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Research Article

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Multiscale habitat selection of an imperiled subspecies of Least Chipmunk (*Neotamias minimus*): when a generalist is really a specialist

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Abstract

Habitat loss is a leading cause of species endangerment, yet information about habitat is anecdotal for most mammals. The Least Chipmunk (*Neotamias minimus*) is the most widespread chipmunk in North America and is purportedly a habitat generalist, which should buffer it against habitat loss. However, the southernmost subspecies (Peñasco Least Chipmunk [*N. m. atristriatus*]) in the Sacramento Mountains of southern New Mexico has declined significantly and has been proposed for listing as endangered under the Endangered Species Act. The declining subspecies presents a conundrum because it could be either a habitat generalist experiencing declines due to factors other than habitat loss or a habitat specialist experiencing habitat loss. We investigated multiscale habitat selection by *N. m. atristriatus* at the landscape, home-range, and within-home-range scales. We hypothesized that habitat selection by the Peñasco Least Chipmunk would be influenced by plant community type, topography, disturbance, ecological edge, and understory structure. For the landscape scale we conducted surveys using remote cameras and tested predictions using occupancy models. At the home-range and within-home-range scales, we obtained used locations via radiotelemetry and tested predictions by comparing habitat features at used and available locations. At all 3 scales, chipmunks selected for open stands of relatively large trees interspersed with meadows containing low cover provided by shrubs. This specialized vegetation structure was principally provided by a distinctive Engelmann Spruce (*Picea engelmannii*)–Gooseberry Currant (*Ribes montigenum*) plant community. Chipmunks avoided disturbance including burnt forests, ski runs, and roads. We conclude that the Peñasco Least Chipmunk is a habitat specialist across multiple scales and that the loss of its required habitat has been the principal cause of its decline.

Key words: habitat selection, habitat specialist, multiscale, niche breadth, *Neotamias minimus atristriatus*, Peñasco Least Chipmunk.

For species of conservation concern, an understanding of habitat requirements is necessary to restore habitat and to prevent further habitat loss. Importantly, species with narrow habitat requirements are often more susceptible to declines related to habitat loss, while habitat generalists are usually buffered (Marvier et al. 2004; Dennis et al. 2011; Habel and Schmitt 2012), and so classifying a species habitat selection on the specialist-generalist continuum can inform management priorities. Additionally, if a species is declining but there is no evidence of habitat loss, this might point to other threats (e.g., poaching, disease, pollutants, and natural disasters; Scheele et al. 2017). However, for many mammalian species, existing habitat descriptions are anecdotal (Schweiger et al. 2021) and generally do not account for detectability (Kellner and Swihart 2014), observer bias in search patterns (Hortal et al. 2008), or observer perception of habitat features (Van Dyck 2012). Rigorous studies of habitat selection are key for understanding species endangerment, making management plans, and recovering species of concern.

The Least Chipmunk (*Neotamias minimus*) is the most widespread chipmunk species in North America, yet literature describing their habitat is almost entirely anecdotal. The species occurs from west-central Yukon Territory south to Arizona and New Mexico, west to California, and as far east as southeastern Ontario (Verts and Carraway 2001). The Least Chipmunk is reported to occur in many biotic communities, including alpine tundra (Sheppard 1971), subalpine forests (Bergstrom and Hoffmann 1991), ponderosa pine forests (Bailey 1931; Conley 1970), pinyon-juniper woodland (Root et al. 2001), and sagebrush steppe (Zeveloff 1988). They are described as associated with a wide range of environmental factors, including rocky meadows (Findley and Negus 1953), dense upland forests (Manville 1949), alpine fell fields (Sheppard 1971), shrubs and forbs (Negus and Findley 1959), grasslands (Dood 1980), rocky cliffs (Whitaker and Hamilton 1998), talus slopes (Chappell 1978), forest edges (Fitzgerald et al. 1994), ski slopes (Hadley and Wilson 2004), and transmission line rights-of-way (Peterson et al. 2017). Given

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this array of habitat associations, the species was characterized as a "cosmopolitan generalist" with "annual weed mode adaptation" (States 1976). However, these purported habitat associations are based on anecdotal reports that depend on a description of places where the species has been sighted. In fact, we are aware of only 3 studies that have explicitly investigated habitat selection by the Least Chipmunk by comparing the use of resources to their availability or to nonuse (Meredith 1976; Root et al. 2001; Rodhouse et al. 2010). The paucity of rigorous habitat selection studies across different community types and scales sheds doubts on the characterization of the species as a generalist.

The Peñasco Least Chipmunk (*N. m. atristriatus*) is restricted to high elevations of the Sacramento Mountains complex in south-central New Mexico (Sullivan 1985) and is the southernmost subspecies of Least Chipmunk (Verts and Carraway 2001). It is genetically distinctive and has been isolated from other populations of least chipmunks for ca 190,000 years (Hope and Frey 2021; Puckett et al. 2021). The Peñasco Least Chipmunk co-occurs with a similar appearing chipmunk, the Gray-footed Chipmunk (*N. canipes*), adding complexity to species identification and modeling (McKibben and Frey 2021; McKibben et al. 2023). The Peñasco Least Chipmunk has apparently experienced a sharp range contraction over the last century and is proposed for listing as endangered under the Endangered Species Act (USFWS 2021). Based on ecological settings of historical captures and their prevalence across the range, it is likely that the subspecies was formerly widespread (Frey and Boykin 2007). The Peñasco Least Chipmunk was common in open Ponderosa Pine (*Pinus ponderosa*) forests and at the edges of meadows with grain fields in the Ponderosa Pine zone (Bailey 1931) and ranged from a glacial cirque above tree line (Conley 1970; Sullivan 1985) to as low as 2,070 m where Ponderosa Pine forest grades into Pinyon Pine (*Pinus edulis*)-juniper (*Juniperus* spp.) woodland (Conley 1970; Frey and Boykin 2007), though it was uncommon or absent in the more dense mixed coniferous forest at middle elevations (Frey and Boykin 2007). However, more recent surveys have failed to document the Peñasco Least Chipmunk throughout much of its historical range. The Peñasco Least Chipmunk has not been verified in the southern Sacramento Mountains subrange since 1966 despite intensive sampling efforts and is only known to persist in the northern Sierra Blanca subrange of the Sacramento Mountains (USFWS 2018). Given the wide range of *N. minimus* and their apparent tolerance for a variety of environmental conditions, this local range contraction presents a conundrum as the Peñasco Least Chipmunk could be either a habitat generalist experiencing declines due to factors other than habitat loss or a habitat specialist experiencing habitat loss.

Our goal was to investigate habitat selection by the Peñasco Least Chipmunk in order to provide context for the conservation of the subspecies and an improved understanding of habitat requirements for the most widespread chipmunk in North America. We considered selection across 3 hierarchical scales (sensu Johnson 1980): landscape, home-range, and within-home-range. We hypothesized that multiscale habitat selection by the Peñasco Least Chipmunk is influenced by 5 general environmental factors: biotic community type, topography, disturbance, edge, and understory structure. While many habitat selection studies test different hypotheses at different scales of selection, we tested each of the 5 environmental factors at every scale of selection (as much as was logical and possible). This approach allowed us to investigate the influence of each factor across scales and to identify factors that were important across all scales. For biotic community type, we predicted: (i) avoidance of dense forests, i.e., mixed coniferous forests predominated by Douglas-fir (*Pseudotsuga menziesii*) or White Fir (*Abies concolor*) and Corkbark Fir (*Abies lasiocarpa* var. *arizonica*); Bailey (1931); Sheppard (1971); Frey and Boykin (2007); (ii) selection for deciduous forests (Turner 1974); (iii) selection for talus fields (Chappell 1978); and (iv) selection for meadows (Vaughan 1974). For topography, we predicted selection for higher elevations (Sheppard 1971) and selection for areas with a gentle slope and less rugged terrain (Bergstrom and Hoffmann 1991). Least chipmunks have been documented using disturbed areas (Hadley and Wilson 2004; Storm and Choate 2012); therefore, we predicted selection for ski runs and for areas with dead trees (e.g., due to bark beetles or wildfire). Least chipmunks have been associated with edge communities between forests and grasslands (Sureda and Morrison 1999; Nagorsen 2004). Edges can either be hard distinctions between 2 community types, or they can grade gradually with an intermingling of the 2 types; the literature suggests that least chipmunks may occur in graded (i.e., intermingled) edges (Meredith 1976; Nagorsen 2004). Therefore, we predicted: (i) selection for ecotones, or the area along the boundary between large patches of forests and large patches of herbaceous cover; (ii) selection for intermingled subalpine edges, where there is a mixing of subalpine tree cover and herbaceous cover; and (iii) selection for intermingled small-scale edges, or areas where trees and herbaceous cover are mixed at a small spatial scale, such as in meadows. Because least chipmunks are often reported from areas with understory cover and rocks (Carleton 1966; Vaughan 1974; Sullivan 1985; Bergstrom and Hoffmann 1991), we predicted selection for low cover provided by rocks, grasses, forbs, and shrubs.

Materials and methods.

Study area and methods overview.

Our study area was above 2,500 m in the Sierra Blanca subrange of the Sacramento Mountains in the Lincoln National Forest and was bounded on the south by the Mescalero Apache Reservation, New Mexico, United States (105°48′56.53″W, 33°23′48.41″N; Fig. 1). The higher elevations of the Sierra Blanca subrange are within the White Mountains Wilderness Area (Alexander et al. 1984) and receive light recreational use. Ski Apache, a developed ski area at the southern border of the wilderness area, is heavily trafficked by recreators during winter and summer months. In 2012, a stand-replacing wildfire burned 17,939 ha of forest in the subrange (McCaffrey et al. 2013). Above ~2,980 m, the dominant biotic communities are subalpine coniferous forests predominated by Engelmann Spruce (*Picea engelmannii*), Corkbark Fir, and subalpine grasslands (Moir 1967; Dye and Moir 1977). Below ~2,980 m is montane coniferous forest predominated by Douglas-fir, White Fir, Ponderosa Pine (*Pinus ponderosa*), Quaking Aspen (*Populus tremuloides*), Gambel Oak (*Quercus gambelii*), and coniferous woodland predominated by Two-needle Pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.; Dick-Peddie 1993).

We evaluated habitat selection at 3 hierarchical scales of selection (sensu Johnson 1980): landscape (first order), home-range (second order), and within-home-range (third order; Fig. 1). The analysis of landscape scale occurred across the study area, while analyses at the home-range and within-home-range scales occurred in the vicinity of Lookout Mountain and adjacent Ice Springs. We used the 5 general categories of environmental factors that we hypothesized would influence habitat selection (biotic community type, topography, disturbance, edge, and understory structure; Table 1) to identify which variables to test and to ensure that we tested the same concepts across the 3 scales. Within categories, we chose variables that the literature indicated might explain Least Chipmunk habitat selection. Field methods were approved by the New Mexico State University Institutional Animal Care and Use Committee (number 2018-005).

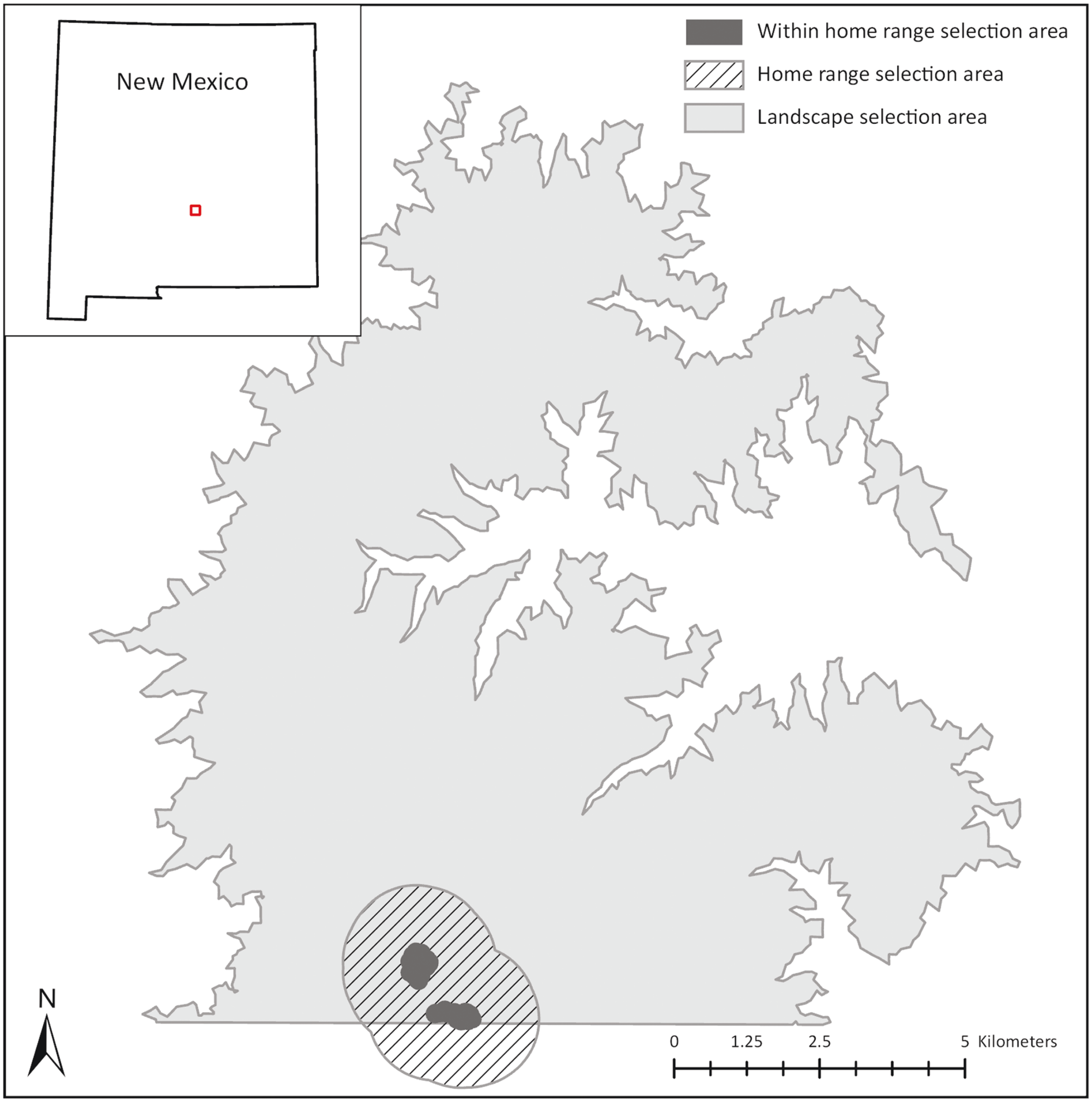

Fig. 1. Location of the study area for 3 scales of habitat selection in the Sierra Blanca subrange of the Sacramento Mountains, New Mexico, United States.

Landscape scale.

To investigate the landscape scale, we conducted surveys for least chipmunks using remote camera-traps and assessed habitat selection using occupancy models, which compare sites where the animal is detected to sites where it is not detected while accounting for imperfect detection (Mackenzie et al. 2002). We conducted a pilot study from June to October 2018 to compare survey techniques and estimate detection probabilities to inform survey design. We conducted the occupancy study from May to October 2019. Because the pilot study suggested that the distribution of chipmunks was spatially clustered, we followed an adaptive cluster sampling design, which is a two-stage sampling approach in which sampling begins at a random set of sites followed by additional effort in areas near sites with detections or sites deemed likely to have detections (Thompson 1990; Brown et al. 2013). The first stage of sampling occurred from 2 June to 1 August, during which we surveyed 124 random sites that were divided evenly between high (>2,800 m) and low (<2,800 m) elevation strata. We also stratified by vegetation types potentially used by chipmunks (shrub predominant, sparse live coniferous, sparse dead coniferous, deciduous, edge, other) within each elevation zone based on a preliminary map of landcover in the study area created by McKibben (2022). Finally, sites were placed within 200 m of roads and backcountry trails to facilitate access. We required a minimum distance of 160 m between survey sites, which is approximately the diameter of the average home range of least chipmunks reported in the literature (Martinsen 1968; Bergstrom and Hoffmann 1991). During the second stage of sampling, we surveyed 115 random sites from 8 August to 7 October within 3 of the highest-elevation peaks in the study area: Lookout Mountain, Nogal Peak, and Monjeau Peak. We did not include 2 other high-elevation peaks (Buck Mountain or White Horse Hill) because surveys in these areas during the 2018 pilot study failed to verify the presence of

Table 1. Variables used for modeling multiscale habitat selection by the Peñasco Least Chipmunk (*Neotamias minimus atristriatus*) in the Sierra Blanca subrange of the Sacramento Mountains, New Mexico, United States, 2019. Variables are grouped by category of environmental factor.

Category	Landscape scale	Home-range scale	Within-home-range scale
Biotic community	Community[a]—Categorical variable with five community types		
	Montane[a]—Categorical variable indicating presence/absence in montane coniferous forest	Montane coniferous tree cover[b]—Percent montane coniferous tree cover (coniferous cover not classified as Corkbark Fir or Englemann Spruce) within 80 m radius, calculated from cover class map	
	Corkbark Fir predominant[a]—Categorical variable indicating presence/absence in Corkbark Fir (*Abies lasiocarpa* var. *arizonica*) predominant forest	Subalpine tree cover[b]—Percent subalpine coniferous tree cover (coniferous cover classified as Corkbark Fir or Englemann Spruce) within 80 m radius calculated from cover class map	
	Engelmann Spruce predominant[a]—Categorical variable indicating presence/absence in Engelmann Spruce (*Picea engelmannii*) predominant forest		
	Open[a]—Categorical variable indicating area with no trees	Herbaceous cover[b]—Percent herbaceous cover within 80 m radius calculated from cover class map	
Topography	Elevation[b]—Mean elevation at 10 m spatial resolution		
		Slope[b]—Mean slope of the terrain within 80 m	
Disturbance	Dead tree count[a]—Count of dead trees along transects	Dead tree cover[b]—Percent dead tree cover within 80 m radius calculated from cover class map	
		Human modified[b]—Hand-digitized categorical variable indicating presence/absence of ski runs and roads	
			Small-diameter spruce count[a]—Count of Engelmann Spruce < 30cm diameter at breast height (DBH) along transects
			Large-diameter spruce count[a]—Count of Engelmann Spruce > 30cm DBH along transects
Edge	Ecotone[b]—Categorical variable indicating presence/absence in 80 m wide ecotone between contiguous conifer tree cover and contiguous herbaceous cover from cover class map	Ecotone[b]—Categorical variable indicating presence/absence in 80 m wide ecotone between contiguous conifer tree cover and contiguous herbaceous cover from cover class map	
	Subalpine edge[b]—Interaction between subalpine coniferous tree cover and herbaceous cover within 80 m radius calculated from cover class map	Subalpine edge[b]—Interaction between subalpine tree coniferous cover and herbaceous cover within 80 m radius calculated from cover class map	
	Small-scale edge[a]—Interaction between count of trees along transects and mean % herbaceous cover	Small-scale edge[b]—Interaction between tree cover and herbaceous cover within 20 m radius calculated from cover class map	Small-scale edge[a]—Interaction between count of trees along transects and mean % herbaceous cover

Table 1. Continued

Category	Landscape scale	Home-range scale	Within-home-range scale
Understory structure	Visual obstruction[a]—Mean % visual obstruction below 1 m		Visual obstruction[a]—Mean % visual obstruction below 1 m
	Herbaceous cover[a]—Mean % herbaceous cover		Herbaceous cover[a]—Mean % herbaceous cover
	Shrub cover[a]—Mean % deciduous shrub cover	Shrub cover[b]—Percent deciduous shrub cover within 20 m radius calculated from cover class map	Gooseberry cover[a]—Mean % Gooseberry Currant (*Ribes montigenum*) cover
	Mixed understory cover[a]—Interaction between mean % herbaceous and shrub cover	Mixed understory cover[b]—Interaction between herbaceous cover and shrub cover within 20 m radius calculated from cover class map	Mixed understory cover[a]—Interaction between mean % herbaceous and gooseberry cover
			Low conifer cover[a]—Mean % conifer limb cover below 1 m
			Boulder count[a]—Count of boulders 0.5 to 5 m width along transects

[a] Collected in the field. We collected landscape-scale field data along three 20-m transects and within-home-range scale data along four 10-m transects.
[b] Collected from a GIS.

least chipmunks. Within each of the core areas, we randomly distributed the maximum number of sites possible while requiring a minimum distance of 80 m between survey sites and sampled a subset of the sites.

We followed the methods of McKibben and Frey (2021) to deploy a single Reconyx PC800 HyperFire camera (Reconyx, Holmen, Wisconsin) at each site. We mounted cameras vertically, approximately 45 cm above the ground, with a PVC frame and placed a peanut butter scent lure in a PVC tube in front of the camera to encourage chipmunks into the field of view. The cameras had a 1-m focal distance and were set to take 3 photographs a second apart for each motion activation. Results from the pilot study suggested that detection probability was higher on days with rain and on days with cooler temperatures, such that 3 survey days would be sufficient to achieve a 90% likelihood of at least 1 detection given that a site was occupied under 81% of the weather conditions observed at the Sierra Blanca weather station in 2018 (Menne et al. 2012; McKibben 2022; Supplementary Data SD1). Consequently, we deployed cameras for at least 3 days. While in the field, we monitored daily weather conditions, and during warm and dry periods (no precipitation and maximum temperatures >22 °C), when detection probabilities were predicted to be lower, we extended survey periods to 5 to 6 days. We considered each 24-h period as a sampling occasion.

We differentiated photographs of the Peñasco Least Chipmunk from the Gray-footed Chipmunk based on pelage characteristics described in McKibben and Frey (2021). Three trained observers reviewed all photographs of chipmunks, and each observer assigned a numeric "confidence-rank" with their identification from: 1 = no confidence; 2 = not very confident; 3 = somewhat confident; to 4 = very confident (McKibben and Frey 2021). We considered an identification to be "verified" if all observers agreed on the identification and reported a confidence rank of 4. Any chipmunk detections that did not meet the criteria to be "verified" were considered nondetections, which is a valid strategy for dealing with false positive detection errors, given an adequate sample size of verified detections (McKibben et al. 2023).

At each camera site we used a geographic information system (GIS) to create variables for ecotone, subalpine edge, and elevation within an 80-m radius. To create the ecotone and subalpine edge variables, we first created a cover class map of the study area by classifying the USGS National Agriculture Imagery Program (NAIP) data using the Support Vector Machine classifier in the Image Analyst extension for ArcGIS Pro (Tso and Mather 2009; Paneque-Gálvez et al. 2013; USGS 2016; ESRI 2017). To classify the map, we identified and recorded the location of trees, shrubs, forbs, grasses, logs, and abiotic ground covers using handheld GPS units on an adlib basis during fieldwork throughout the study area. We used the field-collected cover data to create a training dataset, which we then used to classify the NAIP imagery, creating a cover class map. The cover class map had a 1-m spatial resolution and included 7 cover classes: (i) dead (dead tree, stump, or log); (ii) subalpine (Engelmann Spruce or Corkbark Fir); (iii) montane (Douglas-fir, White Fir, pine [*Pinus* spp.], or juniper [*Juniperus* spp.]); (iv) herbaceous (grass or forb); (v) shrub/deciduous (gooseberry/currant [*Ribes* spp.], New Mexico Locust [*Robinia neomexicana*], Gambel Oak, Quaking Aspen, or unknown shrub or deciduous tree); (vi) rock (talus or bedrock); and (vii) dirt (bare dirt). Ecotone was a categorical variable for presence/absence in an 80-m wide buffer on either side of forest/grassland edges, which was defined as the border of patches of contiguous coniferous tree cover that fell within 40 m of patches of contiguous herbaceous cover. Subalpine edge was the interaction between subalpine coniferous tree cover and herbaceous cover, which mathematically describes the extent of intermingling between the 2 cover types—we predicted that chipmunks would avoid areas with high subalpine tree cover and areas with high herbaceous cover, but select areas with a mixture of both. We used a 10-m digital elevation model raster available from The National Map (USGS 2017) to estimate elevation at each camera site.

At each camera site, we used environmental data collected in the field on 20-m radius plots to create variables for dead tree count, small-scale edge, visual obstruction, shrub cover, herbaceous cover, mixed understory cover, and 5 biotic community types. Along 3 equally spaced belt transects radiating from each camera site, we identified and counted live and dead trees within 1 m, we measured visual obstruction at the site center and every 10 m along each transect using a cover pole modified from Griffith and Youtie (1988), and we recorded ground cover at 1 m from the camera site and then every 2 m using a 20 × 50 cm Daubenmire plot and classing categories (Daubenmire 1959). Dead tree count was the total number of dead trees along belt transects. Visual obstruction was the mean percent of 10-cm bands on cover poles below 1m that were at least 25% covered, averaged across all readings in the plot. Shrub cover was the percent shrub cover of all shrub species averaged across Daubenmire frames. Herbaceous cover was the percent herbaceous cover averaged across Daubenmire frames. Mixed understory cover was the interaction between shrub and herbaceous cover from Daubenmire frames, which mathematically describes a mix of the 2 cover types. The small-scale edge was the interaction between the total count of live trees along belt transects and the mean percent herbaceous cover across Daubenmire frames, which mathematically describes a mix of trees and herbaceous ground cover. Based on descriptions of biotic communities in the Lincoln National Forest (Moir 1967; Alexander et al. 1984; USFS 1997; Ryniker et al. 2006), we used our belt transect data and ground cover data to define 5 biotic community types: dead, montane, Corkbark Fir predominant, Engelmann Spruce predominant, and open.

We defined the detection covariates scent lure age (days since scent lure deployment), precipitation (categorical variable indicating if it rained on a survey day, as recorded at the Sierra Blanca weather station; Menne et al. 2012), maximum daily temperature (recorded on iButtons at each camera site), and visual obstruction at camera site (average percent of bands covered for the 4 cover pole measurements at the site center).

We created an occupancy model to represent landscape-scale habitat selection based on 14 occupancy variables and 4 detection variables (Supplementary Data SD1, Table SD1.1). Following the methods of Morin et al. (2020), we constructed occupancy and detection submodels separately (i.e., varying the occupancy portion while holding detection constant and vice versa). We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) to identify supported submodels, which were those with $\Delta AIC_c < 10$ that did not include uninformative parameters (Arnold 2010; Morin et al. 2020). We tested 15 detection submodels, holding occupancy constant, and we tested 128 occupancy submodels, holding detection constant. We combined all possible pairs of supported occupancy and detection submodels into a final set of 21 models. Additionally, we constructed a model set using only variables collected from a GIS, used the same model selection protocol (Supplementary Data SD1, Tables SD1.2 and SD1.3), and used the top model to create a predictive map of the area selected on the landscape scale.

Home-range scale.

To investigate selection at the home-range scale, we fitted chipmunks with radio collars, relocated the chipmunks using radiotelemetry, and assessed habitat selection using logistic regression models to compare used locations to available locations (Northrup et al. 2022). We captured individual chipmunks using Sherman live traps (model LFATDG; H. B. Sherman, Tallahassee, Florida) baited with oats and peanut butter. We identified all live-captured chipmunks using a suite of morphological characters (Frey 2010). We fit a 1.6-g or 1.7-g radio collar (model BD-2C; Holohil Systems, Carp, Ontario, Canada) to chipmunks that did not appear stressed and appeared to be in healthy physical condition. We did not affix radio collars to chipmunks weighing less than 35 g, so the collar never exceeded the recommended 5% of the body weight of the chipmunk (Sikes et al. 2016). In total, we fit radio collars to 24 chipmunks. Seven of the chipmunks lost their collars, and one of the collars failed and ceased to transmit (see McKibben 2022).

A team of 2 researchers, each with a model R-1000 telemetry receiver (Communications Specialists, Orange, California) attached to a 3-element Yagi antenna (Wildlife Materials International, Inc., Murphysboro, Illinois) located each chipmunk by homing to within 10 to 30 m. When both researchers agreed on the location of the chipmunk, one researcher approached the site to mark the exact location with a handheld GPS device. We searched for chipmunks approximately every other week from 30 May to 25 September 2019, and we located each chipmunk approximately once every 2 search days for the duration of the battery life of the radio-transmitter. We relocated 16 chipmunks at least once via radiotelemetry at a total of 208 locations ($\bar{x}$ = 13 locations/individual, standard errors = ±1.4).

We considered telemetry locations for individual chipmunks as used locations. To reduce autocorrelation, we spatially rarefied the used locations by 10 m ($n = 125$ after rarefication). We did not define availability at the individual level because we did not have sufficient location data to estimate individual home ranges (Haines et al. 2009; McKibben 2022). Instead, we defined the available area as the cumulative minimum convex polygon of all tracked chipmunks with a buffer the width of the maximum distance traveled by a collared chipmunk. This represented the distance a dispersing chipmunk might travel before establishing a home range. We randomly drew available locations from within the available area (Fig. 1).

At chipmunk locations ($n = 125$) and at available locations ($n = 375$), we used a GIS to create variables for montane coniferous tree cover, subalpine tree cover, herbaceous cover, dead tree cover, ecotone, subalpine edge, slope, small-scale edge, human-modified, shrub cover, and mixed understory cover. Following similar methods to the landscape scale, we first created a cover class map specific to the home-range study area (i.e., the available area). However, we did not have ground-truth data points that fell within montane coniferous forest within the study area. Therefore, we classified all montane and subalpine cover as coniferous, and we used the classifications from the landscape-scale cover map to differentiate montane coniferous and subalpine coniferous tree cover. Additionally, we differentiated deciduous shrub from deciduous tree cover based on height of the cover as recorded in the field. We used the cover class map to define cover variables. Montane coniferous tree cover was the percent montane coniferous tree cover (i.e., coniferous cover that was not classified as Corkbark Fir or Englemann Spruce). Subalpine tree cover was the percent subalpine coniferous tree cover (i.e., coniferous cover classified as Corkbark Fir or Englemann Spruce). The herbaceous cover was the percent herbaceous cover. Dead tree cover was the percent dead tree cover. Ecotone and subalpine edge were defined and created as for the landscape scale. We used a 10-m digital elevation model raster available from The National Map (USGS 2017) to estimate mean slope of the terrain. We manually digitized areas of previous forests that had been cut and meadows that had been modified for the construction of ski runs and roads to define the categorical variable human modified. We calculated continuous variables at 3 spatial scales (20, 40, and 80 m). We retained the spatial scale for each variable based on the lowest AIC_c value from univariate logistic regressions (McGarigal et al. 2016). We also included the variable small-scale edge (the interaction between tree cover and herbaceous cover calculated within 20 m, which mathematically describes a mix of the 2 cover types), even though this spatial scale did not have the lowest AIC_c value because we designed the interaction term to match edge variables at other scales of selection. If a variable exhibited perfect separation (i.e., a variable perfectly discriminated between used and available sites), we did not include it in our models.

We used a set of 11 predictor variables (Supplementary Data SD1, Table SD1.3) to create 108 statistical models. We used logistic regression models to compare used locations to available locations while including a random intercept for individual (Manly et al. 2002; Harrison et al. 2018). To fit models with a random intercept for individual without underestimating uncertainty in the parameters of interest, we used a maximum penalized likelihood approach, which is equivalent to assigning a Bayesian prior distribution to the variance parameters (Chung et al. 2013). We used the top model to predict the probability of use across the home-range selection area.

Within-home-range scale.

To investigate selection at the within-home-range scale, we used the same radiotelemetry location data and a use-availability study design with logistic regression models, including a random intercept for individual in a maximum penalized likelihood approach (Manly et al. 2002; Chung et al. 2013; Harrison et al. 2018). We considered a subset of telemetry locations as used locations and they were compared to a paired random available location drawn from within a 160-m radius, which approximated the diameter of a 2-ha home range reported in the literature; this distance represented the distance a chipmunk might regularly travel (Fig. 1; Martinsen 1968; Bergstrom and Hoffmann 1991).

At each used ($n = 78$) and paired available ($n = 78$) location, we used environmental data collected in the field on 10-m radius plots to create variables for the small-diameter spruce count, large-diameter spruce count, small-scale edge, visual obstruction, herbaceous cover, gooseberry cover, mixed understory cover, low conifer cover, and boulder count (Supplementary Data SD1, Table SD1.4). Along 4 equally spaced 2 m width belt transects radiating from each location, we counted boulders; counted trees, which we identified to species and assigned to 10-cm size classes; measured visual obstruction below 1 m at the site center and at the end of each transect using a cover pole modified from Griffith and Youtie (1988); and recorded ground cover every 2 m using a 20 × 50 cm Daubenmire plot and classing categories (Daubenmire 1959). Large-diameter spruce count was the count of Engelmann Spruce >30 cm diameter at breast height (DBH) along belt transects. Small-diameter spruce count was the count of Engelmann Spruce <30 cm DBH along belt transects. The small-scale edge was the interaction between the count of live trees along belt transects and the mean percent herbaceous cover, which mathematically describes a mix of the 2 cover types. Visual obstruction was the mean percent of bands on cover poles below 1 m that were at least 25% covered, averaged across all readings in the plot. The herbaceous cover was the mean percent herbaceous cover across Daubenmire frames. Gooseberry cover was the mean percent Gooseberry Currant (*Ribes montigenum*) cover across Daubenmire frames. Mixed understory cover was the interaction between herbaceous and gooseberry cover. Low conifer cover was the mean percent conifer cover across Daubenmire frames. Boulder count was the count of boulders (width 0.5 to 5 m) along transects. We used this set of 9 predictor variables (Supplementary Data SD1, Table SD1.4) to create 115 statistical models.

Model selection and validation.

For each scale of selection, we did not include pairs of variables that were highly correlated ($r > 0.7$; Dormann et al. 2013) in the same models, and we assessed relative model fit using AIC_c. When a more complex version of a simpler model (i.e., a nested subset model) had a higher AIC_c than the simpler model, and the 85% CIs of the additional parameter overlapped zero, we considered the parameter to be uninformative (Arnold 2010; Leroux 2019). We removed models with uninformative parameters from further consideration. We considered models with $\Delta\text{AIC}_c < 2$ as competitive (Burnham and Anderson 2002). We averaged across all competitive models using a “full” average (i.e., variables are included in every model, but the coefficient is set to 0 if the variable does not appear in a given model; Burnham and Anderson 2002; Lukacs et al. 2010) and implemented in the “MuMIn” package in R. We reported the averaged model as our top model (Arnold 2010). At the landscape scale, we assessed the goodness-of-fit of the top model by examining diagnostic plots of Dunn-Smyth residuals (Warton et al. 2017). For the top home-range and within-home-range models, we calculated marginal and conditional R^2 values (Nakagawa and Schielzeth 2013), and we performed a 10-fold cross-validation repeated 3 times to assess predictive capabilities (Boyce et al. 2002). For competitive models, we assessed the variance inflation factor (VIF) between predictor variables, and we considered variables with a VIF > 5 to be multicollinear (James et al. 2014). We performed the landscape-scale analysis using the “unmarked” package in R and the home-range and within-home-range scale analyses using the “lme4” and “blme” packages in R (Fiske and Chandler 2011; Chung et al. 2013; Bates et al. 2015).

Results

Landscape scale.

There were 5 competitive landscape-scale models that we averaged (Supplementary Data SD2, Table SD2.1). We considered the averaged model as our top model, and it received most of the total model weight ($w = 0.74$). The null model was not competitive ($\Delta\text{AIC}_c = 72.8$). The Dunn-Smyth visual diagnostic plots for occupancy had 95% CIs overlapping 0, which indicates that the model fit the data well and that model assumptions were not violated (Warton et al. 2017). The top landscape-scale model included elevation, small-scale edge, and visual obstruction (Table 2; Supplementary Data SD2, Table SD2.2). Probability of use increased with increased elevation and percent visual obstruction (Fig. 2). For small-scale edge (i.e., the interaction between tree count and herbaceous cover), the probability of use increased with tree count when the herbaceous cover was high but declined with tree count when the herbaceous cover was low (Fig. 2). The top model predicted a probability of use of 0.01 under the average conditions for all variables at survey sites (Fig. 3). The predicted probability of use increased to 0.21 for sites at 3,300 m of elevation with all other conditions held at their average and increased further to 0.71 for sites at 3,300 m of elevation with 1 tree per 20 m of transect, 80% herbaceous cover, and 80% visual obstruction below 1 m. The top model based on only GIS variables included elevation ($\beta = 2.75$, 85% CI = 1.76, 3.75, VIF = 1.71), live conifer cover ($\beta = -1.19$, 85% CI = −2.02, −0.83, VIF = 3.35), dead tree cover ($\beta = -1.70$, 85% CI = −3.29, −0.79, VIF = 1.46), and herbaceous cover ($\beta = 0.23$, 85% CI = −0.81, 1.96, VIF = 2.01), and the predictive map of this model estimated 14.9 ha of habitat with a high probability of use (>0.75), which we interpret as an estimate of occupied habitat (Fig. 3c; Supplementary Data SD2, Tables SD2.3 and SD2.4).

Home-range scale.

The variable for dead tree cover exhibited perfect separation in univariate logistic regression, such that chipmunks did not use any sites with >10% dead tree cover, and so we could not include the variable in our models. There were 2 competitive models, across which we averaged (Supplementary Data SD2, Table SD2.5). The averaged top model accounted for most of the model weight ($w = 0.99$). The null model was not competitive ($\Delta\text{AIC}_c = 211.33$). The marginal and conditional R^2 values were equal ($R^2c = R^2m = 0.76$). Overall model accuracy from the cross-validation process was 84%, true positive prediction rate (sensitivity) was 70%, and true negative prediction rate (specificity) was 89%. The top model included montane coniferous tree cover, slope, human-modified, subalpine edge, and shrub cover (Table 2). The probability of use increased with increasing shrub cover. The probability of use decreased with increasing montane coniferous tree cover, steeper slopes, and in human-modified environments. For the subalpine edge (i.e., the interaction between subalpine tree cover and herbaceous cover), the probability of use increased with higher herbaceous cover and subalpine tree cover,

Table 2. Standardized parameter estimates (β), SE, 85% CI, and VIF for the top model for each scale of habitat selection by the Peñasco Least Chipmunk (*Neotamias minimus atristriatus*) in the Sierra Blanca subrange in the Sacramento Mountains, New Mexico, United States, 2019.

Scale	Variable name	β	SE	85% CI	VIF
Landscape	Elevation	3.62	0.81	2.45, 4.80	1.51
	Tree count × herbaceous cover	1.17	0.63	0.27, 2.07	3.78
	Herbaceous cover	0.85	0.45	0.20, 1.50	1.69
	Tree count	−0.76	1.24	−2.55, 1.03	3.90
	Visual obstruction	1.05	0.47	0.37, 1.73	1.47
Home-range	Montane coniferous tree cover	−1.93	0.73	−2.96, −0.85	1.59
	Slope	−1.14	0.20	−1.43, −0.87	1.08
	Subalpine tree cover × herbaceous cover	0.71	0.22	0.40, 1.04	1.67
	Herbaceous cover	1.50	0.28	1.10, 1.90	2.67
	Subalpine tree cover	1.10	0.23	0.76, 1.44	1.90
	Human modified	−0.54	0.51	−1.60, −0.13	1.04
	Shrub cover	0.31	0.14	0.10, 0.50	1.10
Within-home-range	Visual obstruction	0.99	0.28	0.59, 1.39	1.58
	Gooseberry cover × herbaceous cover	0.84	0.33	0.36, 1.32	1.29
	Gooseberry cover	0.32	0.26	−0.05, 0.70	1.37
	Herbaceous cover	−0.26	0.25	−0.63, 0.11	1.49
	Boulder count	0.81	0.25	0.45, 1.17	1.14
	Large-diameter spruce count	0.53	0.25	0.17, 0.90	1.15

but the probability of use was near 0 when the herbaceous cover was low, regardless of the percent subalpine tree cover (Fig. 2). When we used the top model to predict the probability of use across the home-range selection area, we estimated 13.8 ha of habitat with a high probability of use (>0.75; Fig. 3d).

Within-home-range scale.

There was only 1 competitive model for within-home-range selection, which received over half of the total model weight ($w = 0.59$; Supplementary Data SD2, Table SD2.6). The null model was not competitive ($\Delta AIC_c = 45.99$), and it was the lowest ranked in the model set. The marginal and conditional R^2 values were equal ($R^2c = R^2m = 0.43$). Overall model accuracy from the cross-validation process was 75%, the true positive predication rate (sensitivity) was 71%, and the true negative prediction rate (specificity) was 78%. The top model included large-diameter spruce count, visual obstruction, mixed understory cover, and boulder count (Table 2). The probability of use increased with count of large-diameter spruce, increasing visual obstruction, and count of boulders. For mixed understory cover, i.e., the interaction between herbaceous cover and Gooseberry Currant cover, the probability of use increased with increasing herbaceous cover when gooseberry cover was high but decreased with increasing herbaceous cover when gooseberry cover was low (Fig. 2).

Discussion

A vegetation structure specialist.

Our results provide strong evidence that the Peñasco Least Chipmunk is specialized for specific vegetation structures. At each scale, we found that chipmunks selected for understory structure that provides low cover, such that use increased with increasing visual obstruction at a site at the landscape scale, with increasing shrub cover at the home-range scale, and with increasing Gooseberry Currant, herbaceous, and boulder cover at the within-home-range scale. We also found specialization for a specific forest structure, such that use by chipmunks increased where open stands of trees were interspersed with meadows at the landscape and home-range scales (i.e., the interaction between trees and herbaceous cover) and where there were large-diameter Engelmann Spruce and a mixture of herbaceous and Gooseberry Currant cover at the within-home-range scale. These understory and forest structures are interrelated and are habitat features that were primarily provided by the Engelmann Spruce-Gooseberry Currant plant association (PIEN/RIMO2; USFS 1997), which we only observed in the vicinity of the highest peak in our study area (Lookout Mountain). Gooseberry currants occur in the alpine and subalpine zones and are most commonly associated with stands predominated by Engelmann Spruce (Kearns et al. 2008). Lack of adequate sunlight restricts gooseberry currants from denser closed-canopy forests such as those co-dominated by Corkbark Fir (Zambino 2010), while the more open structure of Engelmann Spruce predominant stands provides partial shade which apparently promotes the growth of Gooseberry Currant—the shrub commonly grows in dense thickets encircling tree islands, patch edges, and the base of trees at timberline (Ellison 1954; Langenheim 1962; Mauk and Henderson 1984; Holtmeier and Broll 1992). Furthermore, we found that chipmunks selected for higher elevation sites at the landscape scale and sites with a gentler slope at the home-range scale, both of which are consistent with selection for the Engelmann Spruce predominant stands that occur at the highest elevations in this forest (Plummer and Gowsell 1904) and that grow best in deep soils with an accessible water table as provided by gentler slopes (Alexander and Shepperd 1990).

We found that the Peñasco Least Chipmunk had a highly restricted distribution, a further indicator of strong habitat specialization. While we might expect a habitat generalist to be widespread on the landscape (Brown 1984), we found chipmunk distribution to

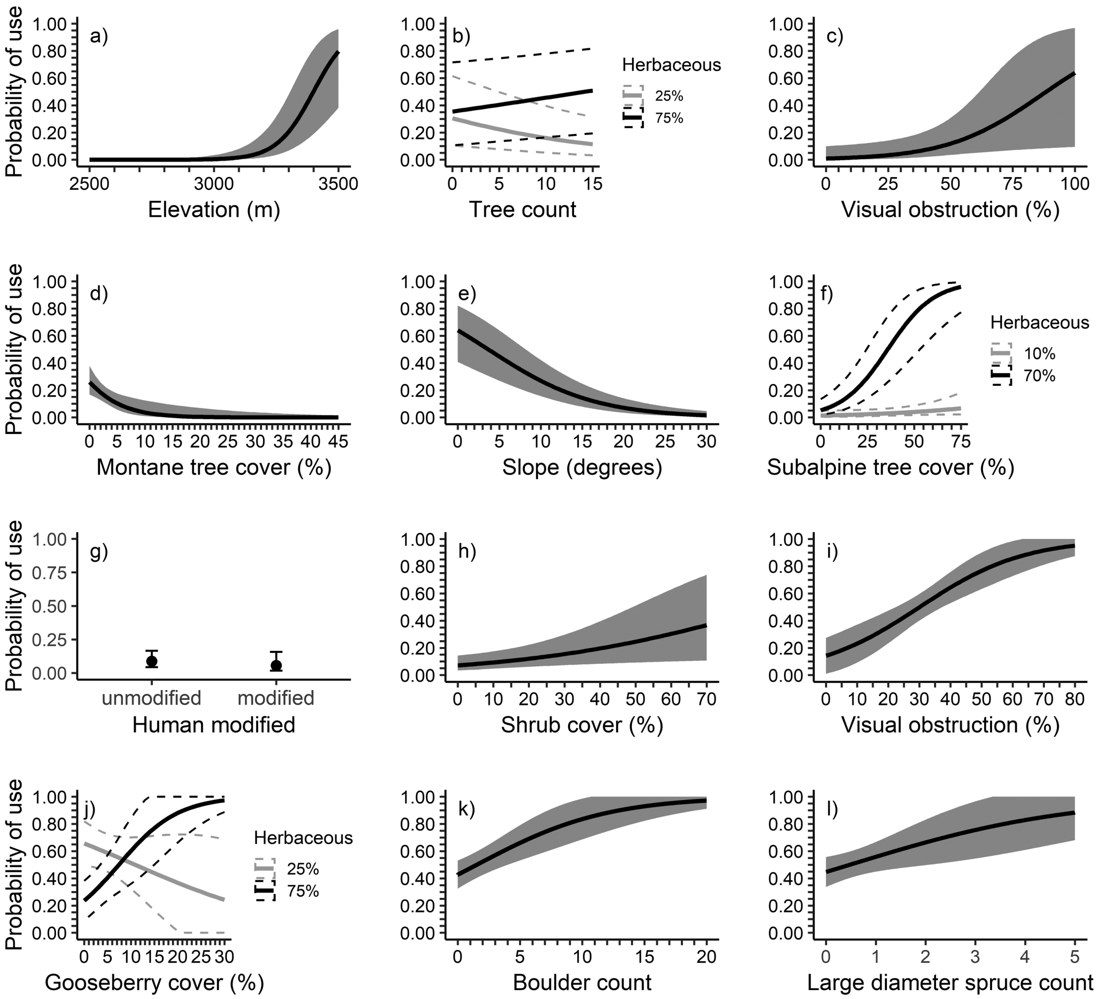

Fig. 2. Predicted probability of use as a function of variables at the landscape a–c), home-range d–h), and within-home-range i–l) scales for the Peñasco Least Chipmunk (*Neotamias minimus atristriatus*) in the Sierra Blanca subrange in the Sacramento Mountains, New Mexico, United States, 2019. Dashed lines and shading represent 95% CI.

be limited; in fact, we found only 2 subpopulations, and we estimated <15 ha of predicted habitat within the 13,218-ha study area. Additionally, if a habitat generalist was experiencing population declines, we would expect its distribution to be independent of patterns of predicted habitat (i.e., areas of unoccupied habitat would be common) because we would expect factors other than habitat loss (e.g., disease, pollution) to drive the decline. In contrast, the distribution of the Peñasco Least Chipmunk was closely aligned with its distinctive habitat, and our models did not predict much-unoccupied habitat—this indicates habitat loss as the driving factor behind the decline of the subspecies, a common story for habitat specialists (Matthews et al. 2014).

Finally, the Peñasco Least Chipmunk avoided areas of disturbance, contrary to expectations for habitat generalists that are often tolerant of environmental change (Dennis et al. 2011) and thrive in areas of disturbance, e.g., European starlings (*Sturnus vulgaris*) and Virginia opossums (*Didelphis virginiana*; Marvier et al. 2004). In our study, chipmunks avoided dead tree cover (landscape and home-range scales), avoided ski runs and roads (home-range scale), and selected old-growth trees (i.e., undisturbed forest; within-home-range scale). The variable dead tree cover was in the top landscape-scale model based on only GIS variables, and it exhibited perfect separation in the home-range-scale analysis, implying that the variable perfectly predicted presence at this scale (i.e., the chipmunks never used dead forest). This finding is especially noteworthy because much of the study area was burned during the 2012 Little Bear Fire (Tillery and Matherne 2013). Other studies reported least chipmunks using ski slopes (Hadley and Wilson 2004) and a transmission line right-of-way (Storm and Choate 2012; Peterson et al. 2017); however, those studies compared chipmunk abundance at the disturbed sites with nearby dense forest stands. Our results suggest that chipmunks avoid dense forest. Furthermore, comparisons of abundances cannot identify habitat preferences (Hall et al. 1997).

While our results indicate that the Peñasco Least Chipmunk exhibits ecological specialization, our approach cannot elucidate absolute habitat quality and does not account for the direct influences of habitat on fitness. For instance, we hypothesize that the northernmost population in the vicinity of Nogal Peak exists in a relatively low-quality habitat that may be relictual or serve as a sink. Future research linking reproduction and survival to habitat factors could have important implications for management and conservation. Additionally, our analyses of home-range and within-home-range selection were conducted at Lookout Mountain and therefore may not be applicable to Nogal Peak, which has different vegetation. Further research into habitat selection in the Nogal Peak area may help shed light on which factors are most predictive of Peñasco Least Chipmunk use throughout its range.

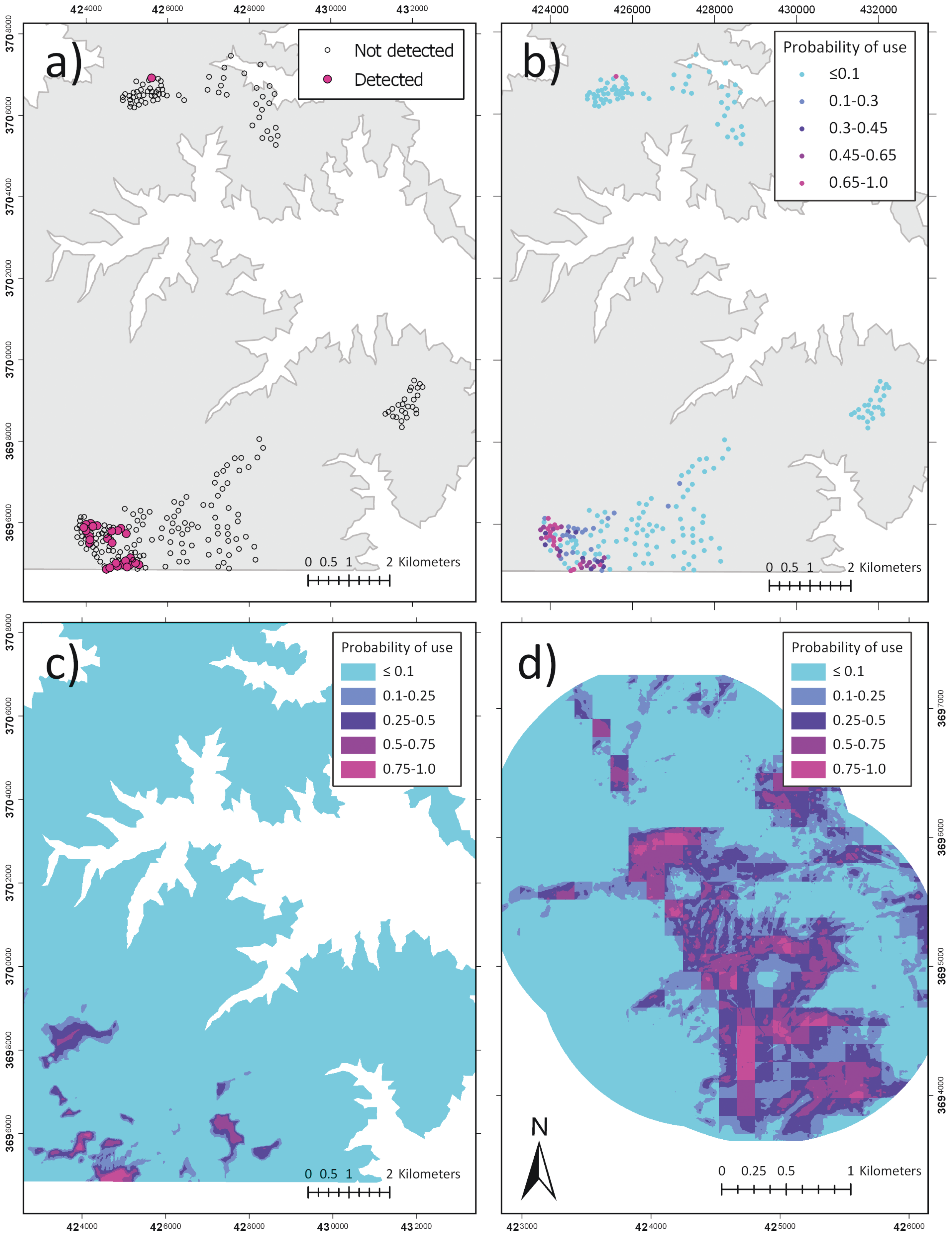

Fig. 3. a) Camera-trap survey sites surveyed May–October 2019 for the Peñasco Least Chipmunk (*Neotamias minimus atristriatus*). Predicted probability of use at b) the landscape scale, projected across camera-trap survey sites; c) the landscape scale, projected across the landscape selection area using the GIS model; and d) the home-range scale, projected across the home-range selection area for the Peñasco Least Chipmunk in the Sierra Blanca subrange of the Sacramento Mountains, New Mexico, United States, 2019. Inset map indicates the location of the home-range selection area within the landscape selection area (see Fig. 1).

Functional roles of variables.

Linking habitat selection to the functional needs of a species can elucidate the importance of environmental components for specific aspects of fitness (e.g., survival and reproduction; Morris 2003). However, as habitat selection by the Peñasco Least Chipmunk was previously unstudied and given the paucity of research into the habitat selection of least chipmunks in general, we could not form compelling a priori hypotheses regarding the functional roles of environmental components. A posteriori, we can hypothesize about the influences of important environmental variables on competition, food availability, predation risk, and den sites. Peñasco least chipmunks avoided dense coniferous forests and lower-elevation montane coniferous forests, which may indicate avoidance of habitat occupied by the larger-bodied Gray-footed Chipmunk (Best et al. 1992). Sheppard (1971) posited that a larger-bodied congener excluded least chipmunks from forested environments through aggressive encounters. Conversely, least chipmunks may outcompete larger-bodied congeners in alpine communities, because their smaller body size is better adapted to the lower primary production (Sheppard 1971). Further research is needed to elucidate the competitive relationship between Peñasco least chipmunks and gray-footed chipmunks.

Understory features may be important to Peñasco least chipmunks as food sources, cover from predators, or den sites. Least chipmunks have a generalist diet consisting of seeds, flowers, fruits, cones, and leaves from a variety of trees, shrubs, forbs, and grasses (Carleton 1966; Vaughan 1974; Bergstrom 1986). A diet study could help tease apart plants that provide food from those that solely provide cover. The variable visual obstruction, which was the amount of low cover (<1 m in height) at a site, likely represents a functional role in predator avoidance. Using radiotelemetry we tracked chipmunks to burrows, which we presumed to be den sites and which were typically located at the base of large-diameter Engelmann Spruce that had limbs growing low to the ground and/or under dense motts of Gooseberry Currant. We also found some presumed den sites under large boulders. These factors may provide dual services, supplying both den sites and escape cover/concealment. Our hypotheses regarding the functional role of environmental factors can help direct future studies investigating the direct impacts of habitat on Peñasco Least Chipmunk fitness.

Habitat loss as a driver of decline of the Peñasco Least Chipmunk.

We posit that specialization for vegetation structure drove historical distribution and subsequent decline of the Peñasco Least Chipmunk. The chipmunk historically occurred in habitat characterized by open forests and shrubby understories, including open Ponderosa Pine stands (Bailey 1931), edges of meadows (Bailey 1931), a glacial cirque at tree line (Conley 1970; Sullivan 1985), aspen stands (Sullivan 1985), talus slopes in a subalpine meadow (Hope and Frey 2000), and shrubby bunchgrass meadows (Frey and Hays 2017). We hypothesize that impacts from wildfire, railroad logging, grazing, road and ski run construction, spruce beetle invasion, and woody plant invasion have changed the vegetation structure and reduced the range to small patches of habitat where suitable structure persists. Most notably, the 2012 Little Bear Fire burned 7,200 ha of the White Mountain Wilderness Area (Tillery and Matherne 2013), likely destroying large patches of habitat (e.g., old-growth Engelmann Spruce stands). The fire burned with moderate or high severity within 53% of the burn area (Tillery and Matherne 2013). Based on our landcover map of the study area, at elevations above 2,800 m (the lower limit for Engelmann Spruce in the area; Plummer and Gowsell 1904), over 26% of the land cover was classified as dead, primarily due to the burn scar from the 2012 fire, while only 5% was classified as living subalpine forest. Additionally, Buck Mountain—a major peak near Lookout Mountain—historically harbored the subspecies (Hope and Frey 2000; Frey and Boykin 2007), but the 2012 fire destroyed swathes of forest on the peak, and subsequent efforts have failed to document the subspecies in the area (Frey and Hays 2017; McKibben 2022).

The area occupied by the population of the Peñasco Least Chipmunk in the vicinity of Lookout Mountain likely represents an environmental refugium in a sea of habitat loss. We posit that declines in the Engelmann Spruce-Gooseberry Currant plant association, which was closely associated with the chipmunk at Lookout Mountain, drove population declines. Following major disturbances such as high-severity wildfires or insect outbreaks Engelmann Spruce stands are usually replaced by other communities (Alexander and Shepperd 1990). Photographs of Sierra Blanca Peak taken in 1914 and 1998 appear to show an expansion of coniferous forest and a profound loss of shrub cover (Fig. 4). Forest expansion likely represents a replacement of large-diameter Engelmann Spruce by Corkbark Fir (Plummer and Gowsell 1904; Veblen et al. 1991). A major die-off of Engelmann Spruce was reported in the region in the early 20th century (Plummer and Gowsell 1904), and a shift away from the mature climax Engelmann Spruce community likely led to a decline in Gooseberry Currant coverage (Reed 1976; Kearns et al. 2008). Loss of Gooseberry Currant may have been further exacerbated by drought (Cook et al. 2007), climate change, and overgrazing (Plummer and Gowsell 1904), while other patches of the Engelmann Spruce-Gooseberry Currant plant association may

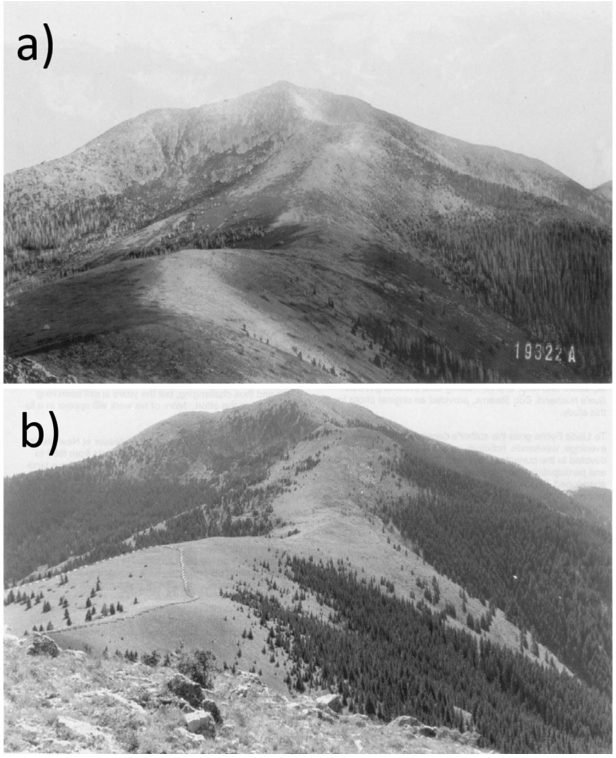

Fig. 4. View from Ski Apache facing south to Sierra Blanca Peak in a) 1914 and b) 1998, in the Sierra Blanca subrange of the Sacramento Mountains, New Mexico, United States, 2019 (photos taken from UHWC 2004). Note the expansion of coniferous forest and loss of understory (likely shrubs) from 1914 to 1998; current vegetation is primarily closed-canopy forest or grassland, neither of which are habitat for the Peñasco Least Chipmunk (*Neotamias minimus atristriatus*). Photo credit a) Rio Grande Historical Collection and b) E Hollis Fuchs.

have been lost in the 2012 fire. Any remaining stands represent relict chipmunk habitat and are threatened by wildfire, spruce bark beetle infestation, recreation, and climate change.

During our surveys, we discovered a subpopulation of the Peñasco Least Chipmunk in the vicinity of Nogal Peak, where chipmunks were associated with a different biotic community from that on Lookout Mountain (Ryniker et al. 2006) but with a similar vegetation structure. The plant community on Nogal Peak is dominated by Gambel Oak in both tree and shrub forms, New Mexico Locust, Snowberry (*Symphoricarpus oreophilus*), and other shrubs and grasses and may represent a long-lived postwildfire disclimax of prior coniferous forest (Guiterman et al. 2018). Within this community, chipmunk detections were associated exclusively with sparse overstory oak trees and a dense understory matrix of shrubs. Further research is needed to elucidate: (i) similarities and differences in finer-scale habitat selection between the Nogal Peak and Lookout Mountain subpopulations; (ii) the historical vegetation community on Nogal Peak; and (iii) the history of succession, stand age, and disturbance in the area. Like the habitat near Lookout Mountain, Nogal Peak may represent a refugium of relict habitat for the Peñasco Least Chipmunk within a broad swathe of habitat loss.

Habitat alteration explains the apparent extirpation of the Peñasco Least Chipmunk from the southern Sacramento Mountains, where railroad logging and fire suppression have significantly altered forest stand composition and structure (Alexander et al. 1984), leading to increased tree density and a loss of old-growth and open-structured stands that support meadows (Covington and Moore 1994). Commercial livestock grazing, which is pervasive throughout most of the historical distribution of the Peñasco Least Chipmunk (Alexander et al. 1984), alters species composition and productivity in meadows and grasslands (Milchunas 2006). These altered vegetation conditions threaten populations of small mammals that depend on herbaceous and shrub cover (Johnston and Anthony 2008) and have negatively impacted the distribution of other small mammal species in the region that also require ample vegetation cover (e.g., Frey and Malaney 2009). We infer that potential extirpation of the subspecies in the southern Sacramento subrange was caused primarily by habitat loss and specifically the loss of open Engelmann Spruce and Ponderosa Pine stands with shrubby meadow understories.

Plague has been suggested as a driver of the decline of the Peñasco Least Chipmunk (Goldberg et al. 2022; but see Frey et al. 2024); however, we would expect plague to result in a distribution that was less tightly explained by habitat covariates—including vacant patches of high-quality habitat—which we did not find. Alternatively, competition with the Gray-footed Chipmunk could be shaping the realized niche of the Peñasco Least Chipmunk, forcing the smaller-bodied chipmunk into suboptimal habitat. However, both species are endemic to the region and have likely coevolved in this system over a long period, so it is unlikely that competition alone is responsible for the decline of the Peñasco Least Chipmunk. Given habitat specialization of the chipmunk and the rarity of these conditions on the landscape, we conclude that habitat loss is the major driver of population decline.

Threats and management recommendations.

Because the Peñasco Least Chipmunk is specialized for a unique vegetation structure, it faces many threats. Wildfires likely pose the most immediate and direct threat to the remaining chipmunk habitat. At the landscape and home-range scales, we found evidence that the chipmunks avoided dead tree cover (i.e., burned forest). Since our field data collection concluded in 2018, several wildfires have threatened occupied chipmunk habitats (NMFWRI 2023). Climate change is predicted to continue to increase the frequency, size, and intensity of wildfires (Hurteau et al. 2014). Climate change may also affect the chipmunk through factors such as altered phenology, drought-induced reductions in food productivity, and increasing prevalence of forest pathogens. For instance, the spruce beetle (*Dendroctonus rufipennis*) threatens chipmunk habitat through a reduction in average tree size (Veblen et al. 1991), a shift in dominance away from Engelmann Spruce trees and towards Corkbark Fir trees (Gonthier and Nicolotti 2013), and an increased chance for high-intensity wildfire (Kulakowski et al. 2003). Grazing by large ungulates may threaten the remaining meadows. Least chipmunks respond negatively to livestock grazing (Medin and Clary 1989), and we suspect that cattle grazing is partially responsible for the extirpation of the Peñasco Least Chipmunk from the southern portion of their historical range. While livestock grazing is not currently authorized in most of the White Mountain Wilderness Area, we observed feral horses at elevations above 2,800 m within the study area. In addition, Elk (*Cervus canadensis*) populations have increased in the region throughout the last century (Wright 2000). Excess grazing by cattle, horses, and Elk may potentially threaten shrubby meadows occupied by the Peñasco Least Chipmunk. Finally, the construction of ski runs and roads and other human disturbances threaten the Peñasco Least Chipmunk through direct mortality and habitat alteration.

Given the small area occupied by the Peñasco Least Chipmunk and the vulnerability of its habitat to degradation and loss, conservation efforts are urgent to prevent its extinction. We recommend prioritizing the protection of existing populations (see McKibben 2022). Furthermore, we recommend the protection and rehabilitation of their habitat, focusing on meadows interspersed with scattered trees and shrubs that provide appropriate understory structure and visual obstruction. Specifically, we suggest that managers protect and rehabilitate meadows and high-elevation shrub species, especially Gooseberry Currant, and that they protect existing Engelmann Spruce predominant stands. Further research could explore methods for restoring Engelmann Spruce stands and rehabilitating and improving ski runs as chipmunk habitat. We recommend ongoing noninvasive monitoring of the known subpopulations and noninvasive research to further investigate the habitat selection, distribution, and abundance of the Nogal Peak subpopulation. Finally, we recommend further survey efforts using noninvasive methods to search for other extant subpopulations.

Implications for least chipmunks range wide.

As one of few comparisons of the use of resources versus their availability for least chipmunks (excepting Meredith 1976; Root et al. 2001; Rodhouse et al. 2010), and the only to evaluate habitat selection across multiple scales, our research provides hypotheses that can be tested throughout the range of the species. Specialization in vegetation structure may partially explain the distribution of least chipmunks throughout North America. Our findings indicate commonalities in anecdotal descriptions of Least Chipmunk habitat: authors have noted associations with rocks/talus (Findley and Negus 1953; Sullivan 1985), meadows (Vaughan 1974; Bergstrom and Hoffmann 1991), shrub cover (Bergstrom and Hoffmann 1991; Rodhouse et al. 2010), edges (Sheppard 1971; Nagorsen 2004; Poffenroth and Matson 2007), and forest openings (Meredith 1976; Nagorsen 2004). Similarly, we found evidence of selection across multiple scales for low cover provided by rocks, shrubs, and herbaceous plants and for meadows with sparse trees at the edges of forests. These habitat features are found in a range of biotic communities, from alpine tundra (Sheppard 1971) to subalpine forests (Bergstrom and Hoffmann 1991) and from Ponderosa Pine parklands (Conley 1970) to sagebrush steppe (Zeveloff 1988). Our results demonstrating the importance of low cover to the Peñasco Least Chipmunk provide a testable hypothesis for factors driving habitat selection by least chipmunks in other geographic regions.

Other Least Chipmunk subspecies occur in isolated subpopulations at the southern range margin (e.g., *N. m. arizonensis*, *N. m. chuskaensis*) and may face threats and local declines similar to the Peñasco Least Chipmunk. As a cold-adapted species, least chipmunks at the trailing edge of their range are especially vulnerable to climate change (Hampe and Petit 2005), and climate models predict that the southwestern United States will become warmer and more arid during the 21st century (Archer and Predick 2008). Increased aridity can exacerbate the loss of shrubs and herbaceous cover by grazing (Caracciolo et al. 2016), increase tree mortality due to insect outbreaks (Allen et al. 2010), and increase the chances of high-severity fire (Hurteau et al. 2014). Throughout the western United States, montane mammals are at risk from habitat alteration and loss (Rowe 2007), wildfire (Zwolak 2009), grazing (Horncastle et al. 2019), anthropogenic disturbance, and climate change (Moritz et al. 2008)—especially at southern range margins (McCain 2019; McCain et al. 2021). In fact, Moritz et al. (2008) documented an upward elevational shift in the lower limits of various *Neotamias* species in Yosemite National Park over a 100-year period, which they attributed to climate warming, while Rowe (2010) documented a contraction in the distribution of *N. minimus* over an 80-year period. Alternatively, at the northern margins of the Least Chipmunk range, we might expect range expansions (e.g., Anderson et al. 2009), an area worthy of future study. Because climate change can have interactive effects with other landcover changes (Rowe 2007; Rowe 2010), it is important to couple research on historical species distributions with rigorous studies of current distributions, habitat requirements, and landcover change. Habitat selection studies of least chipmunks and other montane mammals—especially at trailing edges—are key for understanding habitat loss, niche reduction (Scheele et al. 2017), species risk, and for making informed management plans.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Candidate variables used to test habitat selection at the landscape, home-range, and within-home-range scales.

Supplementary Data SD2. Competitive habitat selection models at the landscape, home-range, and within-home-range scales.

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Author contributions

FM data curation; formal analysis; funding acquisition; investigation; methodology; writing—original draft. JF conceptualization; funding acquisition; methodology; project administration; supervision; writing—review & editing.

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Conflict of interest

None declared.

Data availability

Data are sensitive and therefore not available in a public repository but may be requested from the corresponding author.

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