

Kleptoparasitic Behavior and Species Richness at Mt. Graham Red Squirrel Middens

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Abstract—We used remote photography to assess the frequency of inter- and intra-specific kleptoparasitism and species richness at Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) middens. Remote cameras and conifer cones were placed at occupied and unoccupied middens, and random sites. Species richness of small mammals was higher at red squirrel middens than random sites. Abert's squirrels, potential kleptoparasites, were recorded only at unoccupied middens and random sites. Non-resident red squirrels were most common at unoccupied middens and rare at occupied middens and random sites. Inter- and intra-specific kleptoparasitism of red squirrel middens appears uncommon likely due to territorial behavior.

Introduction

Many animals hoard food for future use. One type of food hoarding, larder hoarding, occurs when individuals store high concentrations of food at one cache site. Benefits of larder hoarding include higher probability of survival during periods of food scarcity, reduction in foraging time, and increased reproductive success. The most significant cost of larder hoarding is that individuals must vigorously defend caches against potential raiders (Vander Wall 1990).

The red squirrel (*Tamiasciurus hudsonicus*) is a small, territorial tree squirrel (~225 g) that larder hoards conifer cones and fungi in cone scale piles known as middens (Steele 1998). Middens can contain $\leq 4,300$ cones (Gurnell 1984) and reach 13 m in diameter and 50 cm in depth (Patton and Vahle 1986). The conspicuous nature of middens may facilitate intra- and inter-specific kleptoparasitic behavior. Kleptoparasitism occurs when an individual takes food from another individual (Brockmann and Barnard 1979). Discarded seeds and fungi at middens (Brown 1984; Hoffmeister 1986) may also provide resources for other small mammals.

In the Pinaleno Mountains of Arizona, endangered Mt. Graham red squirrels (*T. h. grahamensis*) co-occur with an introduced population of Abert's squirrels (*Sciurus aberti*; Hutton et al. 2003). Abert's squirrels are large tree squirrels (~700 g) that eat conifer seeds and fungi, but do not cache or defend food (Hall 1981; Nash and Seamen 1977). Abert's squirrels have been implicated in the decline of Mt. Graham red squirrels through kleptoparasitism of middens (Spicer 1985). Abert's squirrels are known to take cones from red squirrel middens, but the frequency of kleptoparasitic behavior is unknown (Ferner 1974; Hutton et al. 2003). Survivorship or productivity of Mt. Graham red squirrels could be reduced if middens are kleptoparasitized.

Our study quantified the frequency of inter- and intra-specific kleptoparasitism at Mt. Graham red squirrel middens. We

placed Douglas-fir (*Pseudotsuga menziesii*) cones at occupied and unoccupied middens, and random sites and used remote cameras to count potential kleptoparasitic squirrels. In addition, we examined mammalian and avian species richness at middens as an indicator of potential species associations.

Materials and Methods

We conducted our study in the Pinaleno Mountains, 25 km southwest of Safford, Graham County, Arizona. The study area encompassed 110 ha of mixed conifer forest at an elevation of 2,900 m. All Mt. Graham red squirrel middens were marked and examined quarterly for occupancy (Young 1995). Live trapping was conducted regularly on the study area. Captured red and Abert's squirrels were marked with uniquely colored ear tags, and adults were radio-collared.

We selected 9 occupied middens, 7 unoccupied middens, and 7 random sites from the study area. Occupied middens were inhabited by a radio-collared red squirrel. Unoccupied middens exhibited no fresh sign of occupancy (fresh feeding and digging), but still had a well-intact midden structure. Random sites were in forested areas between 50-100 m from middens.

During September-November 2002, we placed 10 Douglas-fir cones on a platform of aged plywood at each site. Remote cameras (15 Trailmaster passive infrared monitors (TM 550) and 3 Trailmaster active infrared monitors (TM 1550) equipped with cameras (TM 35-1, Trailmaster, Lenexa, KS) and 5 deercams (DC-100, Deercam, Park Falls, WI)) were used to photograph animals entering sites. Sites were checked ≥ 2 times a day for 4 d after cone placement. From 5 d to the end of trial, sites were checked once a day until all cones were removed or at least 10 days had past (Mean = 11.2 ± 0.4 days). The sites did not differ in the number of days monitored (1-way ANOVA, $F_{2,20} = 1.80$, $P = 0.191$). We examined photographs

to determine identity of squirrels and recorded the number of uniquely marked Abert's or red squirrel at each site. Unmarked squirrels were counted only once per site. Resident red squirrels were not included in the count at occupied middens. Species richness was measured by tallying the number of mammalian and avian species photographed at each site. We calculated 4 types of species richness: total (all birds and mammals excluding Abert's and red squirrels), small mammal (*Peromyscus maniculatus*, *Tamias dorsalis*, and *Neotoma mexicana*), large mammal (all other mammals), and avian. We identified mammals using Kays and Wilson (2002) and birds using Sibley (2000). All count data were square root transformed to better meet the assumptions of parametric tests; however, means ($\pm SE$) presented are from untransformed values.

Results

Kleptoparasitism

Abert's squirrels were photographed twice at random sites, once at unoccupied middens, and never at occupied middens yielding no differences among sites (table 1: 1-way ANOVA, $F_{2,20} = 1.41$, $P = 0.267$). Red squirrels were observed at all sites in differential numbers (table 1: 1-way ANOVA, $F_{2,20} = 7.60$, $P = 0.004$). More red squirrels were photographed at unoccupied middens than at occupied middens (Tukey-Kramer, $P < 0.05$) and random sites (Tukey-Kramer, $P < 0.05$). No difference existed between occupied middens and random sites in observed number of red squirrels (Tukey-Kramer, $P > 0.05$).

Species Richness

Excluding red and Abert's squirrels, 8 mammalian and 2 avian species were observed at all sites combined (appendix 1). Large mammal and avian species richness were the same between sites (table 2: 1-way ANOVA, $F_{2,20} < 3.00$, $P > 0.100$). Species richness of small mammals differed among sites (table 2: 1-way ANOVA, $F_{2,20} = 4.93$, $P = 0.018$). Small mammal species richness was less at random sites than occupied (Tukey-Kramer, $P < 0.05$) and unoccupied middens (Tukey-Kramer, $P < 0.05$). No difference existed between occupied and unoccupied middens in small mammal species richness (Tukey-Kramer, $P > 0.05$). Total species richness differed among sites (table 2: 1-way ANOVA, $F_{2,20} = 4.43$, $P = 0.026$). Total species richness was higher at occupied middens than at random sites (Tukey-Kramer, $P < 0.05$). No difference was observed in total species richness between occupied and unoccupied middens (Tukey-Kramer, $P > 0.05$) and random sites and unoccupied middens (Tukey-Kramer, $P > 0.05$).

Table 1—Mean number ($\pm SE$) of Abert's squirrels and non-resident red squirrels observed at middens and random sites.

Sites	n	Abert's squirrels	Red squirrels
Occupied middens	9	0.0 $\pm$ 0.1	0.3 $\pm$ 0.2
Unoccupied middens	7	0.3 $\pm$ 0.1	1.6 $\pm$ 0.2
Random sites	7	0.1 $\pm$ 0.1	0.6 $\pm$ 0.2

Discussion

Abert's squirrels do not appear to frequently kleptoparasitize cones from Mt. Graham red squirrel middens; however, we cannot conclusively state that kleptoparasitic behavior is uncommon due to the small sample sizes and short duration of this study. We detected Abert's squirrels twice at random sites, once at an unoccupied midden, and never at an occupied midden. In addition, only 5 observations of Abert's squirrels kleptoparasitizing Mt. Graham red squirrel middens were recorded during 41,000 field hours on our study area (Hutton et al. 2003). Territorial behavior of red squirrels (Gurnell 1984) may prevent Abert's squirrels from successfully raiding middens. Out of 75 agnostic interactions observed between these two species on our study area, red squirrels were the dominant aggressor 98.7% of the time (Hutton et al. 2003). If red squirrels are successfully defending middens against Abert's squirrel incursions, detrimental effects can still occur. Increased territorial defense could lead to energetic costs, decreased foraging time, and increased exposure to predators. Further research is needed to determine the potential effects of introduced Abert's squirrels on the survival of Mt. Graham red squirrels.

Kleptoparasitism of red squirrel middens by Abert's squirrels is not unique to the Pinaleno Mountains and has been noted in Colorado (Ferner 1974) and northern Arizona (Hall 1981). Other known inter-specific kleptoparasites of red squirrels include Clark's nutcrackers (*Nucifragas columbiana*: Bent 1946), black bears (*Ursus americanus*: Kendall 1983), and grizzly bears (*Ursus arctos horribilis*: Mattson and Reinhart 1997). Of these species, only black bears occur in the Pinaleno Mountains (Hoffmeister 1986; Sibley 2000).

Intra-specific kleptoparasitism of occupied Mt. Graham red squirrel middens appears to be an infrequent behavior. Non-resident red squirrels were detected in low numbers at occupied middens and random sites. Territorial behavior likely reduces the number of red squirrels entering an occupied midden area. Territories center around middens and are circular in shape. Red squirrels use calls to maintain territorial boundaries between neighbors and will aggressively chase intruders (Gurnell 1984; Steele 1998). The low numbers of red squirrels at random sites were probably due to the lack of a midden and associated structure. Without visual and olfactory cues associated with middens, red squirrels may have had difficulty locating cones at random sites. The highest numbers of red squirrels were photographed at unoccupied middens. Unoccupied middens have a conspicuous structure (Patton and Vahle 1986) and probably olfactory cues that attract red squirrels. Furthermore, there is no aggressive resident to drive away red squirrels raiding unoccupied middens.

Occupied and unoccupied middens had similar small mammal species richness that was higher than species richness at random sites. Total species richness was highest at occupied middens and lowest at random sites. Red squirrel middens may offer important resources such as food and shelter for small mammals. Middens contain large numbers of cached cones (Gurnell 1984) and small amounts of dried fungi (Hoffmeister 1986). In addition, red squirrels strip conifer cones at middens (Brown 1984) and some seeds likely fall to the ground

Table 2—Mean species richness ($\pm$ SE) at Mt. Graham red squirrel middens and random sites.

Species richness	Occupied middens (n = 9)	Unoccupied middens (n = 7)	Random sites (n = 7)
Small mammal	1.4 $\pm$ 0.3	1.1 $\pm$ 0.3	0.1 $\pm$ 0.3
Large mammal	0.7 $\pm$ 0.2	0.0 $\pm$ 0.2	0.3 $\pm$ 0.2
Avian	0.3 $\pm$ 0.2	0.6 $\pm$ 0.2	0.1 $\pm$ 0.2
Total	2.4 $\pm$ 0.4	1.7 $\pm$ 0.5	0.6 $\pm$ 0.5

uneaten. Food resources at middens could attract granivorous and mycophagous deermice, cliff chipmunks, and Mexican woodrats (Hoffmeister 1986). Red squirrel middens may also provide valuable nest sites for small mammals. Mexican woodrats build nests at Mt. Graham red squirrel middens (A. J. Edelman, personal observation). Predators such as the gray fox (*Urocyon cinereoargenteus*), spotted skunk (*Mephitis mephitis*), and striped skunk (*Spilogale gracilis*; Hoffmeister 1986) may be attracted to middens due to the presence and accessibility of small mammals. Martens (*Martes americana*) utilize subnivean holes created by red squirrels around middens to hunt small mammals (Sherburne 1993). The environment surrounding middens could also favor small mammals and other forest vertebrates. Mt. Graham red squirrel middens differ from random sites by having more basal area, snags, downed logs, foliage volume, and canopy cover (Smith and Mannan 1994).

By storing large quantities of high quality food in visible larder sites, Mt. Graham red squirrels may serve as a keystone species for small mammal diversity in high-elevation forests of the Pinaleno Mountains. Further research is needed to determine the exact effect of red squirrels on species diversity and abundance. Given the precarious state of the Mt. Graham red squirrel population (224 individuals, Arizona Game and Fish Department 2003), it is vital that we understand the relationship of this species with its ecosystem.

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Appendix 1.

Presence (+) or absence (–) of mammalian and avian species found at red squirrel middens and random sites in mixed conifer forest. Number in parentheses indicates number of sites where species were detected.

Species	Occupied middens (n = 9)	Unoccupied middens (n = 7)	Random sites (n = 7)
Deermouse (<i>Peromyscus maniculatus</i>)	+ (5)	+ (4)	+ (1)
Cliff chipmunk (<i>Tamias dorsalis</i>)	+ (2)	+ (1)	–
Mexican woodrat (<i>Neotoma mexicana</i>)	+ (6)	+ (3)	–
Eastern cottontail (<i>Sylvilagus floridanus</i>)	+ (2)	–	–
Striped skunk (<i>Mephitis mephitis</i>)	+ (1)	–	+ (1)
Western spotted skunk (<i>Spilogale gracilis</i>)	+ (1)	–	–
Gray fox (<i>Urocyon cinereoargenteus</i>)	+ (1)	–	–
White-tailed deer (<i>Odocoileus virginianus</i>)	+ (1)	–	+ (1)
Yellow-eyed Junco (<i>Junco phaeonotus</i>)	+ (2)	+ (3)	+ (1)
Hermit thrush (<i>Catharus guttatus</i>)	–	+ (1)	–