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CHARACTERISTICS OF BOLUS NESTS OF RED SQUIRRELS IN THE PINALEÑO AND WHITE MOUNTAINS OF ARIZONA

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ABSTRACT—Red squirrels (*Tamiasciurus hudsonicus*) use cavity, bolus, and underground nests for sleeping, protection, and rearing of young. We compared occurrence and structural characteristics of bolus nests at midden sites (area surrounding the central cache) for red squirrels in the Pinaleño Mountains with those in the White Mountains of southeastern Arizona. Bolus nests were more prevalent in the White mountains, possibly as a result of differing habitat structure; forests of the Pinaleño Mountains had significantly ($P < 0.05$) larger basal area, greater stem densities, and there was less grass on the forest floor than in the White Mountains. Midden sites with more potential cavity nest sites were more likely to have only cavity nests present. Bolus nests were constructed mostly of lichens in the Pinaleño Mountains and of grasses in the White Mountains, whereas most other nest and nest tree characteristics were similar between locations, although nest trees were further from the main cache location at middens in the Pinaleño Mountains.

RESUMEN—Las ardillas rojas (*Tamiasciurus hudsonicus*) utilizan nidos de cavidad, del bola y bajaterra para dormir, protección, y crianza. Comparamos la ocurrencia y characterísticas estructuales de los nidos de bola en territorios de ardillas rojas en las Montañas Pinaleño con arquellas de las Montañas Blancas del sureste de Arizona. Nidos de bola prevelecen en las Montañas Blancas, posiblemente como resultado de las diferencias en la estructura del hábitat; los bosques del las Montañas Pinaleños tuvierion un área basal significativamente más grande ($P < 0.05$), mayores densidades de tallo y tocones, y hubo menos pasto en el suelo quen las Montañas Blancas. Territorios con mayor potencial de tener nidos de cavidad fueron más propensos a tener solamente nidos de cavidad. Los nidos de bola estaban constuidos en su mayoría de líquenes in las Montañas Pinaleño y de pasto en las Montañas Blancas, mientras que las caraterísticas de la mayoria de otros nidos y árboles nidales fueron similares entre ambos lugares. Sin embargo, árboles nidales fueron mas alejaods del lugar principal de almancenamiento en territorios de las Montañas Pinaleños.

Red squirrels (*Tamiasciurus hudsonicus*) are known to use cavity, bolus, and underground nests for sleeping, rearing young, and for protection from predators and weather (Vahle, 1978; Fancy, 1980). Cavity nests are made in hollow logs and snags (standing dead trees), often with several entrances. Bolus nests are found within the foliage of the crown of a tree and are generally bulbous in shape; they are constructed primarily of grass, but may include any readily available material (Hatt, 1929). Bolus nests generally are placed in the densest part of the crown of the nest tree, and generally are located in the interior of a cluster of trees with interlocking branches providing numerous arboreal pathways (Rothwell, 1979). Underground nests consist of several cavities lined with nesting material which are connected by tunnels to food caches and entry-exit holes (Hatt, 1929; Becker, 1992).

Cavity nests are thought to be the preferred nest type for red squirrels (Hatt, 1929; Hamilton, 1939; Hatt, 1943; Layne, 1954; Fancy, 1980). Because a red squirrel in a cavity nest is surrounded by solid walls it would seem to be well protected from terrestrial (Sun, 1989) and avian predators and may also be better protected against adverse weather. Bolus nests appear more exposed to predators and offer less protection from weather than either ground or cavity nests. Red squirrels were more easily routed from bolus nests than cavity nests suggesting that squirrels felt more secure in cavity nests (Layne, 1954). Litters may all be raised in cavity nests prior to weaning (Sun, 1989).

This paper compares occurrence and characteristics of bolus nests used by red squirrels in separated mountain ranges of southeastern Arizona. The White Mountains are on the eastern portion of the Mogollon Plateau, with large expanses of mixed-conifer forest at relatively high elevations (>2,300 m). The Pinaleños Mountains are an isolated range about 140 km south of the White Mountains.

Much of the forest on the White Mountains has been logged since the 1890s, resulting in a patchwork of old and second growth forests. The mixed-conifer forests on the Pinaleños Mountains were similarly logged from the 1880s to the early 1970s. The higher elevation (>3,050 m) spruce-fir forests have been largely untouched by logging, with the exception of a fire-break cut along some forest roads.

The Pinaleños Mountains are home to an endemic and endangered subspecies of red squirrel, the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). The Mt. Graham red squirrel may have been isolated from other populations and subspecies since the major changes in vegetation communities that occurred at the end of the Pleistocene glaciations (approximately 10,000 to 12,000 years BP: Findley and Jones, 1962; Martin and Mehringer, 1965; Patterson, 1984) Relatively little is known about the biology of this subspecies. First described from scientific specimens in 1894 (Allen, 1894), there have been few published accounts dealing with any aspect of its ecology. Hoffmeister (1956) found them to be very rare, and Minckley (1968) found no red squirrels during his survey of the mammals of the range, and incorrectly concluded that they had gone extinct. Several sighting of squirrels by government biologists in the 1970s led to an effort by the Arizona Game and Fish Department to determine the status of the squirrel (Spicer et al., 1985) and the subsequent listing of it as an endangered species in 1987. Habitat loss due to human activity, mostly commercial logging, is blamed for the current endangered status if the population (approximately 528 squirrels in autumn 1999), and it is considered to be under continued threat from habitat loss due to the construction of an astrophysical observatory and recreational facilities, as well as recent insect outbreaks on the mountain range.

Significant differences in some aspects of the ecology, behavior, and life history of the Mt. Graham red squirrel compared to subspecies found in the nearby White Mountains (*T. h. mogollonensis*) may exist, but none has been thoroughly explored. Mt. Graham red squirrels occur at much lower densities than do red squirrels in the White Mountains (P. J. Young, pers. obser.) And do not appear to make use of much of the available habitat on the mountain range. This study was prompted in part by the low incidence of the use of bolus nests by Mt. Graham red squirrels (Froehlich and Smith, 1990; P. J. Young, pers. obser.) And is part of a series of studies designed to compare and contrast the ecology and life history of the Mt. Graham red squirrel to that of its non-endangered counterparts elsewhere in the southwestern United States.

METHODS—The study was conducted in 1994 on the White Mountains and Pinaleños Mountain ranges of southeastern Arizona. Red squirrel nests were examined as midden sites in 2 habitat types on each range. Red squirrel middens are piles of cast off cone scales and other debris from feeding on conifer cones. The midden is the focal point of activity within a territory which is actively defended against other red squirrels and conspecific intruders. Because we could not determine the territorial boundaries surrounding all midden sites during this study, we defined the midden site as the area encompassed within a 10-m radius of the main cone cache. In the Pinaleños Mountains, all active midden sites on the study area of the University of Arizona's Mt. Graham Red Squirrel Monitoring Program were searched for nests. The Pinaleños study areas encompass 107.4 ha of mixed-conifer forests (PM-A area, 2,870 to 3,050 m elevation) and 233.5 ha of spruce-fir forests (PM-B area, 3,050 to 3,267 m elevation). In the White Mountains, 2 study areas (WM-A area, approximately 11 ha mixed-conifer forest, 2,820 m elevation; and WM-B area, approximately 13 ha spruce-fir forest, 2,820 m elevation) were chosen and thoroughly searched for active red squirrel middens. Data on the structure and occurrence of different nest types were collected at all of the active midden sites in all study areas. Each midden site was closely examined for nests of all types. Only those nests that appeared to be in current use were included in the analysis. A nest was considered to be in current use if a squirrel was observed to enter, exit, construct, or repair it, or if there were other signs of recent squirrel use

(e.g., fresh nesting material protruding, debris recently cleaned out, feeding sign below it)

The structure and nature of the surrounding habitat were measured and presence of bolus, cavity, or underground nests was noted at each midden site. Data on construction and location of each bolus nest and the nest tree were recorded. Within each midden site, the following forest structure measurements were taken: species and diameter at breast height (DBH) of all trees and snags ≥3 cm DBH, and canopy cover using a spherical densiometer, at the midden center and at 5 and 10 m from the center in 4 cardinal compass directions (N, E, S, W). Canopy cover of the nest tree was measured at 5 m (N, E, S, W) from the tree. We used methods described by Strickler (1959) for spherical densiometer use to obtain accurate readings with greater efficiency. The number of snags (>22 cm DBH) within a 15 m radius of the midden center also were counted as potential cavity nest sites. Although most cavity nests were found in larger snags (≥40 cm DBH; Froehlich and Smith, 1990), we had previously discovered natal nests in snags as small as 22 cm DBH.

Nest height and height of the nest tree were measured with a clinometer. To avoid disturbing or destroying nests, the size of the nest and distance of the nest from the trunk were measured indirectly from the ground. A ruler was held at a constant distance from the eye of the researcher and measurements were recorded for the nest height (m), width (cm), and distance from trunk (cm). The ratio of the ruler reading of the nest height to the actual nest height as determined from clinometer readings was used to calculate the nest width and distance from the trunk. Nest composition was classified by examination through binoculars and the relative type of each amount of material in the nest was recorded as <50%, 50%, >50%, 100%.

The following measurements were taken to provide a relative measure of the cover provided by the nest tree: number of trees with branches interlocking the nest tree, distance to the 5 nearest trees or snags (DBH ≥15 cm) in meters, position of the tree relative to the 5 nearest trees classified as marginal (on the border of the group) or interior (inside the group), crown density, an estimate of the amount of foliage in the crown classified as thin (<30% foliage), moderate (30 to 60% foliage), or dense (>60% foliage). The crown was defined as the area from the top of the tree to the lowest live branch. Tree position and crown density were described using a modification of the methods of Vahle (1978).

Statistical tests were performed using Statistical Analysis System (SAS Institute Inc., 1985), SigmaStat (SPSS Inc., 1997), and Orianna (Kovach, 1999) statistical packages for personal computers. Differences in the species composition of nest trees versus those available at midden sites were tested using Chi Square tests. Forest structure at midden sites on all study areas was analyzed using analysis of variance (ANOVA) and angular transformations of proportions (Snedcore and Cochrane, 1980). Wilcoxon tests were used to test for differences in habitat structure among midden sites with different nest types present on the Pinaleños Mountain areas. Characteristics of bolus nests and nest trees were analyzed using ANOVA or Wilcoxon tests depending on whether data met assumptions of normality and equal variance. Rayleigh uniformity tests were used to analyze the orientation of nests relative to the trunk of the supporting tree. In all cases an alpha level <0.05 was considered to be statistically significant.

RESULTS—*Habitat Characteristics*—Data on habitat structure were collected at 80 of the active midden sites on the Pinaleños Mountains and at 35 of the active sites on the White Mountains. Time constraints and weather conditions prevented us from collecting these data at all of the midden sites examined for nests.

Midden sites on the PM-A area were located in stands that were dominated by corkbark fir (*Abies lasiocarpa* var. *arizonica*). Engelmann spruce (*Picea engelmannii*), Douglas fir (*Pseudotsuga menziesii*), and other species made up less than 20% of the trees within those sites. Bolus nests were found distributed equally between spruce and fir trees, suggesting that squirrels may have preferred spruce over the more abundant fir for nest locations (Table 1). Stands surrounding midden sites on the PM-B area were co-dominated by Engelmann spruce and corkbark fir, with other species making up less than 1% of the stands. Bolus nests were distributed among spruce and fir trees in proportion to each species abundance at these sites. Douglas fir and quaking aspen (*Populus tremuloides*) were present in many midden sites on the PM-A area, but only 2 middens in the PM-B area had 1 Douglas fir present.

At middens sites on the WM-A area, blue spruce (*Picea pungens)* was dominant and Douglas fir was also abundant. Bolus nests were located predominantly in blue spruce, but Douglas fir trees were chosen as nest locations in greater proportion than their occurrence. Other species present at midden sites included quaking aspen, ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), corkbark fir, white pine (*Pinus strobus*), and Engelmann spruce. Engelmann spruce and corkbark fir

TABLE 1—Species composition of trees (>15 cm DBH) at midden sites versus trees used as nest sites on 4 study areas on the Pinaleños and White Mountains of Arizona, 1994. Other includes quaking aspen, ponderosa pine, white pine, white fir, and miscellaneous deciduous trees and was not included in statistical analyses. Blue spruce does not occur on the Pinaleños Mountains accounting for the differences in degrees of freedom.

Species	PM-A		PM-B		WM-A		WM-B	
	Nest tree	Midden	Nest tree	Midden	Nest tree	Midden	Nest tree	Midden
Engelmann spruce	6 (50.0%)	33 (9.8%)	11 (50.0%)	273 (52.6%)	1 (2.6%)	3 (2.3%)	5 (22.7%)	56 (31.6%)
Blue spruce	—	—	—	—	28 (73.7%)	93 (71.0%)	7 (31.8%)	25 (14.1%)
Corkbark fir	6 (50.0%)	278 (83.5%)	10 (45%)	243 (46.8%)	0	3 (2.3%)	6 (27.3%)	75 (42.4%)
Douglas fir	0	26 (7.7%)	1 (4.5%)	2 (0.5%)	9 (23.7%)	32 (24.4%)	4 (18.2%)	21 (11.9%)
Other	0	12	0	0	0	76	0	9
G-value, *df*	19.19, 2		4.53, 2		0.92, 3		6.03, 3	
P-value	<0.001		0.104		0.921		0.110	

were co-dominant on the WM-B midden sites with blue spruce being less common than at WM-A sites, and other species being incidental. Bolus nests were not preferentially located in any species, except for a tendency for them to be located in spruce trees on the PM-A area (Table 1).

Total basal area of the forest stands at the Pinaleños Mountains midden sites was significantly greater ($P < 0.001$) than in the White Mountains (Table 2). Midden sites on the Pinaleños Mountains had a greater stem density of small (<20 cm DBH) and medium (20 to 40 cm DBH) trees than the White Mountains but the stem density of large (>40 cm DBH) was similar among all sites. Canopy cover at midden sites was similar among all locations, but was greatest in the PM-B area and lowest

TABLE 2—Forest structure at red squirrel midden sites on 4 study areas on the Pinaleños and White Mountains of Arizona, 1994. Superscript letters indicate values that are statistically indistinguishable between study areas based on ANOVA and LSD range tests.

Structural feature	PM-A ($n = 30$)	PM-B ($n = 50$)	WM-A ($n = 20$)	WM-B ($n = 15$)	F, 3 df	P
Total Basal Area (m^2/ha)	61.6^{a} (±3.9*s.e.*)	63.5^{a} (±2.4)	41.3^{b} (±2.9)	48.2^{b} (±4.8)	9.20	<0.001
Ave. DBH (cm)	16.7^{a} (±0.4)	14.7^{b} (±0.3)	17.5^{a} (±0.6)	17.3^{a} (±0.7)	10.04	<0.001
<20 cm DBH stem density (#/ha)	$1{,}227.6^{a}$ (±126.1)	$1{,}733.5^{b}$ (±118.7)	600.0^{c} (±48.7)	$810.6^{a,c}$ (±91.5)	16.63	<0.001
20–40 cm DBH stem density (#/ha)	412.7^{a} (±28.5)	415.1^{a} (±21.1)	248.3^{b} (±30.9)	224.9^{b} (±18.5)	12.58	<0.001
>40 cm DBH stem density (#/ha)	98.8^{a} (±11.2)	111.7^{a} (±7.9)	92.1^{a} (±10.3)	106.9^{a} (±14.0)	0.72	0.543
>22 cm DBH snag density (#/ha)	90.2^{a} (±22.5)	104.4^{a} (±12.5)	6.4^{b} (±3.7)	34.0^{b} (±9.0)	7.39	<0.001
Number of nest snags w/in 15 m	1.6^{a} (±0.5)	2.6^{b} (±0.4)	0.4 (±0.1)	0.5^{c} (±0.1)	20.01	<0.001
Canopy closure (%)	$78.3^{a,b}$ (±1.9)	80.4^{a} (±1.2)	73.5^{b} (±1.8)	78.8^{a} (±2.1)	2.98	0.035

TABLE 3—Comparison of habitat structural features (mean ± *SE*) at red squirrel midden sites on the Pinaleños Mountains having different types of nests within the site. Plots for all measurements except number of snags suitable for cavity nests were 10 m radius (0.0314 ha).

Structural feature	No nest found (n = 19)	Bolus nest only (n = 26)	Cavity nest only (n = 22)	Both (n = 13)	Kruskal-Wallis ANOVA on ranks, 3 *df*	
					H	P
Canopy cover (%)	85.7 ± 1.1	86.1 ± 1.1	85.4 ± 1.7	85.5 ± 1.9	0.365	0.947
Log volume (m^3)	10.1 ± 1.8	9.7 ± 1.7	7.6 ± 1.2	10.7 ± 2.0	1.587	0.662
Basal area (m^2)	2.0 ± 0.2	1.9 ± 0.1	2.2 ± 0.1	1.8 ± 0.1	5.127	0.163
Average DBH (cm)	15.9 ± 0.7	16.7 ± 0.8	16.4 ± 0.7	14.6 ± 0.7	3.332	0.343
Stem density DBH <20 cm (#/plot)	52.3 ± 8.0	44.1 ± 4.8	47.3 ± 5.1	53.4 ± 5.4	2.514	0.473
Stem density DBH 20–40 cm (#/plot)	13.2 ± 1.1	11.8 ± 0.8	15.4 ± 1.1	11.8 ± 0.9	8.860	0.031
Stem density DBH >40 cm (#/plot)	3.6 ± 0.5	3.2 ± 0.4	3.5 ± 0.4	2.5 ± 0.4	2.904	0.407
Slope (°)	16.6 ± 2.2	15.6 ± 2.2	16.1 ± 1.8	16.8 ± 2.5	0.336	0.953
Snags within 15 m (#)	2.6 ± 0.6	2.3 ± 0.5	5.6 ± 0.8	3.1 ± 0.9	13.653	0.003

in the WM-A area. Middens on the Pinaleños Mountains had a much greater density of snags available for cavity nests (>22 cm DBH, within 15 m of midden center) than on the White Mountains.

Nest Types, Structure, and Location—Bolus and cavity nests were found in midden sites in both mountain ranges, but no squirrel was observed using a ground nest during this study. The use of bolus nests was much less common on the Pinaleños Mountains than the White Mountains. On the Pinaleños Mountains, 84 nests (46 bolus; 38 cavity) were found at 62 of the 96 active middens. Bolus nests were found at 40 (42%) of those middens, and were the only type of nest found at 27 (28%) middens. Cavity nests were found at 35 (36%) of the middens and were the only type of nest found at 22 (23%) of the middens. Thirteen midden sites (14%) had both cavity and bolus nests, but no nests of any type were discovered at 35 (36%) of the middens surveyed. In the White Mountains, bolus nests were found at 34 (89%) of the 39 active midden sites examined. Cavity nests also were found at 3 (8%) of these sites. No midden sites were found to have only cavity nests and there were 4 (11%) middens where no nests were discovered. Midden sites in the White Mountains had an average of 2.9 (±0.4 *SE*) bolus nests per midden compared to 0.7 (±0.1 *SE*) per midden site on the Pinaleños Mountains.

For midden sites on the Pinaleños Mountains, we had sufficient data to look for differences in habitat structure at midden sites relative to type of nest found at the site. Because all midden sites on the White Mountain study areas had bolus nests, and only a few had cavity nests, we had insufficient data to perform the same analysis for those areas. Middens with only cavity nests had a greater number of potential nest snags within 15 m than did midden sites with only bolus nests, both cavity and bolus nests, and middens where no nest was found (Table 3).

The location of some nests (e.g., obscured by foliage or witches broom) prevented us from collecting accurate data on their composition and location. We collected these data from 36 nests on the Pinaleños Mountains and for 94 nests on the White Mountains. Bolus nests were constructed almost entirely of grasses in the White Mountains and mostly of lichens in the Pinaleños Mountains (Table 4). Nest height was similar on all study areas, but tended to be highest on the PM-B area and lowest on the WM-A area. Nests were usually located next to the trunk in all habitats (PM-A = 83.3%, PM-B = 58.3%, WM-A = 67.7%, and WM-B = 58.6%). Only 14 nests were built

TABLE 4—Characteristics of red squirrel bolus nests on 4 study areas of the Pinaleños and White Mountains of Arizona, 1994. Superscript letters indicate values that are statistically indistinguishable based on ANOVA and LSD range tests (height and width) and Kruskal-Wallis ANOVA on ranks (distance from trunk). Composition and orientation were not compared statistically between study areas.

Characteristic	PM-A	PM-B	WM-A	WM-B	F, 3 df	P
Composition	Lichen	Lichen	Grass	Grass	—	—
Height above ground (m ± SE)	8.65 ± 0.7	10.37 ± 0.9	7.94 ± 0.4	8.79 ± 0.5	3.22	0.025
Width (cm ± SE)	35.1 ± 4.0	38.0 ± 4.0	38.0 ± 2.0	49.9 ± 6.0	2.66	0.051
Median (and range) distance from trunk (cm)	0 (0.0–39.2)	0 (0.0–8.2)	0 (0.0–5.0)	0 (0.0–29.7)	0.751	0.524
Orientation	random	75°	random	random	—	—

more than 60 cm from the trunks of trees; of these, 3 were on a single straight limb and 11 were built on the forked portion of a branching limb. Nest orientation relative to the tree trunk was random (Rayleigh Test, $P < 0.05$) in all areas except the PM-B habitat where nests tended to be placed at an angle of 75° from true north relative to the trunk.

Trees selected as nest sites had a larger DBH (Table 5) than the average tree (Table 2). There was no significant difference in the DBH of nest trees between locations or habitats (Table 5); however, nest trees in mixed-conifer habitat of both mountain ranges were somewhat smaller than those in spruce-fir habitat. Canopy cover at nest trees was similar at both sites on the Pinaleños Mountains and the WM-A site, but statistically greater at the WM-B sites. Height of the nest trees was not statistically different among the study areas but trees were generally taller in the White Mountains. Nest trees were further from the main cache, and contained fewer nests per tree in the Pinaleños Mountains than in the White Mountains. All other nest tree features were similar within and between habitats and locations (Table 5).

DISCUSSION—With regard to nest building and use, there are measurable differences in the behavior and ecology of the Mt. Graham red squirrels compared to their nearest conspecifics in the White Mountains. However, most of the differences in the type of nests

TABLE 5—Characteristics of trees used for bolus nest location sites by red squirrels on 4 study areas on the Pinaleños and White Mountains of Arizona, 1994. Values with the same superscript letter in each row are statistically indistinguishable (ANOVA or Kruskal-Wallis ANOVA on ranks, LSD range test).

Characteristic	PM-A (n = 12)	PM-B (n = 22)	WM-A (n = 39)	WM-B (n = 23)	F, 3 df	P
DBH (cm)	24.1[a] (±2.9 SE)	35.5[a] (±3.9)	30.2[a] (±2.6)	35.5[a] (±3.8)	1.22	0.306
Canopy closure (%)	78.2[a,b] (±1.7)	77.2[b] (±1.1)	73.5[b] (±1.8)	82.9[a] (±1.2)	14.35	<0.001
Tree height (m)	16.0[a] (±1.6)	19.1[a,b] (±1.5)	18.0[a] (±1.4)	23.9[b] (±1.7)	2.32	0.080
Distance from main cache (m)	8.1[a] (±1.7)	8.3[a] (±1.6)	4.3[b] (±0.6)	2.7[b] (±0.6)	6.61	<0.001
Mean distance to 5 nearest trees (m)	2.9[a] (±0.1)	3.4[a] (±0.2)	3.3[a] (±0.2)	3.4[a] (±0.2)	0.71	0.551
Number of interlocking trees	3.1[a] (±0.4)	3.1[a] (±0.4)	3.1[a] (±0.2)	2.5[a] (±0.3)	1.00	0.397
Tree position (marginal or interior)	marginal[a]	marginal[a]	marginal[a]	marginal[a]	0.423	0.737
Crown density[1]	2.17[a]	2.68[a]	2.54[a]	2.39[a]	1.53	0.211

[1] Light = 1, moderate = 2, dense = 3.

used may be due to differences in the structure and age of the forests on the study areas. In the White Mountains, where snags were scarce, only 3 middens had cavity nests, and these sites also had bolus nests. Bolus nests were abundant and easily located in the White Mountains, and most middens had several bolus nests. One midden in the WM-A area had 14 bolus nests; 7 in 1 tree. The use of multiple bolus nests in an area without cavities also was observed by Hatt (1929) in a coniferous forest in New York, and Finley (1969) reported finding 13 bolus nests at 1 midden in Colorado.

In the Pinaleños Mountains, although both bolus and cavity nests were common, the percentage of middens with cavity nests was only slightly less than middens with only bolus nests. Those middens with bolus nests usually contained only 1 nest and many middens had both nest types. In addition, most, if not all, of the 35 midden sites where no nests were found probably had nests that were not observed; a potential cavity nest was not included unless nesting material was seen in it or a squirrel was seen entering it. Underground nests may have been missed for the same reason.

In most respects the structure and location of bolus nests on both mountain ranges and all habitats were similar. Nests mainly were built close to the trunk on straight limbs or forked branches. If nests were not next to the trunk they were usually on forked branches. Hatt (1929, 1943) also found that red squirrels build their nests in secure places, safe from wind and predators, with several runways to and from the nest. For the greatest security, nests are usually built in the densest part of the crown (Hatt, 1929; Vahle, 1978). Dense branch cover provides protection from wind and rain and hides the nest from view of predators. The many branches also provide various escape routes. In our study, nests averaged 8.7 to 10.4 m (range 2.2 to 27.3 m) from the ground and from 7 to 15 m from the top of the crown. Vahle (1978), in a different area of the White Mountains, found nests from 4.6 to 9.1 m from the ground. In the northeastern United States nests were usually 5 m from the top of the crown (Hatt, 1929).

The only significant difference in the structure of the bolus nests on the 2 mountain ranges can be attributed to qualitative differences in habitat. Bolus nests in the Pinaleños Mountains were made mostly of lichen but in the White Mountains they consisted mostly of grass. Other materials used in nest construction included plastic flagging, small sticks, and toilet paper. Natural clearings and clearing created by logging provided an abundant and easily accessible source of grass in the White Mountains study areas. The forests on the Pinaleños Mountains are less fragmented with fewer open areas than on the White Mountains, and there are very few places where squirrels have access to grass. The larger, older trees on the Pinaleños Mountains, however, provide a readily available source of easily gathered lichen. Although no quantitative analysis was done to compare the amount of lichen growing on trees or the amount of grass available on the different mountain ranges, it appears that the squirrels on each range made use of the most abundant materials for constructing their bolus nests. Nest trees at the Pinaleños Mountains were farther from the main cache than those in the White Mountains. This may be due to the greater incidence in the use of cavity nests on the Pinaleños Mountains compared to the White Mountains which could limit the choice of nest trees. Bolus nests can be placed in nearly any tree but cavity nests require the presence of snags within a narrow range of the state of decay.

Characteristics of trees used as bolus nest trees were similar among all the study areas and are most likely chosen for protection. Red squirrels chose trees with larger than average DBH, moderate crown density, and branches which interlock with other trees. These characteristics provide protection from weather and escape routes from predators. Though spruce trees were not necessarily the most abundant species present, they were preferentially chosen as nest trees on the PM-A site. Because spruce trees retain more of their lower branches for a longer time than other species, they may provide more cover for nests than do other species.

Both Farentinos (1972) and Vahle (1979) found that a majority of the nests on their study areas were oriented to the south. Farentinos suggested this orientation would take advantage of the heat from the sun which stayed in the southern sky in his study. However, Halloran and Beckoff (1994) concluded that the SE orientation of Abert's squirrels' (*Sciurus* *aberti*) nests in Colorado was not related to any thermoregulatory benefits because the squirrels spent little time in the nests when these benefits would be most apparent. We found nests to be oriented randomly with respect to the trunk except in the PM-B habitat where nests were predominantly at a 75° (ENE orientation). Our findings suggest that nest orientation relative to the sun may not be an important consideration for red squirrels in Arizona. Even though middens tend to be located in cool, moist areas that protect stored cones (Smith and Mannan, 1994), nests are placed high in the trees where some sunlight is available. Nests are also well insulated from weather extremes (Pauls, 1981) and are probably kept sufficiently warm with body heat when occupied.

Even with the high number of potential cavity nest sites found at the middens examined in this study, the Mt. Graham red squirrel occurs at much lower densities (0.3 active middens/ha) that the populations on the White Mountains (1.6 active middens/ha; P. J. Young, pers. obser.). The Mt. Graham red squirrel may be more discriminating in its choice of midden sites and type of nests it will use than squirrels on the White Mountains. The presence of suitable snags may be a requirement for the establishment of new midden sites on the Pinaleños. That being said, in recent years there has been an increase in the incidence of the use of bolus nests by Mt. Graham red squirrels. Froehlich and Smith (1990) found only 3 bolus nests among the 22 (14%) nests they located. In 1992, a survey of 102 active midden sites on the same study areas used in the current study found bolus nests at 33 (32%) of those middens (P. J. Young, pers. obser.). During the current study, conducted in 1994, bolus nests were found at 41% of the active midden sites (65% of middens with any type of nest found). During the Froehlich and Smith (1990) study, the Mt. Graham red squirrel population was declining and reached its lowest estimated size (<200 squirrels) between spring 1989 and spring 1990 (Arizona Game and Fish Department, in Litt.). Following a bumper crop of Engelmann spruce and corkbark fir in 1990 the Mt. Graham red squirrel population increased rapidly and by the summer of 1993 was more than 3 times larger than the 1990 population. Even though the presence of snags suitable for cavity nests may be preferred, availability of snags does not seem to limit the size of the population.

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Literature Cited

Allen, J. A. 1894. Description of ten new North American mammals and remarks on others. Bulletin of the American Museum of Natural History 6:320–321.

Becker, C. D. 1992. Proximate factors influencing the timing and occurrence of reproduction in red squirrels. Unpublished Ph.D. dissertation, University of Alberta, Edmonton, Canada.

Fancy, S. G. 1980. Nest-tree selection by red squirrels in a boreal forest. The Canadian Field-Naturalist 94:198.

Farentinos, R. C. 1972. Nests of the tassel-eared squirrel. Journal of Mammalogy 53:900–903.

Findley, J. S., and C. J. Jones. 1962. Distribution and variation of voles of the genus *Microtus* in New Mexico and adjacent areas. Journal of Mammalogy 43:154–166.

Finley, R. B. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. In: Jones, J. K., Jr. editor. Contributions in mammalogy: a volume honoring Professor E. Raymond Hall. Miscellaneous Publications of the University of Kansas Museum of Natural History 51:233–273.

Froehlich, G. F., and N. S. Smith. 1990. Habitat use by the Mt. Graham red squirrel. In: Krausman, P. R., and N. S. Smith, editors. Managing wildlife in the southwest. Arizona Chapter of the Wildlife Society, Phoenix. Pp. 118–125.

Halloran, M. E., and M. Beckoff. 1994. Nesting behaviour of Abert squirrels (*Sciurus aberti*). Ethology 97:236–248.

Hamilton, W. J. 1939. Observations on the life history of the red squirrel in New York. American Midland Naturalist 22:732–745.

Hatt, R. T. 1929. The red squirrel: its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. Roosevelt Wildlife Annals 2:1–146

Hoffmeister, R. 1956. Mammals of the Graham (Pinaleños) Mountains, Arizona. American Midland Naturalist 55:257–288.

Kovach, W. G. 1999. Orianna for Windows. Version 1.05. Kovach Computing Services, Pentraeth, Anglesey, Wales, United Kingdom.

Layne, J. N. 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. Ecological Monographs 24:227–267.

Martin, P. S., and P. J. Mehringer. 1965. Pleistocene pollen analyses and biogeography of the southwest. In: Wright, H. E., and D. G. Frey, editors. The Quaternary of the United States. Princeton University Press, Princeton, New Jersey. Pp. 433–451.

Minkley, W. L. 1968. Possible extirpation of the spruce squirrel from the Pinaleños (Graham) Mountains, southcentral Arizona. Journal of the Arizona Academy of Science 5:110.

Patterson, B. D. 1984. Mammalian extinction and biogeography in the southwestern Rocky Mountains. In: Nitecki, M. H., editor. Extinctions. University of Chicago Press, Chicago, Illinois. Pp. 247–293.

Pauls, R. W. 1981. Energetics of the red squirrel: a laboratory study of the effects of temperature, seasonal acclimation, and use of nest and exercise. Journal of Thermal Biology 6:79–85.

Rothwell, R. 1979. Nest sites of red squirrels (*Tamiasciurus hudsonicus*) in the Laramie Range of southeastern Wyoming. Journal of Mammalogy 60:404–405.

SAS Institute Inc. 1995. SAS/Stat User's guide. Release 6.02 ed. SAS Institute Inc., Cary, North Carolina.

SPSS Inc. 1997. SigmaStat 2.0 for Windows User's Manual. SPSS Inc. Chicago, Illinois.

Smith, A. A., and R. W. Mannan. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. Journal of Wildlife Management 58:437–445.

Snedcor, G. W., and W. G. Cochran. 1980. Statistical methods, Seventh ed. Iowa State University Press, Ames, Iowa. Pp. 290–291.

Spicer, R. B., J. C. DeVos, Jr., and R. L. Glinski. 1985. Status of the Mount Graham red squirrel, *Tamiasciurus hudsonicus grahamensis* (Allen), of southeastern Arizona. Arizona Game and Fish Department, Phoenix, Arizona.

Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. United States Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. Research Note 180:1–5.

Sun, C. 1989. Young dispersal and the seasonal changes of territorial behavior in red squirrels (*Tamiasciurus hudsonicus*). Unpublished M.S. thesis. University of Minnesota, Minneapolis.

Vahle, J. R. 1978. Red squirrel use of southwestern mixed coniferous habitat. Unpublished M.S. thesis, Arizona State University, Phoenix.

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