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Authors: Schweiger, Brittany R., Frey, Jennifer K., and Cain, James W.

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# A case for multiscale habitat selection studies of small mammals

Brittany R. Schweiger, Jennifer K. Frey, \*, and James W. Cain III

Department of Fish, Wildlife and Conservation Ecology, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, NM 88003, USA (BRS, JKF)

U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife and Conservation Ecology, New Mexico State University, P.O. Box 30003 MSC 4901, Las Cruces, NM 88003, USA (JWC)

Habitat information for small mammals typically consists of anecdotal descriptions or infrequent analyses of habitat use, which often are reported erroneously as signifying habitat preference, requirements, or quality. Habitat preferences can be determined only by analysis of habitat selection, a behavioral process that results in the disproportionate use of one resource over other available resources and occurs in a hierarchical manner across different environmental scales. North American chipmunks (Neotamias and Tamias) are a prime example of the lack of studies on habitat selection for small mammal species. We used the Organ Mountains Colorado chipmunk (N. quadrivittatus australis) as a case study to determine whether previous descriptions of habitat in the literature were upheld in a multiscale habitat selection context. We tracked VHF radiocollared chipmunks and collected habitat information at used and available locations to analyze habitat selection at three scales: second order (i.e., home range), third order (i.e., within home range), and microhabitat scales. Mean home range was 2.55 ha ± 1.55 SD and did not differ between sexes. At the second and third order, N. q. australis avoided a coniferous forest land cover type and favored particular areas of arroyos (gullies) that were relatively steepsided and greener and contained montane scrub land cover type. At the microhabitat scale, chipmunks selected areas that had greater woody plant diversity, rock ground cover, and ground cover of coarse woody debris. We concluded that habitat selection by N. q. australis fundamentally was different from descriptions of habitat in the literature that described N. quadrivittatus as primarily associated with coniferous forests. We suggest that arroyos, which are unique and rare on the landscape, function as climate refugia for these chipmunks because they create a cool, wet microclimate. Our findings demonstrate the importance of conducting multiscale habitat selection studies for small mammals to ensure that defensible and enduring habitat information is available to support appropriate conservation and management actions.

Key words: climate refugia, Colorado chipmunk, conservation, multiscale habitat selection, *Neotamias quadrivittatus*, radiotelemetry, rare species, small mammal, telemetry error

Habitat is the ensemble of resources and conditions that allow an organism to survive and reproduce in a location (Hall et al. 1997). Habitat selection is the behavioral process whereby animals select the habitats they use (Johnson 1980; Hutto 1985). Habitat selection is a foundational concept in ecology because it provides understanding about the essential nature of an organism (Johnson 1980; Hutto 1985; Morris 2003). Habitat selection results in the disproportionate use of one resource over other available resources (Hall et al. 1997; Krausman 1999) and is evaluated by comparing the use of particular resources relative to their availability (Manly et al. 2002). Central to the concept of habitat selection is that the behavioral process

is hierarchical across different spatial and temporal scales (Johnson 1980; Mayor et al. 2009). Therefore, evaluating habitat requirements in a multiscale habitat selection framework can provide insight into important habitat characteristics related to an animal's fitness (Uboni et al. 2017).

In contrast, habitat use describes the way an animal uses its environment. Habitat use is not the same as habitat selection because it does not compare resource use versus availability (Krausman 1999). Therefore, habitat use has no implicit consequence to fitness because used resources cannot be interpreted as habitat preferences or requirements (Krausman 1999). As an example, an animal crossed a road, indicating the road was

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<sup>\*</sup> Correspondent: jfrey@nmsu.edu

used, but we do not know if the road is an important component of habitat because we do not know the availability of roads on the landscape. However, an analysis of habitat selection showed that while used, the animal avoided the road relative to its availability, suggesting that the road has a negative influence on fitness.

A review of the mammalogical literature, such as those cited in Mammalian Species accounts, demonstrates that available information about species' habitat typically consists of anecdotal descriptions of places where the species has been observed, or infrequent analyses of habitat use. The main exception is for well-studied large mammals of management interest where studies of habitat selection are more common. McGarigal et al. (2016) reviewed > 800 habitat selection papers and < 3% were for small mammals (rodents and shrews). Problems associated with anecdotal descriptions and analyses of habitat use include: imperfect detection (Neu et al. 1974), focus on accessible or well-studied places (Meyer et al. 2015), observer bias (Schooley and McLaughlin 1992), failure to acknowledge scale (e.g., microhabitat descriptions used to characterize landscape-level habitat), and no link to fitness (Uboni et al. 2017). The litany of anecdotal descriptions and studies of habitat use for small mammals usually are interpreted incorrectly as preference, requirements, or quality (Hall et al. 1997). Consequently, it is possible we have a misunderstanding of habitat requirements for the majority of mammal species, which can limit effective conservation or management actions by misdirected efforts (e.g., Peek et al. 1982; Rettie and Messier 2000; Dussault et al. 2005; Bowyer and Kie 2006). To understand a species' ecology or implement meaningful conservation actions, it is necessary to know the resources preferred by the organism that influence their fitness. This cannot be determined using descriptions of habitat or simple analyses of habitat use.

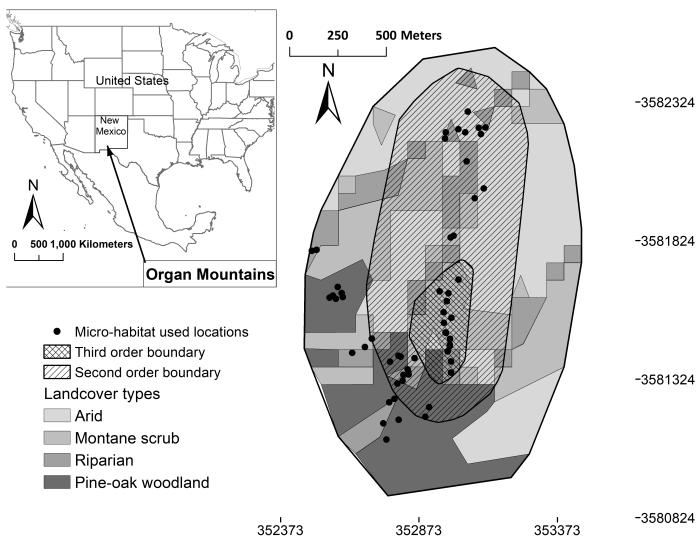
North American chipmunks (Neotamias and Tamias) are a prime example of the lack of studies on habitat selection for small mammal species. Chipmunks are one of the most speciose group of rodents in North America (Burgin et al. 2018), but most literature on habitat for these species is anecdotal or focuses on habitat use. We are aware of only six published studies that evaluated habitat selection in North American chipmunks, none of which evaluated multiple scales. Three studies evaluated microhabitat selection (i.e., third-order selection) in the eastern chipmunk (T. striatus—Geier and Best 1980), the Colorado chipmunk (N. quadrivittatus-Rivieccio et al. 2003), and Palmer's chipmunk (N. palmeri) and the Panamint chipmunk (N. panamintinus—Lowrey and Longshore 2013). Three studies evaluated habitat selection at the landscape scale (i.e., first-order selection) in N. panamintinus (Lowrey et al. 2016) and a subspecies of the Colorado chipmunk, the Oscura Mountains Colorado chipmunk (N. q. oscuraensis-Perkins-Taylor and Frey 2018, 2020). It is possible that mammalogists have a misunderstanding about the habitat needs of many North American chipmunk species because of the lack of habitat selection studies and complete absence of multiscale habitat selection studies. These misunderstandings can influence studies aimed at other aspects of the ecology or evolution of these chipmunk species, particularly any tied to questions about distribution, abundance, or fitness (Uboni et al. 2017).

Neotamias quadrivittatus occurs from Colorado and Utah south to Arizona and New Mexico (Hall 1981). Most of the literature describes it as generally occupying the montane coniferous forest biotic community, which is dominated by large conifer trees (e.g., ponderosa pine [Pinus ponderosa] and Douglas-fir [Pseudotsuga menziesii]—Dick-Peddie 1993), although anecdotal descriptions of habitat suggest a wider array of land cover associations (Best et al. 1994). At the southern distributional limits in the Chihuahuan Desert of New Mexico, there are two subspecies: N. q. oscuraensis and the Organ Mountains Colorado chipmunk (N. q. australis). The state of New Mexico lists these populations as threatened due to their relictual distribution and threats to habitat (New Mexico Department of Game and Fish 2018). Available land cover types in these mountain ranges differ from the typical land cover associations for N. quadrivittatus. For example, the Oscura Mountains contain piñon (Pinus edulis)-juniper (Juniperus monosperma) woodland yet entirely lack montane coniferous forest, whereas in the Organ Mountains, montane coniferous forest is poorly developed and limited to small, scattered stands of ponderosa pine and Douglas-fir. Thus, due to the absence of reliable information about habitat selection at multiple scales, and lack of transferability of most existing information to these populations, it has not been possible to develop sound conservation plans aimed at protecting or enhancing habitat conditions.

Our goal therefore was to evaluate habitat selection by *N. q. australis* at multiple scales to determine whether previous literature and findings were supported in a multiscale habitat selection context. We accomplished this by using radiotelemetry to identify locations used versus randomly sampled available locations. We hypothesized that previous descriptions of habitat in the literature would be upheld in a multiscale habitat selection context. Our objectives were to: 1) estimate home range size; 2) analyze habitat selection at three spatial scales (second order, third order, and microhabitat); 3) interpret results relative to known habitat information about *N. quadrivittatus*; and 4) provide management recommendations based on our findings.

### MATERIALS AND METHODS

Study area.—We studied N. q. australis (hereafter, chipmunks) in the Aguirre Springs Recreation Area (32°21′21.60″N, 106°33′43.20″W) of the Organ Mountains—Desert Peaks National Monument, Doña Ana County, New Mexico from October 2018 to July 2019 (Fig. 1). The Organ Mountains are an isolated, steep mountain range characterized by abrupt rock outcrops that rise to 2,708 m (United States Geological Survey 2017). Elevations in the study area ranged from 1,689 to 2,333 m. Over a 30-year period (1981 – 2010), mean daily summer temperature was 24.7°C, mean daily winter temperature was 6.6°C, and mean annual precipitation was 404 mm (PRISM Climate Group 2019). Summers were lengthy and hot, with monsoonal rains beginning in July, and



**Fig. 1.**—Location of the study area in the Organ Mountains, Doña Ana County, New Mexico, United States. Coordinates are in UTM Zone 13S. Distributions of the four land cover types where available locations were drawn for the second-order and third-order scale analyses and locations used for the microhabitat scale analysis are illustrated.

winters had brief periods below freezing. Dominant shrub and tree species at lower elevations included mountain mahogany (Cercocarpus montanus), gray oak (Quercus grisea), and alligator juniper (Juniperus deppeana). At higher elevations, dominant trees included Gambel oak (Quercus gambelii) mixed with occasional ponderosa pines (P. ponderosa). Riparian corridors existed within steep-sided drainages (i.e., arroyos) that intermittently contained water, and the dominant vegetation included velvet ash (Fraxinus velutina), desert willow (Chilopsis linearis), and, at lower elevations, Fremont's cottonwood (Populus fremontii). The Bureau of Land Management managed the land and prohibited cattle from grazing within the study area. Hiking trails frequently used by people and their dogs were located in the study area.

Overview of study design.—We used a use versus availability design to investigate habitat selection at three spatial scales: second order, third order, and microhabitat (Tables 1 and 2). In our study, the second order represented selection of the combined home ranges of animals in the population, and we

analyzed selection using spatial variables (i.e., study design II of Manly et al. 2002). We defined used locations as telemetry locations for all chipmunks. We defined available locations as random points drawn from a buffered cumulative minimum convex polygon (MCP-Mohr 1947) home range, which was estimated with telemetry locations buffered by the maximum movement distance (175 m) of chipmunks in our study and was created in ArcMap 10.7.1 (ESRI 2019; Redlands, California). We spatially rarified locations used by 10 m to reduce spatial autocorrelation (n = 350). We randomly generated 700 available locations within the buffered cumulative MCP home range. We used logistic regression with binomial distribution and logit link functions to test 120 hypothesis-driven a priori conceptual models (Supplementary Data SD2). We did not use mixed-effects models because preliminary analyses indicated no substantial variation in use among individuals in the population.

Third order represented selection of areas within the home ranges of individual known chipmunks, and we analyzed

**Table 1.—**Variables included in the second- (home range) and third- (within home range) order analyses of habitat selection by *Neotamias quadrivittatus australis* in the Organ Mountains, New Mexico, based on radiotelemetry of captured individuals (n = 20), October 2018 to July 2019.

Category	Variable	Variable nature <sup>a</sup>	Variable description	Scales analyzed	Method
Land cover	Proportion of land cover type	Cont.	Proportion of arid, montane scrub, ri- parian, and woodland land cover types at the radiotelemetry location	10, 30, 90 m	Land cover map
Land cover	Normalized dif- ference vegetation index (NDVI)	Cont.	Measure of state of plant health from -1 (clouds, rocks, bare soil) to 1 (temperate and tropical forests)	30, 90 m	Average of annual NDVI from 2018 to 2019
Water	Distance to drainage	Cont.	Distance from location to the nearest drainage that contained ephemeral water	Meters	ArcMap 10.7 Measuring tool
Slope direction	Folded aspect	Cont.	Aspect in radians folded about the NE–SW line, so that NE becomes 0 radians and SW becomes 3.14 radians.	10, 30, 90 m	ArcMap 10.7 Aspect tool adjusted to NE–SW line following McCune and Keon (2002)
Slope direction	Hill shade	Cont.	Relative amount of illumination based on local topography and sun's location in the sky from 0 (shaded) to 255 (direct sunlight)	10, 30, 90 m	Average of values calculated with ArcMap 10.7 Hillshade tool using azimuth and altitude values for 0900, 1200, and 1500 h on the solstices and equinoxes of 2018–2019
Vertical relief	Slope	Cont.	Slope of the site	10, 30, 90 m	ArcMap 10.7 Slope tool
Vertical relief	Vector ruggedness measure (VRM)	Cont.	Quantifies the ruggedness of terrain based on slope and aspect on a scale of 0 (no terrain variation) to 1 (complete variation)	1-, 3-, 9-cell moving window	ArcMap 10.7 Terrain Ruggedness tool downloaded from Benthic Terrain Modeler toolbox
Vertical relief	Topographic position index (TPI)	Cont.	Index that compares elevation of a cell to neighboring cells, with positive values at the top of the slope and negative values at the bottom (Weiss 2006)	1-, 3-, 9-cell moving win- dows	ArcMap 10.7 Topographic Position Index tool downloaded from Topography Tools toolbox
Vertical relief	Cliff	Cat.	Classified as a cliff if TPI was between -2 and 2 and slope > 15°	10, 30, 90 m	Calculated using values for TPI and slope for each spatial scale
Chipmunk	Unique individual	Cat.	Radiocollared individual	N/A	Random effect included in mixed-effects logistic regression

<sup>&</sup>lt;sup>a</sup>Cont. = continuous; Cat. = categorical.

**Table 2.**—Microhabitat variables collected in the field at locations where *Neotamias quadrivittatus australis* was observed (n = 56) and paired random locations (n = 56) in the Organ Mountains, New Mexico, June 2018 to July 2019.

Category	Variable	Variable nature <sup>b</sup>	Variable description	Method
Food availability <sup>a</sup>	Number of each species of tree by size class	Count	Tree species by size class within 2 m of each 15-m transect.	Belt transect sampling
Food availability <sup>a</sup>	Number of each species of shrub by height class	Count	Shrub species by height class within 2 m of each 15-m transect.	Belt transect sampling
Food availability <sup>a</sup>	Distance to nearest shrub or tree	Cont.	Distance in meters from center of location to the nearest shrub or tree.	Measuring tape
Predation risk	Distance to nearest boulder	Cont.	Distance in meters from center of location to the nearest boulder (rock $\geq 1$ m in diameter).	Measuring tape
Predation risk	Ground cover	Cont.	Percentage ground cover of forbs, grasses, shrubs and trees litter, fine woody debris, bare ground, total rock, rock by type (bedrock, boulder, small rock), and coarse woody debris every 2 m along each 15-m transect.	Standard Daubenmire frame and classing categories
Abiotic factors	Presence of burn	Count	Count of dead standing trees, downed logs or trees, and live shrubs or trees within 2 m of each 15-m transect that display evidence of previous burn.	Belt transect sampling

<sup>&</sup>lt;sup>a</sup>The primary food item of the Organ Mountains Colorado chipmunk diet is conifer seeds, although they also use flowers, fruits, and insects (Patterson 1979). <sup>b</sup>Cont. = continuous.

selection using spatial variables (i.e., study design III of Manly et al. 2002). At the third-order scale, we defined use from telemetry locations of individual chipmunks and defined available locations as randomly generated points within the 100% MCP home range for each chipmunk. The ratio of used:available

points was 1:2. We tested 75 hypothesis-driven a priori models using mixed-effects logistic regression with binomial distribution and logit link function and included a random intercept for each chipmunk (Supplementary Data SD2; Breslow and Clayton 1993; Gillies et al. 2006). We included a random effect

at this scale to allow for the explicit identification of individual variability within the home range (Neter et al. 1996).

In our study, microhabitat represented selection of areas within the home ranges of unknown chipmunks and was analyzed with field-collected and 10-m resolution spatial variables (study design III of Manly et al 2002). At the microhabitat scale, we defined used locations as the area within the immediate vicinity (15 m) of an opportunistically observed chipmunk's location and defined available locations as random locations selected within a 93 m radius of the chipmunk's location, which represented the radius of a 2.7-ha home range for *N. quadrivittatus* (Bergstrom 1988). We opportunistically observed chipmunks at 56 locations and the ratio of used:available points was 1:1. At the microhabitat scale, we used logistic regression with binomial distribution and logit link function to test 32 hypothesis-driven a priori models (Supplementary Data SD2).

We assessed selection of land cover associations at secondand third-order scales using Manly selection ratios (Manly et al. 2002) with the R package *adehabitatHS* (Calenge 2006). At the second-order scale, we compared the proportion of telemetry locations of all chipmunks in each land cover type to the proportion of each land cover type within the buffered cumulative home range. At the third-order scale, we compared the proportion of telemetry locations in each land cover type to the proportion of land cover type available within the home range of each individual chipmunk.

Chipmunk capture and radiotelemetry.—We captured chipmunks with Sherman live traps (model LFATDG; H. B. Sherman, Tallahassee, Florida) baited with a commercial horse feed mixture of grains and molasses. Upon capture, we transferred the chipmunk to a zippered, mesh handling bag for processing and radiocollar attachment. Total handling time of captured chipmunks was < 5 min to minimize stress.

During processing, we recorded body mass by weighing the chipmunk in the bag with a hanging spring scale (Pesola spring scales, PESOLA Präzisionswaagen AG, Schindellegi, Switzerland). We determined sex by visual observation of genitals and assessed reproductive condition as scrotal or nonscrotal for males and open, closed, pregnant (i.e., swollen abdomen), or lactating for females (Schulte-Hostedde et al. 2002). We classified age as juvenile or adult; we considered chipmunks with pelage appearing fluffier, with a body mass  $\leq 50$  g, and not displaying signs of reproductive activity to be juveniles. We fitted a 1.8-g radiotransmitter collar (model BD-2C; Holohil Systems, Carp, Ontario, Canada) to adult chipmunks that did not appear stressed and appeared to be in healthy physical condition. Adult chipmunk body mass was 62.5 g ± 8.43 SD (range = 50 - 84 g), so the collar never exceeded the recommended 5% of the chipmunk's body weight (Sikes et al. 2016). Prior to release, we held radiocollared chipmunks in Sherman traps for ~30 min and then examined them to ensure we properly fitted the collar and each chipmunk had made a full recovery. We recaptured nine chipmunks midway through the study period, at which time we replaced the radiocollar. Capture and handling methods followed recommendations of the American Society of Mammalogists (Sikes et al. 2016) and were approved by the New Mexico State University Animal Care and Use Committee (IACUC 2018-006) and the New Mexico Department of Game and Fish (scientific collecting permit #2868).

We located radiocollared chipmunks with handheld telemetry receivers (model R-1000; Communications Specialists, Orange, California) attached to a 3-element Yagi antenna (Wildlife Materials International, Inc., Murphysboro, Illinois). We recorded observer location with handheld GPS units (model GPSMAP 64st; Garmin, Olathe, Kansas). While recording location data, we made an effort not to disturb the chipmunks or their habitat. We located each chipmunk in random order via triangulation at least twice a day and 5 days/week for the duration of radiotransmitter battery life (~12 weeks). We ascertained compass bearings for a chipmunk from at least two observer locations based on the direction of the strongest telemetry signal. Observers recorded their location and compass bearing within 1 min to reduce potential error due to moving chipmunks. At times when an observer saw a chipmunk without disturbing it, the observer recorded the exact location of that chipmunk with a GPS unit after the chipmunk had left the vicinity. To maintain temporal independence for each chipmunk, we waited ≥ 1 h before obtaining a subsequent location (Brzeziński et al. 2019).

We estimated chipmunk locations using the software Location of a Signal (Ecological Software Solutions LLC 2019), which estimates the point of intersection for two or more locations with bearings. We evaluated the extent and sources of error associated with radiotelemetry to exclude excessively imprecise locations (Withey et al. 2001). We measured the radiotelemetry error using radiotransmitters placed at known locations and developed an equation to predict linear error (i.e., distance between the true position of the radiotransmitter and the triangulated location) following methods of Withey et al. (2001; Supplementary Data SD1). We used the predicted linear error of each telemetry location to define valid telemetry locations. Valid locations included visual observations of identified individuals and triangulated points with a linear error ≤ 30 m (Supplementary Data SD1). Invalid locations were triangulated points with a linear error > 30 m, nonvisual chipmunk locations with only one point, visual observation of unidentified individuals, or triangulation locations that failed to intersect. We only included valid telemetry locations in statistical analyses at the second- and third-order scales.

Home range analysis.—We estimated home range size based on valid telemetry locations using the MCP (Mohr 1947) and 95% fixed kernel density estimator method (KDE—Worton 1989; White and Garrott 1990). For 95% KDE, we used the ad hoc smoothing parameter (h) because reference bandwidth and least squares cross-validation can result in a Type I error by overestimating home range sizes based on small samples (Kie 2013). We used the R package adehabitatHR for home range calculations (Calenge 2006). We determined the number of telemetry points needed to estimate home range using a home range area curve where the asymptote of the curve was considered to represent the number

of locations needed to accurately estimate home range size (Odom and Kuenzler 1955; Haines et al. 2006). We evaluated differences in home range size by sex using an equal variance *t*-test. We tested for normality by sex using the Shapiro–Wilk normality test and tested for equal variance between sexes using an *F*-test.

Collection of spatial variables.—We used spatial variables created in a geographic information system (GIS) that were selected based on their hypothesized importance to habitat selection, including land cover type, normalized difference vegetation index (NDVI), distance to drainage, aspect, hill shade, slope, vector ruggedness measure (VRM), topographic position index (TPI), and cliff (Table 1). Land cover types that included conifer trees have been associated with increased relative likelihood of occurrence for N. q. australis (Frey and Kopp 2013). We included NDVI as a variable because land cover types with conifer trees have been shown to have the greatest NDVI values in the Organ Mountains (Frey and Kopp 2013) and using NDVI would help distinguish among different cover types (i.e., conifer, nonconifer, and nonvegetated areas). Drainages sometimes hold water and water provides more opportunity for drinking and might increase the production of food-producing plants (Moir and Ludwig 1979; Block and Finch 1997). Previous studies have suggested that N. q. australis is adapted to cool climates and associated vegetation types (Patterson 1980; Frey and Kopp 2013); we therefore hypothesized aspect and hill shade would influence habitat selection. Areas with a southwest-facing aspect and decreased hill shade are expected to have more sunlight across the year, hence will not be as likely to support conifers and other cryomesic vegetation (Moir and Ludwig 1979; Block and Finch 1997). Topographic position can influence ecological characteristics of a site, and N. q. australis is thought to be associated with steep slopes (Rivieccio et al. 2003); we therefore hypothesized that slope, VRM, TPI, and cliff would influence habitat selection.

We created all spatial variables in ArcMap 10.7.1 (ESRI 2019). For each variable (except land cover type and distance to drainage), we calculated average values within a 30-m buffer of the location to account for uncertainty associated with the telemetry locations. We selected 30 m as the buffer based on the mean linear error calculated for the study area (Supplementary Data SD1). We created a map of four land cover types—arid, montane scrub, riparian, woodland-based on 1-m resolution satellite imagery available from the National Agriculture Imagery Program (United States Department of Agriculture, Farm Service Agency 2015) and ground-truthed ground cover data (Supplementary Data SD3). The woodland land cover in our study was a ponderosa pine and Gambel oak association and considered a montane coniferous forest biotic community type (Dick-Peddie 1993). We calculated the proportion of each land cover type within the 30-m buffer of the location. We rescaled land cover proportions from 10 m to 30 m and 90 m resolutions. We used NDVI data available at 30 m resolution from Landsat 8 surface reflectance data (United States Geological Survey 2019). We calculated average NDVI over the entire year using Landsat 8 surface reflectance data available monthly for 2019 (Vermote et al. 2016). We rescaled NDVI from 30 to 90 m. We defined drainages, which represented all perennial and intermittent streams, using the National Hydrography Dataset (United States Geological Survey 2019), and calculated the distance in meters from locations to nearest drainage.

To create topographic variables, we used a 10-m Digital Elevation Model raster available from The National Map (United States Geological Survey 2017). We created each topographic variable at three spatial resolutions by using the aggregate tool to rescale variables from 10 m to 30 m and 90 m resolution or from 1-cell to 3-cell and 9-cell moving window (Table 1). We calculated aspect using the aspect tool. We folded aspect to the northeast-southwest line following the equation in McCune and Keon (2002). To calculate hill shade, we obtained data on the sun's altitude and azimuth from the United States Navy Astronomical Applications Department for 0900, 1200, and 1500 h on the 2019 solstices and equinoxes and calculated the average of these values. We calculated the degree of slope using the slope tool and VRM using the Benthic Terrain Modeler toolbox add-on (Walbridge et al. 2018). We calculated TPI as a continuous variable using the Topography Tools toolbox 10.3 add-on (Dilts 2015). We defined cliff as a pixel that had a TPI of -2 to 2 and a slope  $> 15^{\circ}$ .

Collection of field variables for the microhabitat scale.—For the microhabitat scale analysis, we collected data on microhabitat characteristics that could be important for foraging or reducing predation risk. We included all of the spatial variables (except folded aspect, cliff, and NDVI) at a 10-m spatial scale and a suite of field-collected variables. Previous microhabitat use studies found N. q. australis to be associated with increasing litter cover and decreasing shrub and grass cover (Rivieccio et al. 2003), rocks (Sullivan 1996; Rivieccio et al. 2003), and burned areas (Johnson et al. 1998). We measured microhabitat variables along four perpendicular 15-m transects radiating from each location. Variables included tree and shrub species composition and abundance, distance to nearest shrub, tree, and boulder, presence of burned vegetation, and ground cover (Table 2). We defined trees, shrubs, and forbs, using descriptions from the United States Department of Agriculture PLANTS database (United States Department of Agriculture, Natural Resources Conservation Service 2019). Trees were considered woody plants that, at maturity, had a trunk. Shrubs were considered multistemmed woody plants. Forbs were considered vascular plants that lacked significant secondary woody growth. We used the United States Department of Agriculture PLANTS database for plant species names (United States Department of Agriculture, Natural Resources Conservation Service 2019).

We identified to species all trees and shrubs that had trunks or stems located within a 1-m belt on either side of the transects. We recorded the number of each species of shrub by 1-m height classes (< 1, 1 - 2, 2 - 3, 3 - 4, > 4) and the number of each species of tree by 10-cm-diameter size classes (< 10, 10-20, 20-30, 30-40, 40-50, > 50) along each transect. We determined diameter at breast height of trees with a measuring tape. We measured distance from the location to the nearest shrub and to the nearest tree and identified them to species. We calculated woody plant diversity with the Shannon–Weaver index (Shannon and Weaver 1948; Margalef 1957). We measured distance from the location to the nearest boulder, which we defined as a rock  $\ge 1$  m in diameter. We recorded the degree woody plants had been burnt by wildfire: no burn (no evidence

of fire), partial burn (< 75% burn coverage), or complete burn (≥ 75% burn coverage) for shrubs, trees, and dead standing trees.

We collected ground cover data every 2 m along the transects. We used standard  $20 \times 50$  cm Daubenmire plot and classing categories (1: 0-5%, 2: 6-25%, 3: 26-50%, 4: 51-75%, 5: 76-95%, 6: 96-100%) to estimate ground cover by type at 1 m above the ground (Bonham et al. 2004). Ground cover types included forbs, grasses, woody plants, leaf litter, fine woody debris, coarse woody debris, bare, and rock by type. We defined dead leaves as leaf litter. We defined fine woody debris as logs or branches with a diameter < 10 cm and coarse woody debris as logs or branches with a diameter  $\geq 10$  cm (Harmon and Sexton 1996). We classified rock as exposed bedrock, boulders, or small rocks (< 1 m in diameter).

Statistical analysis.—We carried out statistical analyses in Program R (R Foundation for Statistical Computing, Vienna, Austria). For the three habitat selection scales, we created scatterplots of each variable to examine potential outliers and data transformations. We performed a univariate logistic regression on each variable and used the R Package MuMIn (Bartoń 2019) to calculate Akaike's information criterion adjusted for small sample sizes (AIC<sub>c</sub>) to assess model fit to the chipmunk location data (Burnham and Anderson 2002). For spatial variables calculated at three resolutions (10, 30, 90 m), we retained the resolution with the lowest  $\Delta AIC_c$  value (Burnham and Anderson 2002). We then removed any variable that had either 85% CI overlapping zero or were less biologically relevant when the Pearson correlation coefficient between two variables was > 0.70(Arnold 2010). We used 85% CI to ensure we maintained variables that could be included in best-approximating models (Arnold 2010). Based on the scatterplots, we tested for quadratic effects on slope and hill shade at the second-order scale and used AIC, to assess model fit. We retained the quadratic term if the quadratic model had a lower  $\Delta AIC_c$  than the model with the linear term. We hypothesized interactions among NDVI, aspect, hill shade, slope, and VRM at the second- and third-order scales. We retained only those interactions that had 85% CI that did not overlap zero. We standardized the remaining continuous variables around the mean and standard deviation to compare the relative influence of resources on habitat selection (Zar 1986).

We calculated Manly selection ratios and 95% Bonferroniadjusted confidence intervals at the second- and third-order scales to determine if proportion of a land cover type used differed from proportion available (Johnson 1980; Manly et al. 2002). We considered selection ratios > 1 to indicate selection for a specific land cover type and < 1 to indicate avoidance (Manly et al. 2002). At the third order, we evaluated differences in Manly selection ratios between sexes using equal variance t-tests. We tested for normality by sex using the Shapiro–Wilk normality test and tested for equal variance between sexes using an F-test.

For each habitat selection scale, we considered all models with a  $\Delta AIC_c$  value of < 2 as competitive and selected the top model based on  $\Delta AIC_c$  (Burnham and Anderson 2002). We calculated variance inflation factors (VIF) using the R package *car* (Fox and Weisberg 2019) for variables in the top model to assess multicollinearity (James et al. 2014). At the second- and third-order scales, we carried out k-fold cross-validation partitioned into 10 folds to test the predictive capabilities of our top models (Boyce et al. 2002). At the microhabitat selection scale, we undertook k-fold cross-validation partitioned into five folds due to the small sample size. For the second-order scale, we created a map of predicted use based on unstandardized coefficients of variables in our top model (Long et al. 2009).

#### RESULTS

Home range.—We recorded 1,256 locations from 20 adult chipmunks (n = 10 M, n = 10 F), of which 637 locations were valid (31.85 locations  $\pm$  17.38 SD for each animal; Supplementary Data SD4). The home range area curve (100% MCP) appeared to stabilize for most chipmunks at 30 locations (Supplementary Data SD5). We estimated MCP and KDE home range for 10 individuals (n = 5 M, n = 5 F) that had ≥ 30 locations. Home ranges of each sex were normally distributed, and variances were equal between sexes (95% MCP:  $F_{4,4} = 2.81$ , P = 0.34; 100% MCP:  $F_{4,4} = 0.98$ , P = 0.98; KDE:  $F_{4,4} = 2.20$ , P = 0.46). Mean home range did not differ between males and females (95% MCP:  $t_8 = 0.72$ , P = 0.49; 100% MCP:  $t_8 = 0.57$ , P = 0.58; KDE:  $t_8 = 1.87$ , P = 0.10). Estimated mean home ranges for the study population were 95% MCP of 2.55 ha  $\pm$  1.55 SD (range = 1.09 – 4.00 ha); 100% MCP of 3.25 ha  $\pm$  1.32 SD (1.59–5.26 ha); and KDE of 2.09 ha  $\pm$  1.21 SD (0.39–3.96 ha).

Second-order selection.—The only competitive model for second-order selection had proportion of montane scrub land cover at the 90-m scale (MS-90), NDVI at the 90-m scale (NDVI-90), distance to drainage, folded aspect at the 90-m scale (aspect-90), slope<sup>2</sup> at the 90-m scale (slope-90), and an interaction between NDVI-90 and aspect-90 (Table 3; Supplementary SD6). Probability of selection

**Table 3.**—Ranking of logistic regression models for second-order selection (home range) by *Neotamias quadrivittatus australis* (n = 20) in the Organ Mountains, New Mexico, October 2018 to July 2019. Model variables, number of parameters in the model (K), difference in Akaike's information criterion corrected for small sample sizes ( $\Delta$ AIC $_c$ ), Akaike weights ( $w_i$  = estimated probability of model i being the best model given data and model set), and model deviance for candidate models developed to explain differences in selection between used and available radiotelemetry locations. See Supplementary Data SD3 for the full model set; only models that cumulatively made up 95% AIC $_c$  weight are included in this table.

Model <sup>a</sup>	K	$\Delta { m AIC_c}$	$w_{i}$	Deviance
MS + NDVI + DD + FA + Slope + Slope <sup>2</sup> + NDVI * FA	8	0.00	1.00	528.03
MS + W + DD + FA + Hillshade + Hillshade <sup>2</sup> + Slope + Slope <sup>2</sup>	9	22.49	0.00	548.49

<sup>&</sup>lt;sup>a</sup>MS = proportion montane scrub land cover (90 m); W = proportion woodland land cover (90 m); NDVI = normalized difference vegetation index (90 m); DD = distance to drainage (m); FA = folded aspect (90 m); TPI = topographic position index (90 m).

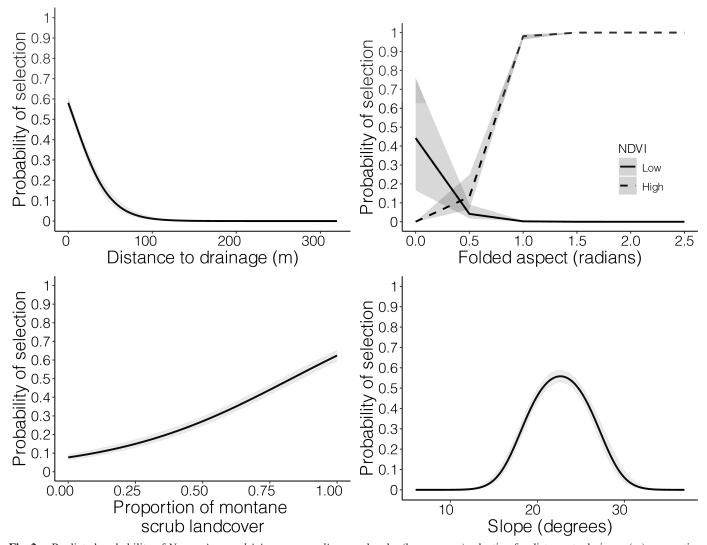
by chipmunks increased with increasing MS-90, NDVI-90, and aspect-90 (Table 4; Fig. 2). Probability of selection by chipmunks decreased as distance to drainage increased (Table 4; Fig. 2). Probability of selection by chipmunks increased until the slope of an area reached  $\geq 20^{\circ}$  and then began to decrease (Table 4; Fig. 2). The interaction between NDVI-90 and aspect-90 suggested that chipmunks

selected for northeasterly facing slopes but also selected more southwesterly facing aspects if they were greener (Table 4; Fig. 2). Ten k-fold cross-validation indicated that the second-order selection model had strong predictive power ( $\rho = 0.81$ , P < 0.0001). The second order predictive map indicated there were very few areas on the landscape with > 25% probability of selection (Fig. 3).

**Table 4.**—Variables, standardized beta coefficient estimates, SE, 85% CI, and variance inflation factors (VIF) for the best-fitting model for second-order selection (home range) by *Neotamias quadrivittatus australis* (n = 20) in the Organ Mountains, New Mexico, October 2018 to July 2019.

Variable	Beta	SE	85% CI	VIF	
Intercept	-2.01	0.28	-2.43, -1.62		
Proportion of montane scrub land cover	0.79	0.14	0.59, 1.01	1.42	
$\stackrel{\circ}{NDVI^a}$	0.31	0.15	0.10, 0.54	1.21	
Distance to drainage	-2.92	0.40	-3.52, -2.37	1.12	
Folded aspect	0.84	0.18	0.57, 1.10	1.48	
Slope	0.52	0.22	0.20, 0.83	1.68	
Slope <sup>2</sup>	-0.36	0.23	-0.70, -0.04	1.45	
NDVI * Folded aspect	1.24	0.22	0.93, 1.57	1.26	

<sup>&</sup>lt;sup>a</sup>NDVI = normalized difference vegetation index.



**Fig. 2.**—Predicted probability of *Neotamias quadrivittatus australis* second-order (home range) selection for distance to drainage (m), proportion of montane scrub land cover type, folded aspect (radians; zero represents NE-facing and 3.14 represents SW-facing), and slope (degrees) in the Organ Mountains, New Mexico, October 2018 to July 2019; shading represents 85% *CI*.

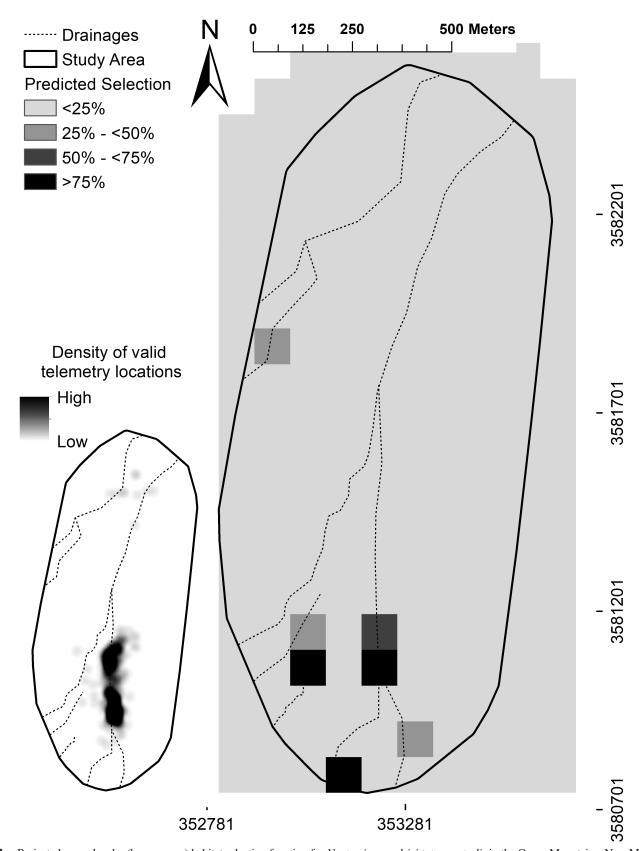


Fig. 3.—Projected second-order (home range) habitat selection function for *Neotamias quadrivittatus australis* in the Organ Mountains, New Mexico, October 2018 to July 2019 (90 m resolution; n = 20). Coordinates are in UTM Zone 13S. Dark areas represent increase in probability of selection; inset map is the density of valid telemetry locations.

At the second-order scale, the highest Manly selection ratio was for riparian land cover (selection ratio = 2.64). Chipmunks also selected for montane scrub land cover (selection ratio = 1.96) and avoided arid and woodland land cover types (selection ratio = 0.16 for both; Fig. 4A).

Third-order selection.—The only competitive model for third-order selection included NDVI at 90-m scale (NDVI-90), distance to drainage, hillshade at 10-m scale (hillshade-10), slope at 90-m scale (slope-90), and TPI at 10-m scale (TPI-10; Table 5;

Supplementary Data SD6). Probability of selection by chipmunks increased with increasing NDVI-90 and slope-90 (Table 6; Fig. 5). Probability of selection by chipmunks increased for strongly negative TPI-10, which we considered as locations within home ranges that were near the base of cliffs in drainages (Table 6; Fig. 5). Probability of selection by chipmunks decreased with increasing distance to drainage and hillshade-10 (Table 6; Fig. 5). The k-fold cross-validation indicated that the top third-order selection model had poor predictive power ( $\rho$  = 0.40, P < 0.0001).

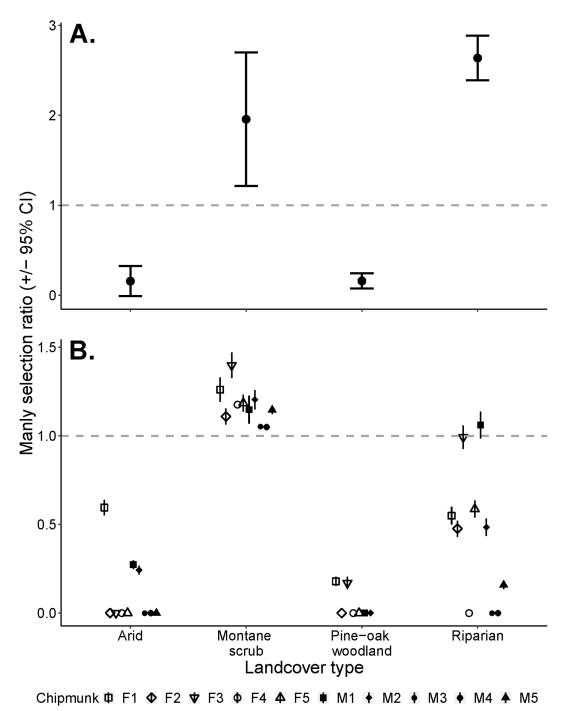


Fig. 4.—Selection ratios and Bonferroni-adjusted 95% CI for ten female (F) and ten male (M) radiotracked *Neotamias quadrivittatus australis* in the Organ Mountains, New Mexico, March–July 2019. Dashed line indicates no selection (i.e., ratios = 1). A) Second-order (home range) selection ratios (n = 20) and B) third-order (within home range) selection ratios for chipmunks with  $\geq 30$  telemetry locations (n = 10).

**Table 5.—**Ranking of mixed-effects logistic regression models for third-order selection (within home range) by *Neotamias quadrivittatus australis* (n = 10) in the Organ Mountains, New Mexico, March–July 2019. Model variables, number of parameters in the model (K), difference in Akaike's information criterion corrected for small sample sizes ( $\Delta$ AIC $_{c}$ ), Akaike weights ( $w_{i}$  = estimated probability of model i being the best model given data and model set), and model deviance for candidate models developed to explain differences in selection between used and available radiotelemetry locations. See Supplementary Data SD3 for full model set; only models that cumulatively made up 95% model weight are included in this table.

Model <sup>a</sup>	K	$\Delta { m AIC}_{ m c}$	$w_{i}$	Deviance
NDVI-90 + DD + Hillshade-10 + Slope-90 + TPI-10	7	0.00	0.91	1,304.91
MS-30 + R-30 + W-90 + NDVI-90 + DD + Hillshade-10 + Slope-90 + TPI-10	10	5.95	0.05	1,304.66

<sup>a</sup>MS = proportion of montane scrub land cover; R = proportion of riparian land cover; W = proportion of pine-oak woodland land cover; NDVI = normalized difference vegetation index; DD = distance to drainage (m); TPI = topographic position index.

**Table 6.**—Variables, standardized beta coefficient estimates, SE, 85% CI, and variance inflation factors (VIF) for the best-fitting model for third-order selection (within home range) by *Neotamias quadrivittatus australis* (n = 10) in the Organ Mountains, New Mexico, March–July 2019.

Variable	Beta	SE	85% CI	VIF
Intercept	-1.12	0.13	-1.31, -0.94	
$NDVI^{a}$	0.14	0.09	0.01, 0.26	1.16
Distance to drainage	-0.55	0.14	-0.75, -0.35	1.94
Hill shade	-0.27	0.09	-0.40, -0.14	1.78
Slope	0.27	0.12	0.09, 0.44	1.41
Topographic position index	-0.89	0.13	-1.07, -0.70	1.88

<sup>&</sup>lt;sup>a</sup>NDVI = normalized difference vegetation index.

At the third-order scale, there were no differences in Manly selection ratios by sex ( $t_{35} = -0.14$ , P = 0.89). All chipmunks selected for montane scrub land cover (selection ratio range = 1.05–1.40; Fig. 4B), and all chipmunks avoided arid land cover (selection ratio range = 0–0.60; Fig. 4B). Most (8) chipmunks avoided riparian land cover, although one chipmunk selected it and one chipmunk did not either select or avoid it (selection ratio range = 0.00–1.06; Fig. 4B). All seven chipmunks with woodland land cover available avoided it (selection ratio range = 0–0.18; Fig. 4B); three chipmunks did not have woodland land cover type within their home range.

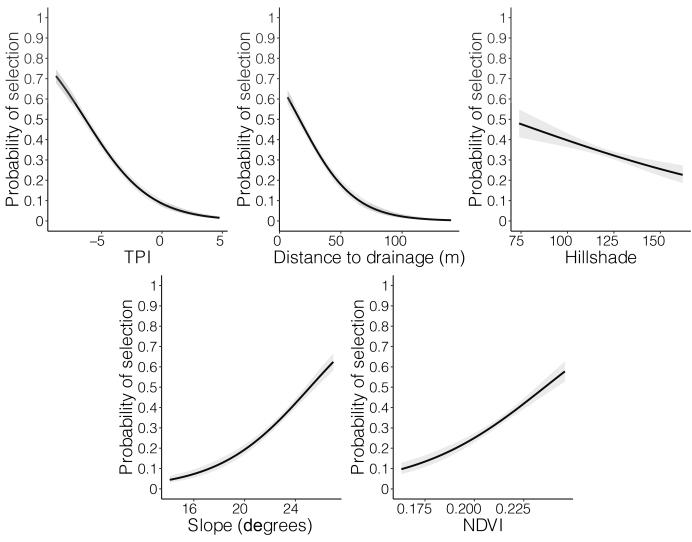
*Microhabitat selection*.—The only competitive model for microhabitat selection included woody plant diversity, distance to nearest tree, coarse woody debris ground cover, rock ground cover, and TPI at 10 m resolution (TPI-10; Table 7). Probability of selection by chipmunks increased with increasing woody plant diversity, coarse woody debris ground cover, and rock ground cover (Table 8; Fig. 6). Probability of selection by chipmunks increased as TPI-10 values became more negative, reflecting areas near the base of slopes (Table 8; Fig. 6). Probability of selection by chipmunks decreased as the distance to nearest tree increased (Table 8; Fig. 6). The k-fold crossvalidation indicated that the top microhabitat selection model had moderate predictive power ( $\rho$  = 0.46, P < 0.0001).

#### **DISCUSSION**

We found that habitat selection by *N. q. australis* was fundamentally different from descriptions of habitat use by the species in

the literature. Prior studies described N. quadrivittatus as primarily associated with montane coniferous forests (Patterson 1980; Best et al 1994). In contrast, N. q. australis in our study area avoided pine-oak woodland land cover type and selected a suite of characteristics associated with relatively deep, steepsided arroyos. At the second order, the study population selected particular areas of arroyos that were relatively green, contained more montane scrub, and had moderate slopes. Similarly, at the third order, chipmunks selected locations within home ranges near the base of arroyo sides that were topographically shadier, steeper, and greener. The second-order predictive map demonstrated that selected habitats only occurred in certain areas of arroyos rather than forested slopes, reinforcing the key difference between our habitat selection results and prior descriptions of habitat use. Because we based our results on a comparison of used versus available locations, we can have more confidence in these results and can interpret them as habitat requirements for N. q. australis in our study area.

Our results demonstrated that failure to consider multiple scales could lead to potential misinterpretation of habitat information. For example, based on the second-order Manly selection ratio results, chipmunks selected riparian land cover nearly twice as strongly as montane scrub land cover, suggesting an association with riparian vegetation. Nevertheless, when we included the context of the third-order and microhabitat scales, we know that chipmunks selected for certain conditions of arroyos—shady, steep sides that were more green—rather than riparian vegetation itself. Without the context of additional scales, managers might misapply conservation efforts for *N. q. australis* by



**Fig. 5.**—Predicted probability of *Neotamias quadrivittatus australis* third-order (within home range) selection for topographic position index (TPI), distance to drainage (m), hill shade, slope (degrees), and normalized difference vegetation index (NDVI) in the Organ Mountains, New Mexico, March–July 2019; shading represents 85% *CI*.

enhancing riparian vegetation in the Organ Mountains. Finally, we demonstrated that extrapolating microhabitat results to a broader, landscape-level scale can lead to misinformation about habitat. At the microhabitat scale, chipmunks selected diverse woody areas with coarse woody debris and rock cover near the base of slopes. Without the information from the coarser scales, we could misinterpret these results and incorrectly conclude that N. q. australis is associated with coniferous forests, as suggested in the previous literature on N. quadrivittatus habitat use. However, given the context of the second- and third-order scales, we know that these microhabitat conditions of rocky sites with downed logs and diverse, woody vegetation near the base of slopes were selected within arroyos. Rivieccio et al. (2003) provided another example of the importance of context when extrapolating microhabitat information. Their study suggested that N. q. australis was positively associated with logs and negatively associated with grass and shrub cover, which could again lead to the inappropriate conclusion of an association with coniferous forests. Nevertheless, that study lacked the ability to draw conclusions from the microhabitat information to the location of chipmunks on the landscape because it did not consider broader scales.

Extrapolating results of a habitat selection study to a different geographic area might lead to misinterpretation of habitat information. Prior studies appropriately used occupancy modeling (Perkins-Taylor and Frey 2018) and species distribution modeling (Perkins-Taylor and Frey 2020) to investigate first-order habitat selection by *N. q. oscuraensis* (Meyer and Thuiller 2006). *N. q. oscuraensis* selected areas at high elevation with piñon woodland and escarpments (Perkins-Taylor and Frey 2018, 2020). In the Oscura Mountains, these selected habitats are broadly distributed due to the relatively uniform topography of the range. In contrast, the Organ Mountains are much more topographically rugged than the Oscura Mountains, resulting in complex patterns of environmental variation and patchy vegetation. This, and the selection of particular areas of arroyos by *N. q. australis*, suggested that the distribution

**Table 7.**—Ranking of logistic regression models for microhabitat selection by *Neotamias quadrivittatus australis* (n = 56) in the Organ Mountains, New Mexico, July 2018 to July 2019. Model variables, number of parameters in the model (K), difference in Akaike's information criterion corrected for small sample sizes ( $\Delta$ AIC<sub>c</sub>), Akaike weights ( $w_i$  = estimated probability of model i being the best model given data and model set), and model deviance for candidate models developed to explain differences in selection between used and available locations. See Supplementary Data SD3 for full model set; only models that cumulatively made up 95% model weight are included in this table.

Model <sup>a</sup>	K	$\Delta { m AIC}_{ m c}$	$W_{i}$	Deviance
SDI + DT + CWD + Rock + TPI-10	6	0	0.58	129.34
DT + DB + CWD + Rock + TPI-10	6	2.41	0.17	131.75
SDI + DT + DB + CWD + Rock	6	2.70	0.15	132.04
DT + DB + CWD + Rock	5	5.23	0.04	136.80
SDI + CWD + Rock + TPI-10	5	5.58	0.04	137.15
SDI + CWD + Rock	4	6.24	0.03	140.00

aSDI = woody plant diversity (Shannon–Weiner diversity index); DT = distance to nearest tree (m); DB = distance to nearest boulder (m); CWD = coarse woody debris ground cover (%); Rock = rock ground cover (%); TPI-10 = topographic position index (10 m).

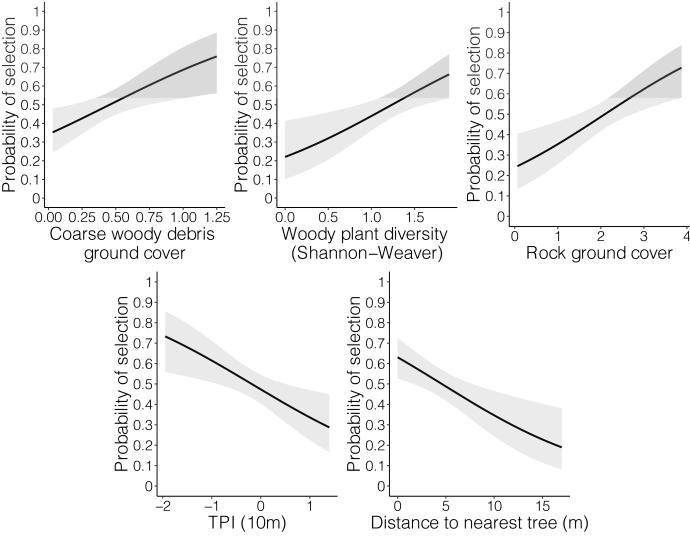
**Table 8.**—Variables, standardized beta coefficient estimates, SE, 85% CI, and variance inflation factors (VIF) for the best-fitting model for microhabitat selection by *Neotamias quadrivittatus australis* (n = 56) in the Organ Mountains, New Mexico, June 2018 to July 2019.

Variable	Beta	SE	85% CI	VIF
Intercept	-0.003	0.21	-0.31, 0.30	
Woody plant diversity	1.06	0.55	0.29, 1.88	1.03
Distance to nearest tree	-0.15	0.06	-0.24, -0.07	1.09
Coarse woody debris ground cover	2.20	0.88	0.97, 3.52	1.12
Rock ground cover	0.79	0.27	0.41, 1.19	1.13
Topographic position index	-0.64	0.32	-1.11, -0.18	1.05

of *N. quadrivittatus* in the Organ Mountains might be more restricted and fragmented than in the Oscura Mountains. For example, piñon woodland is rare in the Organ Mountains and exists only as small relict stands. Although we can only hypothesize what we might expect to find in a first-order model because we did not address first-order selection in this study, this suggests that applying *N. q. oscuraensis* selection for piñon woodland to *N. q. australis* habitat information could be incorrect.

We can have further confidence that our results are reliable because we tested and incorporated telemetry error, which many radiotelemetry studies ignore (e.g., Harris et al. 1990; Withey et al. 2001; Bartolommei et al. 2012). Telemetry error is study site-specific and can lead to incorrect assignment of locations, thereby influencing habitat selection results (White and Garrott 1990). To control for telemetry error in our study, we excluded locations with excessive error from all analyses, we calculated spatial variables for the second- and third-order selection within a circular area around each telemetry location, and we excluded triangulated telemetry locations from the microhabitat analysis. We also selected scales of study based on biologically meaningful levels, which some habitat selection studies fail to consider (Manning et al. 2004; Bowyer and Kie 2006). We defined our scales based on known home range information for N. quadrivittatus instead of human preconceptions to be certain we did not select arbitrary scales for analysis (Manning et al. 2004; Bowyer and Kie 2006). We also calculated spatial variables at multiple spatial scales and used information theory to determine the most informative resolution for analysis (Thompson and McGarigal 2002). We used statistical analyses that were appropriate for our study design and type of attribute data, which some researchers fail to justify adequately (Thomas and Taylor 2006; Jenkins et al. 2019). We chose logistic regression as our method of statistical analysis because the nature of our response variable was binomial: used or available (Garson 2016). We also met the assumptions of logistic regression because we accounted for outliers by using standardized continuous predictors, for multicollinearity among predictors by using Pearson correlation analysis and VIF, and for independence between observations by spacing observations temporally and rarefying locations spatially.

Conservation implications.—Across most of its distribution, N. quadrivittatus occurs in relatively cool, mesic environments of major mountain ranges (Best et al. 1994). In contrast, the Organ Mountains are a small, isolated mountain range located in the Chihuahuan Desert at the species' southern distributional limits. The Organ Mountains have relatively hot and dry conditions compared with other ranges where the species occurs. We found that N. q. australis selected specific areas of certain arroyos that were relatively deep and steep-sided. These arroyos provide a relatively cool microclimate due to topographic shading. In a post hoc test, we found that locations within the arroyos were cooler than locations outside of the arroyos in all seasons except winter (Supplemental Data SD7). The selected areas of the arroyos also were unique in that they held water more consistently than other areas of the study area, due to occurrence of natural springs and precipitation runoff (Blake et al. 2020). Studies have found that water is important for reproductive success in other species of chipmunks (Heller and Poulson 1970; Hirshfield 1975). Arroyos also might have



**Fig. 6**—Predicted probability of *Neotamias quadrivittatus australis* microhabitat selection for coarse woody debris (CWD) ground cover, woody plant diversity, rock ground cover, topographic position index (TPI), and distance to nearest tree (m) in the Organ Mountains, New Mexico, June 2018 to July 2019; shading represents 85% *CI*.

greater diversity of woody vegetation due to the increased availability of water. These physical and ecological conditions of arroyos allow them to function as a "climate change refugia" by increasing the chances of retaining surface water and milder environmental conditions (Morelli et al. 2016:3). That *N. q. australis* selected relatively cool, sparsely distributed mesic areas suggests it is existing on the edge of its ecological tolerances in our study area.

Despite carrying out our study in the supposed core area for chipmunk distribution in the Organ Mountains (Patterson 1980), we found that *N. q. australis* selected for a very specific landform that is unique on the landscape. A post hoc analysis of arroyos within the study area found that they made up 22.52% of the landscape (Supplementary Data SD7); however, based on the second-order predictive map, there only were four 90 m pixels with predicted habitat selection > 50% and only three with > 75%. As a result, *N. q. australis* could have a small and fragmented distribution in the mountain range, thus increasing vulnerability to habitat disturbance and population instability

in occupied patches from recreational activities, military activities, and disturbances such as wildfire (Sullivan 1996; Morrison et al. 2006). Given the limited habitat available to this chipmunk, it therefore is imperative to protect pockets of habitat from disturbance and mitigate impacts of climate change.

As a relict taxon that selects refugial habitat, conservation of *N. q. australis* could focus on protecting arroyos as climate change refugia, following the steps recommended by Morelli et al. (2016). Briefly, beneficial conservation and management plans would be those that focus on maintaining arroyo chipmunk habitat and implementing priority actions such as minimizing disturbance from wildfire and other causes. Future research is needed to determine the climatic buffer that arroyos provide to understand and manage refugia features. Our study did not consider first-order selection; therefore, we are uninformed as to how our habitat selection findings relate to chipmunk distribution across the mountain range. Based on the narrow set of habitat requirements for *N. q. australis* and the uniqueness of the selected portions of arroyos on the landscape,

we hypothesize that first-order selection also will include arroyos and that these conditions will continue to be rare on the landscape. We suggest implementing an occupancy study to examine first-order habitat selection. If the chipmunks are as limited in habitat across their distribution as our study suggests, the conservation stakes for *N. q. australis* could be grim.

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#### SUPPLEMENTARY DATA

Supplementary data are available at Journal of Mammalogy online

**Supplementary Data SD1.**—Study of the radiotelemetry error in the Organ Mountains, New Mexico in March 2019.

**Supplementary Data SD2.**—A priori conceptual models tested using logistic regression to evaluate habitat selection by the Organ Mountains Colorado chipmunk (*Neotamias quadrivittatus australis*).

**Supplementary Data SD3.**—Methods for the creation of a land cover map of the study area in the Organ Mountains, New Mexico.

**Supplementary Data SD4.**—Sex, body mass (g), radiotracking period, number of radiotelemetry locations, and minimum convex polygon and kernel density home range size estimates in a study of habitat selection by the Organ Mountains Colorado chipmunk (*Neotamias quadrivittatus australis*; n = 20) from October 2018 to July 2019 in the Organ Mountains, New Mexico.

**Supplementary Data SD5.**—Relationship between 100% minimum convex polygon home range size and number of valid telemetry locations for 20 Organ Mountains Colorado chipmunks (*Neotamias quadrivittatus australis*) radiotracked in the Organ Mountains, New Mexico from October 2018 to July 2019.

**Supplementary Data SD6.**—Map of topographic variables included in the models for second- and third-order selection by the Organ Mountains Colorado chipmunk (*Neotamias quadrivittatus australis*) radiotracked in the Organ Mountains, New Mexico from October 2018 to July 2019.

**Supplementary Data SD7.**—Post hoc analysis of temperatures in and outside arroyos within the study area in the Organ Mountains, New Mexico.

# LITERATURE CITED

- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1178–2010.
- Bartolommei, P., S. Francucci, and F. Pezzo. 2012. Accuracy of conventional radio telemetry estimates: a practical procedure of measurement. Hystrix, the Italian Journal of Mammalogy 23:12–18.
- BARTOŃ, K. 2019. Package 'MuMIn': multi-model inference. Version 1.43.15. https://CRAN.R-project.org/package=MuMIn. Accessed 7 December 2019.
- BERGSTROM, B. J. 1988. Home ranges of three species of chipmunks (*Tamias*) as assessed by radiotelemetry and grid trapping. Journal of Mammalogy 69:190–193.
- BEST, T. L., S. L. BURT, AND J. L. BARTIG. 1994. *Tamias quadrivittatus*. Mammalian Species 466:1–7.
- BLAKE, J. M., A. C. MITCHELL, Z. SHEPHARD, G. BALL, S. CHAVARRIA, AND K. R. DOUGLAS-MARTIN. 2020. Assessment of soil and water resources in the Organ Mountains-Desert Peaks National Monument, New Mexico. U.S. Geological Survey Scientific Investigations Report 2019-5142. doi:10.3133/sir20195142.
- BLOCK, W. M., AND D. M. FINCH. 1997. Songbird ecology in south-western ponderosa pine forests: a literature review. General Technical Report RM-GTR-292. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experimental Station. Fort Collins, Colorado.
- BONHAM, C. D., D. E. MERGEN, AND S. MONTOYA. 2004. Plant cover estimation: a contiguous Daubenmire frame. Rangelands 26:17–22.
- Bowyer, R. T., AND J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244–257.
- BOYCE, M. S., P. R. VERNIER, S. E. NIELSEN, AND F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 57:281–300.
- Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of American Statistical Association 88:9–25.
- Brzeziński, M., J. Jedlikowski, and E. Komar. 2019. Space use, habitat selection and daily activity of water voles *Arvicola amphibius* co-occuring with the invasive American mink *Neovison vison*. Folia Zoologica 68:21–28.
- BURGIN, C. J., COLELLA, J. P., KAHN, P. L., AND UPHAM, N. S. 2018. How many species of mammals are there? Journal of Mammalogy 99:1–11.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag. New York.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.
- DICK-PEDDIE, W. A., AND W. H. MOIR. 1970. Vegetation of the Organ Mountains, New Mexico. Science Series No. 4, Colorado State University Range Science Department. Fort Collins, Colorado.
- DILTS, T. E. 2015. Topography tools for ArcGIS 10.1. University of Nevada Reno. http://www.arcgis.com/home/item.html?id=b13b3b 40fa3c43d4a23a1a09c5fe96b9. Accessed 7 December 2019.
- Dussault, C., J. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.
- ECOLOGICAL SOFTWARE SOLUTIONS LLC. 2019. Location of a signal. Ver. 4.0. Ecological Software Solutions LLC. Hegymagas, Hungary.

- ESRI. 2019. ArcMap. Ver. 10.7.1. Environmental System Research Institute, Inc. Redlands, California.
- FOX, J., AND S. WEISBERG. 2019. An R companion to applied regression. 3rd ed. SAGE Publications, Inc. Thousand Oaks, California.
- Frey, J. K., AND D. A. KOPP. 2013. Habitat suitability model for the Organ Mountains chipmunk. Final report, Share with Wildlife Program, Conservation Sciences Division, New Mexico Department of Game and Fish. Santa Fe.
- Garson, G. 2016. Logistic regression: binomial and multinomial. Statistical Associates Publishers. Asheboro, North Carolina.
- GEIER, A. R., AND L. B. BEST. 1980. Habitat selection by small mammals of riparian communities: evaluating effects of habitat alterations. Journal of Wildlife Management 44:16–24.
- GILLIES, C. S., ET AL. 2006. Application of random effects to the study of resource selection by animals. The Journal of Animal Ecology 75:887–898.
- HAINES, A. M., F. HERNANDEZ, S. E. HENKE, AND R. L. BINGHAM.
  2006. A method for determining asymptotes of home-range area curves. Pp. 489–498 in Gamebird (S. B. Cederbaum, B. C. Faircloth, T. M. Terhune, J. J. Thompson, and J. P. Carroll, eds.). Warnell School of Forestry and Natural Resources. Athens, Georgia.
- HALL, E. R. 1981. The mammals of North America. 2nd ed. Wiley. New York.
- HALL, L. S., P. R. KRAUSMAN, AND M. L. MORRISON. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.
- HARMON, H. E., AND J. SEXTON. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. LTER Network Office. Seattle, Washington.
- HARRIS, S., W. J. CRESSWELL, P. G. FORDE, W. J. TREWEHELLA, T. WOOLLARD, AND S. WRAY. 1990. Home-range analysis using radio-tracking data: a review of problems and technique particularly as applied to the study of mammals. Mammal Review 20:97–123.
- HELLER, H. C., AND T. L. POULSON. 1970. Circannian rhythms—
  II. Endogenous and exogenous factors controlling reproduction and hibernation in chipmunks (*Eutamias*) and ground squirrels (*Spermophilus*). Comparative Biochemistry and Physiology 33:357–383.
- HIRSHFIELD, J. R. 1975. Reproduction, growth and development of two species of chipmunks: *Eutamias panamintus* and *Eutamias palmeri*. M.Sc. thesis, University of Nevada, Las Vegas. Las Vegas.
- HUTTO, R. J. 1985. Habitat selection by nonbreeding, migratory land birds. Pp. 455–476 in Habitat selection in birds (M. L. Cody, ed.). Academic Press. Orlando, Florida.
- JAMES, G., D. WITTEN, T. HASTIE, AND R. TIBSHIRANI. 2014. An introduction to statistical learning: with applications in R. Springer Science and Business Media. New York.
- JENKINS, J. M. A., D. B. LESMEISTER, AND R. J. DAVIS. 2019. Resource selection analysis. Pp. 199–215 in Quantitative analyses in wildlife (L. A. Brennan, A. N. Tri, and B. G. Marcot, eds.). Johns Hopkins University Press. Baltimore, Maryland.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.
- JOHNSON, K., K. SCORE, H. SMITH, L. DELAY, AND P. MEHLHOP. 1998. Post-fire ecological studies in the Organ Mountains. Monitoring sensitive species and vegetation. Volume 2 animals. Birds, mammals, and snails part 1. Unpublished Report: Environmental Resources Branch, US Army Corps of Engineers. Fort Worth, Texas.

- KIE, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Animal Biotelemetry 1:1–12.
- KRAUSMAN, P. R. 1999. Some basic principles of habitat use. Idaho Forest, Wildlife and Range Experiment Station Bulletin 70:85–90.
- LONG, R. A., J. D. Muir, J. L. Rachlow, and J. G. Kie. 2009. A comparison of two modeling approaches for evaluating wildlifehabitat relationships. Journal of Wildlife Management 73:294–302.
- LOWREY, C., AND K. LONGSHORE. 2013. Habitat interaction between two species of chipmunk in the Basin and Range Province of Nevada. Western North American Naturalist 73:129–136.
- LOWREY, C., K. LONGSHORE, B. RIDDLE, AND S. MANTOOTH. 2016. Ecology, distribution, and predictive occurrence modeling of Palmer's chipmunk (*Tamias palmeri*): a high-elevation small mammal endemic to the Spring Mountains in southern Nevada, USA. Journal of Mammalogy 97:1033–1043.
- MANLY, B. F. J., L. McDonald, D. L. Thomas, T. L. McDonald, AND W. P. ERICKSON. 2002. Resource selection by animals. Kluwer Academic Publishers. Dordrecht, The Netherlands.
- Manning, A. D., D. B. Lindenmayer, and H. A. Nix. 2004. Continua and umvelt: novel perspectives on viewing landscapes. Oikos 104:621–628.
- MARGALEF, R. 1957. Information theory in ecology. General Systems 3:37–71.
- MAYOR, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.
- McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.
- McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.
- MEYER, C., H. KREFT, R. GURALNICK, AND W. JETZ. 2015. Global priorities for an effective information basis of biodiversity distributions. Nature Communications 6:8221.
- MEYER, C. B., AND W. THUILLER. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions 12:288–297.
- MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.
- Moir, W. H., AND J. A. Ludwig. 1979. A classification of spruce-fir and mixed conifer habitat types of Arizona and New Mexico. USDA Forest Service Research Paper RM-207. Rocky Mountain Forest and Range Experiment Station. Fort Collins, Colorado.
- MORELLI, T. L., ET AL. 2016. Managing climate change refugia for climate adaptation. PLoS ONE 11:e0159909.
- MORRIS, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.
- MORRISON, M. L., B. G. MARCOT, AND R. W. MANNAN. 2006. Habitats through space and time: heterogeneity and disturbance. Pp. 254–281 in Wildlife-habitat relationships: concepts and applications (M. L. Morrison, B. G. Marcot, and R. W. Mannan, eds.). 3rd ed. Island Press. Washington, D.C.
- NETER, J., M. H. KUTNER, W. WASSERMAN, C. J. NACHTSHEIM, AND J. NETER. 1996. Applied linear statistical models. 4th ed. McGraw-Hill Publishers. New York.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38:541–545.
- New Mexico Department of Game and Fish. 2018. Threatened and endangered species of New Mexico, 2018 biennial review. New Mexico Department of Game and Fish. Santa Fe.

- ODOM, E. P., AND E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. The Auk 72:128–137.
- Patterson, B. D. 1979. Status of the Organ Mountains population of *Eutamias*. Final report. New Mexico Department of Game and Fish. Santa Fe.
- Patterson, B. D. 1980. A new subspecies of *Eutamias quadrivittatus* (Rodentia: Sciuridae) from the Organ Mountains. Journal of Mammalogy 61:455–464.
- PEEK, J. M., M. D. SCOTT, L. J. NELSON, D. J. PIERCE, AND L. L. IRWIN. 1982. Role of cover in habitat management for big game in Northwestern United States. Transactions of North American Wildlife and Natural Resources Conference 47:363–373.
- Perkins-Taylor, I., and J. K. Frey. 2018. Ecological factors associated with site occupancy of an endemic chipmunk. Journal of Wildlife Management 82:1466–1477.
- Perkins-Taylor, I. E., and J. K. Frey. 2020. Predicting the distribution of a rare chipmunk (*Neotamias quadrivittatus oscuraensis*): comparing MaxEnt and occupancy models. Journal of Mammalogy 101:1035–1048.
- PRISM CLIMATE GROUP. 2019. PRISM climate data. http://www.prism.oregonstate.edu/. Accessed 7 December 2019.
- RETTIE, W. J., AND F. MESSIER. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.
- RIVIECCIO, M., B. C. THOMPSON, W. R. GOULD, AND K. G. BOYKIN. 2003. Habitat features and predictive habitat modeling for the Colorado chipmunk in southern New Mexico. Western North American Naturalist 63:479–488.
- Schooley, R. L., and C. R. McLaughlin. 1992. Observer variability in classifying forested habitat from aircraft. Northeast Wildlife 49:10–16.
- Schulte-Hostedde, A. I., J. S. Millar, and H. L. Gibbs. 2002. Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. Evolution 56:2519–2529.
- SHANNON, C. E., AND W. WEAVER. 1948. The mathematical theory of communication. University of Illinois Press. Urbana.
- SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.
- SULLIVAN, R. M. 1996. Genetics, ecology, and conservation of montane populations of Colorado chipmunks (*Tamias quadrivittatus*). Journal of Mammalogy 77:951–975.
- THOMAS, D. L., AND E. J. TAYLOR. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.

- THOMPSON, C. M., AND K. McGARIGAL. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landscape Ecology 17:259–267.
- UBONI, A., D. W. SMITH, D. R. STAHLER, AND J. A. VUCETICH. 2017. Selecting habitat to what purpose? The advantage of exploring the habitat-fitness relationship. Ecosphere 8:1–13.
- UNITED STATES DEPARTMENT OF AGRICULTURE, FARM SERVICE AGENCY. 2015. National Agriculture Imagery Program. Aerial Photography Field Office. Salt Lake City, Utah.
- UNITED STATES DEPARTMENT OF AGRICULTURE, NATURAL RESOURCES CONSERVATION SERVICE. 2019. The PLANTS database. National Plant Data Team. Greensboro, North Carolina. https://plants.usda.gov. Accessed 7 December 2019.
- UNITED STATES GEOLOGICAL SURVEY. 2017. 1 meter digital elevation models (DEMs) USGS National Map 3DEP downloadable data collection: U.S. Geological Survey. https://apps.nationalmap.gov/. Accessed 7 December 2019.
- UNITED STATES GEOLOGICAL SURVEY. 2019. National Hydrography Dataset (ver. USGS National Hydrography Dataset Best Resolution (NHD) 2001 (published 20191002)). https://apps.nationalmap.gov/. Accessed 7 December 2019.
- Vermote, E., C. Justice, M. Claverie, and B. Franch. 2016. Preliminary analysis of the performance of the Landsat 8/OLI land surface reflectance product. Remote Sensing of Environment 185:46–56.
- WALBRIDGE, S., N. SLOCUM, M. POBUDA, AND D. J. WRIGHT. 2018. Unified geomorphological analysis workflows with benthic terrain modeler. Geosciences 8:94.
- Weiss, A. D. 2006. Topographic position and landforms analysis. http://www.jennessent.com/downloads/tpi-poster-tnc\_18x22.pdf. Accessed 7 December 2019.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife tracking data. Academic Press. San Diego, California.
- WITHEY, J. C., T. D. BLOXTON, AND J. M. MARZLUFF. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. Pp. 45–69 in Radio tracking and animal populations (J. Millspaugh and J. M. Marzluff, eds.). Academic Press. San Diego, California.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.
- ZAR, J. H. 1986. Biostatistical analysis. 2nd ed. Prentice Hall. Englewood Cliffs, New Jersey.

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