggesting recent conifer encroachment (Love and Associates 2006). Today, TDSP is managed as part of a network of public lands in Del Norte County and receives use by hikers, horseback riders, and fishermen accessing the Smith River and nearby Lake Earl.

Although isolated from nearby protected lands in interior Del Norte County by agricultural fields, residential areas, and U.S. Highway 101, TDSP hosts a diversity of native wildlife species. Mountain lions (*Puma concolor*), which do prey on porcupines in other areas (Sweitzer et al. 1997), likely range through TDSP only occasionally, and the porcupine's primary predator in other areas, the fisher (*Pekania pennanti*), was not known to occur within TDSP prior to one nearby sighting by a State Parks employee in 2015 (D. Freeman, pers. comm.). Coyotes (*Canis latrans*) are common in coastal Del Norte County, but across their range they generally prey on porcupines only when more desirable prey are unavailable (Thurber et al. 1992, Prugh 2005) or when deep snow gives them an advantage (Keller 1935, Sweitzer 1996). Additional threats to porcupines in and around TDSP may include vehicle collisions, domestic or feral dogs, and nearby landowners who consider porcupines to be pests.

The climate in coastal Del Norte County is classified as warm-summer Mediterranean or oceanic, with mean temperature in the warmest month reaching only 13.9° C (NOAA 2016a). Average annual rainfall is between 200–254 cm and peaks from November through March (NOAA 2016a). During the summers of 2015 and 2016, temperatures were slightly higher than normal, but precipitation was consistent with recent trends (Figure 2). However, precipitation in winter 2015–16 was much higher than

normal, with 16 days of very heavy rain (≥ 2.54 cm) in December and January (NOAA 2016a). The Smith River reached flood stage on 13 December 2015 and inundated much of the low-lying area within TDSP (USGS 2016).

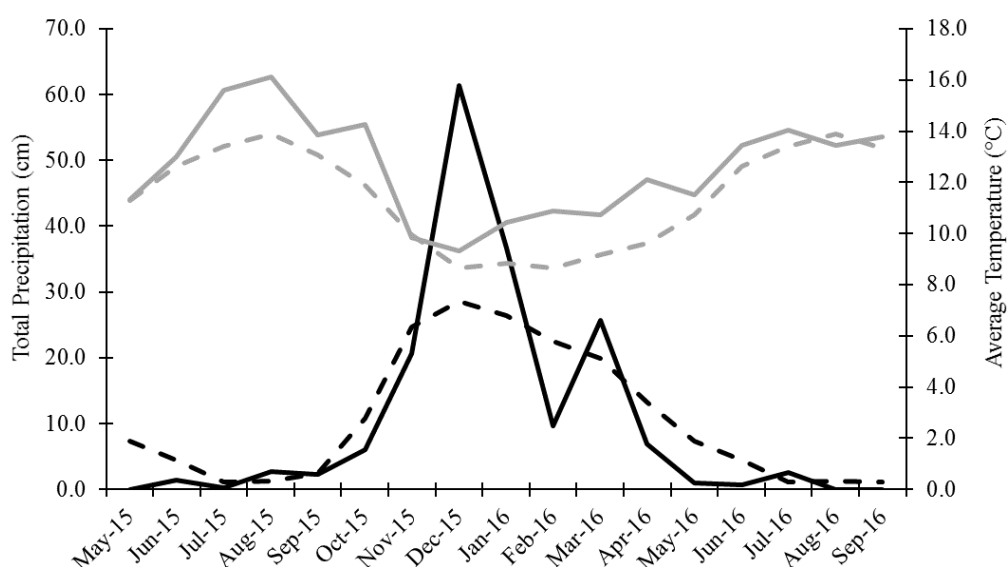


Figure 2. Monthly total precipitation in cm (solid black) and average temperature in °C (solid gray) at a Crescent City, CA, weather station from May 2015 – September 2016. Normal monthly precipitation and average temperature are also shown (dashed black and gray, respectively). Data from National Weather Service Forecast Office, NOAA. [Accessed 19 September 2016. Available from <http://w2.weather.gov/climate/index.php?wfo=eka>.]

Porcupines are observed periodically by visitors to TDSP and nearby lands, and roadkill observations are common in coastal Del Norte County. Public reports submitted from 2012–15 suggest that coastal Del Norte County is the primary hotspot for porcupine sightings on the north coast of California (Appel et al. *In Review*). However, no ecological studies have been conducted on this population, and no estimates of porcupine abundance or distribution in the area are available.

METHODS

I captured, radio-collared, and tracked porcupines in TDSP from May 2015 through September 2016. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at Humboldt State University (protocols #14/15.W.73-A and #15/16.W.32-A) and are consistent with guidelines from the American Society of Mammalogists (Sikes et al. 2011).

Animal Captures

I captured and radio-collared porcupines during three periods: May–July 2015, January–February 2016, and July 2016. With assistance from several crew members, I located porcupines using systematic searches of the study area by walking trails and off-trail areas from late afternoon until approximately four hours after dark, based on my observation that they are most active during this period and therefore most easily spotted. We used flashlights and a thermal camera (FLIR Systems, Inc., Nashua, New Hampshire) to find porcupines either in trees or on the ground, often as they traveled between patches. To mitigate potential bias from this sampling scheme, I divided the study area into search polygons, which we attempted to survey with relatively equal effort until we captured the target number of porcupines. Because we regularly spotted porcupines outside of dedicated search times (e.g., while tracking other collared porcupines or during travel between search sites), approximately half of the porcupine captures ($n = 9$) occurred opportunistically in addition to those found during systematic searches. The

number of animals captured for this study was limited by the availability of VHF transmitters and our tracking effort, in order to obtain a sufficient sample size of relocations for each porcupine. Fifteen VHF transmitters were available for this project, but I only deployed 14 during summer 2015 and saved one in case of transmitter failure. For subsequent captures, I reused transmitters that had been dropped or removed.

We captured porcupines by coaxing them into a 20-gallon plastic trash can from either the ground or low tree branches. We then weighed them in the can using a hanging scale with 0.01-kg precision (UltraSport V2-30; Jennings Scale, Phoenix, Arizona) to adjust drug dosages accordingly. Porcupines were immobilized using an intramuscular injection of ketamine (5 mg/kg) and dexmedetomidine (0.025 mg/kg) or ketamine and xylazine (2 mg/kg) in the muscles at the base of the tail (Morin and Berteaux 2003). This was done by rotating and agitating the can until the porcupine exposed its tail and then having one crew member grasp the guard hairs at the tip of the tail, allowing easy restraint of the tail muscle from underneath. Because no quills grow on the underside of the tail and porcupines often slap with their tails when defensive, restraining the tail in this way allowed for safe control and easy access to the injection site.

Once porcupines were immobilized, I aged and sexed them and collected routine morphometric measurements. I radio-collared adult male and female porcupines, based on a 4-kg threshold for age classification (Dodge 1982). I determined sex by palpating the genital area to expose the penis (Dodge 1982). To ensure long-term identification of each porcupine, I injected a passive integrated transponder (PIT) tag (Biomark, Boise, Idaho) subcutaneously between its shoulder blades.

Finally, I fitted each porcupine with a very high frequency (VHF) radio transmitter (Figure 3; model RI-2D; Holohil Systems Ltd., Carp, Ontario). At 22 g, these transmitters are less than 1% of the average body mass of the porcupines in this study at time of capture (7.71 ± 0.36 kg). I used three different collar designs for attaching the VHF transmitters: a Tygon tubing collar supplied by the manufacturer (Figure 3A), a homemade nylon webbing collar (Figure 3B), and a homemade harness made of the same nylon material (not shown). A subset of porcupines also received 20-g experimental GPS trackers (i-gotU model GT-600 or GT-120; Mobile Action Technologies, New Taipei City, Taiwan) attached by wooden or plastic brackets (Figure 3B). The whole collar including VHF transmitter, bracket, and GPS unit still weighed less than 3% of the porcupines' body mass.

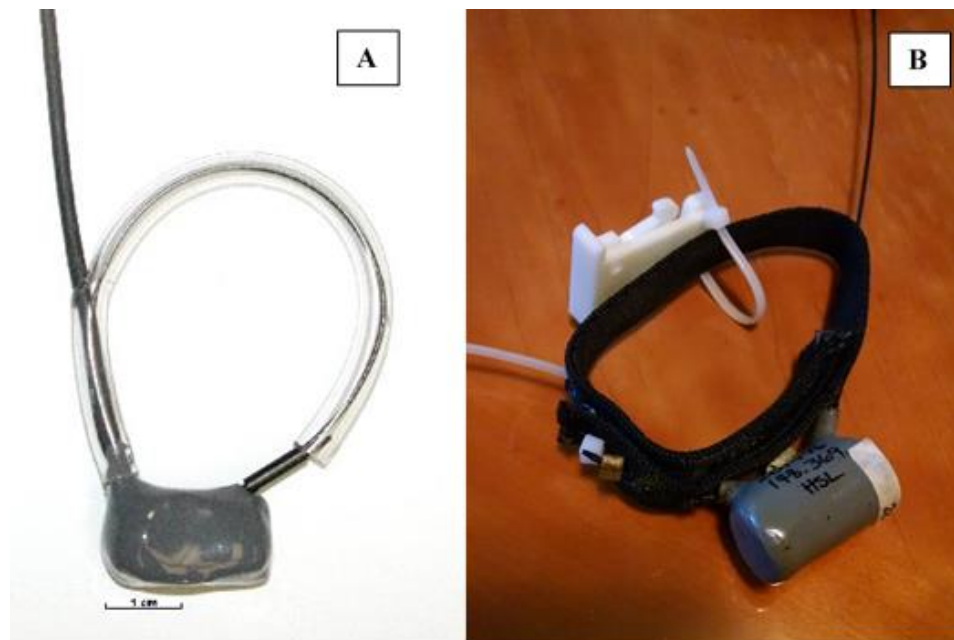


Figure 3. Radio transmitters for porcupine telemetry, shown with two different collar designs: (A) Tygon tubing, and (B) nylon webbing. A plastic bracket for attachment of a GPS tracker is also shown (B). *Image A courtesy of Holohil Systems Ltd., Carp, Ontario.*

I allowed porcupines to recover fully from immobilization before release. Animals immobilized with ketamine and dexmedetomidine received a reversal drug (atipamezole, 0.25 mg/kg) to aid recovery. I placed porcupines back in the trash can and waited until they were able to move naturally and right themselves before releasing them at the site of capture. Beginning in October 2015, I attempted to re-capture all of the original 14 porcupines to weigh them and, when possible, to examine the collar sites for abrasions. Throughout the study, I also periodically recaptured porcupines with GPS trackers to test different attachment mechanisms and settings and exchange them with fully charged units at the end of each unit's battery life.

VHF and GPS Tracking

With assistance from several crew members, I tracked porcupines using handheld VHF receivers (models R-1000, Communications Specialists, Orange, CA; and TRX-2000S, Wildlife Materials, Murphysboro, IL) and 3-element Yagi (Advanced Telemetry Systems, Isanti, MN) or "H" antennas (model RA-14; Telonics, Mesa, Arizona). We used either the homing method or triangulation to locate porcupines and recorded coordinates of each location using handheld GPS units (eTrex Visa HCx or GPSMAP 64s; Garmin, Kansas City, KS). A visual observation was the goal of each tracking session but was not always possible. We recorded "patch-level" locations (estimated to be within 15 m) and triangulations only when physical barriers such as water, burrows, or dense vegetation prevented a visual observation. We found that 15 m was a reasonable distance within which we could be certain that the porcupine was located in the same patch where we

recorded the GPS point, to ensure that it would be matched with the correct vegetation class. For triangulations, we recorded at least three locations and their respective azimuths with a minimum 20-degree difference between them. I used the software program LOAS 4.0 (Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate true locations based on the azimuths and used the results regardless of error polygon size. To reduce autocorrelation among data points, and to minimize the influence of observer presence, we tracked porcupines no more than once during a 24-hour period. Sampling intervals were not equal among porcupines throughout the study, but we attempted to relocate each animal approximately three to four times per week from June–August 2015 and once per week from September 2015 – February 2016. From February–September 2016, I tracked porcupines more sporadically with the primary purpose of testing a new transmitter attachment method. Throughout the study, we tracked porcupines during both day and night so that inference would not be biased towards certain activities like resting or foraging. However, due to logistical constraints, we recorded more observations between sunrise and sunset (75%) than after sunset (25%).

I used data collected from the experimental GPS trackers to augment the telemetry data in subsequent analyses. This allowed me to include several animals that would otherwise have been excluded because of too few locations during a single season. Furthermore, GPS trackers collected locations much more frequently than we were able to obtain locations using VHF telemetry and therefore contributed a more comprehensive data set on porcupines' home ranges and habitat use, particularly at night and during the winter when tracking effort was reduced. We deployed GPS trackers on only a subset of

porcupines ($n = 14$) and, to test battery life and accuracy, we programmed them with varying fix intervals (i.e., the frequency at which locations were recorded) ranging from 10 seconds to 60 minutes.

Based on preliminary stationary trials, the median positional error of these GPS units was less than 10 m in open habitats and under cover (both conifer and willow types), although error was not assessed separately for each device and each fix interval (I. Axsom, unpubl. data). I considered this error highly acceptable given that forest cover can greatly affect GPS performance and accuracy (DeCesare et al. 2005, Moriarty and Epps 2015). To further increase accuracy, I used a data cleaning algorithm (I. Axsom, unpubl. data) to remove suspected outliers, or points that I assumed to be the result of positional error by the device (Figure 4). First, for each deployment, I excluded points within the first eight hours after release to ensure that location data were not affected by our handling of porcupines or their recovery from immobilization. Next, the algorithm compared nearest-neighbor distances between each point (p_2) and its previous (p_1) and subsequent (p_3) neighbors in time. If both distances were greater than the distance between p_1 and p_3 , then the point p_2 was considered an outlier and was removed (Figure 4B). However, if neither of these distances (p_1-p_2 or p_2-p_3) was greater than 20 m, then p_2 was not removed, to prevent unnecessary removal of points within tight clusters. I chose 20 m based on a simulation of the number of outliers identified, erring on the side of removing more potential outliers rather than including them. Finally, for consistency—and to reduce autocorrelation among points—I sub-sampled one random GPS point per 24 hours from the remaining points to augment the VHF telemetry locations (Figure 4C).

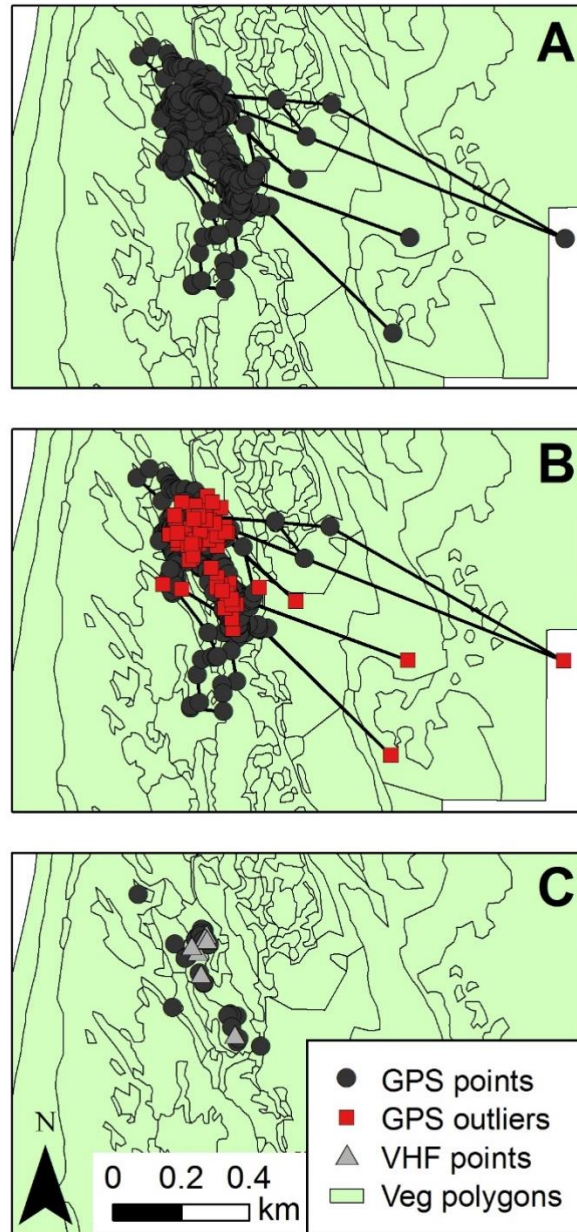


Figure 4. Example of an algorithm used to clean data collected by a global positioning system (GPS) tracker on a male porcupine in Tolowa Dunes State Park, Del Norte County, CA (26 July – 1 September 2016). (A) All GPS points (black circles) were connected to their nearest neighbors in time (black line). (B) Next, points assumed to be the result of positional error were identified as outliers (red squares) based on a comparison of subsequent nearest-neighbor distances, with a minimum nearest-neighbor distance of 20 m required for removal of a point. After outliers were removed, (C) one random point per 24 hours was selected for use in home range and habitat selection analyses. Locations of this animal obtained by very high frequency (VHF) telemetry during the same time period are also shown (gray triangles).

Seasonal Comparisons

I assumed *a priori* that porcupines would select habitats and home ranges differently throughout the year, based on trends reported in the published literature. Even though I hypothesized that seasonal changes in body mass, home range size, and habitat selection would be less extreme than those reported in harsher climates, my objective was to describe the differences between seasons in order to compare with previous studies. Further, Aebischer et al. (1993) recommend that unless seasonal effects can be ignored, tracking data should be compared within a single period. Ideally, I would have been able to compare among summer, fall, winter, and spring, but location sample sizes were not sufficient to allow separation into more than two seasons. Therefore, I divided the study period into summer (1 March – 31 October) and winter (1 November – 29 February).

I based my seasonal delineation on two factors I believed to have biological significance to porcupines: plant phenology and precipitation change. Many authors have acknowledged that seasonal differences in food availability and weather dictate changes in porcupine movements (Gabrielson 1928, Woods 1973, Smith 1979, Roze 1984, Craig and Keller 1986, Coltrane and Sinnott 2013). Porcupine foraging patterns are strongly tied to the seasonal availability of food sources (Roze 2009), and willow and alder trees provide the most available leafy vegetation during the spring and summer in TDSP. I observed leaves remaining on trees until late October 2015 and new growth appearing between late February and early March 2016. Accordingly, the National Weather Service (NWS) classifies the growing season for coastal Del Norte County as 1 March – 15

November (NOAA 2016b). Heavy precipitation may also affect porcupine foraging behavior by restricting their access to seasonally flooded willow swales and by providing a physiological challenge, forcing a tradeoff between foraging and seeking shelter. During my study period, precipitation peaked in TDSP during December 2015 and January 2016 (Figure 2), with the first event of very heavy rainfall (2.54 cm per 24 h) occurring on 8–9 November 2015. I therefore chose seasonal cutoff dates of 1 November and 1 March to reflect the local conditions of both plant phenology and precipitation.

Home Range Analysis

I calculated individual porcupine home ranges using 95% minimum convex polygons (MCPs) and kernel density estimation (KDE) at the 50%, 90%, and 95% isopleths using the *adehabitatHR* package (Calenge 2006) in Program R (R Core Team 2015). For KDEs, I calculated grid and extent parameters separately for each animal, based on a desired cell size of 10×10 m. This cell size was computationally appropriate and was slightly larger than the error from VHF and GPS telemetry. I tested three different bandwidth selection methods and visually assessed the resulting utilization distributions (UDs). Least-squares cross-validation (LSCV) did not converge for all animals, and a reference bandwidth did not appear to accurately portray space use. The third option, fixed bandwidth, appeared to be the best across all animals. To select a biologically meaningful fixed bandwidth, I estimated the average radius of the circular equivalents for all of the vegetation patch polygons within TDSP and arrived at

approximately 60 m. KDEs estimated using a bandwidth of 60 m do appear to accurately represent porcupine space use and were therefore used for all UD estimates.

I calculated MCPs and KDEs for porcupines based on summer and winter locations separately. I then used paired *t*-tests to compare changes in home range size (using 95% KDEs) between summer and winter for animals that had at least five relocations in each season, as well as non-paired *t*-tests to assess differences between males and females. I also used linear regression to test whether total home range size was related to maximum body mass attained by porcupines. Finally, I calculated utilization distribution overlap indices (UDOI; Fieberg and Kochanny 2010) to test for home range overlap among all porcupines, as well as between each individual's summer, winter, and overall home range. The UDOI is a function of space use overlap between two individuals using the same area uniformly (i.e., with constant UDs), where $UDOI = 0$ indicates no overlap and $UDOI = 1$ indicates complete overlap. The same concept can be applied to compare an individual animal's home ranges over two different time periods. Therefore, by incorporating probabilistic space use measured by the UD, the UDOI indicates whether overlap is greater ($UDOI > 1$) or less ($UDOI < 1$) than would be expected relative to uniform use (Fieberg and Kochanny 2010).

Habitat Selection Analysis

Vegetation Classification

To classify available habitat within the study area, I digitized polygons of vegetation classes by hand using satellite imagery and a geographic information system

(GIS; ArcMap 10.3.1, ESRI, Redlands, CA). I used base imagery from ESRI (NAIP 2014, USDA FSA) and digitized consistently at a 1:4,000 scale, as this is the highest resolution available for the most recent set of imagery and provides enough detail to distinguish vegetation features. I categorized vegetation into 14 classes that I believe to have biological significance for porcupines, based on composition and structure of dominant species. These classes were based on habitat descriptions from a previous ecological assessment of TDSP (MRB 2009). However, to reduce the likelihood that some vegetation classes would not be available within every animal's home range, and to ensure that the number of covariate levels was smaller than the number of animals tracked during each season (Aebischer et al. 1993), I collapsed these categories into nine vegetation classes (Table 1).

Table 1. Vegetation classes and their availability within the study area at Tolowa Dunes State Park, Del Norte County, CA. (continued)

Vegetation class	Description	% Available
Conifer forest	Mature trees, including <i>Pinus contorta contorta</i> , <i>Picea sitchensis</i> , <i>Abies grandis</i> , and <i>Pseudotsuga menziesii</i> . Understory dominated by <i>Vaccinium ovatum</i> , <i>Gaultheria shallon</i> , <i>Arctostaphylos uva-ursi</i> , <i>Rubus parviflorus</i> , <i>Berberis aquifolium</i> , <i>Polystichum munitum</i> , <i>Pteridium aquilinum</i> .	19.29
Pasture	Primarily non-native grasses, including <i>Phalaris arundinaceae</i> . Partially inundated seasonally.	16.40
Dune	Nearshore dunes, sparsely vegetated by non-native (<i>Ammophila arenaria</i>) and native vegetation (<i>Baccharis pilularis</i> and dune mat species). Trees (e.g., <i>Pinus contorta contorta</i> , <i>Picea sitchensis</i> ,	15.26

Vegetation class	Description	% Available
	<i>Morella californica</i>) are sparse and grow as shrubby life forms.	
Swale	Combines two classes of seasonally inundated swales. Shrub swales are dominated by <i>Salix sp.</i> with an understory of herbaceous swale (see Marsh). Wooded swales are more diverse and contain mature <i>Salix sp.</i> , <i>Alnus rubra</i> , and <i>Malus fusca</i> mixed with <i>Pinus contorta contorta</i> and <i>Picea sitchensis</i> , with herbaceous swale understory.	14.92
Coastal scrub	Stabilized dunes vegetated by <i>Baccharis pilularis</i> , <i>Morella californica</i> , <i>Pinus contorta contorta</i> , and <i>Spiraea douglasii</i> , with an understory of dune mat species and <i>Ammophila arenaria</i> in some areas.	11.81
Marsh	Both freshwater and brackish marshes, inundated with standing water either year-round or seasonally. Dominated by <i>Persicaria hydropiperoides</i> , <i>Nuphar lutea</i> , and emergent species. All marshes are freshwater except for Yontocket Slough, which receives overflow from the Smith River. Also includes seasonally inundated herbaceous swales dominated by <i>Carex sp.</i> and <i>Juncus sp.</i> , with some <i>Spiraea douglasii</i> , <i>Rubus ursinus</i> , herbs, and nonnative <i>Phalaris arundinaceae</i> in some areas.	9.78
Meadow	Coastal meadows contain <i>Juncus sp.</i> , native and nonnative grasses, <i>Berberis aquifolium</i> , dune mat forbs, and exotics such as <i>Rumex sp.</i>	7.30
Beach	Open sand (beach strand).	5.23
Fruit	Remnant cultivated apple (<i>Malus domestica</i>) and English walnut (<i>Juglans regia</i>) trees.	0.01

Weighted Compositional Analysis

I quantified habitat selection at both the home-range scale (second-order selection) and the within-home-range scale (third-order selection), according to Johnson (1980), for both summer and winter. To model second-order selection, I followed design II as defined by Thomas and Taylor (2006), in which use is measured for individuals but habitat availability is measured at the population level and assumed to be the same for each animal. I defined the extent of habitat available to the population by the study area boundary. My third-order selection analysis followed design III, in which both use and availability were measured for individuals at the home range level (Thomas and Taylor 2006). Here, I restricted available resources to the extent of each individual's home range, defined as its overall 95% KDE.

I used weighted compositional analysis (WCA) to quantify porcupine habitat selection in relation to vegetation classes, according to methods proposed by Millspaugh et al. (2006). Weighted compositional analysis is a variation on traditional compositional analysis (CA), a commonly used approach to assessing habitat selection in relation to categorical covariates by using multivariate analysis of variance (MANOVA; Aebischer et al. 1993). It improves on traditional CA by using the height of the UD as the response variable instead of discrete location points, and thus treats space use within an animal's home range as a continuous and probabilistic process rather than relying on the assumption of random use (Marzluff et al. 2004, Millspaugh et al. 2006). Traditional compositional analysis assumes that habitat use within an animal's home range boundary is proportional to the availability of habitat types present, ignoring that nonrandom use

(i.e., the selection of some habitats over others) should be the biological expectation (Millspaugh et al. 2006). Finally, WCA preserves the benefits of traditional compositional analysis, including the use of animals as the sample unit instead of individual location points and the ability to rank habitats in order of relative selection and test for differences among groups (Aebischer et al. 1993, Pendleton et al. 1998, Alldredge and Griswold 2006).

I conducted WCA separately for summer and winter location data at both the second and third orders of selection. I calculated two or three separate UD's on the same grid for each animal: an overall UD using all locations, as well as a summer UD and a winter UD using only locations from each respective season, when available. The height of the UD at each cell within these three grids represented the probability of use of that cell by the animal during each season. To avoid bias introduced by values in the tails of the distribution, I clipped UD's to their 95% contours, which then became the individual home range boundaries for delineating use in second-order analysis and availability in third-order analysis (Millspaugh et al. 2006). However, to compare seasonal use with the entire area available to each animal at the third order—as opposed to just its seasonal home range—I defined home ranges for all seasons as the outer boundary created by merging the overall, summer, and winter 95% contours. This outer boundary (hereafter referred to as the total home range) differed from the 95% contour of the overall UD in only a few instances, but using the outermost extent was necessary to avoid excluding habitat that was considered available in one season and not another. The remaining UD heights represented seasonal use relative to each animal's total home range (Figure 5).

Because a few UD grids extended outside the study area (i.e., into the ocean), I also clipped grids to the study area boundary.

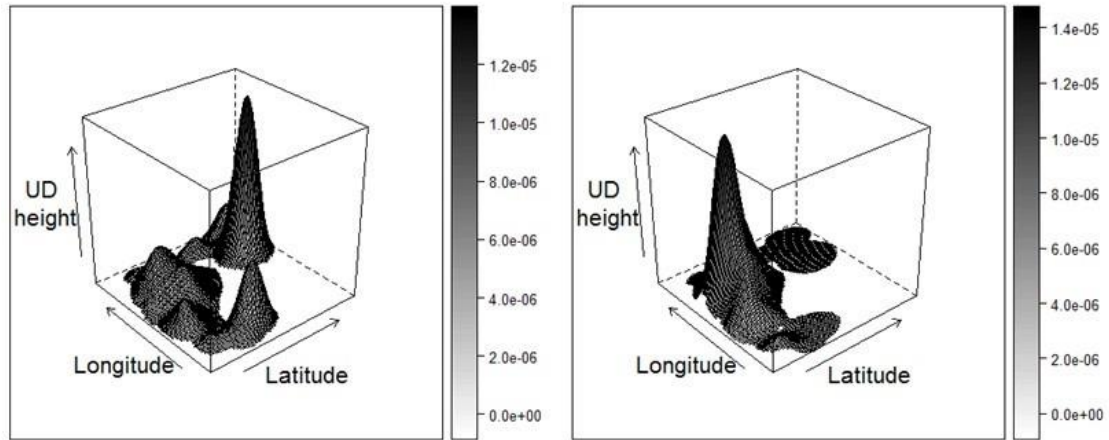


Figure 5. Summer (left) and winter (right) utilization distribution (UD) grids clipped to the total 95% home range for a female porcupine in Tolowa Dunes State Park, Del Norte County, CA (2015-16).

To relate use data to the covariate values, I used the spatial overlay function *over* in package *sp* (Pebesma and Bivand 2005) for Program R to assign a category from the vegetation polygons shapefile to each grid cell within the seasonal UDs. I then calculated the proportional use of each vegetation class by summing the UD heights of all grid cells by class in each animal's home range and dividing the sum by the total UD height of all grid cells within the home range. These proportions represented individual UD-weighted estimates of use for each vegetation class within each animal's home range for both second- and third-order analysis (Millsaugh et al. 2006).

Defining availability is difficult and often arbitrary in habitat selection studies, because it is generally not possible to account for all biological factors that may constrain an animal's access to resources, such as seasonal changes in vegetation or the presence of

competitors (Johnson 1980, Aebischer et al. 1993, Morrison et al. 2012). Because my study area had meaningful boundaries, for the most part (Figure 1), I considered it a reasonable delineation of available habitat for this population of porcupines. Thus, for second-order analysis, I defined the extent of available habitat as the entirety of the study area. Using the layer of vegetation class polygons, I calculated the proportional availability of each vegetation class within the study area (Table 1). This allowed me to compare porcupines' use of habitats constituting their home ranges with those available in the entire study area. Availability data were therefore the same for each animal at the second order. For third-order analysis, I calculated habitat availability separately for each animal as the proportion of its total home range belonging to each vegetation class. Because I was interested in whether animals used different areas of their home ranges seasonally, I used the same availability data for both summer and winter, considering the entirety of each animal's home range to be available during both seasons.

One drawback to compositional analysis is the need to substitute zero values of use and availability with non-zero numbers, in order to avoid negative infinity results in subsequent log-transformations (Aebischer et al. 1993, Bingham and Brennan 2004). When habitat types were available to but not used by an animal, I replaced zero-use values with a number that was one order of magnitude smaller than the lowest UD height (see pheasant example from Aebischer et al. 1993). These values represent the biologically meaningful scenario of complete avoidance of a particular habitat type (or use too low to be detected). When certain habitat types were not available within an individual's home range, I followed the suggestions of Aebischer et al. (1993) for

replacing these missing values with the mean selection ratio for that vegetation type, as explained subsequently. Aebischer et al. (1993) acknowledged that while it is ideal for all habitat types to be available to each animal (i.e., present within its home range), removing animals from analysis to satisfy this constraint may result in a considerable loss of data and can even introduce bias. I therefore chose not to remove any animals to preserve data but recognize that this replacement may not be ideal.

I first tested for significant non-random use of habitats (Wilks' test, $\alpha < 0.05$) at both the second and third orders (Millsaugh et al. 2006). For those instances when overall selection was significant, I then calculated log-ratios and conducted pairwise t -tests to rank habitat types by their relative use. Compositional analysis uses a log-transformation of the use and availability data to account for the unit-sum constraint, which requires proportional use among all habitat types to sum to one—an assumption that is often violated by other analysis methods (Aebischer et al. 1993). The log-transformation is computed as $use_i = \ln(u_i/u_j)$, in which u_i is the proportional use for habitat type i and u_j is the proportional use for habitat type j , and similarly for availability as $avail_i = \ln(a_i/a_j)$. The log-ratio for selection of habitat type i is then defined as $use_i - avail_i$. Habitat type j is used as a reference category—the denominator for the log-transformation of use and availability for each other habitat type. This reduces the dimensionality of the response variable matrix by one habitat type and satisfies the unit-sum constraint (Pendleton et al. 1998, Alldredge and Griswold 2006). Because all information is preserved in subsequent matrices and the log-ratios are

relative, choice of the reference category has no effect on the overall analyses (Pendleton et al. 1998).

I log-transformed the use and availability proportions for each animal and computed pairwise log-ratios in order to rank habitat types according to the methods of Aebischer et al. (1993). I created matrices of log-ratios using an iterative process in which each vegetation class served as the denominator in computing log-ratios for each other vegetation class. I then conducted one-sample t -tests on the mean log-ratios across individuals for each vegetation class to assess whether it was selected significantly differently from the reference category ($H_0: \mu = 0$). For each vegetation type as a reference category, I counted the number of vegetation classes with mean log-ratios greater than zero—representing selection greater than the reference category—and used these counts to rank vegetation classes in order of their relative selection (Aebischer et al. 1993). I considered differences between ranks and between all pairs of vegetation classes to be statistically significant at a level of $\alpha < 0.05$ if overall selection was significantly nonrandom, as recommended by Aebischer et al. (1993). For vegetation types containing missing values of log-ratios (due to some habitat types not being available to all animals at the third order), I computed the mean log-ratio of all non-missing values for that vegetation type and used this mean as a replacement for the missing values (see Appendix 2, Aebischer et al. 1993). In this way, the mean log-ratio for each vegetation type remained unchanged but the problem of missing values was resolved.

In order to summarize the relative differences in selection among habitats, I computed the geometric means of selection ratios, as recommended by Pendleton et al.

(1998). The selection ratio w_i is defined as $w_i = u_i/a_i$ for each habitat type i (Manly et al. 2002). The geometric mean of selection ratios is an appropriate summary statistic because it preserves the lognormal distribution of compositional analysis and has been shown to reflect the rankings from compositional analysis more closely than other summary measures (Pendleton et al. 1998). I also computed 95% confidence intervals for the geometric means to assess whether vegetation classes were used significantly differently from their availability (i.e., selected or avoided), with confidence intervals not overlapping 1.

RESULTS

Animal Captures

I captured and radio-collared a total of 20 porcupines: 14 between 27 May – 23 July 2015 (nine females and five males), an additional four between 27 January – 20 February 2016 (two females and two males), and two in July 2016 (both males). Porcupine captures occurred throughout the study area (Figure 6). Initial body mass for the porcupines captured during summer 2015 was not significantly different between females (7.91 ± 0.44 kg) and males (8.96 ± 0.59 kg; $t_{12} = -1.44$, $P = 0.176$). Both porcupines initially captured during summer 2016 were small males, with body mass less than the average for summer 2015 (5.90 kg and 5.98 kg). Body mass of females (6.28 ± 1.93 kg) and males (6.90 ± 0.27 kg) captured during winter 2015–16 was also not significantly different ($t_2 = -0.32$, $P = 0.778$); however, this includes one female believed to be a subadult with a body mass of 4.35 kg. Because this female was above my threshold of 4 kg for an adult, she received a radio-collar; however, her morphological features resembled those of a subadult. Her collar fell off within one week of capture and her locations are therefore not included in any analyses.

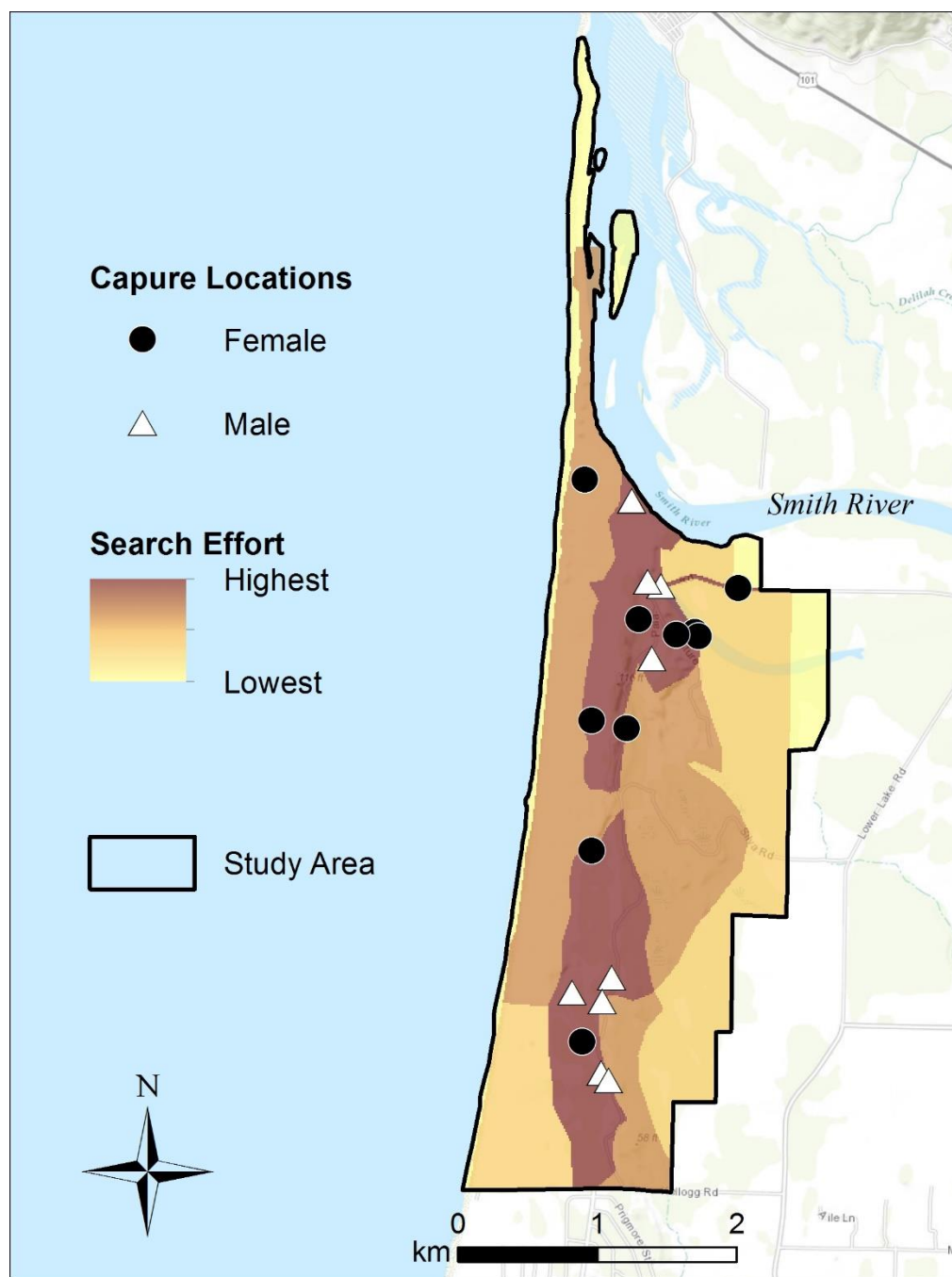


Figure 6. Capture locations of female ($n = 10$, black circles) and male ($n = 9$, white triangles) porcupines in Tolowa Dunes State Park, Del Norte County, CA (2015–16). Approximate search effort is represented from highest (dark) to lowest (light).

Male and female porcupines both had larger body mass in summer than winter, with a difference of approximately 0.66 kg (paired $t_{11} = 4.45$, $P = 0.001$). The difference was larger for males, which had a mean difference of 0.82 kg (paired $t_5 = 3.34$, $P = 0.021$). Females were, on average, 0.51 kg heavier in summer than winter (paired $t_5 = 3.04$, $P = 0.029$). For animals that were weighed multiple times during summer or winter, I averaged all data points within each season in order to use paired t -tests between summer and winter body mass. However, seasonal averages do not reflect fluctuations in body mass that occurred (Figure 7).

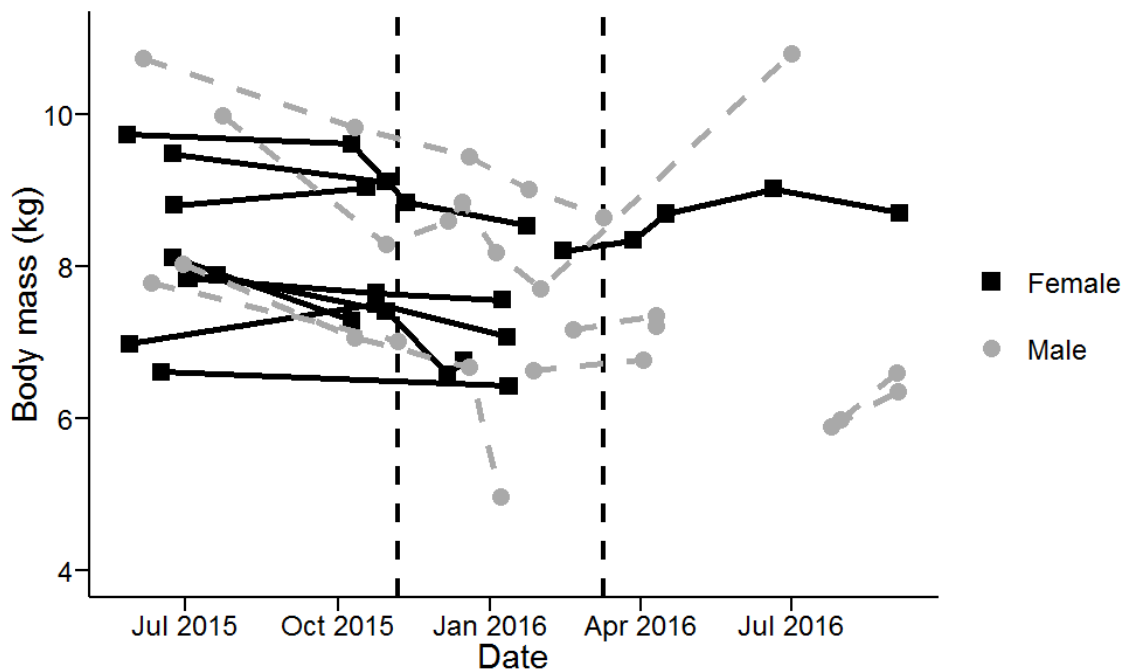


Figure 7. Changes in body mass (kg) of female (black squares) and male (gray circles) porcupines in Tolowa Dunes State Park, Del Norte County, CA (2015–16). Only porcupines for which multiple body mass measurements were recorded are shown ($n = 17$). Dashed vertical rules indicate seasonal delineation for summer 2015 (< 1 November), winter (1 November 2015 – 29 February 2016), and summer 2016 (≥ 1 March 2016).

VHF and GPS Tracking

From May–October 2015, we located the original 14 porcupines between 17–45 times each ($\bar{x} = 30$, $SE = 2$). During this time period, one collared male left the study area and one female died, resulting in a change in the composition of porcupines that we tracked through the fall and winter. Further, in December 2015 and January 2016, two porcupines lost their collars (one female and one male) and four died (two females and two males). Because of these losses, I collared the four previously mentioned additional porcupines in January and February 2016 to increase the sample size of winter location data. Therefore, although we tracked 15 porcupines total during the winter period from November 2015 – February 2016, the number of locations obtained during this time ranged from 2–16 per animal ($\bar{x} = 8$, $SE = 1$). Finally, during the summer period from March–September 2016, I relocated seven porcupines between 2–8 times each ($\bar{x} = 5$, $SE = 2$). Among all telemetry locations, 79.2% were visual observations, 11.3% were “patch-level,” and 9.5% were recorded by triangulation.

I deployed GPS trackers on 14 porcupines and collected between nine and >10,000 location points per animal ($\bar{x} = 1,517$, $SE = 755$) over 1–4 deployments each. The amount of data collected was limited by a variety of factors including battery life and unit failure (Table 2). I deployed four additional GPS units that were not recovered, either because they became detached from the collar ($n = 3$) or the entire collar fell off ($n = 1$). After removing outliers and subsampling one point per 24 hours, I added between 1–38 points per animal to augment the telemetry data for these 14 porcupines ($\bar{x} = 11$, $SE = 3$).

Table 2. GPS data collected on porcupines at Tolowa Dunes State Park, Del Norte County, CA (2015–16). I assumed unit failure (e.g., due to water damage) if data collection stopped after < 10 days and the end of battery life if data collection lasted \geq 10 days with fix interval at \geq 10 min. Various fix intervals were used to test unit battery life and accuracy.

Animal ID	Deployment date	Total days	Fix interval (min.)	Limiting factor
15.12 ♀	20 July 2015	9	10	Testing
15.12 ♀	3 August 2015	9	10	Testing
15.12 ♀	30 October 2015	28	10	Battery ended
15.12 ♀	6 December 2015	5	10	Unit failed
15.01 ♀	11 November 2015	2	0.1	Battery ended
15.14 ♂	15 December 2015	3	10	Unit failed
15.03 ♂	19 December 2015	14	10	Battery ended
15.11 ♂	7 January 2016	1	60	Mortality
15.13 ♀	8 January 2016	2	60	Collar removed
15.02 ♀	11 January 2016	4	60	Unit failed
15.07 ♀	12 January 2016	1	60	Unit failed
15.03 ♂	24 January 2016	25	60	Battery ended
16.17 ♀	14 February 2016	11	60	Battery ended
16.18 ♂	20 February 2016	13	60	Battery ended
16.17 ♀	27 March 2016	9	30	Battery ended
16.15 ♂	2 April 2016	9	20	Battery ended
15.14 ♂	1 July 2016	1	20	Harness lost
16.19 ♂	25 July 2016	38	20	Battery ended
16.20 ♂	30 July 2016	31	20	Battery ended

Home Ranges

I estimated porcupine home range sizes using both minimum convex polygon (MCP) and kernel density estimate (KDE) methods (Table 3). Porcupines with fewer than five locations in a given season were omitted from the respective analyses, as was one male that left the study area in July 2015 and whose movements may therefore represent a dispersal event rather than part of his home range. Home range sizes were statistically equivalent for males and females during both summer ($t_{16} = 1.122$, $P = 0.279$) and winter ($t_9 = 0.252$, $P = 0.807$). Porcupine home ranges were larger during summer than winter (paired $t_{10} = 3.941$, $P = 0.003$). For females, home ranges were significantly larger during the summer than during the winter by approximately 0.179 km^2 (paired $t_5 = 3.69$, $P = 0.015$). Male home ranges were statistically equivalent during summer and winter (paired $t_4 = 1.109$, $P = 0.330$). Finally, I found a very strong correlation between the heaviest body mass attained by male porcupines and their overall home range sizes ($r^2 = 0.94$, $F_{1,6} = 92.57$, $P < 0.001$) but no correlation between body mass and home range sizes for females ($r^2 = 0.12$, $F_{1,8} = 1.10$, $P = 0.33$; Figure 8).

Table 3. Estimated home range sizes (mean \pm 1 SE) for porcupines in Tolowa Dunes State Park, Del Norte County, CA, during summer and winter 2015–16. Home ranges were calculated using both kernel density estimation (KDE) and minimum convex polygon (MCP) methods at various isopleths.

Season	Sex	<i>n</i>	50% KDE (km ²)	90% KDE (km ²)	95% KDE (km ²)	95% MCP (km ²)
Overall	Female	10	0.087 \pm 0.013	0.306 \pm 0.046	0.386 \pm 0.057	0.261 \pm 0.057
	Male	8	0.061 \pm 0.010	0.254 \pm 0.045	0.329 \pm 0.057	0.177 \pm 0.060
	Both	18	0.075 \pm 0.002	0.283 \pm 0.008	0.360 \pm 0.009	0.224 \pm 0.010
Summer	Female	10	0.079 \pm 0.011	0.288 \pm 0.042	0.363 \pm 0.052	0.232 \pm 0.055
	Male	8	0.058 \pm 0.013	0.218 \pm 0.039	0.282 \pm 0.048	0.125 \pm 0.046
	Both	18	0.070 \pm 0.002	0.257 \pm 0.007	0.327 \pm 0.009	0.185 \pm 0.009
Winter	Female	6	0.048 \pm 0.006	0.180 \pm 0.025	0.229 \pm 0.031	0.063 \pm 0.024
	Male	5	0.047 \pm 0.006	0.167 \pm 0.018	0.219 \pm 0.028	0.075 \pm 0.030
	Both	11	0.048 \pm 0.001	0.174 \pm 0.005	0.224 \pm 0.006	0.069 \pm 0.005

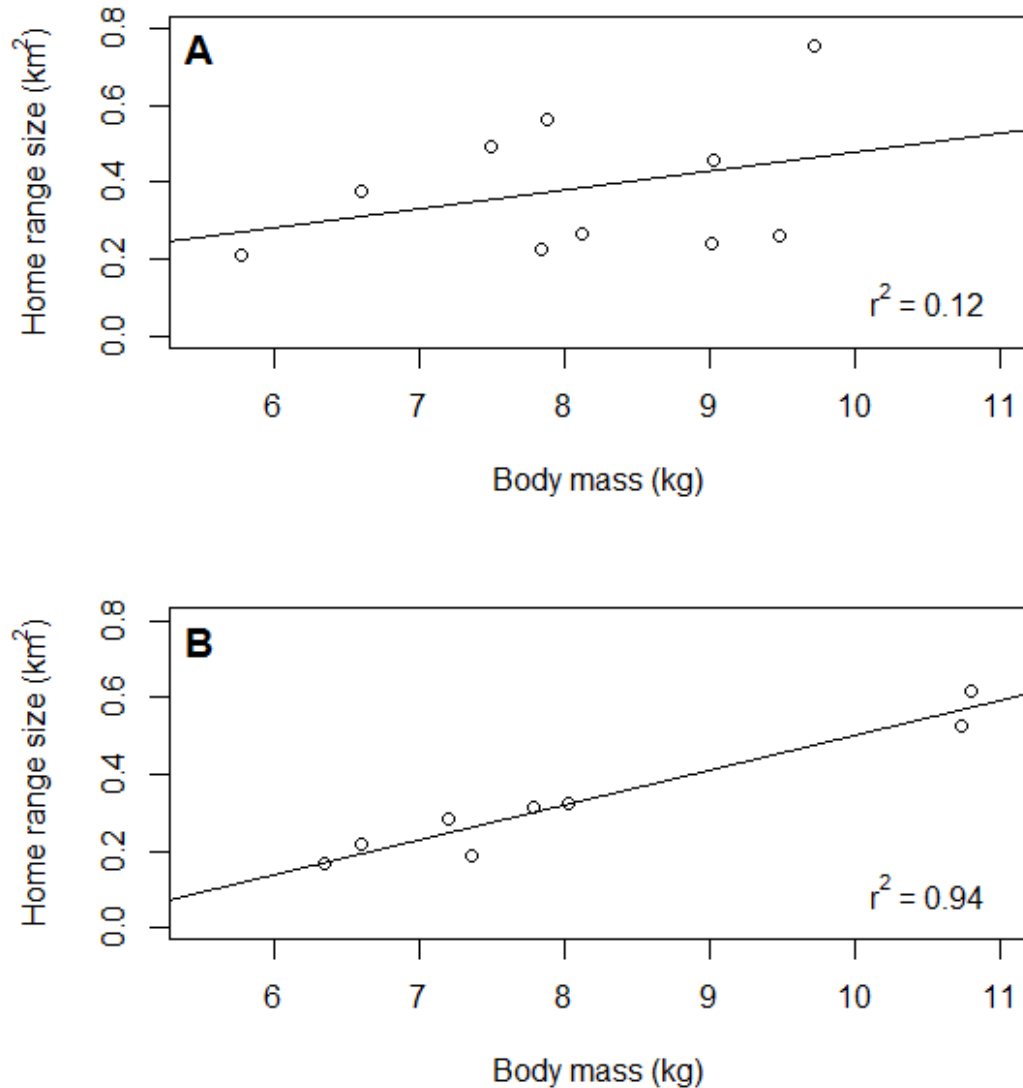


Figure 8. Porcupine home range sizes (95% kernel density estimates) in relation to maximum body mass attained (kg) for females (A) and males (B) in Tolowa Dunes State Park, Del Norte County, CA (2015–16). Males had a very strong correlation between heaviest body mass attained and overall home range size ($r^2 = 0.94$, $F_{1,6} = 92.57$, $P < 0.001$) but females had no correlation ($r^2 = 0.12$, $F_{1,8} = 1.10$, $P = 0.33$).

Among porcupines for which I collected both summer and winter location data, the overlap between their summer and winter home ranges was much less than would be expected under uniform use based on UDOI values ($\bar{x} = 0.29$, $SE = 0.08$, $n = 11$).

Summer home ranges overlapped with overall home ranges more than expected, with mean $UDOI > 1$ ($\bar{x} = 1.32$, $SE = 0.11$, $n = 11$), and winter home ranges overlapped with overall home ranges less than expected, with mean $UDOI < 1$ ($\bar{x} = 0.82$, $SE = 0.11$, $n = 11$). Only one porcupine, a male, had a $UDOI < 1$ between its summer and overall home ranges, and, along with two other males, also had $UDOI > 1$ between its winter and overall home ranges. Most porcupines used less of their total home ranges during winter than during summer, as indicated by the lower overlap. For some porcupines, this meant using mostly separate areas in each season (Figure 9A) while others used a restricted part of their summer home range during winter (Figure 9B).

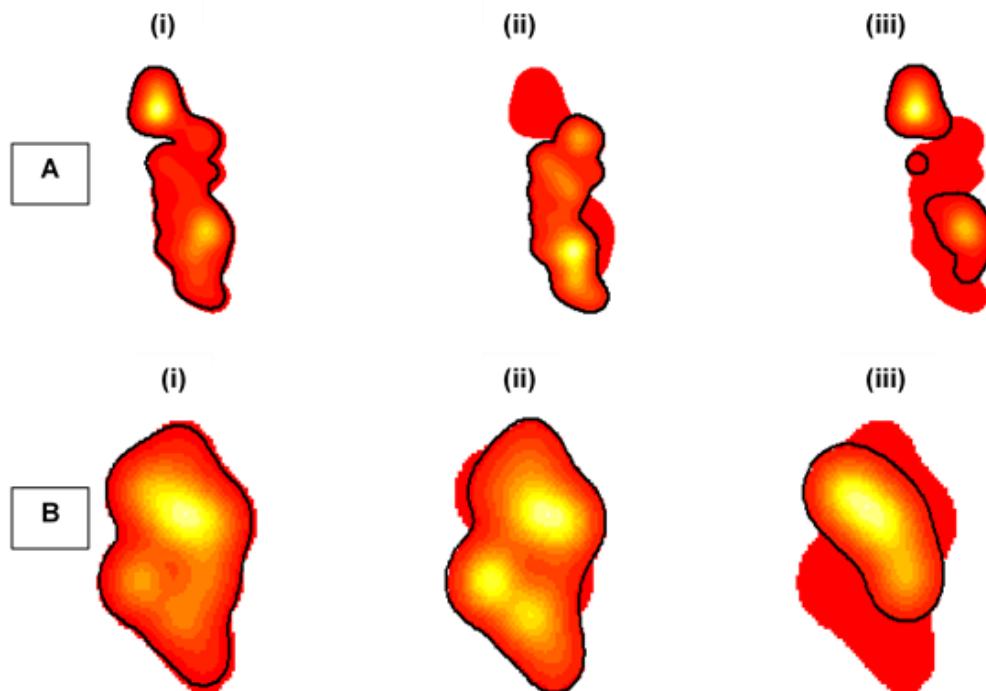


Figure 9. Examples of home range utilization by two porcupines: (A) a male; and (B) a female, in Tolowa Dunes State Park, Del Norte County, CA (2015–16). Utilization distributions (absence of black perimeters) and 95% KDE contours (black perimeters) were calculated over the course of the entire study (i) as well as for summer only (ii) and winter only (iii).

During summer, all porcupine home ranges (95% KDEs) overlapped with at least one other marked porcupine's home range (Figure 10A), and many overlapped with home ranges of several animals (median = 8 for females, 5 for males). Among overlapping pairs, UDOI values ranged from 0.01–1.04 (Table 4). During winter, many porcupine home ranges did not overlap any other home ranges (median = 0.5 for females, 1 for males; Figure 10B), and UDOI values among overlapping pairs ranged from 0.01–0.22 (Table 5). Overlap was lower among porcupine core areas, defined as their 50% KDEs (Figure 10C–D). However, in summer, most porcupine core areas still overlapped at least one other marked porcupine's core area (median = 3 for females, 3 for males), with UDOI among overlapping pairs ranging from 0.01–0.18 (Table 4). During winter, only two pairs of marked porcupines had overlapping core areas (Table 5). Fewer animals were tracked during winter, so the spatial arrangement of home ranges and core areas of marked animals is very likely correlated with observer effort.

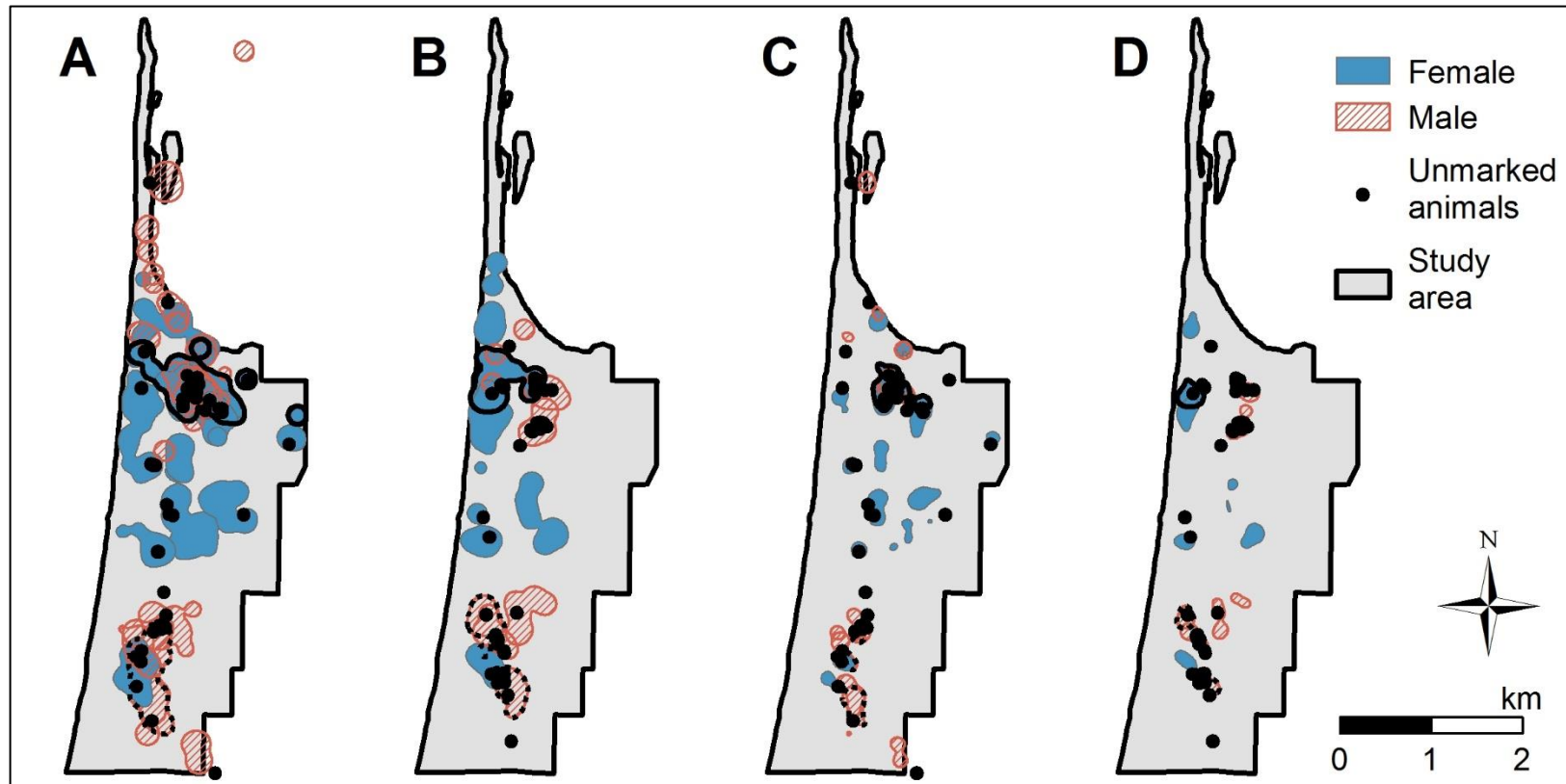


Figure 10. Home ranges (A-B) and core areas (C-D) of female (solid blue) and male (hashed red) porcupines in Tolowa Dunes State Park, Del Norte County, CA, during 2015–16. Home ranges were calculated as 95% kernel density estimates (KDE) for (A) summer ($n = 10$ ♀, 9 ♂) and (B) winter ($n = 6$ ♀, 5 ♂). Core areas were calculated as 50% KDE for (C) summer ($n = 10$ ♀, 9 ♂) and (D) winter ($n = 6$ ♀, 5 ♂). Home range and core area of one female (solid line) and male (dashed line) are outlined to illustrate that single home ranges may be represented by multiple polygons. Locations of unmarked porcupines observed during each respective season are indicated by black circles.

Table 4. Pairwise comparisons of utilization distribution overlap indices (UDOI) for home ranges (95% KDEs, shaded gray) and core areas (50% KDEs, no shading) of porcupines in Tolowa Dunes State Park, Del Norte County, CA, in summer 2015–16. Pairs of animals whose home ranges did not overlap are indicated by a 0 value. Quadrants are separated by sex: female (♀) and male (♂).

ID/ sex	1 ♀	2 ♀	5 ♀	7 ♀	8 ♀	9 ♀	10 ♀	12 ♀	13 ♀	17 ♀	3 ♂	4 ♂	6 ♂	11 ♂	14 ♂	15 ♂	18 ♂	19 ♂	20 ♂
1 ♀	NA	<0.1	0.53	0	0.29	<0.1	<0.1	0.31	0	0	0	0	0	0	0.39	0.31	0	0	0.46
2 ♀	0	NA	<0.1	0	<0.1	<0.1	0	0	0	0	0	0	<0.1	0	0.42	<0.1	0	0	<0.1
5 ♀	<0.1	0	NA	0	0.17	<0.1	<0.1	0.22	0	0	0	0	0	0	0.27	0.52	0	0	0.81
7 ♀	0	0	0	NA	0	0	<0.1	0	<0.1	0	0	0	0	0	0	0	0	0	0
8 ♀	<0.1	<0.1	<0.1	0	NA	0.28	<0.1	<0.1	0	0	0	0	0	0	0.13	0.24	0	0	0.36
9 ♀	<0.1	0	<0.1	0	<0.1	NA	<0.1	<0.1	0	0	0	0	0	0	<0.1	<0.1	0	0	<0.1
10 ♀	0	0	0	0	0	0	NA	0	0	0	0	0	0	0	<0.1	<0.1	0	0	<0.1
12 ♀	<0.1	0	<0.1	0	0	0	0	NA	0	0	0	0	0	0	<0.1	<0.1	0	0	<0.1
13 ♀	0	0	0	0	0	0	0	0	NA	0	0	0	0	0	0	0	0	0	0
17 ♀	0	0	0	0	0	0	0	0	0	NA	0.27	<0.1	0	0	0	0	<0.1	0.27	0
3 ♂	0	0	0	0	0	0	0	0	0	<0.1	NA	0.33	0	<0.1	0	0	<0.1	0.17	0
4 ♂	0	0	0	0	0	0	0	0	0	<0.1	<0.1	NA	0	0	0	0	0	<0.1	0
6 ♂	0	0	0	0	0	0	0	0	0	0	0	0	NA	0	<0.1	0	0	0	0
11 ♂	0	0	0	0	0	0	0	0	0	0	<0.1	0	0	NA	0	0	0.34	<0.1	0
14 ♂	<0.1	<0.1	<0.1	0	<0.1	0	0	<0.1	0	0	0	0	0	0	NA	0.31	0	0	0.30
15 ♂	<0.1	0	<0.1	0	<0.1	0	0	0	0	0	0	0	0	0	<0.1	NA	0	0	1.04
18 ♂	0	0	0	0	0	0	0	0	0	0	<0.1	0	0	<0.1	0	0	NA	0.26	0
19 ♂	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.1	NA	0
20 ♂	<0.1	<0.1	<0.1	0	<0.1	<0.1	0	0	0	0	<0.1	0	0	0	<0.1	0.18	0	0	NA

Table 5. Pairwise comparisons of utilization distribution overlap indices (UDOI) for home ranges (95% KDEs, shaded gray) and core areas (50% KDEs, no shading) of porcupines in Tolowa Dunes State Park, Del Norte County, CA, in winter 2015–16. Pairs of animals whose home ranges did not overlap are indicated by a 0 value. Quadrants are separated by sex: female (♀) and male (♂).

ID/ sex	1 ♀	2 ♀	7 ♀	12 ♀	13 ♀	17 ♀	3 ♂	11 ♂	14 ♂	15 ♂	18 ♂
1 ♀	NA	0	0	0.22	0	0	0	0	<0.1	0	0
2 ♀	0	NA	0	0	0	0	0	0	0	0	0
7 ♀	0	0	NA	0	0	0	0	0	0	0	0
12 ♀	<0.1	0	0	NA	0	0	0	0	<0.1	0	0
13 ♀	0	0	0	0	NA	0	0	0	0	0	0
17 ♀	0	0	0	0	0	NA	<0.1	0	0	0	0
3 ♂	0	0	0	0	0	0	NA	0	0	0	0.19
11 ♂	0	0	0	0	0	0	0	NA	0	0	0
14 ♂	0	0	0	0	0	0	0	0	NA	<0.1	0
15 ♂	0	0	0	0	0	0	0	0	0	NA	0
18 ♂	0	0	0	0	0	0	<0.1	0	0	0	NA

Habitat Selection

I ran compositional analysis on 19 animals and nine habitat types for summer 2015–16 and on 11 animals and nine habitat types for winter 2015–16. At the second order of selection, representing the home-range level, porcupines used vegetation classes significantly differently from their availability in the study area during both summer (Wilks' $\lambda = 1.58 \times 10^{-32}$, $P < 0.001$) and winter (Wilks' $\lambda = 0$, $P < 0.001$). During summer, porcupines selected meadows and swales (Figure 11A); however, the three highest-ranking vegetation classes—meadow, swale, and marsh—were not selected differently from one another according to paired *t*-tests (Table 6). Porcupines avoided coastal scrub, fruit, dune, pasture, and beach (Figure 11A), but use was not different among the three least-selected vegetation classes (Table 6). During winter, porcupines avoided dune, marsh, fruit, beach, and pasture, and although they selected coastal scrub, this was not significant (Figure 11B; Table 7).

Porcupines also used vegetation classes significantly differently from availability at the third order of selection, within their home ranges, during both summer (Wilks' $\lambda = 0.35$, $P < 0.001$) and winter (Wilks' $\lambda = 0.46$, $P < 0.001$). During summer, porcupines selected swale and marsh—which were not significantly different from one another (Table 8)—and avoided coastal scrub, conifer forest, pasture, dune, and beach (Figure 12A). During winter, porcupines avoided marsh and pasture (Figure 12B), which were not significantly different from each other (Table 9).

I did not test for differences in habitat selection between male and female porcupines during each season. Aebischer et al. (1993) recommended sample sizes of 10 or more animals when comparing between groups—or at least a greater number of animals than of resource categories. Because this was not satisfied during either summer ($n = 9$ females, 5 males) or winter ($n = 6$ females, 5 males), I pooled location data between the sexes for habitat selection analysis in both seasons.

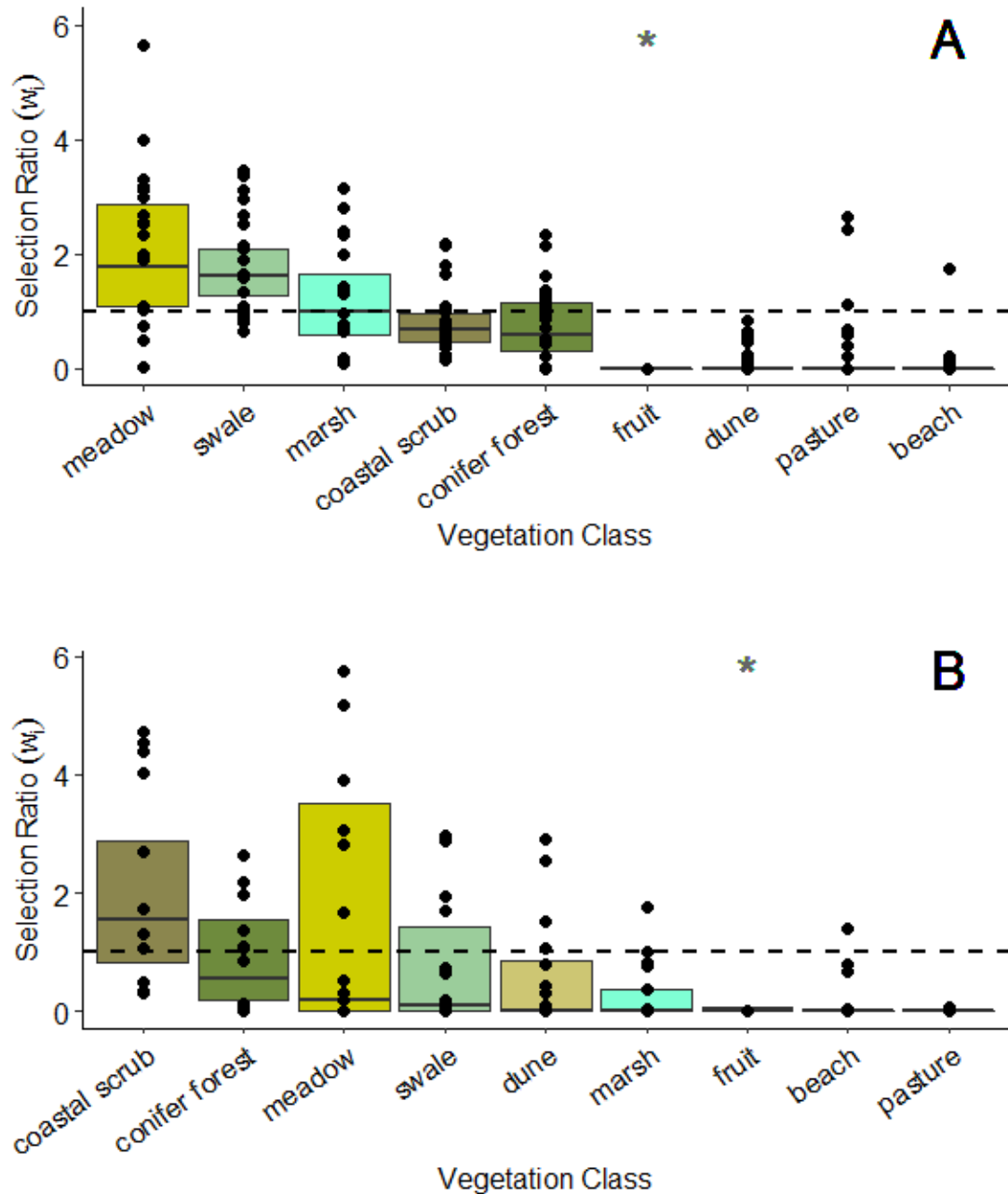


Figure 11. Geometric means and 95% confidence intervals of 2nd-order selection ratios (w_i) for vegetation classes used by porcupines in Tolowa Dunes State Park, Del Norte County, CA, during (A) summer and (B) winter 2015–16. Classes are ordered by their relative selection according to weighted compositional analysis. Individual porcupine w_i are shown as dots, with asterisks indicating classes from which outliers ($w_i > 6$) were omitted: (A) $n = 6$ from fruit, and (B) $n = 2$ from fruit. The dashed line represents neither selection nor avoidance ($w_i = 1$).

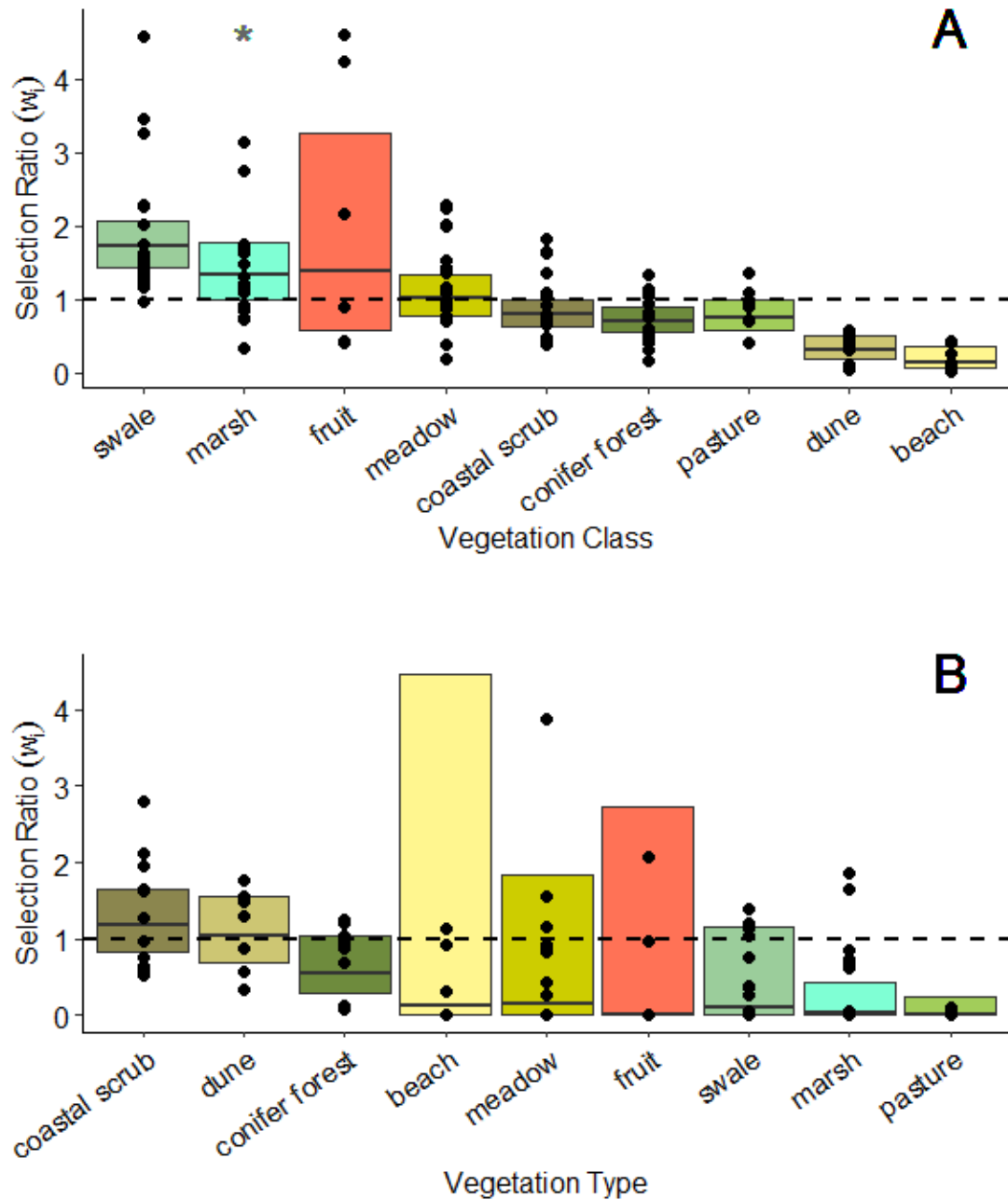


Figure 12. Geometric means and 95% confidence intervals of 3rd-order selection ratios (w_i) for vegetation classes used by porcupines in Tolowa Dunes State Park, Del Norte County, CA, during (A) summer and (B) winter 2015–16. Classes are ordered by their relative selection according to weighted compositional analysis. Individual porcupine w_i are shown as dots, with asterisks indicating classes from which outliers ($w_i > 6$) were omitted: (A) $n = 1$ from marsh. The dashed line represents neither selection nor avoidance ($w_i = 1$).

[illegible]

[illegible]

Table 9. Paired comparisons between habitat types used by porcupines at the 3rd order (within home range level) in Tolowa Dunes State Park, Del Norte County, CA, during winter 2015–16. Vegetation classes appear in relative order of most- to least-selected based on weighted compositional analysis. Signs represent the significance level at which each vegetation class (row) was selected over each other vegetation class (column): no difference, or $P > 0.05$ (–); $P < 0.05$ (++); $P < 0.001$ (+++); and $P < 0.0001$ (++++).

Winter (3rd)	Coastal scrub	Dune	Conifer forest	Beach	Meadow	Fruit	Swale	Marsh	Pasture
Coastal scrub	NA	–	–	+++	–	++++	–	++	++++
Dune		NA	++	+++	–	+++	++	++	++++
Conifer forest			NA	–	–	++++	–	++	++++
Beach				NA	–	–	–	++	+++
Meadow					NA	++	–	–	++++
Fruit						NA	– – – ¹	–	–
Swale							NA	–	++++
Marsh								NA	–
Pasture									NA

¹ For this pair, fruit was selected less than swale ($P < 0.001$).

DISCUSSION

Porcupines exhibited strong seasonal differences in body mass, home range size, and habitat selection in TDSP, a coastal dune habitat in northern California. These results are inconsistent with my hypotheses that porcupines in a mild, coastal climate would (1) not undergo a strong decrease in body mass and survival during the winter and would (2) have similar home range sizes between summer and winter. My third hypothesis was partially upheld; porcupines used broadleaf-dominated vegetation classes when leaves and fruits were available but did rely on conifer trees for feeding in the winter, as in other parts of their range.

Body Mass and Survival

Both male and female porcupines declined in body mass between summer and winter and gained mass back in spring. This is consistent with the findings of previous studies and supports the existence of a winter nutritional bottleneck in TDSP similar to that experienced by northern populations (Coltrane and Barboza 2010), despite a milder climate. Over the course of the winter, porcupines lost 34% of their body mass in Alaska (Coltrane et al. 2011), between 20–31% in the Great Basin Desert (Sweitzer and Berger 1993), 17% in Wisconsin (Pokallus and Pauli 2016), 40% in Quebec (Berteaux et al. 2005), and 25% in New York's Catskill Mountains (Roze 1984). In my study, female porcupines lost up to 17% of their body mass while males lost up to 38%. The mean differences between winter and summer body mass (females: $7.54\% \pm 0.54\%$, $n = 9$;

males: $17.80\% \pm 2.26\%$, $n = 6$) were comparatively lower than those reported elsewhere but are consistent with a seasonal decrease in nutrition.

Even though porcupine body mass loss in winter at TDSP was less than reported elsewhere, most mortalities occurred during winter. Of the five porcupines that died during this study, four died during December and January. The first mortality occurred in late summer 2015, and analysis of the cementum annuli in this porcupine's teeth revealed its age to be between 9–12 years, which is fairly old for a porcupine in the wild (Woods 1973, Earle and Kramm 1980). This female's body mass was below average at only 5.98 kg, which is also consistent with advanced age (Earle and Kramm 1980). We were only able to perform a necropsy on one of the porcupine carcasses recovered in winter 2015–16. Among the others, starvation or disease seemed the most likely cause of death for two porcupines, but we were unable to rule out predation for the third. Necropsy of the remaining porcupine showed that it had suffered from both pneumonia and starvation, with very little body fat present. Similarly, necropsy of an unmarked porcupine that I found deceased in January 2016 revealed the absence of nearly all body fat. Although further study is needed on porcupine physiology and survival in TDSP, these findings are consistent with the conclusion that winter presents a survival bottleneck for porcupines in coastal climates due to poor diet or physiological stressors—the same factors limiting survival in northern populations (Coltrane and Barboza 2010, Pokallus and Pauli 2015).

During summer in TDSP, porcupines fed primarily on leaves of willows, red alders, and Douglas' spirea; herbaceous plants like water pepper; and the fruits of apple (*Malus domestica*) and coast man-root (*Marah oregana*; P. Belamaric, unpubl. data).

None of these food sources were available during the winter months, and porcupines switched to feeding primarily on bark and needles of shore pines (P. Belamaric, unpubl. data). Conifer bark and needles are both low in nutritional value and high in toxin concentrations, requiring porcupines to decrease energy expenditure, rely on body fat stores, and consume a variety of alternate foods in winter (Coltrane and Barboza 2010, Coltrane 2012). We regularly observed porcupines grazing in coastal meadows during periods of new growth from October–February—notably, during the day and sometimes in inclement weather. This suggests a tradeoff between nutritional demands and a need for shelter, which may prove costly given the plant phenology and climate of coastal habitats. Although porcupines possess certain physiological tolerances to extreme cold and low-quality diets (Coltrane and Barboza 2010), it has been suggested that rain presents a particular challenge (Gabrielson 1928, Hooven 1971). In one Oregon population, porcupines remained in relatively unsheltered trees during cold, snowy winters but retreated to dens at the onset of wet weather (Gabrielson 1928). The author suggested that porcupine quills soften when wet, thus providing less protection against predators, although this hypothesis has not been tested (Gabrielson 1928). As an alternative explanation, when pathogens are present, porcupines are particularly susceptible to pneumonia in damp conditions due to their small lung capacity (Hooven 1971). Although the species evolved in a wet tropical climate (Vilela et al. 2009), the combination of high precipitation and relatively cold temperatures at TDSP could still be at their limit of physiological tolerance. Further study of porcupine metabolic responses in this population—as well as the nutritional content and toxin concentrations of dietary

components—is necessary to understand the mechanisms behind this nutritional bottleneck in wet, coastal climates.

The pattern of body mass loss I observed is consistent with other studies, with the exception that body mass loss appeared to begin earlier in TDSP. Most porcupines in my study lost mass between summer and fall (Figure 7), whereas porcupine body mass typically peaks in the fall and declines throughout winter (Roze and Ilse 2003, Coltrane et al. 2011). Changes in plant phenology, diversity, and weather may explain this discrepancy. In mixed deciduous forests, porcupines rely on high-caloric items such as acorns, beechnuts, and apples to maintain their body mass through the fall breeding season and to maximize body fat stores in preparation for winter (Roze 2009). In TDSP, I have found no trees producing hard mast aside from one remnant cultivated English walnut (*Juglans regia*), in which I did not ever find a porcupine. Several shrubs produce soft mast in the form of berries, but these are typically produced during spring and summer, and we found no evidence of porcupines foraging on them (P. Belamaric, unpubl. data). Porcupines did appear to take advantage of remnant or naturalized cherry plum (*Prunus cerasifera*) and apple trees, as expected. In summer 2015, we found one porcupine regularly occupying two different cherry plum trees during the time of fruit ripening, and both cherry plum leaves and fruit were identified in the porcupine's scat (P. Belamaric, unpubl. data). The only apple tree present in the study area, to my knowledge, received extremely high use by porcupines during July and August of both years. I observed multiple porcupines foraging on apples simultaneously on several occasions; most notable was a congregation of at least four adults and one juvenile on 30 July 2016.

Similar foraging clusters occurred in a Catskills Mountains population (Roze 2009).

Apples provide a source of energy for body mass gain during summer but are likely all eaten by early fall. In TDSP, porcupines may lose body mass during the fall when no high-caloric mast sources are available, and although willows still have leaves, they are senescing during this stage and provide lower concentrations of critical nutrients such as nitrogen (Rytter and Ericsson 1993, Bollmark et al. 1999).

Importantly, I was not able to assess reproductive status of porcupines during this study. Female porcupines are either pregnant or lactating for 11 months out of the year, which has obvious effects on body mass changes (Roze 2009). Knowing when pregnancy and breeding occur in this population would allow me to account for body mass changes due to reproduction irrespective of nutritional status. In studies from Nevada, New York, and Wisconsin, researchers found that porcupine mating occurred during the months of September–November (Sweitzer 2003, Roze 2009, Pokallus and Pauli 2015). Although I did not observe any porcupine mating behavior, I confirmed one pregnancy in April 2016 with parturition occurring in late May or early June. Along with regular observations of young porcupines with adult females during the summer, this is consistent with—but does not confirm—the occurrence of mating season in the fall.

Home Ranges

Porcupine home range sizes in TDSP were consistent with others reported in the literature (Table 10). Several studies have estimated porcupine home ranges, and I calculated both MCPs and KDEs for comparison. However, MCP estimates are often biased low when sample sizes are small, as is likely the case with my winter data when each animal had fewer relocations (Table 3), and kernel estimates are highly dependent on choice of bandwidth and other parameters (Girard et al. 2002). As an example, my winter MCP estimates of 0.063 km^2 for females and 0.075 km^2 for males are likely biased low, compared to their 95% KDE counterparts of 0.229 km^2 and 0.219 km^2 , respectively. For these reasons, the KDE method has been recommended for calculating home ranges of porcupines (Coltrane and Sinnott 2013). Nevertheless, my MCP results were comparable to those from several other studies. Reported winter porcupine MCPs vary from 0.001 km^2 in Idaho shrub desert (Craig and Keller 1986) to over 1.710 km^2 in Alaska (Coltrane and Sinnott 2013). Compared to porcupine home ranges reported from nearby regions, my estimates are most similar to those from Oregon (0.060 km^2 ; Smith 1979) but are larger than those from British Columbia (0.015 km^2 ; Zimmerling and Croft 2001) and much smaller than those from Washington (0.835 km^2 ; Dodge and Barnes 1975). My summer MCP estimates of 0.232 km^2 and 0.125 km^2 for female and male porcupines, respectively, most closely resemble summer MCP estimates of 0.154 km^2 (females) and 0.209 km^2 (males) from Quebec, Canada (Morin et al. 2005).

Table 10. Sample of porcupine home range sizes (km²) reported from previous studies. Authors estimated home ranges in various ways, including minimum convex polygons (MCP), other minimum area methods, or kernel density estimates (KDE).

Author	Year	Location	Season	Method	Sex	Mean home range size (km ²)	SE (km ²)
Coltrane and Sinnott	2013	Alaska	Winter	MCP	♀	0.94	1.64
					♂	2.77	2.75
			Winter	KDE (95%)	♀	0.89	0.26
					♂	1.11	0.38
Dodge and Barnes	1975	Washington	Winter	Min. area	♀♂	0.81	-
Roze	1987	New York	Summer	MCP	♀♂	0.65	0.19
			Winter		♀♂	0.07	0.01
Morin et al.	2005	Quebec	Summer	MCP	♀	0.21	0.06
					♂	0.15	0.06
Smith	1979	Oregon	Winter	Min. area	♀♂	0.01	-
Shapiro	1949	New York	Winter	Unknown	♀♂	0.01	-
Zimmerling and Croft	2001	British Columbia	Winter	Forage locations	♀♂	<0.01	-
Craig and Keller	1986	Idaho	Winter	Min. area	♀♂	<0.01	<0.01

Most previous studies have only quantified porcupine home ranges either specifically for winter or for non-winter, but not both (Table 10). However, one study, in the Catskills Mountains of New York, found an 89% decrease in home range size (based on MCP estimates) from 0.649 km² in summer to 0.074 km² in winter (Roze 1987, 2009).

Similarly, porcupines in my study had larger home ranges during summer than winter (Table 3), although decreases of 73% for females and 40% for males are likely inflated due to skewed winter MCP estimates, as discussed previously. Decreases of 37% for females and 22% for males, based on 95% KDE estimates, are likely more realistic. In New York, Roze (1987, 2009) attributed the decrease in home range sizes to porcupines' reduced mobility in deep snow and reported that during a subsequent winter with abnormally low snowfall, porcupines increased their home ranges to a size not significantly different from their summer home ranges. Snow is not a factor in coastal Del Norte County, and although many areas are seasonally inundated with water, this does not appear to restrict porcupines' movements. We observed porcupines moving back into flooded willow swales during February and March, as soon as new growth appeared, suggesting that porcupines avoid these habitats during winter not because they are flooded but because of a lack of available forage. We did observe porcupine feeding sign on willow bark, but the extent to which this contributes to their winter or summer diet is not known.

The difference in home range use between summer and winter is also apparent in the higher degree of overlap between summer and overall home ranges ($\bar{x} = 1.32$, $SE = 0.11$, $n = 11$) than between winter and overall home ranges ($\bar{x} = 0.82$, $SE = 0.11$, $n = 11$). This suggests that porcupines may select home range areas based on their habitat needs during both seasons; however, some animals appeared to use mostly non-overlapping areas for their summer and winter home ranges (Figure 9A), and overall overlap between them was very low ($\bar{x} = 0.29$, $SE = 0.08$, $n = 11$). Closer examination of data collected

from GPS trackers could further illustrate whether porcupines are completely avoiding these areas in alternate seasons or are just using them too infrequently to be detected by VHF tracking. As an example, GPS tracking data revealed that one female porcupine made short, regular movements (≤ 24 hrs) away from willow patches and into dune and coastal scrub habitat during summer, when no apparent resource needs could explain these movements. During the following winter, this porcupine was located many times within the same habitat patches she had visited in summer, and where I found two heavily used den sites. These observations suggest that porcupines may make regular movements throughout their home ranges during summer, either to patrol and defend territories, or to scout for suitable den sites for use in winter, similar to the process of prospecting in birds (Reed et al. 1999). Further use of GPS trackers to study the fine-scale movements by porcupines in TDSP could test these two hypotheses.

Several studies have found that male porcupines have larger home ranges than females (Dodge and Barnes 1975, Craig and Keller 1986, Sweitzer 2003, Roze 2009), and others have found no significant difference (Morin et al. 2005, Coltrane and Sinnott 2013). In my study, female and male overall home range sizes were not statistically different ($t_{15.74} = 0.70$, $P = 0.492$). However, my seasonal delineation of summer and winter was likely too coarse to detect changes in home range size that may occur for specific life history events. According to Roze (2009), adult males will expand their home ranges during the breeding season—generally September through November—while females and subadult males will not. This trend was borne out in studies by both Roze (2009) and Sweitzer (2003). I did not classify any male porcupines as subadults, but

it is worth noting that males with larger body mass did have significantly larger home ranges in my study (Figure 8). I also excluded one male from home range analysis because he left the study area in July 2015, making a movement of approximately 3.5 km to the southeast. I assumed this to be a dispersal event rather than a typical movement within his home range, which seems likely given that we did not locate him in TDSP again during the course of this study. Another male porcupine left the study area in September 2015—remarkably, crossing the main channel of the Smith River—but returned to his previous home range area. Given the timing of this event, this male may have been attempting to seek out females during the breeding season.

The positive correlation between male body mass and home range size in my study is concordant with results from the Great Basin Desert during breeding season (Sweitzer 2003) but not with winter home range sizes in Alaska, where no such correlation existed (Coltrane and Sinnott 2013). This supports the hypothesis that male porcupine home range size is tied to reproductive success rather than to increased metabolic demands (Sweitzer 2003). Because porcupines exhibit mate-defense polygyny, larger males are better able to access and successfully defend females, therefore increasing their mating success (Sweitzer 2003). I found a correlation between male home range size and largest body mass attained during both summer ($r^2 = 0.851$, $F_{1,6} = 34.15$, $P = 0.001$) and winter ($r^2 = 0.891$, $F_{1,3} = 24.43$, $P = 0.016$). A finer-scale analysis of home range size and body mass during the breeding season could better explain this relationship among porcupines in TDSP.

Overlap among porcupine home ranges in my study was greater than I expected. Female porcupines reportedly maintain exclusive core areas—except when resources are scarce—but males will overlap one another's home ranges as well as those of females (Sweitzer 2003, Roze 2009). During summer, I observed a high degree of overlap not only between females' home ranges but between their 50% KDEs, which are often used as a measure of core areas. Males' home ranges and core areas overlapped both other males' and females', as expected. We regularly observed unmarked porcupines occupying the same patches or even the same trees as collared porcupines, during all times of the year, but because we did not know sex or age class of the unmarked porcupines, it is difficult to make inference about these interactions. Several porcupines were observed feeding in the apple tree simultaneously, as mentioned previously, but pairs of porcupines were also commonly observed in willow trees together. Sweitzer (2003) hypothesized that the high degree of female-female home range overlap in the Great Basin Desert was due to the clumped dispersion of limited resources, but it may also be true that defending a core area is less necessary where resources are overly abundant (e.g., Powell 1987). In TDSP during the summer, porcupines forage primarily in willow trees, which are very abundant. Maintaining exclusive access to dens or important food resources may be more critical in the winter; however, because we tracked fewer porcupines during that time, the lower degree of overlap observed is likely due to reduced effort and the spatial distribution of these porcupines and cannot be interpreted as biologically meaningful.

Social dynamics may also influence porcupine home range size and overlap. Agonistic behavior has been reported in porcupines, particularly between males during the breeding season (Sweitzer and Berger 1997, Roze 2009). We witnessed two instances of adult porcupines vocalizing loudly to each other, but both occurred during the summer—one was a female-male pair, and the others were unmarked animals of unknown sex. A couple of marked porcupines had quills impaled in their bodies at the time of capture, but none to an extent that would suggest a fight of the magnitude described by Sweitzer and Berger (1997) or Roze (2009). These same authors have presented evidence of a female-biased dispersal structure in porcupines (Sweitzer and Berger 1998, Roze 2009), but it is not known to what extent females face competition from philopatric male offspring or engage in agonistic behavior with dispersing female offspring. Further research into the genetic relatedness of porcupines in TDSP could shed light on how social structure affects the patterns of home range size and overlap observed in this study.

Habitat Selection

Porcupines in TDSP selected habitats disproportionately to their availability at both the home-range and within-home-range levels. Porcupines also selected habitats differently between summer and winter at both levels. Although relatively few of the selection ratios show statistical significance for either selection or avoidance due to the high amount of individual variation (Figure 11, Figure 12), the changes in relative selection rankings between seasons and levels are perhaps more useful for interpreting

porcupine habitat selection and providing ecological insights. These patterns of selection are consistent with porcupine habitat use according to food availability within their home ranges, but foraging requirements alone do not explain habitat selection at the home range level, suggesting that other factors are also operating. Further, differences in habitat selection between seasons likely reflect the changing availability of food items and the onset of physiological constraints imposed by seasonal weather conditions.

Porcupines' selection of vegetation classes at the third order (within their home ranges) is consistent with their diet composition based on preliminary microhistological analysis of fecal materials. During summer, coastal willow (*S. hookeriana*) leaves made up approximately 58% of their diet in TDSP and Pacific willow (*S. lasiandra*) leaves made up an additional 9% (P. Belamaric, unpubl. data). No other diet components were identified at greater than 5% (P. Belamaric, unpubl. data), but the majority of all summer dietary components—including water pepper, bracken fern, coast man-root, red alder, Douglas' spirea, apple, cascara buckthorn, twinberry, and yellow pond lily—were most prevalent within the top three selected vegetation classes: swale, marsh, and fruit (Figure 12A). These other components may be seldom used but biologically important resources for porcupines—for instance, as sources of carbohydrates or sodium. As herbivores, porcupines' diet is naturally deficient in sodium, requiring them to seek out additional sources in order maintain a sodium-to-potassium ratio sufficient for muscular and nervous system function (Roze 2009). Many herbivores seek out aquatic vegetation as a sodium source, and plants in the water pepper (*Persicaria sp.*) and yellow pond lily (*Nuphar sp.*) genera—both common in TDSP—have been found to contain between 44–

781 times more sodium than terrestrial plants, respectively (Botkin et al. 1973). In my study, several female porcupines made heavy use of Yontocket Slough (the remnant Smith River channel) and a nearby seasonal pond during summer, contributing to the high selection for marsh vegetation (Figure 12A). This could correspond to a seasonal salt drive associated with the demands of lactation, or a general exploitation of aquatic plants during times of the year when these areas are not inundated with water. Both hypotheses are plausible, but, in any case, sodium is likely less limiting overall for herbivores in coastal marine environments, where aerosolized sea salt deposition and highly saline soils provide for sodium-rich food sources (Botkin et al. 1973). This would explain why not all porcupines used marsh habitats (Figure 11, Figure 12) or had aquatic vegetation in their diets (P. Belamaric, unpubl. data). Further, porcupines did not respond to salt-soaked wood blocks I deployed in TDSP for a separate study, in contrast to findings from other areas (R. Callas, pers. obs., Roze 2009). Finally, the least-selected vegetation classes, dune and beach (Figure 12A), offered virtually no food sources during the summer, which is consistent with the hypothesis that porcupines selected habitats based on food resources at the third-order.

Winter diet analyses are not yet available, but preliminary results suggest that the most prevalent components were shore pine and California wax myrtle, an evergreen shrub (P. Belamaric, unpubl. data). Both shore pine and wax myrtle are dominant in two of the highest-ranked winter vegetation classes (coastal scrub and conifer forest) and are present in the third (dune). Despite my regular observations of porcupines grazing in meadows during the winter, meadow habitat was not as highly selected in the winter.

Similar to the minority diet components used in summer, forbs and grasses may be an important but seldom-used food source for porcupines during the winter, due to the risks of physiological exposure or predation associated with foraging in meadows (Sweitzer and Berger 1992). Alternatively, porcupines may have used other vegetation classes proportionally more than meadows because they offered both forage and shelter, which is likely more important during the winter months. As with summer, the least-selected habitat types at the third order—marsh and pasture (Figure 12B)—offered no food resources during the winter.

Porcupine habitat selection at the home-range level is likely influenced by the availability of food resources but may also depend on other factors, such as den availability or social dynamics. At the second order of selection, porcupines placed their summer home ranges according to the availability of meadows and swales while avoiding coastal scrub, fruit, dune, pasture, and beach (Figure 11A). The selection of swales correlates with porcupines' summer food preferences, as discussed previously, and marshes were neither selected nor avoided, on average (Figure 11A). Fruit trees, which porcupines also selected within their home ranges, were not selected at the home range level, suggesting that porcupines used fruit trees when available but did not place their home ranges according to their availability. In TDSP, this was likely due to the very low availability of fruit trees, and it should be noted that six porcupines did have extremely high selection ratios for fruit at the second order (outliers on Figure 11A). The top ranking of meadows does not correlate with any diet components used by porcupines in the summer—except possibly man-root fruits—suggesting that meadows are either

important for another reason, or this ranking is an artifact of variability among porcupines or the proximity of meadows to other habitat types that were used frequently, such as fruit trees, marshes, and swales. The apparent selection for meadows could also be influenced by my coarse seasonal delineation, as I did observe porcupines grazing in meadows during October, which fell within my summer classification. Porcupines placed their winter home ranges according to the availability of coastal scrub vegetation while avoiding dune, marsh, fruit, beach, and pasture (Figure 11B). Swales were ranked lower in winter than during summer while conifer forests were ranked higher (Figure 11). These rankings are consistent with porcupines' selection of winter habitats based on resources for food and shelter, as discussed previously. Meadows were ranked higher than at the third order, confirming that they may be important—if seldom-used—resources for porcupines during the winter (Figure 11B). Two hypotheses may explain why porcupine foraging patterns more closely resemble third-order than second-order habitat selection: either (1) factors other than forage availability influence selection at the second order, or (2) porcupines are most selective at the third-order, and any apparent patterns in second-order selection are just artifacts of this fine-scale selection. In this study, patterns in second-order selection may be more reflective of the patchy landscape structure than porcupine habitat choices. Both hypotheses, along with the high degree of core area overlap where resources are abundant, fit a broader pattern of habitat selection by generalist species.

In some parts of their range, porcupines rely heavily on dens for shelter in the winter and shape their foraging patterns and home ranges around den site selection (Roze

1987, Zimmerling and Croft 2001). In other areas, porcupines use dens opportunistically throughout their home ranges (Dodge and Barnes 1975, Morin et al. 2005, Coltrane and Sinnott 2013). Although my observations suggest that porcupines in TDSP follow the latter trend, I did not systematically assess den site selection or use, which could have unknown effects on home range size, overlap, and habitat selection in this study. We found porcupines in dens 22 times, during both seasons, but all observations were of the same five females. Higher den use by females is consistent with two previous studies (Roze 1987, Morin et al. 2005). The structures we found porcupines using included underground holes on forested hillsides, root system cavities, downed logs, stumps, overhanging banks, and even the abandoned lodge of a beaver (*Castor canadensis*), similar to observations in Washington (Dodge and Barnes 1975). During 20 out of the 22 observations, the weather was either rainier ($n = 10$) or windier ($n = 10$) than on surrounding days, according to NWS data (NOAA 2016a). Coltrane and Sinnott (2013) proposed that den use may be more important for porcupines in temperate climates than in Alaska, where body sizes are much larger, although porcupines in TDSP were on average still larger than those in New York, Massachusetts, and Quebec (Roze and Ilse 2003). Shelter from the rain should be particularly important for porcupines in a coastal climate, as discussed previously, so our limited observations of den use could be due to a lack of dens on the landscape or the fact that porcupines are also using other habitat features for shelter, such as dense vegetation. In coastal scrub habitat, which porcupines selected during the winter, most conifers grow short and stunted, providing cover under thick mats of branches and duff.

Variation in use among porcupines was higher for some vegetation classes than for others. The observed variation may occur for many reasons, including the replacement of zero-use values when a vegetation class was not available within a porcupine's home range. This resulted in binomial or right-skewed distributions of selection ratios for the fruit tree category, because it was not available to all porcupines but was used very heavily by porcupines for which it was available (see outliers on Figure 11, Figure 12). A corresponding biological consequence is that when not all habitats are available within an animal's home range, its use of other habitats is necessarily higher—an acknowledged flaw of compositional analysis (Bingham and Brennan 2004, Thomas and Taylor 2006). The exclusion of some habitat types from individual home ranges could occur due to a resource's sparse or patchy occurrence—like fruit trees in my study area—or social dynamics such as territoriality or resource defense. Importantly, the exclusion of some habitat types and corresponding increase in the use of others was highly variable among porcupines in this study.

Further demographic study could reveal whether the observed variation in habitat selection is biologically meaningful and will be a necessary component of understanding porcupine ecology at this edge of their range. Age- and sex-specific differences among porcupines may help explain the home range overlap, variation in habitat selection, and patterns in den use observed in this study. For example, across age classes, porcupines likely differ in their access to resources, nutritional and metabolic needs, tooth wear, and climbing ability, among other things. Male and female porcupines may select habitats differently due to their dissimilar breeding movements, needs for shelter, and dietary and

sodium demands (Roze 2009). Due to small sample sizes, I was not able to analyze male and female habitat selection separately. However, it is clear that individual porcupines may have different strategies for coping with seasonal nutritional, physiological, and reproductive demands, as evidenced by females' exclusive use of dens in this study. As an example, one female was found in a tree only once out of 24 relocations, while our observations of all porcupines combined were more evenly split between the ground (54%) and trees (46%). Anecdotally, males appeared to forage in meadows more than females. Sweitzer and Berger (1992) found a relationship between larger body size and more frequent use of high-risk open areas for foraging; however, unlike other studies (Sweitzer and Berger 1997), I did not find sexual dimorphism in body mass, and foraging differences may be more pronounced between juveniles and adults than between the sexes. Alternatively, future studies could test the hypothesis that porcupines with smaller fat stores during winter are more dependent on food intake and may therefore spend more time foraging during the winter (Coltrane et al. 2011). Preliminary analysis of porcupine diet in TDSP revealed a high degree of similarity among individual summer diets (P. Belamaric, unpubl. data). The only extreme outlier was an adult female whose scat had no willow fragments but was composed almost entirely of bracken fern, which was not found in any other porcupine's diet (P. Belamaric, unpubl. data). Further determination of the age classes, reproductive status, and relatedness of porcupines in this study would help reveal whether these outliers represent extraneous circumstances or biologically meaningful differences. Despite individual variation, porcupines in this study exhibited a similar strategy to that reported elsewhere: to feed on leaves and fruits when available,

switch to bark and needles otherwise, and rely on built-up fat stores to survive harsh winters.

Overall, my results agree with some previous studies that have found porcupines to be selective in their habitat use at the second order (Tenneson and Oring 1985, Mally 2008) but contrast with others (Morin et al. 2005). Disagreement in the literature on whether or not porcupines select home ranges with regard to habitat availability may explain the lack of consensus regarding their classification as habitat generalists or specialists. The inconsistencies between analytical methods likely also explains why few commonalities have been found across porcupine habitat selection studies. It is apparent that the inference of selection is highly dependent on both delineation of the study area and variation in the landscape. For example, Morin et al. (2005) found that porcupines did not select specific habitat features at the home range level in areas where preferred forage was highly abundant throughout the landscape, while Mally (2008) found that porcupines did select specific habitat features where the available forage was more variable. In TDSP, where vegetation is patchily distributed across the landscape, I found that porcupines were selective at the home range level, but that this was likely a reflection of foraging decisions within their home ranges. At the third order, all previous hierarchical habitat selection studies of which I am aware agree that porcupines are selective within their home ranges (Morin et al. 2005, Mally 2008, Coltrane and Sinnott 2013)—this study included. Even with this apparent selectivity, my overall results are consistent with the classification of porcupines as habitat generalists. Their strategy for acquiring resources by adapting to seasonal forage availability and body mass loss

appears to be broadly effective—whether in coastal climates, deserts, or snowy hardwood forests. With regard to feeding, porcupines have been found to select among individual trees at the fourth order (Snyder and Linhart 1997, Morin et al. 2005), which is consistent with their classification as facultative feeding specialists (Coltrane 2012). Because porcupines in this study appeared to select habitats primarily based on forage availability—and they consumed a difficult diet seasonally, as in other parts of their range—my results agree with this classification. Fine-scale, seasonal analysis of resource use by porcupines in TDSP would provide further insight into dietary specialization at this edge of their range. Finally, studying porcupine selection on a microhabitat scale could identify additional resources important for porcupines—such as tree- or stand-level differences, den sites, access to water, and sodium sources—not detected by this study.

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