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Severely insect-damaged forest: A temporary trap for red squirrels?

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ABSTRACT

Recent insect infestations in the spruce-fir forest in the Pinaleño Mountains of southeastern Arizona provided an opportunity to document response to severe forest disturbance and existence of an ecological trap for an endemic montane isolate, the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). From September 2003 to December 2005 we assessed habitat selection and home range dynamics, and monitored potential correlates of fitness (body mass, reproduction, survivorship) in red squirrels living in insect-damaged forest, while drawing comparisons to squirrels inhabiting undamaged mixed-conifer forest. Although Mt. Graham red squirrels demonstrate equal-preference for habitat within insect-damaged forests and reproduce as well as individuals in undamaged forest, poor survivorship and reduced potential to reproduce suggest insect-damaged forest may function as an ecological trap. In addition, areas selected within insect-damaged forest had <69% dead trees, suggesting an upper limit to the extent of tree mortality tolerated by red squirrels. Habitat selection and sensitivity to disturbance will influence use of insect-damaged areas by forest-dwelling species. Although insect-damaged forest may retain habitat patches for a few individuals, low survivorship may generate an ecological trap.

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1. Introduction

Natural and anthropogenic disturbances create temporal and spatial heterogeneity of resources and cause short- and long-term changes to habitat (Sousa, 1984; Bengtsson et al., 2000). Disturbance often results in habitat alterations that may fragment and isolate populations of taxa (Ceballos and Ehrlich, 2002; Ewers and Didham, 2006). In addition, severe disturbance may dramatically alter habitat structure and in turn reduce reproductive success and site fidelity (Jones et al., 2001; Penteriani et al., 2002). Geographic isolation often increases risk of population extinction by increasing susceptibility to stochastic events (Lande, 1998; Alvarez, 2001).

Insect infestation alters forest structure by reducing live basal area and increasing understory vegetation, which transforms animal communities (Matsuoka et al., 2001; Suring et al., 2006). Responses of small mammals to structural change from insect infestation are largely unknown but may include temporary decreased abundance, particularly for seed-eating forest obligates dependent on mature conifers (Matsuoka et al., 2001; Koprowski et al., 2005; McDonough and Rexstad, 2005). Rapid changes to forest composition and structure may function as an 'ecological trap' for some species (Flaspohler et al., 2001).

Ecological traps occur when animals make maladaptive habitat selections using cues that formerly were positively correlated with habitat quality (Schlaepfer et al., 2002), thus individuals do not avoid habitat where measures of fitness, such as reproduction and survival, are lower relative to other available habitat (Robertson and Hutto, 2006). 'Equal-preference traps', when animals equally prefer high and low quality habitat, and 'severe traps', when animals prefer lower quality habitat, are known (Robertson and Hutto, 2006). A key requirement for demonstrating ecological traps is observing individual preference, which is often influenced by competition and aggression from conspecifics (Robertson and Hutto, 2006). Recolonization of an unoccupied area is an ideal opportunity to understand habitat preference and, when coupled with measures of individual fitness, determine potential for an ecological trap.

Tree squirrels are an indicator of mature forest structure (Carey, 2000) due to their dependence on mature trees for food, nests, and cover (Gurnell, 1987). We selected red squirrels (*Tamiasciurus hudsonicus*) as a model organism to determine response to insect infestation and potential for resulting ecological traps. In the western part of their range, red squirrels are territorial and defend

conspicuous larderhoards or middens (Steele, 1998); therefore, occupancy of an area by red squirrels is easily determined. Furthermore, red squirrels likely demonstrate demographic and behavioral responses to severe insect infestation due to dependence on conifer seeds as a primary food source (Gurnell, 1987); secondary foods include epigeous fungi and branch tips (Steele, 1998). The Mt. Graham red squirrel (*T. h. grahamensis*), a federally listed subspecies of red squirrel, occupies spruce-fir and mixed-conifer forests isolated in the Pinaleño Mountains in southeastern Arizona (USFWS, 1993). Recent infestations of western balsam bark beetle (*Drycoetes confusus*), spruce beetle (*Dendroctonus rufipennis*), and introduced spruce aphid (*Elatobium abietinum*) severely damaged spruce-fir forest in the Pinaleños in the late 1990s, reducing seed crop and basal area of live trees and causing numbers of red squirrels inhabiting spruce-fir to fall nearly to zero (Koprowski et al., 2005). Subsequently in 2003, red squirrels began to recolonize patches of spruce-fir forest in a mosaic of recovering forest, providing an opportunity to examine response to insect infestation and assess if insect-damage functions as an ecological trap. With basal area of live trees severely reduced, we expected squirrels to select areas with fewer dead trees, range over larger areas in search of food, and have reduced survival and reproductive success due to overall reduction in habitat quality. We expected squirrels to recolonize the insect-damaged area when available habitat in adjacent undamaged areas had few unoccupied middens. If insect-damage functions as a severe ecological trap, we would find greater occupancy of available midden habitat in damaged areas relative to undamaged. Alternatively, if insect-damage functions as an equal-preference trap, we would expect similar occupancy of available midden habitat in both areas. Thus to examine response to insect-damage and assess the possibility of an ecological trap, we: (1) assessed habitat selection, (2) documented home range, and (3) examined correlates of fitness in red squirrels that recolonized insect-damaged forest. We draw comparisons to squirrels inhabiting mixed-conifer forest that is relatively undamaged and examine support for the potential existence of an 'equal preference' ecological trap induced by insect-damage.

2. Methods

2.1. Study area and trapping

We studied Mt. Graham red squirrels from September 2003 to December 2005 within the insect-damaged, spruce-fir forest (529 ha, 3048–3267 m) in the Pinaleño Mountains of southeastern Arizona. The forest was dominated by Engelmann spruce (*Picea engelmannii*) and cork-bark fir (*Abies lasiocarpa*) in the upper elevations, but included Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), southwestern white pine (*Pinus strobiformis*), ponderosa pine (*Pinus ponderosa*), and aspen (*Populus tremuloides*) in greater numbers as elevation approached 3048 m. Beginning in 1996, all spruce-fir forest (termed 'insect-damaged') in the Pinaleños was impacted by insect infestation (Wood et al., 2007). Therefore, we simultaneously collected data in a portion of relatively undamaged mixed-conifer forest (termed 'undamaged'), 130 ha, 2850–2979 m) dominated by cork-bark fir, but that included previously listed species. The study areas contained 34% of all known middens in the Pinaleños (Koprowski et al., 2005) and were demographically linked by dispersal in both directions (C.A.Z. and J.L.K, unpublished data).

We used the trapping and handling methods of Koprowski et al. (2007) to capture and uniquely mark all squirrels, and radio collar all adults (>200 g). We assessed mass, sex, age class, and reproductive status of all squirrels.

2.2. Habitat preference

We examined habitat preference by quantifying available midden habitat within both forest types. We evaluated occupancy each December, as cached cones are visible and occupancy is easily assessed (Mattson and Reinhart, 1996). Midden habitat is limited in the Pinaleños and important for red squirrel survival (Smith, 1968; Smith and Mannan, 1994). We selected midden occupancy as our measure of preference rather than density of squirrels, a calculation that includes areas with no midden habitat. Middens were recorded as occupied or unoccupied based on sign of red squirrel activity and/or observations of squirrels displaying resident behavior (Mattson and Reinhart, 1997). We used midden occupancy from 1990 to 1997 to examine historical occupancy prior to insect infestation. Available middens, both pre- and post-infestation, were occupied at least once in the previous 3 years.

2.3. Home range and space use

We used a receiver and Yagi antenna (receiver: Model TRX-2000S, antenna: Model F164-165-3FB, Wildlife Materials International Inc., Carbondale, IL) to obtain radio-telemetric locations by homing and biangulation (White and Garrott, 1990). We tracked squirrels in daylight throughout each month. Consecutive locations were separated by ≥1 h to reduce autocorrelation.

We calculated seasonal home ranges from January 2004 to August 2005. Seasons were defined as winter (December to February), spring (March to May), summer (June to August), and fall (September to November). Locations were spread across the 3-month season. Incremental area plots reached an asymptote for most squirrels at 20 locations, setting the minimum number of locations per home range. Although squirrels in the undamaged area had greater mean number of locations per home range, both areas had significantly more than the minimum 20 locations (insect-damaged, 41 ± 2 locations; undamaged, 48 ± 1 locations; $t = -3.79$, $P = 0.0002$). We used Animal Movements (Hooge and Eichenlaub, 2000), with smoothing parameters calculated by least squares cross-validation, to determine 95% (termed 'range') and 50% (termed 'core') fixed-kernels (Millspaugh and Marzluff, 2001), and Ranges 6 (Anatrack, 2003) to calculate 95% and 50% minimum convex polygons (MCP). Ranges varied by season but not by estimator, fixed-kernel or MCP (Table 1). Cores varied by season and estimator, with fixed-kernel cores larger than MCP cores (Table 1). Since we found little to no variation in home range estimators, we use only fixed-kernel ranges and cores for analyses and report MCP values for comparison with other studies.

We used two simultaneous directional bearings, with inter-bearing angles between 70 and 110° (White and Garrott, 1990), to obtain biangulations and calculated locations with LOAS (Ecological Software Solutions, 2003). We used a beacon to estimate location error (Millspaugh and Marzluff, 2001). Within insect-damaged forests, steep drainages increased the bearing and linear error associated with biangulation (mean ± S.D., $n = 32$, bearing error, $8.6 \pm 6.2°$; linear error 42.9 ± 28.7 m) relative to undamaged forests (mean ± S.D., $n = 64$, bearing error, $5.6 \pm 4.5°$; linear error, 12 ± 6 m; Koprowski et al., 2008). Thus, we increased homing in insect-damaged forests (mean ± S.D., % homing 2004 = 35.9 ± 30.9%, % homing 2005 = 87.6 ± 17.3%) and used biangulation most frequently (mean homing = 28 ± 23% S.D.) in undamaged forest.

Within insect-damaged forest, squirrels typically select midden habitat in areas with <64% tree mortality and greater basal area of live trees (Zugmeyer and Koprowski, in press). To quantify habitat selected by squirrels in insect-damaged forest at a larger scale, we used high-resolution satellite imagery (0.6 m Quickbird) classified by pixel into 9 cover classes: (1) deep shadow; (2) shadow; (3)

Table 1

Results of a two-factor ANOVA examining main effects of home range estimator (fixed-kernel or MCP) and season on range and core size (±S.E.) for home ranges of Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona, winter 2004 to summer 2005.

| | Home range size | | Main effect | |
	Fixed-kernel	MCP	Estimator	Season
Range	2.97 ± 0.26	2.48 ± 0.22	$F_{1,427} = 1.38$, $P = 0.24$	$F_{3,427} = 19.08$, $P < 0.001$
Core	0.45 ± 0.05	0.36 ± 0.04	$F_{1,427} = 6.79$, $P = 0.01$	$F_{3,427} = 11.53$, $P < 0.001$

Sample size (range, core): $n = 216, 216$.

large live conifers; (4) small live trees; (5) dying/dead trees; (6) grass/aspen; (7) tan soil; (8) bright rock; and (9) road, dark rock, or soil (Wood et al., 2007). Shadows were unlit sides of live tree canopies (Wood et al., 2007). We used Hawth's tools (Beyer, 2006) to determine cover composition within seasonal home range polygons. We compared cover composition in selected areas with random areas by centering each seasonal home range about a random location. For each observed and random range and core we estimated percent dead trees (total number of class 5/sum of classes 1–6), percent open (sum of classes 7, 8, and 9/total classes), and number of live trees (sum of classes 1–4, and 6).

2.4. Body mass and demography

We determined seasonal body mass and reproductive condition (Koprowski, 2005a) for adult males and females in both study areas. We examined ratios of adults to subadults (young of the year < 200 g) and males to females for newly captured squirrels. Litter size was determined by homing to nests of all lactating females during 2004 and 2005; we counted juveniles at time of emergence. To examine potential lifetime reproductive success of mortalities, we calculated the number of potential reproductive events attained since first capture. We used peak frequency of scrotal condition and presence of lactation in Mt. Graham red squirrels (Koprowski, 2005a) to set limits for potential reproduction to March 31 for males and July 31 for females in a given year. Thus if an individual died prior to these dates, we assumed they had not reproduced in their last year.

We used radio-telemetry, trapping, and observation at middens to monitor survival of squirrels. If a squirrel could not be found or the radio-signal remained in one location, we attempted to capture missing squirrels at middens to determine their fate. Squirrels were considered dead if remains and radio collar were found, radio collar was found with no new sign and/or a new squirrel captured at the midden, or the missing individual was not captured and a new squirrel was observed at the missing individual's midden. Red squirrels are territorial, and if alive, tolerance of other squirrels at their midden is unlikely (Smith, 1968).

2.5. Statistical analyses

We conducted statistical analysis in JMP 5.1 (SAS Institute, 2003). We used the natural logarithm to transform data when necessary to meet the assumption of normality; we report means

(±S.E.) as untransformed values. To determine squirrel habitat preference, we used ANOVA and Fisher's exact test to compare historical and current occupancy, respectively, of available middens in each forest type. To determine severity of insect-damage tolerated by squirrels, we compared percent dead trees, percent open, and number of live trees between observed and random ranges and cores. We used multiple-regression to examine effect of home-range type (random vs. observed), while accounting for size and season, and ANOVA to examine effect of home-range type in each season, while accounting for size.

Range and core size did not vary between years in either forest type and were pooled (insect-damaged: range, $t_{44} = 1.32$, $P = 0.20$; core, $t_{44} = 1.07$, $P = 0.29$; undamaged: range, $t_{168} = -0.10$, $P = 0.92$; core, $t_{168} = -0.73$, $P = 0.47$). We used ANOVA, multiple regression, and Tukey–Kramer post hoc analyses, to examine effect of season, home range estimator, sex, and forest type on range and core size.

To determine dispersal patterns, we used Fisher's exact test to compare ratio of adults to subadults and males to females among newly captured individuals. We used *t*-tests and ANOVA to compare litter size, number of potential reproductive events, and body mass of squirrels between forest types. Mt. Graham red squirrels can demonstrate sex and seasonal differences in body mass (Koprowski, 2005a) so we compared body mass separately for each sex, while including season as a covariate. Body mass did not vary with year so data were pooled (mean ± S.E., insect-damaged: male, 233.8 ± 1.8 g, $F_{3,42} = 0.09$, $P = 0.96$; female, 232.4 ± 2.6 g, $F_{3,37} = 1.8$, $P = 0.16$; undamaged: male, 231.6 ± 1.1 g, $F_{3,148} = 0.90$, $P = 0.44$, female, 226.2 ± 1.2 g, $F_{3,122} = 1.45$, $P = 0.23$). We used Kaplan–Meier analysis (Kaplan and Meier, 1958) to compare survival between forest types and sexes; we determined fate, number of days survived since first capture, of each squirrel as of December 2005. We used linear regression to examine the relationship between survival within insect-damaged forests and home range size and percent of home range classified as dead trees or open area; we used the last home range calculated prior to death.

3. Results

3.1. Habitat available in both forests

Ample opportunities appeared to exist for settlement in each forest type. Prior to insect infestation (1990–1997), percent of available middens occupied did not differ between 'undamaged forest' and 'insect-damaged forest' (Table 2; $F_{1,14} = 0.69$, $P = 0.42$).

Table 2

Mean (±S.E.) December midden occupancy for Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) before insect-infestation (1990–1997) and during recolonization of insect-damaged forest (2003–2005) in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona.

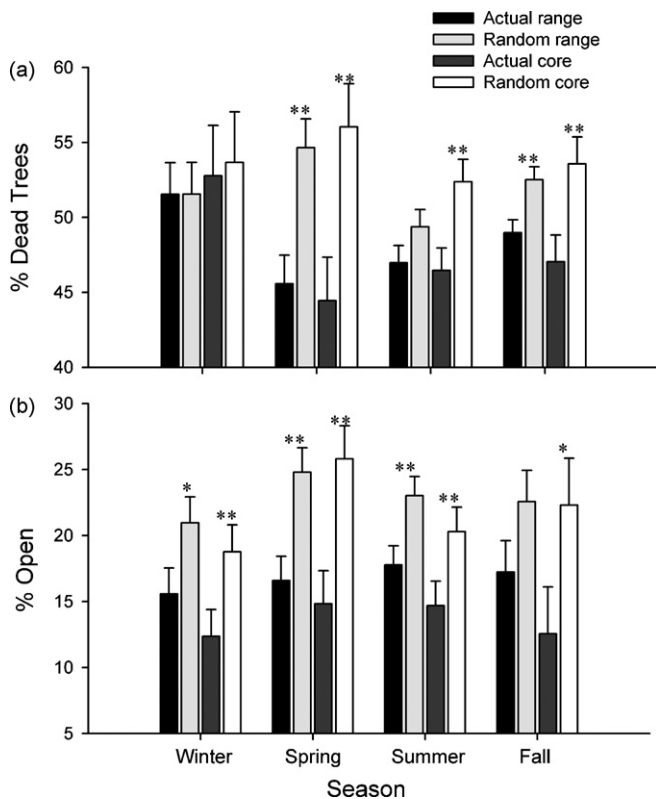| Years	Forest	% occupied	Occupied	Available	Range occupancy (%)
1990–1997	Insect-damaged	53 ± 5	82 ± 17	153 ± 22	35–81
	Undamaged	59 ± 5	38 ± 5	65 ± 6	42–85
2003–2005	Insect-damaged	14 ± 7	8 ± 5	46 ± 11	3–28
	Undamaged	20 ± 3	13 ± 1	65 ± 4	15–25

Table 3
Results of six multiple regression models comparing percent dead trees, percent open, and number of live trees within observed or randomly generated (Type) ranges and cores for Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged forest in the Pinaleño Mountains, Arizona, winter 2004 to summer 2005.

	d.f.	% dead trees		% open		Number live trees	
		F	P	F	P	F	p
95% range							
Full Model	5.86	3.35	0.008	8.6	<0.001	865.1	<0.001
Type	1.86	12.25	<0.001	23.6	<0.001	11.1	0.001
Season	3.86	1.30	0.280	0.51	0.67	2.25	0.09
Size (ha)	1.86	0.01	0.938	17.42	<0.001	3488.36	<0.001
50% core							
Full Model	5.86	3.54	0.006	6.1	<0.001	380.3	0.001
Type	1.86	13.97	<0.001	23.5	<0.001	10.4	0.002
Season	3.86	0.52	0.672	1.28	0.29	1.26	0.29
Size (ha)	1.86	1.29	0.260	2.75	0.101	1558.78	<0.001

Table 4
Seasonal fluctuations in mean 95% range and 50% core ($\pm$S.E.) for Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona, winter 2004 to summer 2005.

Season	Forest type	95% range (ha)		50% core (ha)	
		Kernel[a]	MCP[b]	Kernel	MCP
Winter	Insect	3.33 ± 0.89	3.57 ± 0.91	0.50 ± 0.16	0.38 ± 0.17
	Non-insect	1.24 ± 0.17	0.92 ± 0.12	0.16 ± 0.03	0.2 ± 0.03
Spring	Insect	4.29 ± 0.98	4.39 ± 1.29	0.62 ± 0.16	0.38 ± 0.09
	Non-insect	2.22 ± 0.31	1.74 ± 0.19	0.38 ± 0.07	0.25 ± 0.04
Summer	Insect	8.77 ± 2.06	7.74 ± 1.75	1.25 ± 0.45	1.11 ± 0.35
	Non-insect	3.66 ± 0.62	2.76 ± 0.43	0.60 ± 0.13	0.45 ± 0.08
Fall	Insect	3.54 ± 1.07	3.25 ± 0.97	0.33 ± 0.10	0.36 ± 0.13
	Non-insect	1.54 ± 0.33	1.30 ± 0.29	0.21 ± 0.06	0.21 ± 0.04

Sample sizes (insect damaged, undamaged): winter, n = 10, 42; spring, n = 14, 45; summer, n = 13, 58; fall, n = 9, 25.
[a] Fixed-kernel.
[b] Minimum convex polygon.

As recently as December 2000, percent of available middens occupied within undamaged forest was as high as 50% (occupied, n = 42; available, n = 84). During recolonization of insect-damaged forest (September 2003 to December 2005), percent of available middens occupied in undamaged forest was similar to insect-damaged forest (Table 2; Fisher's exact test, P = 0.67).

3.2. Habitat selection with reduced damage

Squirrels living in insect-damaged forest had home ranges in areas with less damage (Table 3). Percent dead trees in observed ranges and cores were 4.1% and 6.7% lower than respective random ranges and cores (observed, range: 47.9 $\pm$ 0.8%, core: 47.3 $\pm$ 1.3%; random, range: 52.1 $\pm$ 0.8%, core: 54 $\pm$ 1.3%). Except for one male with a winter core of 84% dead trees, observed ranges and cores had less than 69% dead trees (core, n = 45, range = 12.0–64.7%; range, n = 46, range = 30.9–68.5%). Observed ranges and cores had less percent dead trees in all seasons (Fig. 1a, ANOVA, all F > 6.6, all P < 0.02), but did not differ in summer (ranges) and winter (ANOVA, all F < 2.3, all P > 0.14).

Random and observed ranges and cores differed in percent open area (Table 3). Percent open area in observed ranges and cores was 6.2% and 8.2% lower than in respective random ranges and cores (observed, range: 16.8 $\pm$ 0.9%, core: 13.8 $\pm$ 1.2%; random, range: 23.0 $\pm$ 0.9%, core: 22.0 $\pm$ 1.2%). Observed ranges and cores were less open in winter, spring, and summer (Fig. 1b, ANOVA, all F > 4.5, all $P \leq$ 0.07), but not in fall (range, $F_{1,15}$ = 2.5, P = 0.13).

Random and observed ranges and cores differed in number of live trees (Table 3). Median number of live trees in observed ranges and cores was 8.3% (95%CI 3.4–14.0) and 12.1% (95%CI 4.5–20.2) higher than respective random ranges and cores. Observed ranges and cores had more live trees in summer, spring, and fall (ANOVA, all F > 5.4, all P < 0.04), but not in winter (ANOVA, range, $F_{1,17}$ = 0.03, P = 0.87; core, $F_{1,17}$ = 0.12, P = 0.74).

3.3. Home ranges enlarge

Ranges varied with season ($F_{3,210}$ = 9.41, P < 0.001), forest type ($F_{1,210}$ = 12.48, P < 0.001), and sex ($F_{1,210}$ = 4.56, P = 0.034), as did cores (season, $F_{3,210}$ = 11.03, P < 0.001; forest type, $F_{1,210}$ = 11.85, P < 0.001; sex, $F_{1,210}$ = 3.86, P = 0.051). Squirrels in insect-damaged forest had larger home ranges than squirrels in undamaged forest in summer and spring (Table 4, ANOVA, summer range, $F_{1,68}$ = 13.30, P < 0.001; summer core, $F_{1,68}$ = 8.50, P = 0.005; spring range $F_{1,56}$ = 2.97, P = 0.090; other seasons all F < 2.1, all P > 0.15). Squirrels living in undamaged forest demonstrated seasonal variation in ranges and cores; summer ranges were larger than fall and winter, spring ranges larger than winter, and summer and spring cores larger than winter and fall (Table 4, ANOVA, range, $F_{3,165}$ = 6.81, P < 0.001; core, $F_{3,165}$ = 8.51, P < 0.001; Tukey–Kramer post hoc, all P < 0.05). Squirrels living in insect-damaged forest demonstrated less seasonal variation in range and core, with only summer ranges being larger than winter ranges (Table 4, ANOVA, range, $F_{3,41}$ = 2.68, P = 0.059; core, $F_{3,41}$ = 2.58, P = 0.066; Tukey–Kramer post hoc, P < 0.05). In undamaged forest, females had larger ranges and cores than males (Table 5, ANOVA, range, $F_{1,165}$ = 6.30, P = 0.013; core, $F_{1,165}$ = 4.42, P = 0.037), whereas sex

Fig. 1. Seasonal fluctuations in mean percent pixels ($\pm$S.E.) classified as (a) dead trees and (b) open areas, within observed and randomly generated ranges and cores for Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged forest in the Pinaleño Mountains, Arizona, winter 2004 to summer 2005. Asterisk (*) denotes 0.05 < P < 0.1, 2 asterisks (**) denote P < 0.05 comparing observed to random. Sample sizes: winter, n = 10; spring, n = 14; summer, n = 13; fall, n = 9.

Table 5
Mean 95% range and 50% core (±S.E.) for male and female Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona, winter 2004 to summer 2005.

Forest type	95% range (ha)		50% core (ha)	
	Male	Female	Male	Female
Insect	4.41 ± 0.70	6.23 ± 1.51	0.59 ± 0.11	0.88 ± 0.30
Non-insect	1.76 ± 0.23	3.20 ± 0.47	0.29 ± 0.06	0.49 ± 0.09

Sample sizes (male, female): insect-damaged, $n = 26, 20$; undamaged, $n = 98, 72$.
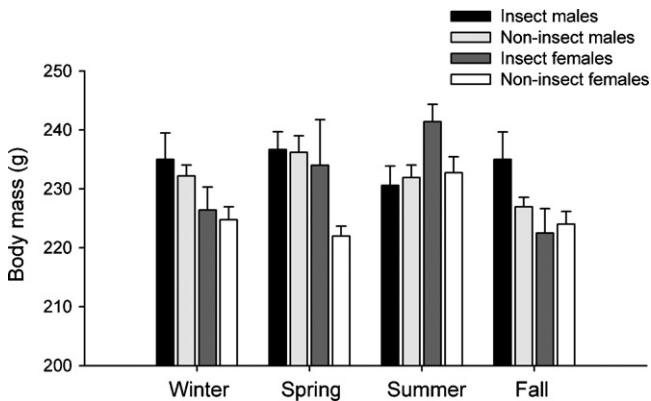
Fig. 2. Mean body mass (±S.E.) for adult male and female Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona, spring 2002 to fall 2005. Sample sizes (insect-damaged, undamaged): male: winter = 7, 34; spring = 12, 33; summer = 17, 44; fall = 10, 41; female: winter = 7, 22; spring = 10, 35; summer = 14, 38; fall = 10, 31.

did not influence range or core size in insect-damaged forest and all individuals traversed large home ranges (ANOVA, range, $F_{1,41} = 0.12$, $P = 0.73$; core, $F_{1,41} = 0.16$, $P = 0.69$).

3.4. Body mass similar

Body condition, as indicated by body mass, varied by season in both sexes (Fig. 2; males, $F_{3,193} = 2.9$, $P = 0.037$; females, $F_{3,162} = 7.1$, $P < 0.001$). Females were heavier in insect-damaged forest than in undamaged forest (insect-damaged, 232.4 ± 2.1 g; undamaged, 226.2 ± 1.2 g; $F_{1,162} = 5.6$, $P = 0.019$); male body mass did not vary with forest type (insect-damaged, 233.8 ± 1.9 g; undamaged, 231.6 ± 1.1 g; $F_{1,193} = 0.8$, $P = 0.37$).
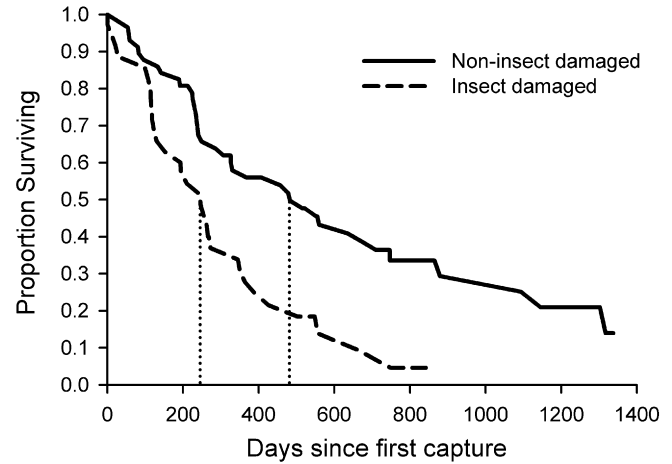
3.5. Demographics similar, survivorship reduced

Neither adult:subadult nor male:female ratios differed between forests (Table 6). All females alive during the breeding season

Fig. 3. Proportion of Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) surviving since first captured in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona, summer 2003 to summer 2005. Dotted line indicates median number days alive since first capture. Sample sizes: insect-damaged, $n = 35$; undamaged, $n = 57$.

within insect-damaged forest ($n = 15$) and undamaged forest ($n = 23$) lactated at least once. Litter size did not differ in insect-damaged and undamaged forest (Table 6). All males alive during the breeding season within insect-damaged ($n = 20$) and undamaged forest ($n = 32$) were reproductive at least once.

Survivorship was lower in insect-damaged relative to undamaged forest (Fig. 3, Table 6). Median survival since first capture did not differ between males and females living in insect-damaged forest (Table 6), nor between males and females in undamaged forest (Table 6). Reduced survivorship results in fewer potential reproductive events; squirrels in undamaged forest (1.93 ± 0.23, $n = 13$) had nearly double the opportunities to reproduce as squirrels in insect-damaged forest (1.25 ± 0.21, $n = 16$; $t_{27} = -2.09$, $P = 0.045$).

Within insect-damaged forest, days survived and range or core size were not related (linear regression: range, $F_{1,12} = 0.026$, $P = 0.81$; core area, $F_{1,12} = 0.057$, $P = 0.82$); nor were days survived and percent of range or core classified as dead trees or open area (linear regression, range: % dead, $F_{1,12} = 0.19$, $P = 0.67$, % open $F_{1,12} = 0.043$, $P = 0.84$; core: % dead, $F_{1,12} = 1.41$, $P = 0.26$, % open, $F_{1,12} = 0.18$, $P = 0.68$).

4. Discussion

Although Mt. Graham red squirrels equally preferred habitat within insect-damaged forest and reproduced as well as individuals in undamaged forest, reduced survivorship and reproductive potential suggest that insect-damaged forest may represent an

Table 6
Summary of demographic data: (a) ratios of %adult:%subadult and %male:%female, (b) mean (95%CI) litter size, and (c) median days survived (95% CI) since first capture for Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in insect-damaged and undamaged forest in the Pinaleño Mountains, Arizona, winter 2004 to summer 2005.

	Insect-damaged	Undamaged	P
(a)			
%adult:%subadult	85:15	85:15	Fisher's exact $P = 1.00$
%male:%female	55:45	52:48	Fisher's exact $P = 0.707$
(b) Litter size	2.7 young (1.9 to 3.4 young)	3.1 young (2.6 to 3.6 young)	$t = -0.91$ $P = 0.37$
(c) Squirrel survival	247 d (141–345 d)	483 d (286–710 d)	Log-rank $\chi^2 = 11.57$ $P < 0.001$
	Male	**Female**	**P**
Insect-damaged	211 d (115–364 d)	247 d (99–557 d)	Log-rank $\chi^2 = 0.25$ $P = 0.62$
Undamaged	458 d (236–747 d)	560 d (240–1317 d)	Log-rank $\chi^2 = 0.58$ $P = 0.45$

Sample sizes are: (a) insect-damaged: 82, undamaged: 269; (b) insect-damaged: 7, undamged: 17; (c) (all, male, female) insect-damaged: 35, 20, 15; undamaged: 57, 32, 25.

ecological trap. The insect-damaged forest was essentially unoccupied as of 2002 (Koprowski et al., 2005), and colonizers dispersed from contiguous relatively undamaged forest at low elevations. Dispersal patterns in small mammals are often sex or age biased (Gaines and McClenaghan, 1980). Similar age (adult:-subadult) and sex ratios among newly caught individuals suggest that natal and breeding dispersal occurred in both forest types. Occupancy of middens in undamaged forest was lower than recent occupancy in 2000, suggesting habitat was available during recolonization. Therefore, available habitat and similar age and sex ratios indicate individuals were not relegated to insect-damaged forest. Although spruce-fir forest was thought the preferred forest type prior to infestation (USFWS, 1993), similar midden occupancy, historically and during recolonization, suggests squirrels equally prefer both forest types. In addition, occupied midden habitat in insect-damaged forest is characterized by features (high basal area, log volume, and canopy cover) found at middens prior to insect-damage as well as across red squirrel distribution (Zugmeyer and Koprowski, in press). This suggests cues for habitat selection have not changed and may no longer correlate with habitat quality, with individuals currently inhabiting insect-damaged forest possibly succumbing to an equal-preference ecological trap (Robertson and Hutto, 2006).

Habitat selection in home ranges within insect-damaged forest indicated severity of insect infestation that individuals tolerated. Squirrels inhabiting insect-damaged forest demonstrated little seasonal variation in habitat selection with nearly all individuals selecting home ranges with <69% dead trees. Food resources likely influence home range selection, as number of live trees was greater than found at random. Additionally, live trees create canopy cover that affords protection from predators (Hughes and Ward, 1993). Selection of greater cover suggests influence of predation risk; red squirrels perceive greater predation risk in and avoid crossing forest openings (Bakker and Van Vuren, 2004). Alternatively, dry open areas offer fewer mushrooms, a secondary food resource for squirrels (Steele, 1998). Middens are important for survival, thus midden establishment may influence habitat selection at the larger scale of the home range. Squirrels living in insect-damaged forest occupied middens in areas with <64% dead trees (Zugmeyer and Koprowski, in press). Studies of forest thinning practices suggest similar results with a decline in squirrel density after removal of > 50% stem density (Koprowski, 2005b); with more severe damage, squirrels may not find an area habitable.

Squirrels living within insect-damaged forest had larger home ranges than individuals living in undamaged forest. Home ranges must satisfy an individual's resource needs (Gurnell, 1987); thus home range size may increase when food is less abundant (Lurz et al., 2000). Food resources and high body mass are important for reproductive success (Wauters and Dhondt, 1989), thus decreased seed and epigeous fungi crops in insect-damaged forest (Koprowski et al., 2005) and large home ranges would suggest decreased reproduction within insect-damaged forests. However, squirrels obtained adequate resources as body masses did not differ between forest types and all females and males were in reproductive condition. Furthermore, litter size did not differ between forest types. Juvenile survival and dispersal may differ between forest types, but remain unknown. Population density can impact reproductive success (Wauters and Lens, 1995); density likely had minimal or no impact on reproduction with few squirrels living in insect-damaged forest and the notably low density of this endangered species (USFWS, 1993).

While most demographic characteristics did not differ between forest types, squirrels living in insect-damaged forest had low survivorship relative to individuals in undamaged forest. Differences in survival can be linked to low food availability leading to

decreased body size and condition (Wauters and Dhondt, 1989); however, body mass of squirrels was similar in both forest types. Large home ranges may decrease survival by increasing energy expenditure (Smith, 1968) and exposure to predators because of greater movement (Martel and Dill, 1995). We found no relationship between home range size and survival, perhaps due to considerable size of home ranges in the Pinaleños. Raptors are primary predators of Mt. Graham red squirrels (Schauffert et al., 2002) and reduced canopy cover may increase predation risk, particularly by northern goshawks (Accipiter gentilis) that inhabit similar forests and kill in areas with dead trees (Greenwald et al., 2005). However, we found no relationship between survival and percent dead trees or percent open area within home ranges. Regardless of the cause, low survivorship reduces the number of potential reproductive events attained by an individual by 50%, dramatically reducing individual fitness for squirrels living in insect-damaged forest. Equal-preference for both forest types combined with low survival suggest that insect-damaged forest currently represents an ecological trap for red squirrels in this habitat isolate (Schlaepfer et al., 2002; Robertson and Hutto, 2006). However, this equal-preference trap is a temporary condition that will likely disappear with time as the forest recovers and basal area of live trees increases. In addition, as there was no replication with this current study, response of red squirrels to severe insect-infestation should be examined across their distribution to determine if this pattern exists among populations that are not isolated.

Forests with severe insect infestation (>69% tree mortality as suggested by this study) may not represent habitat (Matsuoka et al., 2001). Although insect-damaged forest may retain patches of habitat, low survivorship suggests an ecological trap (Schlaepfer et al., 2002; Robertson and Hutto, 2006) and potentially a population sink if net fitness is negative (Pulliam and Danielson, 1991), though presence of a population sink in the study area is unknown. While their existence does not necessitate population decline (Robertson and Hutto, 2006), ecological traps are a concern for the persistence of isolated and/or endangered populations inhabiting insect-damaged forests. Additionally, fuel build-up from fire suppression (Grissino-Mayer and Fritts, 1995) combined with dead trees increase risk of wildfire for individuals inhabiting remnant patches. In summer of 2004 a stand-replacing wildfire burned a large portion of insect-damaged forest in the Pinaleño Mountains (Koprowski et al., 2006), destroying habitat for red squirrels and many forest-dwelling species. Climate change is altering natural disturbance regimes (Dale et al., 2000). While species may adapt to changing climate, many will demonstrate a shift in range distribution (Parmesan, 2006). Populations occupying isolated habitats, those on mountaintops and in fragmented areas, lack that option and face greater risk of extinction that can be exacerbated by ecological traps created by an array of disturbances.

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