

HABITAT SELECTION IS UNALTERED AFTER SEVERE INSECT INFESTATION: CONCERNS FOR FOREST-DEPENDENT SPECIES

CLAIRE A. ZUGMEYER* AND JOHN L. KOPROWSKI

Wildlife Conservation and Management, School of Natural Resources, University of Arizona,
Tucson, AZ 85721, USA

Present address of CAZ: Sonoran Institute, 7650 East Broadway Boulevard #203, Tucson, AZ 85710, USA

Severe disturbance may alter or eliminate important habitat structure that helps preserve food caches of food-hoarding species. Recent recolonization of an insect-damaged forest by the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) provided an opportunity to examine habitat selection for midden (cache) sites following disturbance. From September 2003 to December 2005, we examined surface temperature and physical and vegetative characteristics associated with random locations and midden sites in insect-damaged forests. Red squirrel use of midden sites that are similar in structure to those used before insect infestation indicates that insect infestation did not eliminate midden habitat. However, differences between occupied middens and historical middens that are unoccupied reflect the severity of insect infestation tolerated by red squirrels. Occupied middens had <64% tree mortality, high basal area of live trees, and cooler surface temperatures during snow-free months. Forest areas with greater tree mortality would likely not represent habitat, threatening the persistence of an isolated population. Although conservation efforts can protect remaining habitat, disturbance events continually represent a threat. Habitat loss and predictions of increased disturbance due to climate change highlight the importance of documenting response to disturbance.

Key words: Arizona, disturbance, ecological trap, endangered species, habitat selection, isolation, larderhoard, midden, red squirrel, *Tamiasciurus*

Disturbance, both natural and anthropogenic, creates temporal and spatial heterogeneity of resources that can cause short- and long-term changes to habitat and disrupt interactions between individuals and resources (Bengtsson et al. 2000; Sousa 1984). Severe disturbance may dramatically alter habitat structure, causing reduced reproductive success or site abandonment (Jones et al. 2001; Penteriani et al. 2002). These impacts may be of increased concern if available habitat is isolated or limited or both. Furthermore, rates and impacts of natural disturbances are predicted to increase with current trends in climate change (Dale et al. 2000), thus highlighting the need to understand species' responses to disturbance.

Habitat is any area that provides resources and conditions that promote survival and reproduction of an individual (Hall et al. 1997). Therefore, habitat selection is critical for completion of life-history stages. Although understanding the actual

process of habitat selection may not be feasible, examining areas used by individuals may suggest environmental variables used in the selection process. Furthermore, identification of important microhabitat features is necessary for effective conservation efforts, particularly if habitat is limited (Fernandez and Palomares 2000; Oppel et al. 2004).

Habitat selection of sites to cache and hoard food for later consumption has evolved in many birds, mammals, and arthropods (Smith and Reichman 1984; Vander Wall 1990). To reduce loss of cached items due to decomposition or pilferage, food-hoarding animals evolved many food-handling behaviors, including selection of the cache site (Vander Wall 1990). Selected cache sites may be dry (burrows of steppe rodents—Formozov 1966), inaccessible (deep crevices sealed by red-headed woodpeckers—MacRoberts 1975), or wet (scavenged carcasses placed in water by hyenas—Kruuk 1972) and will vary with species needs. Disturbance may damage or alter features about cache sites and reduce the quality of a site to preserve food. Thus disturbance could be detrimental to a food-hoarding animal, particularly if the cache site is lost altogether.

Red squirrels (*Tamiasciurus hudsonicus*) in western North America defend territories surrounding conspicuous, centrally

* Correspondent: czugmeyer@yahoo.com

located larderhoards (C. C. Smith 1968) and therefore provide an excellent model system to examine questions relating to habitat selection of cache locations following disturbance. Red squirrels cache conifer cones in large cone-scale piles or middens resulting from concentrated feeding (Finley 1969). Middens create a cool, moist environment that prevents desiccation of stored cones (Brown 1984; Shaw 1936; USFWS 1993), thereby providing an important food source for winter and times of cone failure (M. C. Smith 1968; Steele and Koprowski 2001). Midden locations are associated with forest vegetation characteristics, such as high basal area and canopy cover, that help to maintain microclimates necessary to preserve cones (Finley 1969; Mattson and Reinhart 1997; Smith and Mannan 1994; Uphoff 1990; Vahle and Patton 1983). Vegetation structure surrounding middens may be damaged or altered after disturbance such as severe insect infestation. Frequency and impacts of insect infestations are projected to increase with current trends in global climate change (Ayres and Lombardero 2000), a trend that may have significant impacts if midden function is impaired. Although numbers of red squirrels decrease in insect-disturbed areas (Koprowski et al. 2005; Matsuoka et al. 2001), the response of squirrels to structural and vegetation disturbance is poorly known.

The Mt. Graham red squirrel (*T. h. grahamensis*), a federally listed subspecies of red squirrel (Sullivan and Yates 1995; USFWS 1987), occupies high-elevation coniferous forests (spruce–fir and mixed conifer) of the Pinaleño Mountains, Graham County, Arizona (Hoffmeister 1986). Midden sites may be limited because the Pinaleño Mountains are located at the southern terminus of the distribution of red squirrels and have increased exposure to hot and dry conditions relative to those in higher latitudes (Smith and Mannan 1994), the very environment that might necessitate a need for cool midden microclimates. Recent insect infestations of western balsam bark beetle (*Drycoetes confusus*), spruce beetle (*Dendroctonus rufipennis*), and the introduced spruce aphid (*Elatobium abietinum*) beginning in the late 1990s severely damaged spruce–fir forest and reduced basal area of live trees and seed crop (Koprowski et al. 2005; USDA 2000). Consequently, occupied middens in an area with severe insect damage decreased 96% from 23 in 1997 to 1 in 2001 (Koprowski et al. 2005). In 2003, red squirrels began to recolonize high-elevation forests that now consist of a mosaic of forest conditions with varying levels of insect damage, providing an opportunity to examine habitat selection of midden sites in response to disturbance. Although establishment of territories and middens by red squirrels can be investigated by documenting displacement (C. C. Smith 1968), conducting removal experiments (Larsen and Boutin 1995), and determining settlement of dispersing individuals (Larsen and Boutin 1994; Haughland and Larsen 2004a, 2004b), recolonization of an unoccupied area is an ideal opportunity to understand territory establishment, because individuals are able to select habitat from a suite of environments with little or no influence of the presence of conspecifics. Our objectives were to determine which traits distinguish midden locations from random forest locations, to determine if any traits distinguish occupied midden locations

from historical middens (those occupied before insect damage that now remain unoccupied), to examine relationships between habitat selection and occupancy with level of insect damage, and to examine interactions between forest structure and midden microclimate.

MATERIALS AND METHODS

Study area.—We collected data from September 2003 to December 2005 within the insect-damaged spruce–fir forest (529 ha, >3,048 m elevation) in the Pinaleño Mountains of southeastern Arizona. The forest was dominated by Engelmann spruce (*Picea engelmannii*) and cork-bark fir (*Abies lasiocarpa*), but included Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), southwestern white pine (*Pinus strobiformis*), and aspen (*Populus tremuloides*).

Midden occupancy.—Historical middens, those found during initial surveys by the Arizona Game and Fish Department in the 1980s, are permanently marked. We searched for new middens and sign of squirrel activity during ground surveys each fall (September–November, 2003–2005) and while tracking radiocollared squirrels (Zugmeyer and Koprowski 2009). We conducted quarterly surveys of middens ($n = 377$) to monitor and evaluate midden occupancy. Middens were recorded as occupied or unoccupied based on sign of red squirrel activity, observations of squirrels displaying resident behavior, or both (Mattson and Reinhart 1997). Sign of red squirrel activity included remnants of feeding (fresh cone scales and cores), cone caching, and clipped cones (Finley 1969). Resident behaviors were defined as territorial vocalizations, chasing of other squirrels, or caching cones within a midden (Gurnell 1987).

Midden characteristics.—To determine whether features at midden sites within insect-damaged forests were similar to features found before insect infestation (Smith and Mannan 1994), we compared characteristics among occupied middens ($n = 18$), a random subset of unoccupied historical middens ($n = 28$), and random forest locations ($n = 26$). To determine if squirrels were selecting specific historical middens to occupy, we compared characteristics of occupied and unoccupied middens. To obtain random locations, we used ArcView 3.3 (Environmental Systems Research Institute 2002) to generate random points in the same general area as occupied middens, followed distances and bearings from known locations, and tagged trees within 10 m of the located point.

At each occupied midden, unoccupied historical midden, and random location, we measured 3 physical and 14 vegetation characteristics within circular plots (radius = 10 m, area = 0.3 ha) centered on a tree. We measured percent slope, slope aspect, and elevation from the center of the plots. We used a global positioning system (GeoExplorer II; Trimble Navigation, Sunnyvale, California) to obtain elevation. Direction was determined from slope aspect as: N, if $315^\circ < \text{aspect} \leq 45^\circ$; E, if $45^\circ < \text{aspect} \leq 135^\circ$; S, if $135^\circ < \text{aspect} \leq 225^\circ$; and W, if $225^\circ < \text{aspect} \leq 315^\circ$. We recorded species, diameter at breast height (DBH), and snag class (dead or alive) for all trees > 3 cm DBH, and noted number of logs and decayed logs (≥ 20 cm

DBH at the large end and ≥ 2 m in length) within each circular plot. We used densiometer readings at 0, 5, and 10 m in the 4 cardinal directions to determine canopy cover. Finally, we placed temperature data loggers (Thermochron iButtons, model DS1921G-F5; Dallas Semiconductor, Dallas, Texas) at each site to measure surface temperature from 1 September 2004 to 31 August 2005. Data loggers were housed in open-ended plastic containers covered in hardware cloth for protection and placed open side down, 1 m north of the center of the plot, and elevated approximately 1 cm to allow air circulation. We programmed data loggers to record temperature every 91 min from May to November and 121 min from December to April. While downloading data loggers on 11 May 2005, we visually estimated percent snow cover remaining on each plot.

Level of insect damage.—To assess level of insect damage throughout the study area, we used high-resolution satellite imagery (0.6 m Quickbird) classified by pixel into 9 ground cover classes: deep shadow; shadow; healthy large conifers; small healthy trees or shrubs; dying or dead trees; cienega, grass, or aspen; tan soil; bright rock; and asphalt road, dark rock, or dark soil (Wood et al. 2007); shadows were unlit sides of live tree canopies. We used the classified image to generate a map of insect damage where each pixel represented the percent of dead trees (total number of class 5/sum of classes 1–6) found within a 10-m circular buffer. Using this map, we examined relationships between level of insect damage and midden location and occupancy.

Statistical analyses.—We examined physical and vegetative characteristics of all 3 types of sites (random, unoccupied midden, and occupied midden) separately with linear contrasts and simultaneously with stepwise logistic regression. For each variable, we used linear contrasts in 2 comparisons: middens (occupied and unoccupied) versus random locations, and occupied versus unoccupied middens. When examining differences in vegetation structure, we included all physical characteristics as covariates.

We used logistic regression to determine variables that were most important in predicting whether a site was a midden or random location, and occupied or unoccupied midden. Because we had no a priori models to explain differences between middens and random locations, we used stepwise selection ($P < 0.25$ for entry, $P > 0.1$ for removal) of variables to include in a logistic regression model. We only included variables for selection that had correlation < 0.75 with each other to reduce impacts of multicollinearity (Edelman and Koprowski 2006; McGarigal et al. 2000).

To examine monthly variation in surface temperature, we compared 3 measures of surface temperature between random locations, unoccupied middens, and occupied middens. Maximum, minimum, and maximum daily range temperatures were the highest, lowest, and highest range (daily high – daily low) of temperatures respectively recorded during the first 7 days of every month. For each measure of temperature in each of the 12 months, we used linear contrasts to make the same comparisons as previously described. Elevation, slope, and direction were included as covariates. Because vegetation measures were obtained during summer, we examined July temperatures

with stepwise ($P < 0.25$ for entry, $P > 0.1$ for removal) multiple regression to determine the variables that best explained variation in midden temperature.

Insect infestation has primarily affected the upper elevations. Proportion of dead trees increased with elevation ($F = 7.39$, $df. = 1, 64$, $P = 0.008$) and was included as a covariate when examining variation in level of insect damage, measured as percent dead trees from the damage map. We used linear regression to examine relationships between midden type (occupied versus unoccupied) and midden occupancy (percent of quarterly surveys that a midden is occupied) with level of insect damage.

RESULTS

Midden occupancy.—Forty-five middens were occupied during ≥ 1 of 10 surveys from September 2003 to December 2005; 31% were either new middens ($n = 8$) or shifts of previously designated midden sites ($n = 6$, mean distance from original scale pile = 16 m, range = 7.5–26 m). New middens had minimal or no scale pile, with cached cones (>30) sometimes found on the ground rather than in a scale pile.

Midden occupancy was not associated with percent dead trees ($n = 24$, $F = 0.12$, $df. = 1, 21$, $P = 0.73$). Historical middens that were reoccupied ($n = 17$, mean time since last occupied = 29 months, 95% confidence interval [95% CI] 22–36 months) during our study had been occupied more recently than middens that remained unoccupied ($n = 100$, mean time since last occupied = 42 months, 95% CI 39–45 months; $t = 3.21$, $df. = 115$, $P = 0.002$).

Midden characteristics.—Physical characteristics of midden and random sites differed only in slope and elevation (Table 1). All midden sites (occupied and unoccupied) were located in areas with lower slope than random locations. Occupied middens were on lesser slopes and located at lower elevations than unoccupied middens (Table 1).

Middens and random locations did not differ in number of total trees, live trees, dead trees, decayed logs, and logs, or in average canopy cover at the plot center (Table 1). However, midden sites had higher canopy cover at 5 and 10 m, total canopy cover, number of large live trees (>40 cm DBH), basal area of total, live, and dead trees, and volume of logs. Basal area of live trees was the only vegetation measure that was higher at occupied middens than at unoccupied middens (Table 1).

Total basal area, log volume, number of decayed logs, and number of live trees were important variables for distinguishing middens from random locations (Table 2). A location increased in likelihood of being a midden by 3% (95% CI 1–5%) with a 1-m² increase in total basal area, by 206% (95% CI 43–558%) with a 1-m³ increase in log volume, by 40% (95% CI 2–98%) with an increase of 1 decayed log, and decreased by 4% (95% CI 2–6%) with a decrease of 1 live tree. Slope, basal area of live trees, and elevation were important variables for distinguishing occupied middens from unoccupied middens (Table 2). A location decreased in likelihood of being an occupied midden by 13% (95% CI 3–33%) with a 1° decrease in slope, increased in likelihood by 2% (95% CI 100–105%)

TABLE 1.—Mean ($\pm SE$) physical and vegetation measurements for random locations ($n = 26$) and Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) unoccupied middens ($n = 28$) and occupied middens ($n = 18$) in the insect-damaged forest above 3,000 m in the Pinaleño Mountains, Arizona, fall 2003 to summer 2005.

Physical or vegetation characteristic	Random location	Unoccupied midden	Occupied midden	Random versus midden P^a	Unoccupied versus occupied P^a
Slope (%)	29.0 \pm 2.0	25.6 \pm 1.9	16.1 \pm 2.4	0.012	<0.001
Elevation (m)	3,115 \pm 7	3,146 \pm 7	3,118 \pm 10	0.603	0.001
Aspect (°)	217 \pm 12	225 \pm 12	239 \pm 16	0.410	0.582
Total canopy cover (%)	64.7 \pm 2.6	73.1 \pm 2.6	78.6 \pm 3.4	0.022	0.950
Center	72.5 \pm 3.1	73.7 \pm 3.1	82.9 \pm 4.1	0.413	0.469
5 m from center	60.5 \pm 3.1	71.8 \pm 3.1	78.5 \pm 4.1	0.017	0.949
10 m from center	60.9 \pm 2.9	73.6 \pm 2.8	74.3 \pm 3.8	0.007	0.587
Total trees (no./ha)	1,578 \pm 135	1,827 \pm 132	2,059 \pm 175	0.589	0.752
Live trees	894 \pm 111	839 \pm 108	1,115 \pm 144	0.512	0.660
Live trees (>40 cm DBH)	1.4 \pm 1.3	11.8 \pm 1.3	10.2 \pm 1.7	<0.001	0.957
Dead trees	685 \pm 87	988 \pm 85	944 \pm 113	0.097	0.942
Total basal area (m ² /ha)	54.8 \pm 3.7	68.6 \pm 3.6	80.7 \pm 4.8	<0.001	0.106
Live tree basal area	15.8 \pm 2.7	16.0 \pm 2.6	33.1 \pm 3.5	0.022	0.018
Dead tree basal area	39.0 \pm 3.5	52.5 \pm 3.4	47.6 \pm 4.6	0.008	0.896
Total logs (no./ha)	72 \pm 12	89 \pm 11	78 \pm 15	0.368	0.953
Volume logs (m ³ /ha)	27 \pm 8	60 \pm 8	52 \pm 10	0.019	0.855
Total decayed logs (no./ha)	82 \pm 19	155 \pm 18	133 \pm 24	0.169	0.155

^a Results of linear contrasts comparing 1) random locations versus middens and 2) unoccupied middens versus occupied middens.

with a 1-m² increase in basal area of live trees, and decreased in likelihood by 2% (95% CI 1–3%) with a 1-m decrease in elevation.

Midden microclimates.—Surface temperatures varied monthly (Fig. 1). May temperatures varied greatly; percent snow cover in May differed between random and midden locations ($F = 9.10$, $df. = 2, 63$, $P < 0.001$; site mean percent cover $\pm SD$: random = 22% \pm 32%, unoccupied = 45% \pm 41%, occupied = 70% \pm 32%). With exception of July, when maximum temperatures at midden sites tended to be higher, maximum surface temperatures tended to be lower at midden sites than at random locations (Fig. 1a; Table 3). Minimum temperatures at midden sites tended to be warmer than random locations during fall and early winter months (Fig. 1b; Table 3).

TABLE 2.—Results of stepwise logistic regression models to assess odds of a) a site being a Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) midden ($n = 46$) versus random location ($n = 26$), or b) a midden being occupied ($n = 18$) versus unoccupied ($n = 28$) in the insect-damaged forest above 3,000 m in the Pinaleño Mountains, Arizona, fall 2003 to summer 2005.

Source	Estimate	SE	P	Odds ratio
a)				
Intercept	-7.46	2.32	0.001	—
Total basal area (m ²)	0.035	0.011	0.002	1.03
Log volume (m ³)	1.12	0.39	0.004	3.06
No. decayed logs	0.35	0.17	0.036	1.4
No. live trees	-0.039	0.021	0.058	0.96
b)				
Intercept	73.60	38.78	0.058	—
Slope (°)	-0.14	0.058	0.013	0.869
Live basal area (m ²)	0.028	0.014	0.043	1.02
Elevation (m)	-0.023	0.012	0.057	0.977

Differences in maximum and minimum surface temperatures were reflected in the lower maximum daily ranges of midden sites (Fig. 1c; Table 3). Patterns were similar when comparing occupied and unoccupied middens. Occupied middens had lower maximum temperatures and higher minimum temperatures than unoccupied middens during snow-free months (Figs. 1a and 1b; Table 3). Differences were reflected in the lower maximum daily range of temperatures at occupied middens during snow-free months (Fig. 1c; Table 3).

Maximum July temperature on the midden surface was cooler at random locations and occupied middens than at unoccupied middens ($F = 7.03$, $df. = 1, 54$, $P = 0.011$). In addition, maximum July temperature was decreased with higher average canopy cover at plot center ($F = 12.23$, $df. = 1, 54$, $P < 0.001$) and was increased with greater number of logs ($F = 3.89$, $df. = 1, 54$, $P < 0.053$). Minimum July temperature was cooler at middens facing south and east than at middens facing north and west ($F = 43.30$, $df. = 1, 55$, $P < 0.001$) and was warmer with higher basal area of live trees ($F = 25.22$, $df. = 1, 55$, $P < 0.001$) and higher average canopy cover at plot center ($F = 10.53$, $df. = 1, 55$, $P = 0.002$). Maximum July daily range was smaller at random locations and occupied middens than at unoccupied middens ($F = 7.35$, $df. = 1, 55$, $P = 0.009$), was smaller with higher average canopy cover at plot center ($F = 17.92$, $df. = 1, 55$, $P < 0.001$), and larger with higher numbers of logs ($F = 4.56$, $df. = 1, 55$, $P = 0.037$).

Level of insect damage.—Insect damage did not differ among random, unoccupied, and occupied sites where vegetation was measured (random: $n = 26$, $\bar{X} = 52.1\%$, range = 16.2–78.4%; unoccupied: $n = 26$, $\bar{X} = 53.4\%$, range = 38.2–74.2%; occupied: $n = 16$, $\bar{X} = 45.3\%$, range = 24.5–63.2%; $F = 2.28$, $df. = 2, 64$, $P = 0.110$). Percent dead trees

determined from imagery was similar to those measured in the field (paired t -test: $t = 0.487$, $d.f. = 71$, $P = 0.63$). Percent dead trees at unoccupied middens was 7.07% higher than occupied middens (unoccupied: $n = 237$, $\bar{X} = 59.1\%$, 95% CI 57.6–60.7%; occupied: $n = 39$, $\bar{X} = 50.8$, 95% CI 46.4–55.3%; $F = 12.24$, $d.f. = 1, 273$, $P < 0.001$).

DISCUSSION

Despite changes to forest structure, adequate midden sites continue to exist after insect infestation. Middens selected by Mt. Graham red squirrels within insect-damaged forest were characterized by indicators of high forest density, such as high basal area, log volume, and canopy cover. Results were congruent with features at middens before insect infestation (Smith and Mannan 1994) as well as across the distribution of red squirrels (Finley 1969; Mattson and Reinhart 1997; Uphoff 1990; Vahle and Patton 1983). In addition, approximately 70% of occupied middens were historical locations, further evidence that insect infestation has not eliminated midden habitat. However, differences between occupied middens and historical middens, which are presently unoccupied, reflect the severity of insect infestation that red squirrels will tolerate. Midden sites occupied during our study were found in areas with <64% dead trees. Large trees produce the most cones (USDA and USFS 1965) and proximity to a food source is economical for hoarding because reduced time and energy spent traveling (Charnov 1976). Although number of large trees did not differ, occupied middens had greater potential for cone production with greater basal area of live trees than historic midden sites. Establishment of middens near a food source may be important in disturbed forests, such as our study area, where availability of food is reduced and basal area of live trees around middens has decreased 63.3% after onset of insect infestation (Koprowski et al. 2005).

Occupied middens experienced cooler surface temperatures than unoccupied middens during snow-free months when sun and heat have strong desiccating effects on middens. As cones age, scales open and seeds disperse by gravity and wind (USDA and USFS 1965), at which point squirrels no longer benefit from cone harvesting (Shaw 1936). Cone opening is prevented by storage in a midden's cool, moist environment (Brown 1984; Shaw 1936), suggesting that locations with cool surface temperatures will better preserve cones. Squirrels are not likely selecting midden locations solely on surface temperature, because random locations occasionally had temperature regimes similar to occupied middens. Cool surface temperatures were associated with high basal area, log volume, and canopy cover, likely cues used for selection because squirrels demonstrate preference and ability to discern differences in these microhabitat characteristics (Bakker 2006). The ability of vegetation structure to create a cool, moist microclimate was further demonstrated in May when percent snow cover remaining on occupied middens was 3 times greater than cover at random locations. Canopy cover at the center of the plot was associated with maximum, minimum, and maximum daily range of surface temperature and may be more important

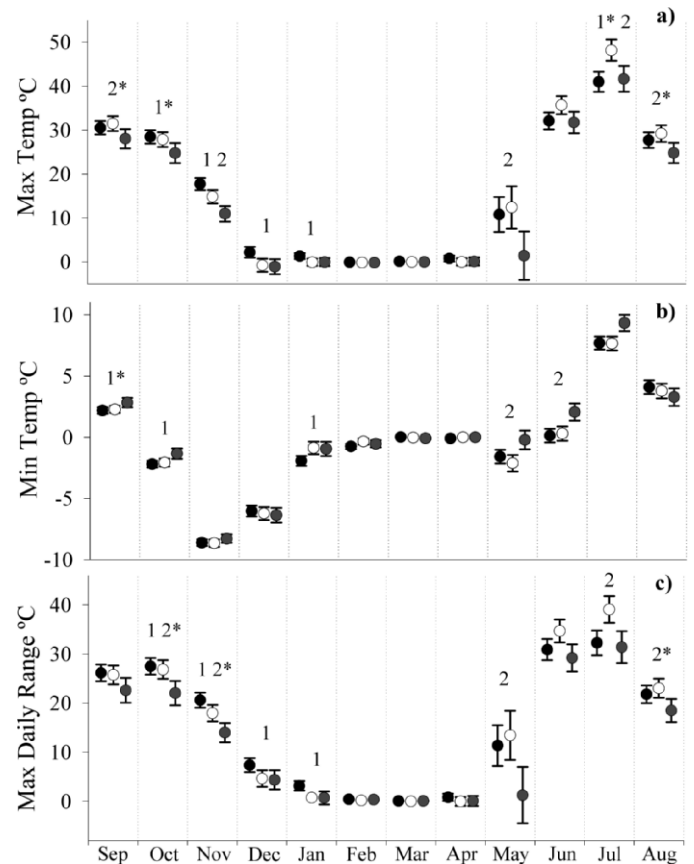


FIG. 1.—Mean (\pm SE) a) maximum, b) minimum, and c) maximum daily range of ground surface temperature from September 2004 to August 2005 for random locations (\bullet) and unoccupied (\circ) and occupied (\bullet) Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) middens in the insect-damaged forest above 3,000 m in the Pinaleno Mountains, Arizona. A “1” indicates $P < 0.05$ for linear contrast of middens and random locations, “2” indicates $P < 0.05$ for linear contrast of unoccupied and occupied middens. An asterisk (*) indicates $0.1 > P > 0.05$. Sample sizes are (random, unoccupied, occupied): September–October (26, 23, 12); November (26, 23, 16); December–May (24, 20, 11); June–July (22, 23, 15); August (22, 23, 14).

in insect-damaged forest where canopy cover at midden sites decreased 68% from 1990 to 2002 (J. L. Koprowski, pers. obs.). Sites with greater canopy cover may also provide protection from raptors, the most commonly observed predator (Schauffert et al. 2002). Furthermore, within insect-damaged forest, areas of reduced canopy cover equate to areas with increased dead trees and fuel loads that can result in increased frequency and intensity of fire that further decreases survival (Koprowski et al. 2006). Thus, reduced canopy cover from severe insect infestation has potential to alter midden microclimate and increase rates of predation and fire, important influences on survival of red squirrels.

Recolonization of insect-damaged forest provided increased understanding of what constitutes midden habitat, because individuals were able to select a midden location within a mosaic of forest conditions and levels of insect damage without residents already in the forest to influence site selection. Many habitat selection models assume that individuals are selecting

TABLE 3.—Comparisons of maximum, minimum, and maximum daily range of ground surface temperature from September 2004 to August 2005 for random locations, and unoccupied and occupied Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) middens in the insect-damaged forest above 3,000 m in the Pinaleno Mountains, Arizona. Sample sizes (random, unoccupied, occupied): September–October (26, 23, 12); November (26, 23, 16); December–May (24, 20, 11); June–July (22, 23, 15); August (22, 23, 14).

Temperature	September	October	November	December	January	May	June	July	August	Other months
Midden versus random										
Maximum		$t_{58} = -1.71$ $P = 0.093$	$t_{62} = -3.44$ $P = 0.001$	$t_{52} = -2.69$ $P = 0.01$	$t_{52} = -2.16$ $P = 0.036$			$t_{57} = 1.95$ $P = 0.057$		$ t < 1.8$ $P > 0.31$
Minimum	$t_{58} = 1.79$ $P = 0.079$	$t_{58} = 1.95$ $P = 0.056$			$t_{52} = 2.31$ $P = 0.025$					$ t < 1.4$ $P > 0.16$
Range		$t_{58} = -2.09$ $P = 0.041$	$t_{62} = -2.97$ $P = 0.004$	$t_{52} = -2.01$ $P = 0.051$	$t_{52} = -2.51$ $P = 0.016$					$ t < 1.5$ $P > 0.14$
Occupied versus unoccupied										
Maximum	$t_{58} = -1.87$ $P = 0.067$		$t_{62} = -1.98$ $P = 0.052$			$t_{52} = -2.21$ $P = 0.032$		$t_{57} = -2.04$ $P = 0.046$	$t_{56} = -1.87$ $P = 0.067$	$ t < 1.5$ $P > 0.13$
Minimum						$t_{52} = 2.59$ $P = 0.013$	$t_{57} = 2.13$ $P = 0.038$			$ t < 1.6$ $P > 0.11$
Range		$t_{58} = -1.95$ $P = 0.057$	$t_{62} = -1.85$ $P = 0.069$			$t_{52} = -2.30$ $P = 0.026$		$t_{57} = -2.09$ $P = 0.042$	$t_{56} = -1.84$ $P = 0.072$	$ t < 1.5$ $P > 0.15$

the highest quality habitat available (Fretwell and Lucas 1969; Pulliam and Danielson 1991). Although individuals presumably did not sample the entire 529-ha study area, Mt. Graham red squirrels have large home ranges (Koprowski et al. 2008) and explore large areas of forest while foraging. Squirrels presumably selected the best unoccupied midden location within areas sampled (Pulliam and Danielson 1991). Social dominance and availability of vacant territories influence habitat selection and territory establishment in many taxa (Jacquot and Solomon 2004; Petit and Petit 1996; Stiver et al. 2006). Red squirrels are excluded from areas by territorial defense of conspecifics (C. C. Smith 1968) and midden acquisition is often influenced by vacant territories (Gurnell 1984; Price et al. 1986) or bequeathal by females (Boutin and Price 1993; Price and Boutin 1992). Such effects are minimized in our study because of recolonization of unoccupied forest.

The importance of middens for survival of red squirrels, particularly during times of low food availability, has long been acknowledged (M. C. Smith 1968; Steele and Koprowski 2001). However, characteristics that define a midden location may not be consistent throughout the range or under varying forest conditions. Aspects of midden structure associated with surface temperature may be more important in the southern portion of the distribution of red squirrels, where temperatures are warmer and drier. In contrast, in parts of the Rocky Mountains, risk of midden excavation by grizzly bears (*Ursus arctos horribilis*—Mattson and Reinhart 1997) may have a greater influence on midden site selection than features influencing surface temperature. Because the midden is critical for survival, selection of midden location will influence selection of habitat at a larger scale. If numbers of live trees in a forest are severely reduced (>64% tree mortality in this study), squirrels may not find adequate midden locations and as a result may not select or use any forest in the area. Studies of forest thinning practices suggest similar results with a decline in squirrel density after removal of >50% stem density (Koprowski 2005). Unless red squirrels alter habitat selection

after severe insect infestation, forests receiving greater damage will likely no longer represent habitat. In addition, although red squirrels appear to equally prefer insect-damaged to healthy forest, individuals living in insect-damaged forest had significantly lower survival than individuals living in healthy forest (Zugmeyer and Koprowski 2009). Although the cause remains unknown, low survivorship reduced the number of potential reproductive events attained by an individual by 50%, dramatically reducing individual fitness for squirrels living in insect-damaged forest (Zugmeyer and Koprowski 2009). Ultimately, equal preference of insect-damaged forests combined with low survival suggests that response of squirrels to insect disturbance may result in an ecological trap (Robertson and Hutto 2006; Schlaepfer et al. 2002). Decreased food storage abilities, increased risk of predation, and greater likelihood of catastrophic fire further reduce the quality of insect-damaged habitat, which provides additional support for the possibility of an ecological trap. Although ecological traps do not necessitate population declines (Robertson and Hutto 2006), they remain a concern for the persistence of populations in isolated or fragmented forests with no opportunity to move to undamaged habitat.

Impacts of forest insect infestations and other natural disturbances are projected to increase in the future with the current trends in global climate change (Ayres and Lombardero 2000; Dale et al. 2000) and therefore have the potential to affect many forest-dwelling species. Ecological and evolutionary traps (Schlaepfer et al. 2002) may become more common as climate change creates asynchronous relationships between species and their environments (e.g., yellow-bellied marmots [*Marmota flaviventris*] emerging early from hibernation causing asynchrony with phenology of food plants [Parmesan 2006]). Disturbance and climate change commonly result in range shifts (Parmesan 2006), but high rates of habitat loss may eliminate that option for many species. Although conservation efforts can help preserve remnant habitat for threatened and endangered species, there remains the threat of disturbance

events that may damage or severely alter the ecological integrity of critical areas. Therefore, documenting response and ability, or lack thereof, to adapt to impacts of disturbance is a priority for future research and a necessity for aiding conservation efforts, especially in the face of predicted climate change.

ACKNOWLEDGMENTS

We thank C. J. Conway, K. M. Leonard, R. W. Mannan, K. E. Munroe, M. G. Rheude, D. J. A. Wood, and an anonymous reviewer for comments on earlier drafts as well as thoughtful discussion, and M. Banville, S. R. Bertelsen, V. L. Greer, M. Griffiths, L. Helleckson, J. L. Jolley, S. R. B. King, M. J. Merrick, G. H. Palmer, K. Pokorny, A. Potter, M. Proctor, A. Stead, V. Steen, C. Steimer, M. Watson, and B. D. Weise for much field and logistical assistance. Field efforts were conducted under permits from the United States Department of Agriculture Forest Service, Arizona Game and Fish Department, United States Fish and Wildlife Service, and the University of Arizona's Institutional Animal Care and Use Committee. In particular we are indebted to B. Van Pelt, Arizona Game and Fish Department, for his efforts to procure funds. Funding and in-kind support for this research were provided by Arizona Game and Fish Department, United States Department of Agriculture, United States Forest Service, University of Arizona's Office of the Vice President for Research, Steward Observatory, Arizona Agricultural Experiment Station, and T&E Incorporated.

LITERATURE CITED

- AYRES, M. P., AND M. J. LOMBARDO. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262:263–286.
- BAKKER, V. J. 2006. Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *Journal of Mammalogy* 87:124–130.
- BENGTSSON, J., S. G. NILSSON, A. FRANC, AND P. MENOZZI. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management* 132:39–50.
- BOUTIN, S., AND K. PRICE. 1993. Post-breeding dispersal by female red squirrels (*Tamiasciurus hudsonicus*): the effect of local vacancies. *Behavioral Ecology* 4:151–155.
- BROWN, D. E. 1984. Arizona's tree squirrels. Arizona Game and Fish Department, Phoenix.
- CHARNOV, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- DALE, V. H., L. A. JOYCE, S. McNULTY, AND R. P. NEILSON. 2000. The interplay between climate change, forests, and disturbances. *Science of the Total Environment* 262:201–204.
- EDELMAN, A. J., AND J. L. KOPROWSKI. 2006. Characteristics of Abert's squirrel (*Sciurus aberti*) cavity nests. *Southwestern Naturalist* 51:64–70.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 2002. ArcView GIS: release 3.3. Environmental Systems Research Institute, Redlands, California.
- FERNANDEZ, N., AND F. PALOMARES. 2000. The selection of breeding dens by the endangered Iberian lynx (*Lynx pardinus*): implications for its conservation. *Biological Conservation* 94:51–61.
- FINLEY, R. B. J. 1969. Cone caches and middens of tamiasciurus in the Rocky Mountain region. *Miscellaneous Publications, Museum of Natural History, University of Kansas* 51:233–273.
- FORMOZOV, A. N. 1966. Adaptive modifications of behavior in mammals of the Eurasian steppes. *Journal of Mammalogy* 47:208–223.
- FRETWELL, S. D., AND H. L. LUCAS, JR. 1969. On territorial behavior and other factors influencing habitat distribution in birds, I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- GURNELL, J. 1984. Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. *Animal Behaviour* 32:1119–1131.
- GURNELL, J. 1987. The natural history of squirrels. Facts on File Inc., New York.
- HALL, L. S., P. R. KRAUSMAN, AND M. L. MORRISON. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:173–182.
- HAUGHLAND, D. L., AND K. W. LARSEN. 2004a. Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. *Journal of Mammalogy* 85:225–236.
- HAUGHLAND, D. L., AND K. W. LARSEN. 2004b. Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. *Journal of Animal Ecology* 73:1024–1034.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. University of Arizona Press, Tucson.
- JACQUOT, J. J., AND N. G. SOLOMON. 2004. Experimental manipulation of territory occupancy: effects on immigration of female prairie voles. *Journal of Mammalogy* 85:1009–1014.
- JONES, J., R. D. DEBRUYN, J. J. BARG, AND R. J. ROBERTSON. 2001. Assessing the effects of natural disturbance on a neotropical migrant songbird. *Ecology* 82:2628–2635.
- KOPROWSKI, J. L. 2005. Management and conservation of tree squirrels: the importance of endemism, species richness, and forest condition. Pp. 245–250 in *Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II* (G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster, eds.). *Proceedings RMRS-P-36*. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona.
- KOPROWSKI, J. L., M. I. ALANEN, AND A. M. LYNCH. 2005. Nowhere to run and nowhere to hide: response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biological Conservation* 126:491–498.
- KOPROWSKI, J. L., S. R. B. KING, AND M. MERRICK. 2008. Home ranges are expanded in a peripheral population: space use of endangered Mt. Graham red squirrels. *Endangered Species Research* 4:227–232.
- KOPROWSKI, J. L., K. M. LEONARD, C. A. ZUGMEYER, AND J. L. JOLLEY. 2006. Direct effects of fire on endangered Mt. Graham red squirrels. *Southwestern Naturalist* 51:59–63.
- KRUUK, H. 1972. *The spotted hyena: a study of predation and social behavior*. University of Chicago Press, Chicago, Illinois.
- LARSEN, K. W., AND S. BOUTIN. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75:214–223.
- LARSEN, K. W., AND S. BOUTIN. 1995. Exploring territory quality in the North American red squirrel through removal experiments. *Canadian Journal of Zoology* 73:1115–1122.
- MACROBERTS, M. H. 1975. Food storage and winter territory in red-headed woodpeckers in northwestern Louisiana. *Auk* 92:382–385.
- MATSUOKA, S. M., C. M. HANDEL, AND D. R. RUTHRAUFF. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. *Canadian Journal of Zoology* 79:1678–1690.

- McGARIGAL, K., S. CUSHMAN, AND S. STAFFORD. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York.
- MATTSON, D. J., AND D. P. REINHART. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology* 34:926–940.
- OPPEL, S., H. M. SCHAEFER, V. SCHMIDT, AND B. SCHRODER. 2004. Habitat selection by the pale-headed brush-finch (*Atlapetes pallidiceps*) in southern Ecuador: implications for conservation. *Biological Conservation* 118:33–40.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- PENTERIANI, V., M. MATHIAUT, AND G. BOISSON. 2002. Immediate species responses to catastrophic natural disturbances: windthrow effects on density, productivity, nesting stand choice, and fidelity in northern goshawks (*Accipiter gentilis*). *Auk* 119:1132–1137.
- PETIT, L. J., AND D. R. PETIT. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell–Lucas model. *Ecological Monographs* 66:367–387.
- PRICE, K., AND S. BOUTIN. 1992. Territorial bequeathal by red squirrel mothers. *Behavioral Ecology* 4:144–150.
- PRICE, K., K. BROUGHTON, S. BOUTIN, AND A. R. E. SINCLAIR. 1986. Territory size and ownership in red squirrels: response to removals. *Canadian Journal of Zoology* 64:1144–1147.
- PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137:S50–S66.
- ROBERTSON, B. A., AND R. L. HUTTO. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87:1075–1085.
- SCHAUFFERT, C. A., J. L. KOPROWSKI, V. L. GREER, M. I. ALANEN, K. A. HUTTON, AND P. J. YOUNG. 2002. Interactions between predators and Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*). *Southwestern Naturalist* 47:498–501.
- SCHLAEPFER, M. A., M. C. RUNGE, AND P. W. SHERMAN. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- SHAW, W. T. 1936. Moisture and its relation to the cone-storing habit of the western pine squirrel. *Journal of Mammalogy* 17:337–349.
- SMITH, A. A., AND R. W. MANNAN. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. *Journal of Wildlife Management* 58:437–445.
- SMITH, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. *Ecological Monographs* 38:31–63.
- SMITH, C. C., AND O. J. REICHMAN. 1984. The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics* 15:329–351.
- SMITH, M. C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. *Journal of Wildlife Management* 32:305–317.
- SOUSA, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353–391.
- STEELE, M. A., AND J. L. KOPROWSKI. 2001. North American tree squirrels. Smithsonian Institution Press, Washington, D.C.
- STIVER, K. A., J. FITZPATRICK, J. K. DESJARDINS, AND S. BALSHINE. 2006. Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. *Animal Behaviour* 71:449–456.
- SULLIVAN, R. M., AND T. L. YATES. 1995. Population genetics and conservation biology of relict populations of red squirrels. Pp. 193–208 in *Storm over a mountain island: conservation biology and the Mt. Graham affair* (C. A. Istock and R. S. Hoffmann, eds.). University of Arizona Press, Tucson.
- [USDA] UNITED STATES DEPARTMENT OF AGRICULTURE. 2000. Forest insect and disease conditions in the Southwestern region. United States Department of Agriculture, Flagstaff, Arizona.
- [USDA AND USFS] UNITED STATES DEPARTMENT OF AGRICULTURE AND UNITED STATES FOREST SERVICE. 1965. Silvics of forest trees of the United States. Agriculture Handbook 271. United States Department of Agriculture and United States Forest Service, Washington, D.C.
- [USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 1987. Endangered and threatened wildlife and plants; determination of endangered status for the Mount Graham red squirrel. Federal Register 52:20994–20999.
- [USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 1993. Mount Graham red squirrel recovery plan. United States Fish and Wildlife Service, Phoenix, Arizona.
- UPHOFF, K. C. 1990. Habitat use and reproductive ecology of red squirrels (*Tamiasciurus hudsonicus*) in central Arizona. M.S. thesis, Arizona State University, Tempe.
- VAHLE, J. R., AND D. R. PATTON. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. *Journal of Forestry* 81:14–15.
- VANDER WALL, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois.
- WOOD, D. J. A., S. DRAKE, S. P. RUSHTON, D. RAUTENKRANZ, P. W. W. LURZ, AND J. L. KOPROWSKI. 2007. Fine scale analysis of Mount Graham red squirrel habitat following disturbance. *Journal of Wildlife Management* 71:2357–2364.
- ZUGMEYER, C. A., AND J. L. KOPROWSKI. 2009. Severely insect-damaged forest: a temporary trap for red squirrels? *Forest Ecology and Management* 257:464–470.

Submitted 9 December 2007. Accepted 18 June 2008.

Associate Editor was Gerardo Ceballos.