

DO RED SQUIRREL MIDDENS PROMOTE VERTEBRATE SPECIES DIVERSITY?

by

Erin Elizabeth Posthumus

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A Thesis Submitted to the Faculty of the

SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT

In Partial Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE
WITH A MAJOR IN WILDLIFE CONSERVATION AND MANAGEMENT

In the Graduate College

THE UNIVERSITY OF ARIZONA

2013

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SIGNED:

Erin E. Posthumus

APPROVAL BY THESIS ADVISOR

This thesis has been approved on the date shown below:

John L. Koprowski

John L. Koprowski

School of Natural Resources and the Environment

April 30, 2013

Date

ACKNOWLEDGEMENTS

First I would like to thank my Masters Thesis advisor, John L. Koprowski, for his guidance and support throughout my graduate program. Thank you to my thesis committee members, R. William Mannan and Robert. J. Steidl for suggestions and contributions throughout the project. I would also like to thank William M. Block for supporting and funding this endeavor. Thank you to David G. Allen, Maria M. Altemus, Hsiang Ling Chen, Theresa M. Crimmins, Jonathan J. Derbridge, Kathy L. Gerst, Rosa R. Jessen, Jherime Kellerman, Allyssa Kilanowski, Melissa J. Merrick, Alyssa H. Rosemartin, and Kathleen M. Stetz for providing helpful review comments and contributions to this manuscript. Thank you to Samantha K. Barnett, Alejandro Grajal-Puche, Vicki L. Greer, Melissa J. Merrick, Bonnie J. Raschke, Valerie A. Roundtree, Stephanie A. Snedecker, Alesha Williams, and especially Laura J. McHugh for providing assistance in the field. Mark Borgstrom at the Statistical Consulting Laboratory at the University of Arizona provided assistance with statistical analysis and interpretation. Funding was provided by the Forest Service Rocky Mountain Research Station, T&E Incorporated's Grants for Conservation Research, and the American Society of Mammalogists' Grants-in-Aid Program. Georgia Ehlers and the Peace Corps Coverdell Fellows program provided tuition assistance during my program and an internship at the USA National Phenology Network that helped me develop as a professional. A special thank you to my family and friends for their endless love and support.

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ABSTRACT

The modifications animals make to their environments can be critical to species diversity. Red squirrels (*Tamiasciurus hudsonicus*) create large piles of conifer cone debris (middens) and are hypothesized to function as a keystone species due to positive associations between middens and other vertebrate species. We assessed vegetation and landscape structure at middens with a resident red squirrel for varying consistencies over the prior 5 years and surveyed mammals and birds at the community and population level. After accounting for vegetation and landscape characteristics, red squirrel-created resources positively influenced species richness of medium and large mammals and ground foraging birds, abundance of deer mice (*Peromyscus maniculatus*) and ground foraging birds, and activity of cliff chipmunks (*Tamias dorsalis*). Increased knowledge of the interaction strength of the red squirrel with its environment may be used to inform decisions in forest management and restoration and offer insight on the conservation value of larderhoarding mammals.

INTRODUCTION

Biological diversity is a critical component of ecosystems, each ecosystem containing species with unique functions and interspecific interactions (Primack 1995). Species influence energy pathways and material flows; loss of species can alter ecosystems and disrupt ecosystem services (Hooper et al. 2005). Certain species have disproportional impact on their ecosystems (Power et al. 1996, Cardinale et al. 2006), perform unique functions (Kotliar 2000), and when extirpated, may negatively impact diversity and ecosystem function (Parmesan 2006), earning them the moniker of keystone species (Paine 1969). Although the utility of the keystone species concept has been debated, a focus on understanding the interaction strength of particular species may aid managers and policy makers (Mills et al. 1993, Power et al. 1996).

A suite of mammals have been hypothesized to function as keystones, such as beaver (*Castor canadensis*; Naiman et al. 1986), prairie dogs (*Cynomys* spp.; Miller et al. 1994), and bison (*Bison bison*; Knapp et al. 1999). Tests of these hypotheses have included effects of re-establishment of hypothesized keystones on vegetation or landscapes after extirpation (e.g. bison; Knapp et al. 1999) and comparisons of vegetation or animal communities in the presence or absence of potential keystone species (e.g. red-naped sapsuckers, *Sphyrapicus nuchalis*, Daily et al. 1993; prairie dogs, Goguen 2012; kangaroo rats, *Dipodomys* spp., Prugh and Brashares 2012). The variety of these taxa show the wide applicability of the keystone concept, which may pertain to species due to a diversity of 'keystone effects' (Mills et al. 1993).

Some species have been classified as keystone modifiers (Mills et al. 1993) or ecosystem engineers (Jones et al. 1994). Although all species are ecosystem engineers to some extent (Wright and Jones 2006), certain species modify ecosystems by redistributing resources or creating structures (Jones et al. 1994). This may be done on a large scale, such as beaver, which alter hydrology and community productivity through dams and feeding activities (Naiman et al. 1986) and prairie dogs, which alter soil structure and vegetation composition through burrowing and feeding (Kotliar et al. 1999) or on a small scale such as badgers, *Taxidea taxus*, which create mounds that maintain diversity of prairie flora (Platt 1975) and woodrats, *Neotoma* spp., which alter nitrogen mineralization in soils and create a nest with a unique microclimate that is used by other animals (Whitford and Steinberger 2010). Species that function as ecosystem engineers or modifiers contribute to the biodiversity of their ecosystems, and ecosystem function may decline as a result of their extirpation.

In addition to engineering landscapes through changing hydrology, altering vegetation, and changing soil chemistry, species may also alter environments through the concentration of food resources (MacRoberts and MacRoberts 1976, Vander Wall 1990). Handling and storage of food by animals for later use, termed larderhoarding, is a strategy used by many species from acorn woodpeckers (*Melanerpes formicivorus*; MacRoberts and MacRoberts 1976) to pika (*Ochotona* spp.; Kawamichi 1976), which enables animals to satisfy energy requirements during times of fluctuating resources (Vander Wall 1990). Food may be stored for short or long periods, and in the case of the

North American red squirrel (*Tamiasciurus hudsonicus*; hereafter red squirrel), food may be stored for multiple years (Gurnell 1987, Vander Wall 1990).

The red squirrel is a territorial tree squirrel distributed throughout large portions of the coniferous forests of the United States and Canada (Steele 1998). Red squirrels disperse seeds, serve as prey for forest predators, and create structure via conspicuous cone-scale piles, known as middens, which result from concentrated feeding in a single location (Fig. 1: Steele 1998). Middens are central to a single red squirrel's well-defended territory (Steele 1998), which can vary from 1 to >10 ha (Gurnell 1984, Koprowski et al. 2008). Middens may be used over generations of red squirrels (Gurnell 1987), and can reach 13 m in diameter and 50 cm in depth (Patton and Vahle 1986). Typically located in forests with unusually dense canopies, high stem densities and thick foliage (Thomas et al. 1988, Smith and Mannan 1994, Merrick et al. 2007), middens have a cool, moist microclimate optimal to larderhoard conifer cones and fungi (Fitzpatrick et al. 1993, Zugmeyer and Koprowski 2009). Cones, protected within the midden from wind exposure and solar radiation, remain moist and do not release their seeds (Finley 1969). In addition to seeds dropped by squirrels during feeding (Finley 1969), a single midden may contain over 10,000 stored cones collected from throughout a red squirrel's territory (Finley 1969). Cones stored during summer and autumn meet dietary requirements of squirrels for up to 2 years (Hurly and Lourie 1997, Vander Wall 1990).

Large numbers of cones, dropped seeds, and a large structure comprised of conifer cone-scales and cores that facilitate tunneling, nesting and access to food resources (Finley 1969), create the potential to influence diversity of other vertebrates at

middens. These resources may attract small mammals and birds, which may, in turn, attract mesocarnivores and avian predators (Pearson and Ruggiero 2001, Edelman et al. 2005). Positive associations with red squirrel middens have been reported for mesocarnivores and large mammals (Sherburne 1993, Mattson and Reinhart 1997). Subnivean tunnels are used by marten (*Martes americana*) more often when the access points are close to red squirrel middens (Sherburne 1993), and grizzly bears (*Ursus arctos horribilis*) excavate middens to obtain the majority of whitebark pine (*Pinus albicaulis*) seeds that they consume (Mattson and Reinhart 1997). Richness and abundance of mammals and bird species is higher at middens than in surrounding forest (Pearson and Ruggiero 2001, Edelman et al. 2005). However, these studies were limited by their landscape scale and were only indirectly examining middens (Pearson and Ruggiero 2001), or used methods of survey that only permitted detection of large animals by remote camera (Edelman et al. 2005).

Although associated positively with middens, species may be selecting for similar forest features and structure due to coincident habitat affinities with red squirrels (Pearson and Ruggiero 2001), rather than selecting for the localized resources created by red squirrels. Red squirrels select sites with high canopy cover, large cone bearing trees (Smith and Mannan 1994, Merrick et al. 2007), and large amount of coarse woody debris (Pearson and Ruggiero 2001). Deer mice (*Peromyscus* spp.), chipmunks (*Tamias* spp.), voles (*Microtus* spp.), and woodrats consume conifer seeds (Hoffmeister 1986) and den in coarse woody debris (Lee 2004, Fauteux et al. 2012). Insectivores such as shrews (Soricidae) may be attracted to high insect abundance from conifer seeds and moist

woody microhabitats, and flying squirrels (*Glaucomys* spp.) and voles may select areas with woody debris conducive to fungal growth (Amaranthus et al. 1994). Why high species diversity occurs at red squirrel middens remains unknown, as does the question of whether red squirrels function as keystone modifiers in their ecosystem.

To determine whether animals are attracted to midden sites beyond an attraction to similar types of resources as those favored by red squirrels, we assessed associations between midden locations and mammals and birds at the community and population level. Our first objective was to determine the vegetation and structural features with which middens were associated. We predict that middens will be located in areas with higher forest stand density, more conifer cone seed fall, and cooler, more humid microclimates than random locations. We also predict that middens with a greater consistency of red squirrel residency over time will have larger cone-scale piles than middens with a lower consistency of red squirrel residency.

Our second objective was to determine if resources created by red squirrels influence community and population characteristics of other vertebrates associated with middens. If midden structure or food resources are influential, we predict that mammal and avian species richness and abundance will be higher at middens than random locations, and will be positively associated with the presence of red squirrels and red squirrel created resources above and beyond the vegetation and landscape characteristics selected by red squirrels.

STUDY AREA

The study area was 100 ha of mixed-conifer forest in the Pinaleño Mountains, 25 km southwest of Safford, Graham Co., Arizona, dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and southwestern white pine (*Pinus strobiformis*), interspersed with cork-bark fir (*Abies lasiocarpa* var. *arizonica*), Engelmann spruce (*Picea engelmannii*), aspen (*Populus tremuloides*) and ponderosa pine (*Pinus ponderosa*), at an elevation of 2,870 to 3,050 m (Sanderson and Koprowski 2009). Middens in this area have been surveyed for residency by red squirrels every 3 months since 1996 (Sanderson and Koprowski 2009).

The federally endangered Mt. Graham red squirrel (MG red squirrel; *T. h. grahamensis*), at the southernmost extent of the red squirrel range (Steele 1998), is a subspecies restricted to the Pinaleño Mountains of southeastern Arizona (Hoffmeister 1986). The entire population has remained < 300 squirrels since 2004 (Arizona Game and Fish Department, unpublished data). The MG red squirrel creates middens primarily in stands of Engelmann spruce, cork-bark fir, or mixed conifer at elevations above 2,425 m (Fitzpatrick et al. 1993). The diet of MG red squirrels consists mainly of cones from 5 conifer species: Engelmann spruce, white fir, Douglas-fir, cork-bark fir, southwestern white pine, and fungi (Smith 1981).

METHODS

We selected 40 red squirrel middens in 2011 based upon a gradient of residency; we determined residency for each midden as the proportion of quarterly surveys where a red squirrel was detected at the midden (hereafter ‘residency’). Survey methods involve a visit to each midden location, examination of the midden for sign of red squirrel activity (tracks, feeding sign, nesting material, etc), and determination if the midden is occupied, and observation of the site for up to 3 h, with multiple visits as necessary to observe a squirrel (Sanderson and Koprowski 2009). As red squirrels are highly territorial and solitary, a midden site is nearly always occupied by one adult and is defended aggressively (Sanderson and Koprowski 2009). In 2011 and 2012, from a pool of 166 middens we randomly selected 10 middens without a resident red squirrel for the 5 years prior to the study (0% residency), 10 middens with <50% residency and without a resident red squirrel for at least 1 year prior to the study, 10 middens with a resident red squirrel during 50-75% of surveys in the 5 years prior to the study, and 10 middens with $\geq 75\%$ residency in the 5 years prior to the study. We used 15 of these 40 middens again in 2012 due to limited number of middens for this endangered species. Due to correlations <60% in dependent variables between years at sites sampled in both years, we treated all sites as independent. We used ArcGIS 9.0 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to buffer known middens by 60 m to ensure that our area for surveying species diversity would not overlap middens and random locations, and then randomly selected 10 non-midden locations within the study area.

Habitat Features Selected by Red Squirrels

We surveyed vegetation at each location along 2-m wide transects radiating from the center to 30 m in each of 4 cardinal directions (total area surveyed = 0.02 ha/location). We used a spherical densitometer to estimate canopy closure (Lemmon 1956), and averaged readings as we stood facing away from the center at 0, 2, 10, 20, and 30 m in each direction. We counted number of live and dead trees (<20 cm, 20-40 cm, >40 cm dbh), measured tree diameter at breast height (dbh), and calculated basal area/ha for all live and dead trees. We recorded species of live trees and calculated the Shannon-Weiner diversity index. We measured volume of hard downed logs >20 cm in diameter and counted snags >40 cm dbh. We measured slope and aspect in absolute degrees from the center of each location.

We used data loggers (HOBO Pro v2 Temp/RH, Onset Computer Corporation, Bourne, MA) to measure temperature and humidity at 25 middens randomly selected from the 40 total, and 10 random locations in each year. We placed HOBOs on the surface of the cone-scale pile at middens and on the ground at random locations. At a subset of 10 middens with a red squirrel in residence we paired HOBOs on the surface and buried 15 cm inside of the cone-scale pile. HOBOs logged temperature and humidity at 0600, 1200, 1800, and 2400 h each day of the year. We calculated mean temperature, mean maximum temperature, mean minimum temperature, range in temperature, mean humidity, mean maximum humidity, mean minimum humidity, and range in humidity. We used data from July, August, and September when red squirrels store cones (Steele 1998), but prior to snowfall that would influence microclimate.

Features Created by Red Squirrels

We used a binary variable to indicate presence or absence of red squirrels during each survey. We measured area and depth of cone-scale piles and counted number of visible cached cones in September and December. We used an index (1, 2, 3, 4) to represent cone numbers (1-25, 26-50, 51-75, >75, respectively) and selected the highest index in either September or December of the year prior to survey to approximate cone availability. We used 50 cm by 50 cm wire mesh collectors to measure fallen conifer seeds (Koprowski et al. 2005) at 10 middens with a resident squirrel and 10 random locations from May to November. We identified viable seeds to species, counted, summarized as mean number of viable seeds per site, and converted to seeds/m².

To meet assumptions of normality (Ramsey and Schafer 2002), we transformed canopy cover and low temperature by squaring, transformed log volume and slope with the natural log, and transformed aspect with the square root. We used 2-tailed *t*-tests to compare vegetation and structural characteristics and microclimate at middens and random locations and paired *t*-tests to compare microclimate on the surface and inside the cone-scale pile. We conducted regression analyses and fit linear, quadratic and cubic polynomials to examine the relationships between vegetation and structural characteristics with residency. We used JMP 9.0 (SAS Institute INC., Cary, NC) for all statistical analyses.

Mammalian and Avian Community Composition

To survey small mammals at middens and random locations, we used a web design, centered on each midden or random location (Anderson et al. 1983). Trapping webs were

comprised of 30-m lines radiating in 8 directions at 45° angles from center of the midden or random location. We set folding galvanized Sherman live traps (7.5 by 9 by 23 cm, Large Folding Trap 0.02 Aluminum, H. B. Sherman Traps, Inc., Tallahassee, FL) at 2, 10, 20, and 30 m and one at the center (total of 29 traps per web). For 1 4-night period at each location, we opened traps at sunset, baited with peanut butter, rolled oats, and alfalfa pellets, checked at sunrise, and reset traps and checked again in mid-morning. We identified each individual to species, weighed and measured following McDiarmid and Wilson (1996), and marked each with ear tags (Monel #1005-1, National Band and Tag Company, Newport, KY), before release at the capture location. Handling methods followed American Society of Mammalogists (Sikes and Gannon 2011) and University of Arizona Institutional Animal Care and Use Committee guidelines (Protocol #11-248).

We used a Pearson's chi-square test to compare presence of small mammal species between middens and random locations and at high residency middens with or without a current resident squirrel. As we were unable to calculate species richness with varying detection probability, we calculated species richness of small mammals (and all subsequent richness estimates) assuming detection = 1, and used Huggins closed capture-recapture analysis in Program MARK (White and Burnham 1999) to estimate abundance of small mammals at each location. We tested a series of models for detection probability that included a null model (M_0) permitting no variation in capture probabilities, and models allowing variation in capture probabilities by time (M_t), with respect to individual heterogeneity (M_h), and a combination of response by time and heterogeneity (M_{ht}). We used Akaike's Information Criterion with a correction for finite sample sizes (AICc) to

rank and evaluate models (Burnham and Anderson 2002). We considered models within 2 Δ AIC of the top model to be competing for all analyses. We estimated abundance of the more frequently trapped *Peromyscus maniculatus* and *Tamias dorsalis*, and combined detections of the remaining 4 less frequently trapped species (*Microtus longicaudus*, *Neotoma mexicana*, *P. boylii*, and *Sorex monticolus*). We used abundance estimates from the top models for each of these species for subsequent analyses.

We calculated mean body mass for adults for 5 of the small mammal species (we excluded *P. boylii* from these analyses because we only captured 9 individuals), and used a 2-tailed *t*-test to compare mean body mass at middens and random locations. We used linear regression to compare mean body mass to residency. We calculated total biomass of all adults, subadults and juveniles of all 6 species combined, and used a 2-tailed *t*-test to compare biomass of small mammals at middens and random locations and middens of high residency with and without a resident red squirrel, and linear regression to compare total biomass to residency.

To determine activity of small mammals near the midden center relative to the total trapping area, we used an analysis of variance (ANOVA) to compare numbers of unique individuals captured at distances of 0, 2, 10, 20 and 30 m from middens and random locations. We corrected for variable area and trap number at each distance of the trapping web by dividing the total number of unique individuals for each species at each distance by the effective trap area for each distance. We calculated effective trap area as a ring with a width from midpoint to midpoint between each trap in the 8 trap lines then divided by number of traps in the ring, except for the center, which we estimated as a

circle of radius 1 m. Effective trapping area for the center of the web was 1 m², for traps at 2 m: 27.5 m², traps at 10 m: 74.2 m², traps at 20 m: 157.1 m², and traps at 30 m: 235.6 m².

We used remote cameras (Bushnell Trophy Cam 119436c, TrailCamPro, Springfield, MO) to survey medium and large mammals at middens and random locations (Edelman et al. 2005). We set 3 cameras facing the location, 5-10 m from the center and 1-2 m above the ground for a randomly-assigned 6-day period in each year from May to September. We set an additional camera at occupied middens within 1 m of the cone-scale pile to detect activity. We did not include detections from this additional camera in species richness or detection estimates. We set cameras at maximum sensitivity to record one photo upon detection, with a 3-sec delay between photographs. We identified animals in photographs to species, and calculated species richness over 6 days for each location. We used Pearson's chi-square test to compare presence of medium and large mammal species between middens and random locations and at middens with high occupancy with or without a current resident squirrel. We calculated total number of detections as number of days in which each species was detected, and summed over 6 days. We used 2-tailed *t*-tests to compare total number of detections at middens and random locations and at middens with high occupancy with or without a current resident, and linear regression to compare number of detections to residency.

We used 10-min point counts to survey birds for 4 consecutive days (Ralph et al. 1993) at each midden and random location in early morning (0500-0900 hour) just before small mammal trapping sessions. We detected birds by sight and sound and classified

distances to the observer of 0-10 m, 11-20 m, 21-30 m, 31-50 m, 51-100 m, and >100 m. We truncated bird detections at 100 m, to include only those in proximity to middens and discarded detections with less confident distance estimates. We included birds in the ground foraging guild, characterized as those that search for seeds or insects on the ground (Elphick et al. 2001), in subsequent analyses.

We used ANOVA to compare total species richness at each of 4 levels of residency of middens and random locations. For small mammals, medium and large mammals, and birds, we used 2-tailed *t*-tests to compare species richness at middens and random locations. To determine whether red squirrel-created resources had an effect on species richness at middens after accounting for vegetation and landscape characteristics, we first developed a set of 11 *a priori* candidate models comprised of combinations of our 3 principal component variables (forest density, tree diversity, and forest floor) for vegetation and landscape features as well as mean low temperature and precipitation from the US Forest Service's weather station at Columbine, Arizona (Latitude: 32° 42' 14" Longitude: 109 ° 54' 50") for the 4 day period. We used AIC values from standard least squares to rank and evaluate models and determine the top model for species richness of mammals and birds and abundance of small mammals. We developed an additional set of 10 *a priori* candidate models including covariates from this top model with combinations of red squirrel presence, cone-scale pile volume, and number of cached cones, to determine if red squirrel-created resources improved the model. For ground foraging birds, we created hierarchical models for abundance with a distance sampling function in the R package 'unmarked' (Fiske and Chandler 2011). We compared null models with

half normal, hazard rate, and uniform detection functions, determined that the hazard rate detection function resulted in the top model, and developed 11 *a priori* candidate models including our principal component variables for vegetation and landscape features, mean low temperature and precipitation. We also included covariates for detection probability in these models. After selecting the top model, we developed an additional set of 10 *a priori* candidate models including covariates from this top model with combinations of red squirrel presence, cone-scale pile volume, and number of cached cones, to determine if red squirrel-created resources improved the model.

RESULTS

Vegetation Surrounding Middens

Middens differed in structure and composition from random locations. Middens had higher canopy cover, larger basal area, lower tree diversity, more large trees, greater log volume, and more level slope than random locations (Table 1). Middens had more conifer seeds than random locations ($t_{38} = 1.95$, $P = 0.059$), especially in 2012 ($t_{18} = 3.28$, $P = 0.004$) but not 2011 ($t_{18} = 0.17$, $P = 0.864$). A 10-fold increase in numbers of seeds (mean \pm SE) occurred from 2011 (7.9 ± 3.0 seeds/m²) to 2012 (79.8 ± 12.1 seeds/m², $t_{38} = 5.78$, $P < 0.001$). Interannual difference was greater at middens (2011: 7.3 ± 4.2 seeds/m², 2012: 112.0 ± 16.4 seeds/m², $t_{18} = 6.17$, $P < 0.001$) than random locations (2011: 8.4 ± 4.5 seeds/m², 2012: 47.6 ± 10.8 seeds/m², $t_{18} = 3.36$, $P = 0.004$).

To reduce dimensionality among 7 habitat variables, we used principal components analysis with the correlation matrix. The first principal component, forest density (29.5% of variation), had high loadings for basal area (factor weight = 0.56), percent canopy cover (0.52), and number of trees >40 cm dbh (0.48). The second principal component, tree diversity (20.2% of variation), had high loadings for tree diversity (0.58) and number of snags >40 cm dbh (0.48), and the third, forest floor (16.0% of variation), included log volume (0.78) and slope (-0.51).

From July to September when squirrels collect and store cones, the surface of middens had lower maximum daily temperature than random locations (midden: $15.7 \pm 2.7^\circ\text{C}$; random: $17.5 \pm 5.1^\circ\text{C}$; $t_{67} = 1.90$, $P = 0.059$) and higher mean daily humidity than random locations (middens: $84.4 \pm 6.1\%$; random $80.9 \pm 4.4\%$; $t_{67} = 2.30$, $P = 0.022$).

During the same months, mean daily temperature (\pm SE) inside the cone-scale pile was 11.8 ± 0.6 , with a maximum range of 4.4 ± 0.6 . The interior of cone-scale piles had less extreme temperatures with a lower maximum daily temperature ($t_{65} = 3.01$, $P = 0.004$), higher minimum daily temperature ($t_{65} = 2.70$, $P = 0.009$), and less range in temperature ($t_{65} = 4.52$, $P < 0.001$) compared to the surface of the cone-scale pile (Fig. 2). Mean daily humidity (\pm SE) inside cone-scale piles was $96 \pm 1.21\%$, with a maximum range of $20 \pm 6.32\%$. The inside of cone-scale piles had higher, more stable humidity than the surface, with higher mean daily humidity ($t_{65} = 7.23$, $P < 0.001$), higher maximum daily humidity ($t_{65} = 3.19$, $P = 0.002$), higher minimum daily humidity ($t_{65} = 3.91$, $P < 0.001$), and less range in daily humidity ($t_{65} = 3.11$, $P = 0.003$; Fig. 2).

Middens with high residency were associated with high canopy cover, high basal area, low log volume, and steep slopes (Table 1). Predictably, cone-scale pile volume increased with increasing residency, as did number of cached cones (Table 1). Residency did not increase with the number of fallen seeds ($F_{1,18} = 0.49$, $P = 0.495$, $R^2 = 0.03$). Residency was influenced by temperature and humidity, except for mean daily humidity, which had a quadratic relationship, highest at middens of low and high residency, and lowest at intermediate residency ($F_{1,45} = 4.13$, $P = 0.023$, $R^2 = 0.16$).

Influence of Midden versus Vegetation Characteristics on Vertebrates

Community level.—Mean (\pm SE) species richness of mammals and birds combined was $13.0 (\pm 0.7)$ species at middens of residency $>75\%$, $13.2 (\pm 0.6)$ species at middens of 50-75% residency, $10.8 (\pm 0.5)$ species at middens of $<50\%$ residency and without a resident for at least a year prior to the study, $11.7 (\pm 0.6)$ species at middens of

0% residency, and $11.0 (\pm 0.81)$ species at random locations ($F_{4,95} = 2.99$, $P = 0.023$). Species richness of small mammals was higher at middens (3.4 ± 0.1 species) than random locations (2.8 ± 0.2 species; $t_{98} = 2.48$, $P = 0.019$). Among middens, species richness of small mammals was positively influenced by an interactive effect of our principal components of tree density and forest floor (Table 2). Adding covariates for red squirrel-created resources did not significantly improve the model, although a competing model contained a positive association with an interactive effect of presence of red squirrel, volume of the cone-scale pile, and number of cached cones (Table 3). Species richness of medium and large mammals was higher at middens (1.7 ± 0.1 species) than random locations (1.3 ± 0.2 species; $t_{98} = 1.82$, $P = 0.078$). Among middens, species richness of medium and large mammals was positively influenced by tree diversity, forest floor, and tree diversity (Table 2). Adding covariates of presence of red squirrel and volume of cone-scale pile improved each of our 5 competing models (Table 3). Species richness of birds was not different at middens and random locations ($t_{98} = 0.17$, $P = 0.863$). Among middens, species richness of birds was positively influenced by tree density and forest floor, but negatively influenced by tree diversity (Table 2). Adding presence of red squirrels and number of cached cones significantly improved this model (Table 3).

We detected 6 species of small mammals during 11,600 trap nights. In 2011 and 2012, we captured 53 *Microtus longicaudus* (46 unique individuals), 121 *Neotoma mexicana* (66 unique individuals), 9 *Peromyscus boylii* (8 unique individuals), 1355 *P. maniculatus* (730 unique individuals), 70 *Sorex monticolus* (41 unique individuals), and

564 *T. dorsalis* (350 unique individuals; Appendix A). We detected *P. maniculatus* at every site and *T. dorsalis* at 94% of our sites (Table 4). We detected *N. mexicana* at 64% of middens and 40% of random locations (Table 4). We detected *S. monticolus* at 45% of middens and 20% of random locations (Table 4). Current residency status of high residency middens did not influence presence of small mammal species ($\chi^2 \leq 1.13$, $P \geq 0.287$ for all species).

We detected 10 species of medium to large mammals in 1722 camera days (Table 4) in addition to Mt. Graham red squirrels: Abert's squirrel (*Sciurus aberti*; 14 detections), black bear (*Ursus americanus*; 39 detections), bobcat (*Lynx rufus*; 11 detections), elk (*Cervus canadensis*, 1 detection), gray fox (*Urocyon cinereoargenteus*; 3 detections), mountain lion (*Puma concolor*; 3 detections), white-tailed deer (*Odocoileus virginianus*; 156 detections), rock squirrel (*Spermophilus variegatus*; 18 detections), and striped skunk (*Mephitis mephitis*; 45 detections). We detected bobcat and lions only at middens, with no detections at random locations. All other species were detected at both middens and random locations, although black bear were detected more frequently at middens than random locations. Frequency of detection of all mammals combined was not greater at middens with a current resident red squirrel than at middens of high residency but without a resident ($\chi^2 \leq 2.43$, $P \geq 0.119$ for all species). Total number of detections of the 10 species of medium to large mammals combined did not differ between middens (2.8 ± 0.4 detections) and random locations (3.1 ± 0.8 detections; $t_{98} = 0.24$, $P = 0.814$), high residency middens with (3.2 ± 0.8 detections) or without a current

resident red squirrel (2.5 ± 0.7 detections; $t_{38} = 0.67$, $P = 0.508$) nor were total detections associated with increasing residency ($F_{1,78} = 0.06$, $P = 0.814$, $R^2 < 0.001$).

We detected 25 bird species, including 4 that we classified as ground foragers: American robin (*Turdus migratorius*; 63 detections), hermit thrush (*Catharus guttatus*; 147 detections), Stellar's jay (*Cyanocitta stelleri*; 17 detections), and yellow-eyed junco (*Junco phaeonotus*; 222 detections). Additional cameras placed within 2 m of middens detected 3 species of birds on cone-scale piles that were all classified as ground foragers: American robin, hermit thrush, and yellow-eyed junco.

Population level. —For *P. maniculatus*, we used abundance estimates from our top model, in which detection varied with individual heterogeneity and over the trapping period (M_{ht} : Table 5). Abundance of *P. maniculatus* (mean \pm SE # individuals/ha) was similar at middens (19.2 ± 1.2) and random locations (16.9 ± 2.2 ; $t_{98} = 0.91$, $P = 0.375$), and higher in 2011 (23.6 ± 1.5 individuals) than in 2012 (13.8 ± 1.2 ; $t_{98} = 5.25$, $P < 0.001$). Abundance of *P. maniculatus* was positively influenced by tree diversity and precipitation and mean temperature during the trapping period (Table 2). Adding covariates for red squirrel-created resources significantly improved the model; abundance was positively influenced by the volume of the cone-scale pile and negatively influenced by the presence of red squirrels and the number of cached cones (Table 3).

We used abundance estimates for *T. dorsalis* generated from our top model, in which detection varied with individual heterogeneity (M_h : Table 5). Abundance of *T. dorsalis* (mean \pm SE # individuals/ha) was higher at middens (10.8 ± 1.0) than at random locations (4.9 ± 1.1 ; $t_{98} = 4.10$, $P < 0.001$), and did not differ between 2011 and 2012 (t_{98}

= 0.65, $P = 0.519$). Abundance of *T. dorsalis* was positively influenced by temperature and negatively influenced by precipitation (Table 2). Adding covariates for red squirrel-created resources did not significantly improve the model, although a competing model contained an interactive effect of presence of red squirrel, volume of the cone-scale pile, and number of cached cones (Table 3).

We used abundance estimates for the other 4 small mammals, *M. longicaudus*, *N. mexicana*, *P. boylii*, and *S. monticolus*, from our top model, in which detection varied with individual heterogeneity (M_h ; Table 5). Abundance of the 4 species combined (mean \pm SE # individuals/ha) was similar at middens (4.2 ± 0.4) and random locations (3.5 ± 0.9 ; $t_{98} = 0.81$, $P = 0.427$), and did not differ between years ($t_{98} = 0.06$, $P = 0.952$). Abundance of the 4 small mammal species was positively influenced by tree density, tree diversity, forest floor, precipitation and temperature (Table 2). Adding covariates for red squirrel-created resources improved 1 of 5 top models; presence of red squirrel both positively and negatively influenced abundance, and volume of cone-scale pile and number of cached cones negatively influenced abundance (Table 3).

Within our ground foraging bird guild, detection was positively influenced by tree density and forest floor (Table 2). Abundance of ground foraging birds was positively influenced by tree density, tree diversity and both positively and negatively influenced by forest floor (Table 2). Adding red squirrel-created resources did not significantly improve the model, but competing models contained a positive association with presence of red squirrels and negative associations with the volume of the cone-scale pile and the number of cached cones (Table 3).

Mean body mass of adult small mammals did not differ between middens and random locations (Table 6). Total biomass including adults, subadults, and juveniles of all small mammals was not different between middens and random locations (Table 6) or at middens of high residency with or without a resident red squirrel ($t_{38} = 0.790$, $P = 0.435$). Body mass of small mammals and total biomass was not associated with residency (Table 6). *S. monticolus* showed a slight quadratic trend in body mass with increasing residency, with higher body mass at middens with the lowest and highest residency, but lower body mass at mid-levels of residency (Table 6).

P. maniculatus tended to have a high number of unique individuals near the center of the midden, although this trend was also seen at random locations for number of unique individuals (Table 7). *T. dorsalis* showed a similar tendency in high number of unique individuals near the center of the midden, which was not seen at random locations (Table 7). We photographed *T. dorsalis* on 3 separate occasions holding a conifer cone on a midden inhabited by a resident red squirrel. *S. monticolus* showed a trend in higher number of unique individuals at mid-distances from the midden, but not at random locations (Table 7).

DISCUSSION

Middens Are Located in Dense Forest

Consistent with previous studies (Smith and Mannan 1994, Pearson 2000), middens differed from random locations with regard to multiple structural characteristics, especially indicators of forest density such as basal area, canopy cover, number of large trees, and coarse woody debris. Middens with high residency also had high canopy cover and basal area. Red squirrels likely select and persist at these sites for protection from avian predators (Schauffert et al. 2002), presence of large amounts of cone-bearing trees (Koprowski et al. 2008), and due to their moderate temperatures with higher humidity to aid thermoregulation (Gurnell 1987) and cone storage (Finley 1969). Cone-storage piles provided a microclimate with stable temperatures and high, stable, humidity that further inhibits cones from desiccating and opening to release seeds (Finley 1969, Zugmeyer and Koprowski 2009).

Log volume, a critical habitat component for small mammals (Loeb 1999, Lee 2004, Fauteux et al. 2012) and a microhabitat conducive to fungal growth (Amaranthus et al. 1994), was higher at middens than random locations but did not lead to increased residency. Although red squirrel middens can contain large amounts of coarse woody debris (Smith and Mannan 1994, Merrick et al. 2007), decreasing residency at middens with greater log volume demonstrates that red squirrels may not persist at sites with high amounts of forest decadence.

Community-Level Effects of Red Squirrels on Species Richness

Species richness of small mammals was higher at middens than random locations, but red squirrel-created resources contributed little to models after accounting for vegetation and landscape characteristics. Small mammals may be generally attracted to the same locations as red squirrels due to favored forest characteristics (Pearson and Ruggiero 2001), but the majority of species may not be associated with red squirrel-created resources or presence of red squirrels but rather red squirrel-selected resources. Closed canopy likely provides protection from predators, a moderate microclimate, and nesting locations for a variety of species (Carey and Johnson 1995, Azeria et al. 2009). Coarse woody debris is a critical habitat component for animals that use logs and stumps for nests or feed on fungus that is more abundant with increased coarse woody debris (Loeb 1999, Lee 2004, Fauteux et al. 2012).

Medium and large mammal species richness was higher at middens than at random locations, and both presence of red squirrels and volume of the cone-scale pile improved models for richness. Bobcats and lions may be attracted to middens due to potential prey (Schauffert et al. 2002), and black bears excavate middens in search of pine cones (Kendall 1983). Mammals in this size class may also use middens for thermoregulatory properties, as marten use middens as resting sites in winter (Buskirk 1984).

Avian species richness was not higher at middens than random locations, but avian richness was influenced by the presence of red squirrels and number of cached cones. Our cameras also detected three avian ground foragers on the surface of the cone-

scale pile with a red squirrel in residence, suggesting these birds may be using the cone-scale piles to some degree, perhaps to forage for seeds or insects (Elphick et al. 2001).

We recommend further study on the abundance and diversity of arthropods in cone-scale piles to understand whether middens are a hotspot for arthropod diversity as found at structures created by other keystone modifiers such as packrats and kangaroo rats (Whitford and Steinberger 2010, Prugh and Brashares 2012).

Some Species and Guilds Associated with Red Squirrel-Created Resources

We detected *P. maniculatus* at all sites, and *T. dorsalis* at all but 6 sites. These 2 species are both generalists, and their diet may include seeds of conifers, shrubs, grasses and forbs, insects, snails, fungi, bones, leaves or bark (Hoffmeister 1986). Many small mammals, such as *P. maniculatus*, undergo yearly population fluctuations that can drastically change abundance (Wolff 1984), as noted in our study. Midden structure was positively associated with *P. maniculatus* abundance, and this species was often photographed on the surface of the midden cone-scale pile. *P. maniculatus* live and nest in logs and under debris piles, and even make use of human created structures (Hoffmeister 1986), which may result in an association of *P. maniculatus* with the structure and size of the midden cone-scale pile.

T. dorsalis abundance was most influenced by abiotic factors, showing the activity of individuals may be affected by limiting temperature or precipitation. *T. dorsalis* may also be associated with habitat features that we did not measure because they are uncommon at our sites such as shrub cover or rock cover (Block et al. 2011). However, we detected higher activity of *T. dorsalis* individuals near midden centers and

individuals may spend more time at middens than other areas of the forest. *T. dorsalis* may spend more time at middens due to favored food resources such as conifer seeds (Hart 1992) *T. dorsalis* also tunnels and creates dens and nests in many substrates (Hart 1992), which may be facilitated by the microclimate and structure of the cone-scale pile.

Red squirrel presence was a significant component of models for abundance of ground foraging birds, which were also the only birds that we detected with cameras at the midden cone-scale pile. The diet of these birds is composed primarily of seeds and invertebrates (Elphick et al. 2001), which may be higher with a resident red squirrel dropping seeds while feeding (Finley 1969), and might explain the detections of these avian species on top of the cone-scale pile. Our sample size of fallen seeds was limited, so we were not able to detect whether numbers of fallen seeds were higher at middens with a resident red squirrel than at middens without a resident, but middens had more fallen conifer seeds than random locations.

Our study provides evidence that red squirrels function as keystone modifiers in the mixed conifer forest, and highlights the importance of larderhoarding as a community-level process that drives patterns in mammalian and avian species richness. Because we often understand little of the importance of species to ecosystem function, and find difficulty predicting which species have the greatest influence on ecosystem processes (Cardinale et al. 2006), we must maintain biodiversity to the greatest extent possible in order to provide resistance to environmental change (Chapin et al. 2000, Loreau et al. 2001). Increasing our knowledge of how potential keystone modifiers such

as the red squirrel can influence species diversity will aid in the persistence of species critical to maintenance of diversity and ecosystem function.

CONSERVATION IMPLICATIONS

Species richness of mammals and birds was associated with closed dense forest and large amounts of coarse woody debris. Forest thinning may increase densities of some small mammals in conifer forests, but retention of slash and maintenance of shrub cover and coarse woody debris is also important to maintain densities (Converse et al. 2006). Maintaining these aspects of mature forest with structural heterogeneity in mixed conifer forests may preserve diversity of mammals and birds (Carey and Johnson 1995, Azeria et al. 2009). Forest management practices that also maintain red squirrel middens or even create artificial structures (Sullivan et al. 2012) may sustain diversity of mammals and birds.

The MG red squirrel persists at the southernmost extent of the red squirrel distribution, an area with warmer, drier forests than in much of the rest of the species range. This subspecies has home ranges 3 to 10 times greater than red squirrels in other parts of their distribution (Koprowski et al. 2008); therefore the effects of red squirrels on species diversity that we have observed may be exacerbated in areas with higher density of middens. At the southern end of the range, forest disturbances such as loss of canopy cover from insect infestations or fire, made more common by current trends in climate change (Parmesan 2006), threaten to alter midden microclimate to the detriment to food storage (Zugmeyer and Koprowski 2009). With predicted global change creating warm, dry climates, and threatening montane diversity (McCain and Colwell 2011) such southern forests may portend the future of forest communities at northern latitudes.

APPENDIX A TABLES

TABLE 1. Vegetation and landscape characteristics (mean \pm SE) at red squirrel middens and random locations ($n = 100$), and over the gradient of red squirrel (*Tamiasciurus hudsonicus*) residency ($n = 80$). Mt. Graham, Graham Co. Arizona, 2011-2012.

Middens versus random locations				
Characteristic	Midden	Random	<i>t</i>	<i>P</i>
Percent canopy cover	75.7 \pm 13.0	65.1 \pm 18.3	2.94	0.008
Basal area (m ² per ha)	6696.9 \pm 271.7	5480.1 \pm 543.4	2.10	0.044
Tree diversity (Shannon Index)	0.9 \pm 0.1	1.13 \pm 0.1	3.07	0.005
Log volume (m ² per ha)	73.79 \pm 1.1	55.52 \pm 1.2	1.70	0.100
# of snags >40 cm dbh (per ha)	30.43 \pm 3.2	29.61 \pm 6.3	0.11	0.911
# of trees >40 cm dbh (per ha)	304.2 \pm 1.1	175.53 \pm 1.3	2.22	0.034
Slope (degrees from horizontal)	10.8 \pm 1.1	15.1 \pm 1.1	2.07	0.049
Aspect (degrees from North)	53.0 \pm 0.1	71.9 \pm 0.5	1.39	0.175
Cone-scale pile volume (m ²)				
Cached conifer cones (index)				
Residency gradient				
Characteristic	Estimate	<i>F</i>	<i>P</i>	<i>R</i> ²
Percent canopy cover	35.9 \pm 19.7	11.13	0.001	0.13
Basal area (m ² per ha)	1415.4 \pm 774.1	3.34	0.071	0.04
Tree diversity (Shannon Index)	0.1 \pm 0.1	0.05	0.830	< 0.01
Log volume (m ² per ha)	2.9 \pm 0.7	6.78	0.011	0.08
# of snags >40 cm dbh (per ha)	12.7 \pm 8.9	2.04	0.157	0.03
# of trees >40 cm dbh (per ha)	1.7 \pm 0.4	0.48	0.492	0.01
Slope (degrees from horizontal)	3.5 \pm 0.7	9.54	0.003	0.11
Aspect (degrees from North)	0.2 \pm 1.1	0.02	0.887	< 0.01
Cone-scale pile volume (m ²)	4.7 \pm 0.7	45.09	< 0.001	0.37
Cached conifer cones (index)	2.7 \pm 0.4	49.55	< 0.001	0.39

TABLE 2. Influence of vegetation, landscape and weather characteristics on species richness and abundance of birds and mammals. Best models of species richness and abundance of mammals and birds at red squirrel (*Tamiasciurus hudsonicus*) middens ($n = 80$), selection statistics and performance measures, including vegetation, landscape, and weather covariates. All models within 2 ΔAIC are reported, as well as the null model. (-) = negative association. Mt. Graham, Graham Co. Arizona, 2011-2012.

	Model ^a	K^b	ΔAIC^d	w_i^e
Species richness of small mammals (min AICc ^c = 229.1)	tree density \times forest floor	1	0.0	0.6
	null		3.6	0.1
Species richness of medium and large mammals (min AICc = 252.1)	tree diversity + forest floor	2	0	0.2
	forest floor	1	0.3	0.2
	null	0	1	0.1
	tree diversity	1	1.3	0.1
Species richness of birds (min AICc = 371.8)	tree density + tree diversity + forest floor	3	1.8	0.1
	tree density - tree diversity + forest floor	3	0	0.8
Abundance of <i>Peromyscus maniculatus</i> (min AICc = 595.4)	null		22.7	0.0
	tree diversity + precipitation + temperature	3	0	0.7
Abundance of <i>Tamias dorsalis</i> (min AICc = 514.9)	null		13.57	0.0
	(-) precipitation + temperature	2	0	0.4
	forest floor - precipitation + temperature	3	1.9	0.1
Abundance of <i>Microtus longicaudus</i> , <i>Neotoma mexicana</i> , <i>P. boylii</i> , and <i>Sorex monticolus</i> (min AICc = 416.1)	null		3.27	0.1
	tree diversity + precipitation + temperature	3	0	0.3
	precipitation + temperature	2	0.1	0.2
	tree density + precipitation + temperature	3	0.4	0.2
	forest floor + precipitation + temperature	3	0.7	0.2
	tree density + tree diversity + forest floor + precipitation + temperature	5	1.9	0.1
Abundance of ground foraging birds (min AICc = 1002.9)	null		20.2	0.0
	abundance: tree density + (-)tree diversity + forest floor	6	0	0.3
	detection: null			
	abundance: null	3	0.4	0.2
	detection: null			
	abundance : (-)tree density + (-)tree diversity + forest floor	7	0.4	0.2
detection: tree density				
abundance: tree density + (-)tree diversity + (-)forest floor	7	1.2	0.1	

detection: forest floor

^a squirrel = presence of red squirrel, cone-scale pile = volume of cone-scale pile, cached cones = index of cached cones, forest density = PCA variable including % canopy cover, basal area, and number of trees > 40 cm dbh, tree diversity = PCA variable including Shannon Index of live tree diversity and number of snags > 40 cm dbh, forest floor = downed log volume and slope, precipitation = mean daily precipitation during survey, temperature = mean daily low temperature during survey, ^b K = number of parameters, ^c AIC = Akaike's Information Criterion values, ^d Δ AIC = AIC relative to the most parsimonious model, ^e w_i = AIC model weight.

TABLE 3. Influence of red squirrel-created resources, vegetation, landscape and weather characteristics on species richness and abundance of birds and mammals. Best models of species richness and abundance of mammals and birds at red squirrel (*Tamiasciurus hudsonicus*) middens ($n = 80$), selection statistics and performance measures, including vegetation, landscape, and weather covariates and red squirrel-created resource covariates. All models within 2 Δ AIC are reported, as well as the top model from Table 2. (-) = negative association. Mt. Graham, Graham Co. Arizona, 2011-2012.

	Model ^a	K^b	Δ AIC ^c	w_i^d
Species richness of small mammals (min AICc ^e = 229.1)	tree density \times forest floor	1	0	0.3
	tree density \times forest floor + squirrel \times cone-scale pile \times cached cones	2	1.9	0.1
Species richness of medium and large mammals (min AICc = 237.0)	tree diversity - forest floor + squirrel	3	0	0.6
	tree diversity - forest floor	2	15.0	0.1
Species richness of birds (min AICc = 369.2)	tree density - tree diversity + forest floor + cached cones	4	0	0.4
	tree density - tree diversity + forest floor + squirrel + cached cones	5	2.0	0.1
	tree density - tree diversity + forest floor	3	2.6	0.1
Abundance of <i>Peromyscus maniculatus</i> (min AICc = 592.3)	tree diversity + precipitation + temperature + cone-scale pile	4	0	0.4
	tree diversity + precipitation + temperature + cone-scale pile - cached cones	5	1.4	0.2
	tree diversity + precipitation + temperature - squirrel + cone-scale pile	5	1.7	0.2
	tree diversity + precipitation + temperature	3	3.2	0.1
Abundance of <i>Tamias dorsalis</i> (min AICc = 514.9)	(-) precipitation + temperature	2	0	0.4
	precipitation + temperature - squirrel \times cone-scale pile \times cached cones	3	1.9	0.1
Abundance of <i>Microtus longicaudus</i> , <i>Neotoma mexicana</i> , <i>P. boylii</i> , and <i>Sorex monticolus</i> (min AICc = 416.1)	tree diversity + precipitation + temperature - squirrel	4	0	0.3
	tree diversity + precipitation + temperature - cone-scale pile	4	0.9	0.2
	tree diversity + precipitation + temperature	3	1.2	0.1
	tree diversity + precipitation + temperature + squirrel - cone-scale pile	5	1.9	0.1
Abundance of ground foraging birds (min AICc = 1002.6)	abundance: tree density + (-)tree diversity + forest floor + squirrel - cone-scale pile detection: null	8	0	0.2
	abundance: tree density + (-)tree diversity +	6	0.3	0.2

forest floor			
detection: null			
abundance: tree density + (-)tree diversity + forest floor + squirrel	7	1.0	0.1
detection: null			
abundance: tree density + (-)tree diversity + forest floor – cone-scale pile	7	1.6	0.1
detection: null			
abundance: tree density + (-)tree diversity + forest floor + squirrel - cone-scale pile - cached cones	9	2.0	0.1
detection: null			

^a squirrel = presence of red squirrel, cone-scale pile = volume of cone-scale pile, cached cones = index of cached cones, forest density = PCA variable including % canopy cover, basal area, and number of trees > 40 cm dbh, tree diversity = PCA variable including Shannon Index of live tree diversity and number of snags > 40 cm dbh, forest floor = downed log volume and slope, precipitation = mean daily precipitation during survey, temperature = mean daily low temperature during survey, ^b K = number of parameters, ^c AIC = Akaike's Information Criterion values, ^d Δ AIC = AIC relative to the most parsimonious model, ^e w_i = AIC model weight.

TABLE 4. Frequency of detection of mammal species at middens and random locations ($n = 100$), Pearson's chi-squared ($n = 100$), and logistic regression of frequency of detection over gradient of red squirrel (*Tamiasciurus hudsonicus*) residency ($n = 80$), for small and medium-large mammals. Mt. Graham, Graham Co. Arizona, 2011-2012.

Species	Middens versus random locations				Residency gradient	
	Midden	Random	χ^2	P	χ^2	P
<i>Microtus longicaudus</i>	0.31	0.35	0.10	0.748	0.005	0.947
<i>Neotoma mexicana</i>	0.64	0.40	3.73	0.053	0.020	0.888
<i>Peromyscus boylii</i>	0.09	0.00	1.88	0.170	4.176	0.041
<i>Peromyscus maniculatus</i>	1.00	1.00				
<i>Sorex monticolus</i>	0.45	0.20	4.17	0.041	0.125	0.723
<i>Tamias dorsalis</i>	0.95	0.90	0.71	0.400	1.163	0.281
<i>Lynx rufus</i>	0.15	0.00	3.41	0.065	2.566	0.109
<i>Mephitis mephitis</i>	0.29	0.15	1.57	0.210	0.251	0.616
<i>Odocoileus virginianus</i>	0.53	0.55	0.04	0.841	1.781	0.182
<i>Otospermophilus variegatus</i>	0.08	0.15	1.1	0.295	0.231	0.631
<i>Puma concolor</i>	0.03	0.00	0.51	0.475	0.124	0.725
<i>Sciurus aberti</i>	0.09	0.10	0.03	0.861	0.037	0.847
<i>Urocyon cinereoargenteus</i>	0.04	0.05	0.07	0.797	2.527	0.112
<i>Ursus americanus</i>	0.30	0.10	3.33	0.068	1.764	0.184

TABLE 5. Models for detection probability run in Program MARK to estimate abundance of small mammals. Top 3 models shown for each species or group. Mt. Graham, Graham Co. Arizona, 2011-2012.

Species	Model ^a	K^b	ΔAIC^d	w_i^e
<i>Peromyscus maniculatus</i> (min AICc ^c = 4118.4)	M _{ht} (heterogeneity x time)	3	0.00	0.99
	M _t (time)	6	15.16	< 0.01
	M _o (null)	2	40.69	< 0.01
<i>Tamias dorsalis</i> (min AICc = 1922.4)	M _t (time)	6	0.00	1.00
	M _{ht} (heterogeneity x time)	3	7.27	0.03
	M _h (heterogeneity)	1	13.78	0.00
<i>Microtus longicaudus</i> , <i>Neotoma mexicana</i> , <i>P. boylii</i> , and <i>Sorex monticolus</i> (min AICc = 815.1)	M _{ht} (heterogeneity x time)	3	0.00	0.59
	M _h (heterogeneity)	1	2.47	0.29
	M _t (time)	4	2.74	0.25

^a Mode I= models for abundance estimates, ^b K = number of parameters, ^c AIC = Akaike's Information Criterion values, ^d ΔAIC = AIC relative to the most parsimonious model, ^e w_i = AIC model weight.

TABLE 6. Mean body mass \pm SE (n) of adult individuals at middens and random locations for 5 small mammal species, and over the gradient of red squirrel (*Tamiasciurus hudsonicus*) residency frequency. Mt. Graham, Graham Co. Arizona, 2011-2012.

Species	Middens versus random locations				Residency gradient		
	Midden	Random	t	P	F	P	R^2
<i>Microtus longicaudus</i>	50.1 \pm 2.3 (17)	48.1 \pm 3.5 (7)	0.49	0.633	0.20	0.662	0.01
<i>Neotoma mexicana</i>	160.5 \pm 4.9 (30)	157.0 \pm 12.0 (5)	0.27	0.790	0.16	0.694	0.01
<i>Peromyscus maniculatus</i>	19.9 \pm 0.3 (79)	19.7 \pm 0.5 (18)	0.33	0.740	< 0.01	0.994	< 0.01
<i>Sorex monticolus</i>	5.6 \pm 0.2 (24)	4.7 \pm 0.7 (2)	1.17	0.253	2.63	0.095	0.20
<i>Tamias dorsalis</i>	70.5 \pm 0.9 (53)	70.4 \pm 1.8 (14)	0.03	0.973	1.25	0.296	0.05
Total biomass ^a	460.6 \pm 28.3 (80)	391.6 \pm 56.5 (20)	1.09	0.279	0.21	0.810	0.01

^a = all of above species and also including *Peromyscus boylii*.

TABLE 7. Mean unique small mammal captures per day by distance (m) from red squirrel (*Tamiasciurus hudsonicus*) middens ($n = 80$) or random location ($n = 20$). All numbers of captures multiplied by 10^4 . Mt. Graham, Graham Co. Arizona, 2011-2012.

Species	Middens					SE	<i>F</i>	<i>P</i>
	0 m	2 m	10 m	20 m	30 m			
<i>Microtus longicaudus</i>	0.0	2.2	2.5	1.7	2.0	0.9	1.20	0.311
<i>Neotoma mexicana</i>	29.8	9.1	3.4	3.4	2.9	7.8	2.19	0.069
<i>Peromyscus maniculatus</i>	109.0	37.5	52.6	52.6	36.8	17.1	3.71	0.006
<i>Sorex monticolus</i>	0.0	6.8	5.1	33.8	2.8	1.5	3.07	0.016
<i>Tamias dorsalis</i>	89.5	30.7	24.4	14.9	14.5	13.2	5.61	< 0.001
Random Locations								
<i>Microtus longicaudus</i>	0.0	4.6	11.8	0.0	2.7	3.3	2.17	0.078
<i>Neotoma mexicana</i>	0.0	0.0	3.4	3.2	1.1	1.3	1.71	0.154
<i>Peromyscus maniculatus</i>	199.0	50.0	48.8	31.8	29.2	36.9	3.78	0.007
<i>Sorex monticolus</i>	0.0	4.5	3.4	4.0	1.6	2.8	0.46	0.763
<i>Tamias dorsalis</i>	39.8	27.3	23.6	12.0	84.9	19.0	0.44	0.783

APPENDIX B FIGURES



FIGURE 1. Photographs of (a) red squirrel (*Tamiasciurus hudsonicus*) midden cone-scale pile, (b) cached cones inside pit dug by red squirrel, and (c) stored cones, which may number in the thousands at a single midden. Photo credits, E. E. Posthumus. Mt. Graham, Graham Co. Arizona, 2011-2012.

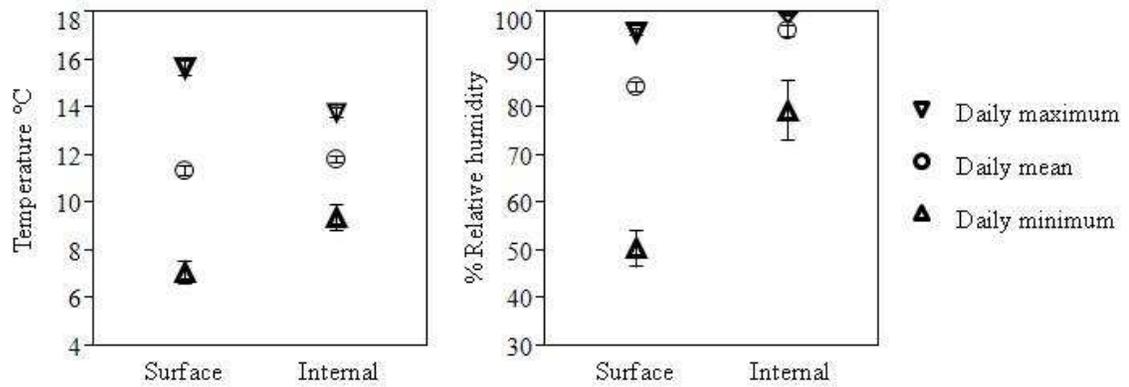


FIGURE 2. Mean, maximum, and minimum daily temperature (°C) and mean, maximum, and minimum daily relative humidity (%) from HOBO Pro v2 Temp/RH loggers placed on surface of cone-scale pile (surface) and 15 cm below surface (internal) at red squirrel (*Tamiasciurus hudsonicus*) middens ($n = 66$). Mt. Graham, Graham Co. Arizona, 2011-2012

APPENDIX C SMALL MAMMAL CAPTURES

Number of unique adult and juvenile individuals of each small mammal species captured in 2011 and 2012. Mt.Graham, Graham Co. Arizona, 2011-2012.

2011							
Species	Female			Male		Total	Total
	Adult	Juv	Total	Adult	Juv		
<i>Microtus longicaudus</i>	5	8	13	3	2	5	18
<i>Neotoma mexicana</i>	13	4	17	11	4	15	32
<i>Peromyscus boylii</i>	2	2	4	3		3	7
<i>Peromyscus maniculatus</i>	157	96	253	85	91	176	429
<i>Sorex monticolus</i>	5	2	7	4		4	11
<i>Tamias dorsalis</i>	51	44	95	17	48	65	160
Total	233	156	389	123	145	268	657

2012							
Species	Female			Male		Total	Total
	Adult	Juv	Total	Adult	Juv		
<i>Microtus longicaudus</i>	18	6	24	4		4	28
<i>Neotoma mexicana</i>	15	7	22	7	5	12	34
<i>Peromyscus boylii</i>				1		1	1
<i>Peromyscus maniculatus</i>	114	49	163	74	64	138	301
<i>Sorex monticolus</i>	20	2	22	8		8	30
<i>Tamias dorsalis</i>	62	13	75	92	23	115	190
Total	229	77	306	186	92	278	584

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