

# Seasonal changes in home ranges of Abert's squirrels: impact of mating season

A.J. Edelman and J.L. Koprowski

**Abstract:** We compared home ranges of introduced Abert's squirrels (*Sciurus aberti* Woodhouse, 1853) in mixed-conifer forests of Arizona during non-mating and mating seasons. Because Abert's squirrels are reported to depend on ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forests, the mixed-conifer forest in our study represented a novel habitat. Home-range size, home-range overlap with females, and movement distances increased for males from non-mating to mating seasons. Home-range size and overlap characteristics of females remained consistent between seasons, but movement distances were reduced during the mating season. Males probably increased home-range size, home-range overlap with females, and movement distances during the mating season to maximize contact with scarce females. Home-range size and overlap characteristics of female Abert's squirrels likely remained stable between seasons because females do not search for mates. Restricted movements by females during the mating season may be due to changes in resource use in preparation for reproduction. Non-mating season home ranges in our study were smaller than home ranges observed in ponderosa pine forest. Abert's squirrels in mixed-conifer forest may have small home ranges because resource quality is higher than in ponderosa pine forest or competition for space with co-occurring Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis* (J.A. Allen, 1894)).

**Résumé :** Nous avons comparé les aires vitales des écureuils d'Abert (*Sciurus aberti* Woodhouse, 1853), une espèce introduite, dans des forêts de conifères mixtes de l'Arizona durant la saison de reproduction et en dehors de cette période. Puisque qu'on a signalé que les écureuils d'Abert sont dépendants des forêts de pins ponderosa (*Pinus ponderosa* P. & C. Lawson), la forêt de conifères mixte de notre étude représente un habitat inusité. Chez les mâles, la taille de l'aire vitale, le chevauchement avec les aires vitales des femelles et les distances des déplacements sont plus grands durant la saison de reproduction que durant le reste de l'année. Chez les femelles, la taille de l'aire vitale et les caractéristiques du chevauchement restent semblables d'une saison à l'autre, quoique les distances des déplacements diminuent durant la saison de reproduction. Les mâles augmentent probablement la taille de leur aire vitale, le chevauchement de leur aire avec celles des femelles et les distances de leurs déplacements afin de maximiser leurs contacts avec les femelles qui sont peu nombreuses. Chez les écureuils d'Abert femelles, la taille de l'aire vitale et les caractéristiques du chevauchement d'aire restent stables en toutes saisons probablement parce que les femelles ne recherchent pas de partenaire. Les déplacements restreints des femelles durant la saison de reproduction peuvent être dus à des modifications de leur utilisation des ressources en préparation pour la reproduction. Les aires vitales hors de la saison de reproduction dans notre étude sont plus restreintes que celles observées dans la forêt de pins ponderosa. Les écureuils d'Abert peuvent avoir des aires vitales plus petites dans la forêt de conifères mixte à cause de la qualité supérieure des ressources par comparaison à la forêt de pins ponderosa ou à cause de la compétition pour l'espace avec les écureuils roux de Mount Graham (*Tamiasciurus hudsonicus grahamensis* (J.A. Allen, 1894)) qui y cohabitent avec eux.

[Traduit par la Rédaction]

## Introduction

Home-range size is affected by a variety of biotic and abiotic factors, including body size, mating system, population density, climate, and resource distribution and abundance (McNab 1963; Boutin 1990; Fisher and Owens 2000; Lurz et al. 2000; Dahle and Swenson 2003a, 2003b). Seasonality in any of these factors can lead to variation in

home-range size of individuals throughout the year. In most mating systems, males and females differ in strategies used to maximize reproductive success (Wilson 1975; Crook et al. 1976; Clutton-Brock 1989). In polygynous and promiscuous species with little or no male parental care, ability to obtain and to convert food into offspring is a primary determinant of female reproductive success. Therefore, spatial distribution and abundance of resources are expected to have the greatest impact on home-range size of females (Ostfeld 1985; Davies 1991). For males that do not provide parental care, reproductive success is principally influenced by the number of females with which males successfully copulate. Thus, spatial distribution and abundance of females will strongly affect home-range size of males (Emlen and Oring 1977; Ims 1987; Clutton-Brock 1989). The difference in factors affecting home-range size between sexes can be temporarily reduced in species with seasonal reproduction. Outside the mating season, exploiting resources can become the prin-

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A.J. Edelman<sup>1,2</sup> and J.L. Koprowski. Wildlife Conservation and Management, School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA.

<sup>1</sup>Corresponding author (e-mail: [andrew@unm.edu](mailto:andrew@unm.edu)).

<sup>2</sup>Present address: Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM 87131, USA.

cial factor influencing home-range size of males, as well as females (Erlinge and Sandell 1986; Dahle and Swenson 2003a).

The promiscuous mating system of Holarctic tree squirrels (genera *Sciurus* L., 1758 and *Tamiasciurus* Trouessart, 1880) results in divergent reproductive strategies between sexes (Gurnell 1987; Koprowski 1998). During the mating season, each female tree squirrel is in estrus for <1 day and mates with multiple males (Thompson 1977; Gurnell 1987). Because tree squirrels lack male parental care (Steele and Koprowski 2001), males should monitor and mate with as many females as possible to maximize reproductive success (Clutton-Brock 1989). Female tree squirrels, however, should maximize reproductive success by obtaining resources (e.g., food and nest sites) to reproduce and to care for young (Clutton-Brock and Harvey 1978). Sexual differences in reproductive strategies of tree squirrels suggest that space use may vary between sex and season. Patterns of seasonal changes in home-range size of tree squirrels are ambiguous, with some studies reporting that home-range size does (Thompson 1978; Farentinos 1979; Koford 1982; Kenward 1985; Wauters and Dhondt 1992; Lema 2001) or does not vary between non-mating and mating seasons (Cross 1969; Foster 1992; Halloran and Bekoff 2000; Linders et al. 2004). Other factors besides reproductive strategies, such as food and nest resources, and population density may affect tree squirrel home-range size between seasons (Don 1983; Linders et al. 2004; Lurz et al. 2000; Wauters and Dhondt 1992).

Abert's squirrels (*Sciurus aberti* Woodhouse, 1853) are native to montane areas of the southwestern United States and northern Mexico, where ponderosa pine (*Pinus ponderosa* P. & C. Lawson) dominates forests (Brown 1984). The Abert's squirrel is reportedly a specialized herbivore thought to depend on ponderosa pine for food and nest sites (Keith 1965; Patton and Green 1970; Stephenson 1975; Pederson et al. 1976; Hall 1981; Snyder 1993; Halloran and Bekoff 1994; States and Wettstein 1998). Both sexes are similar in size (Nash and Seaman 1977) and non-territorial with overlapping home ranges (Farentinos 1979; Halloran and Bekoff 2000). Abert's squirrels consume a variety of seasonally available food items that include fungi and conifer seeds, staminate flowers, buds, and inner bark (Stephenson 1975). Abert's squirrels have among the lowest reported densities and largest home-range sizes for Holarctic tree squirrels (Gurnell 1987). Previous studies on home-range characteristics of Abert's squirrels have found contradictory evidence for sexual differences in home-range size (Farentinos 1979; Halloran and Bekoff 2000; Lema 2001). Home ranges from these studies, however, were either created from opportunistic sightings rather than from random locations (Farentinos 1979; Halloran and Bekoff 2000) or were based on low numbers of locations per individual (Lema 2001).

Our aim was to examine variation in seasonal home-range characteristics of male and female Abert's squirrels in relation to mating activities. Our study focused on an introduced population of Abert's squirrels occupying mixed-conifer forest in the Pinaleño Mountains of Arizona. Abert's squirrels were introduced to the Pinaleño Mountains in the 1940s (Davis and Brown 1988) and, unlike natural populations, inhabit forests that contain little to no ponderosa pine (Hutton

et al. 2003; Edelman and Koprowski 2006). Thus, an additional objective was to compare home-range size of Abert's squirrels in this novel habitat with past studies conducted in ponderosa pine forest. Based on reproductive strategies, we expected males to expand home-range size and overlap with females during the mating season and move long distances to monitor and mate with females. Variation of female home ranges and movements between mating and non-mating seasons are more difficult to predict because their reproductive success likely depends on food resource abundance and distribution.

## Materials and methods

### Study area

The study area was located in the Pinaleño Mountains, 25 km southwest of Safford, Arizona, USA. Our site encompasses 110 ha of mixed-conifer forest from ca. 2850 to 3170 m in elevation. Dominant tree species were corkbark fir (*Abies lasiocarpa* (Hook.) Nutt. var. *arizonica* (Merriam) Lemmon, 41%), Engelmann spruce (*Picea engelmannii* Parry ex Engelm., 20%), quaking aspen (*Populus tremuloides* Michx., 17%), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco, 10%), with smaller amounts of southwestern white pine (*Pinus strobiformis* Engelm., 8%), ponderosa pine (2%), and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., 1%) (A.J. Edelman and J.L. Koprowski, unpublished data).

### Radiotelemetry

We used 48 cm × 15 cm × 15 cm box traps constructed of 1.3 cm × 2.5 cm wire mesh (custom model No. 202; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanuts and peanut butter to trap squirrels. Captured squirrels ( $n = 47$  individuals) were transferred to a cloth handling cone (Koprowski 2002) to assess sex, reproductive condition, age class, and body mass. Uniquely numbered metal ear tags (model No. 1005-1; National Band and Tag Co., Newport, Kentucky, USA) with plastic colored washers (1 cm, model No. 1842; National Band and Tag Co., Newport, Kentucky, USA) were attached to squirrels. Adults (>600 g,  $n = 34$  individuals) were fitted with radio collars (model No. SOM 2380; Wildlife Materials, Inc., Murphysboro, Illinois, USA) that weighed <5% of body mass. Handling of animals was in accordance with the University of Arizona Institutional Animal Care and Use Committee and the guidelines of the Canadian Council on Animal Care.

From July 2002 to June 2003, we used biangulation and homing (White and Garrott 1990) to locate radio-collared squirrels during daylight hours. Most locations (84.9%) of the same individual were taken on separate days; however, consecutive locations during the same day were taken  $\geq 90$  min apart ( $364.9 \pm 13.9$  min; mean  $\pm$  SE).

Biangulation accounted for the majority of locations (67%). To reduce location error, only bearings with inter-bearing angles of  $\geq 60^\circ$  and  $\leq 120^\circ$  were used to estimate animal locations (White and Garrott 1990). Consecutive bearings on the same animal were taken  $\leq 30$  min apart ( $8.8 \pm 0.2$  min; mean  $\pm$  SE) to reduce error associated with animal movement. Estimated locations from bearings were calculated using LOAS (Ecological Software Solutions 2003). Accuracy of estimated bearings and locations were obtained by con-

ducting a beacon study (Withey et al. 2001). Twenty radio collars were placed randomly throughout the study area at locations whose coordinates had been mapped using a GPS unit (GeoExplorer II; Trimble Navigation, Sunnyvale, California, USA). We positioned radio collars both in trees (ca. 2 m) and slightly off the ground (ca. 0.2 m) to simulate typical squirrel locations. Bearings were taken for each radio collar by an observer unaware of actual locations. Bearing and linear error were calculated from actual and estimated bearings and locations using LOAS. A trend for bearing error ( $3.8^\circ \pm 2.2^\circ$ ; mean  $\pm$  SE) to differ from zero existed (one-sample Student's  $t$  test,  $t_{[39]} = 1.7$ ,  $P = 0.089$ ), possibly indicating a small bias in estimated bearings. The standard deviation of the bearing error (SD = 13.7) showed some loss of precision in estimated bearings, but the short distance (usually <200 m) between observer and squirrel limited the impact of the bearing error on location estimates (linear error of  $19.4 \pm 2.4$  m (mean  $\pm$  SE),  $n = 20$ ).

Locations obtained by homing were mapped using a GPS unit or with a compass bearing and estimated distance from a known location. In the latter case, locations were calculated using the ArcView<sup>®</sup> extension distance/azimuth tools (Jenness Enterprises 2003).

### Data analysis

We used Ranges 6 (Anatrack Ltd. 2003) to estimate home-range size, home-range overlap, and interfix distance during non-mating (July 2002 – January 2003) and mating (February 2003 – June 2003) seasons. Mating season was defined as the period during which females could possibly enter estrus. We used similar season lengths as other studies on Abert's squirrels (Farentinos 1979; Halloran and Bekoff 2000) to facilitate comparison. A plot of home-range size versus number of locations reached an asymptote at approximately 25–30 fixes. Therefore, only individuals with  $\geq 25$  locations ( $35.6 \pm 0.78$  locations (mean  $\pm$  SE),  $n = 30$ ) during a season were used for home-range estimates.

The fixed-kernel method with a fixed multiplier of 1.0 as a smoothing parameter was used to estimate home-range size. For each individual, 3 home-range estimates were created: 95% minimum convex polygon (MCP), 95% fixed kernel, and 80% fixed kernel. The 80% fixed kernel was selected by examining the utilization distribution (Wauters and Dhondt 1992). The 95% and 80% fixed kernel estimates were used to compare home-range size between seasons and sexes in our study. The 95% MCP and 95% fixed kernel estimates were used to compare home-range sizes with other studies. The total percentage of a home range overlapped by neighboring squirrels (total percent overlap) was calculated for 95% fixed kernels. Distances moved between consecutive locations (i.e., interfix distance) during a month were calculated for each individual from July 2002 to June 2003 (Linders et al. 2004).

Mating chases were found by homing on radio-collared squirrels when several individuals were located in close proximity or when long-range movements were detected. Within each mating chase, number of individuals and identity of marked squirrels were recorded at time of sighting.

We conducted all statistical analyses using JMP-IN<sup>®</sup> (SAS Institute Inc. 2003). Home-range estimates were log-transformed and total percent overlap was arcsine-transformed to better

meet assumptions of parametric tests (Zar 1984); however, the mean  $\pm$  SE values presented in the Results are from untransformed data. For all individuals within a season, two-tailed Student's  $t$  tests were used to analyze home-range size, total percent overlap, interfix distances, and interfix intervals between sexes. For individuals that were monitored in both seasons, two-tailed Wilcoxon's signed-rank tests were used to compare home-range size, total percent overlap, interfix distances, and interfix intervals for females and males between seasons.

## Results

### Home-range size

Size of home ranges was similar between males (95% fixed kernel:  $6.4 \pm 1.2$  ha; 80% fixed kernel:  $4.2 \pm 0.7$  ha;  $n = 8$ ) and females (95% fixed kernel:  $8.8 \pm 1.3$  ha; 80% fixed kernel:  $5.8 \pm 0.8$  ha;  $n = 8$ ) during the non-mating season (all  $t_{[14]} < 1.65$ ,  $P > 0.13$ ). Size of male home ranges (95% fixed kernel:  $25.4 \pm 6.5$  ha; 80% fixed kernel:  $15.8 \pm 4.1$  ha;  $n = 9$ ) was over 4 times larger than the size of female home ranges (95% fixed kernel:  $7.0 \pm 1.9$  ha; 80% fixed kernel:  $4.4 \pm 1.0$  ha;  $n = 5$ ) during the mating season (all  $t_{[12]} > 3.10$ ,  $P < 0.01$ ).

Home ranges of six males increased about 3.5 times in size from the non-mating season to the mating season (all  $Z = 10.5$ ,  $P = 0.031$ ; Figs. 1A, 1B). Five females exhibited no difference in home-range size between non-mating and mating seasons (all  $Z < 1.6$ ,  $P > 0.8$ ; Figs. 1A, 1B).

### Home-range overlap

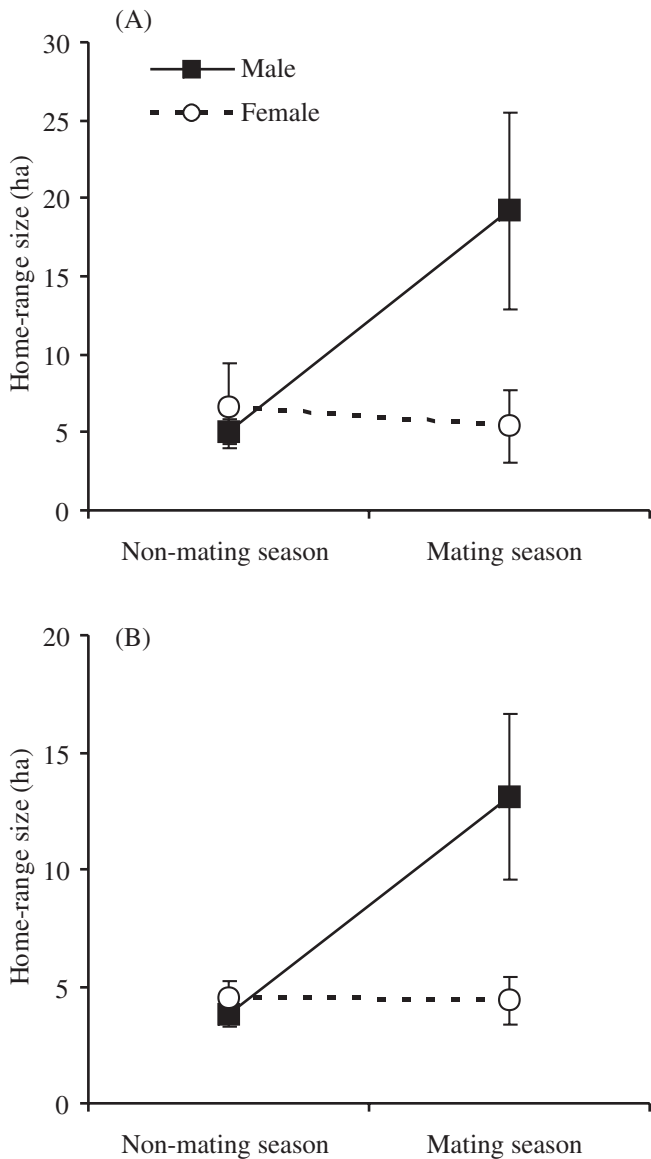
During the non-mating season, total percent overlap of home ranges by males (females:  $32.3\% \pm 13.2\%$ ,  $n = 8$ ; males:  $40.5\% \pm 10.0\%$ ,  $n = 8$ ) and females (females:  $27.1\% \pm 8.2\%$ ,  $n = 8$ ; males:  $28.3\% \pm 15.0\%$ ,  $n = 8$ ) did not differ between sexes (all  $t_{[14]} < 1.5$ ,  $P > 0.15$ ). Total percent overlap of home ranges by males was approximately 1.5 times higher for females ( $94.5\% \pm 3.5\%$ ,  $n = 5$ ) than for males ( $62.1\% \pm 8.6\%$ ,  $n = 9$ ) during the mating season ( $t_{[12]} = 2.80$ ,  $P = 0.016$ ). Male ( $24.2\% \pm 8.1\%$ ,  $n = 9$ ) and female ( $17.6\% \pm 0.8\%$ ,  $n = 5$ ) home ranges did not differ during the mating season in total percent overlap by females ( $t_{[12]} = 0.62$ ,  $P = 0.55$ ).

No difference in total percent overlap of home ranges by females was observed between non-mating and mating seasons for either sex (all  $Z < 4.0$ ,  $P > 0.20$ ; Fig. 2A). Total percent overlap of home ranges by males approximately doubled for individual females ( $n = 5$ ) from the non-mating season to the mating season ( $Z = 7.5$ ,  $P = 0.031$ ; Fig. 2B). Total percent overlap of home ranges by males did not change for individual males ( $n = 6$ ) from the non-mating season to the mating season ( $Z = 5.5$ ,  $P = 0.313$ ; Fig. 2B).

### Interfix distances

Distance moved between consecutive locations was similar between males ( $132.5 \pm 18.5$  m,  $n = 8$ ) and females ( $143.6 \pm 13.6$  m,  $n = 8$ ) during the non-mating season ( $t_{[14]} = 0.49$ ,  $P = 0.635$ ). Distance moved between consecutive locations was 2 times larger for males ( $202.4 \pm 12.5$  m,  $n = 9$ ) than for females ( $98.5 \pm 10.9$  m,  $n = 5$ ) during the mating season ( $t_{[12]} = 5.55$ ,  $P < 0.001$ ). Time interval between

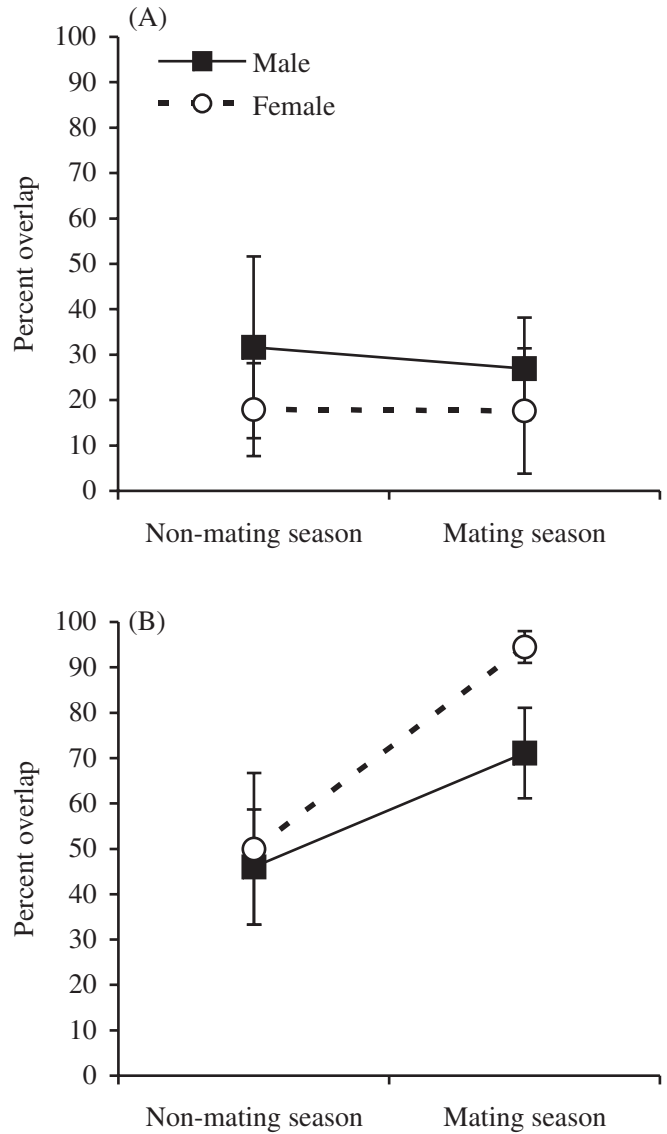
**Fig. 1.** Ninety-five percent (A) and 80% (B) fixed kernel home-range estimates (mean  $\pm$  SE) for female ( $n = 5$ ) and male ( $n = 6$ ) Abert's squirrels (*Sciurus aberti*) during non-mating and mating seasons in the Pinaleno Mountains, Arizona.



interfix distances did not differ between males (non-mating season:  $76.3 \pm 3.3$  h; mating season:  $54.8 \pm 1.6$  h) and females (non-mating season:  $71.8 \pm 2.0$  h; mating season:  $55.6 \pm 1.5$  h) for either the non-mating season or the mating season (all  $t < 1.2$ ,  $P > 0.25$ ).

Female movement was more limited during the mating season with over 65% of consecutive interfix distances occurring at  $<100$  m (Fig. 3A). Male movement distances increased during the mating season with more frequent occurrences of large interfix distances (Fig. 3B). Interfix distances almost doubled for individual males from the non-mating season ( $112.1 \pm 8.2$  m) to the mating season ( $208.1 \pm 18.2$  m) ( $Z = 10.5$ ,  $P = 0.016$ ;  $n = 6$ ). Interfix distances for individual females appeared to decrease from non-mating season ( $125.6 \pm 17.3$  m) to mating season ( $98.5 \pm 10.9$  m) ( $Z = 7.5$ ,  $P = 0.063$ ,  $n = 5$ ). Time interval between interfix

**Fig. 2.** Total percent overlap (mean  $\pm$  SE) of female ( $n = 5$ ) and male ( $n = 6$ ) Abert's squirrel home ranges by neighboring females (A) and males (B) between non-mating and mating seasons in the Pinaleno Mountains, Arizona.



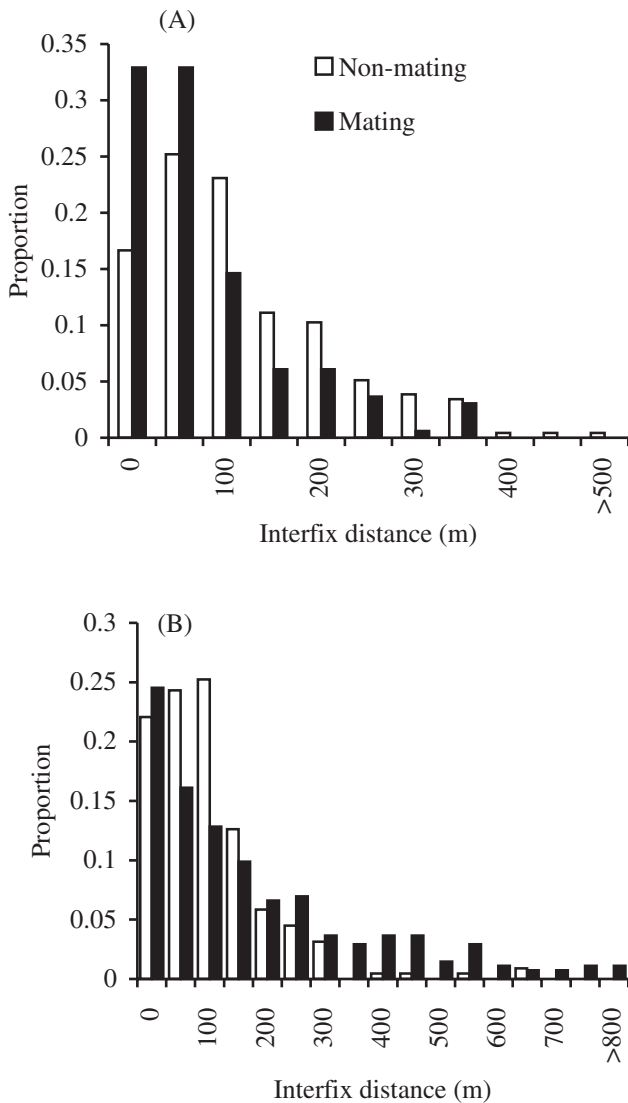
distances did differ between non-mating season (males:  $74.2 \pm 3.7$  h; females:  $71.6 \pm 2.7$  h) and mating season (males:  $53.4 \pm 2.1$  h; females:  $55.8 \pm 1.5$  h) for individual males ( $Z = 10.5$ ,  $P = 0.031$ ) and females ( $Z = 7.5$ ,  $P = 0.063$ ).

**Mating chases**

Seven mating chases were observed in and around the study area during mid-May 2003. Four of five radio-collared females and two unmarked females (outside the study area) were observed in mating chases. All four radio-collared females in mating chases subsequently produced young, while the other radio-collared female did not. The number of males recorded in mating chases was  $3.9 \pm 0.3$  (range 3–5). Marked males participated in  $2.2 \pm 0.4$  mating chases (range 1–4).



**Fig. 3.** Proportion of interfix distances for individual female ( $n = 5$ ; A) and male ( $n = 6$ ; B) Abert's squirrels during non-mating and mating seasons in the Pinaleno Mountains, Arizona.



## Discussion

### Home ranges of males

Seasonal variation in home-range characteristics and movements of male Abert's squirrels appears to reflect the difference in male reproductive strategies between non-mating and mating seasons. Male tree squirrels provide no parental care (Steele and Koprowski 2001), thus reproductive success is maximized by successfully mating with as many females as possible (Emlen and Oring 1977; Ims 1987; Clutton-Brock 1989). During the mating season, males increased home-range size, home-range overlap with females, and movement distances, likely to maximize contact with females and engage in multiple mating chases. The low density of Abert's squirrels (Gurnell 1987) likely contributed to the magnitude of the increase in home ranges of males during the mating season. Males should increase movement

patterns to maximize contact with scarce females (Clutton-Brock 1989). The reduced home-range size, home-range overlap, and movement distances of male Abert's squirrels during the non-mating season, as well as a similarity in these characteristics with females, may reflect a focus on exploiting food resources and minimizing energy expenditures and predation risk. During the non-mating season, male reproductive strategies should change to maximizing future reproductive success through survival and maintenance of body condition if tracking of females is not necessary for reproductive success (Erlinge and Sandell 1986; Dahle and Swenson 2003a).

Male Abert's squirrels in ponderosa pine forests also expanded home ranges greatly in the mating season in some populations (Farentinos 1979; Lema 2001). Halloran and Bekoff (2000), however, did not detect any difference in home-range size of males between seasons on the same study site used by Farentinos (1979). Male eastern gray squirrels (*Sciurus carolinensis* Gmelin, 1788) and Douglas squirrels (*Tamiasciurus douglasii* (Bachman, 1839)) expand home-range size during the mating season (Thompson 1978; Koford 1982; Kenward 1985). Male eastern gray squirrels also increase encounters with females by visiting nests and home ranges of several females each day (Steele and Koprowski 2001). In Eurasian red squirrels (*Sciurus vulgaris* L., 1758) occurring at relatively high densities, home ranges of males did not increase in size during the mating season, likely because males do not leave their home range to mate and will exit a mating chase if it extends beyond a home-range boundary (Wauters et al. 1990). Male western gray squirrels (*Sciurus griseus* Ord, 1818) did not increase home-range size during the mating season, but did have more home-range overlap with neighboring squirrels and larger movement distances (Linders et al. 2004).

### Home ranges of females

The similarity in home-range size and overlap characteristics of female Abert's squirrels between non-mating and mating seasons suggests that mating activities do not greatly affect space use. Female tree squirrels, unlike males, do not search for mates and rely on pheromones that attract males from >500 m (Gurnell 1987). Thus, unlike males, female Abert's squirrels did not increase home-range size and overlap during the mating season. The trend for decreasing movement distances during the mating season may indicate a change in resource use by females or reduction in energy expenditure in preparation for reproduction.

Abert's squirrels studied in ponderosa pine forests yielded conflicting results regarding home-range size of females between non-mating and mating seasons. Home-range size of females varied little between seasons in Colorado (Halloran and Bekoff 2000), whereas home-range size decreased from non-mating season to mating season in Arizona (Lema 2001). Relative stability in home-range size of females between seasons also occurs in eastern gray squirrels (Thompson 1978; Kenward 1985) and Eurasian red squirrels (Wauters and Dhondt 1992). Female western gray squirrels did not change home-range size between non-mating and mating seasons, but did show limited movement during the mating season (Linders et al. 2004).

**Table 1.** Comparison of mean home-range size (ha) of Abert's squirrels (*Sciurus aberti*) during non-mating and mating seasons between mixed-conifer forest in the Pinaleno Mountains, Arizona, versus ponderosa pine forest in Colorado and Arizona.

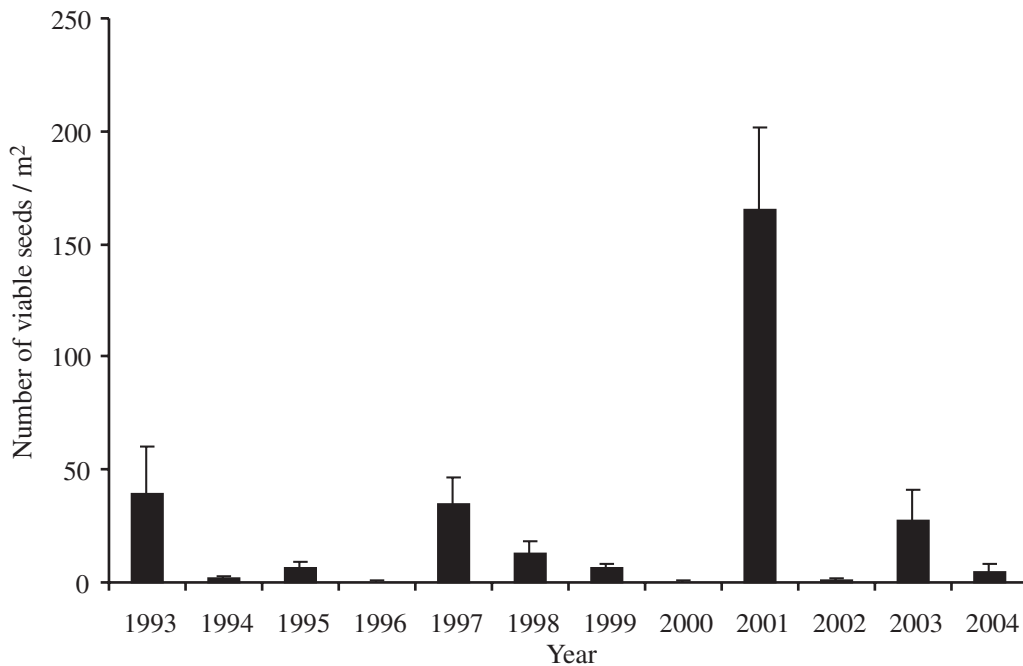
|                          | Mixed-conifer forest |                  |          | Ponderosa pine forest |          |                      |          |
|--------------------------|----------------------|------------------|----------|-----------------------|----------|----------------------|----------|
|                          |                      |                  | <i>n</i> | Colorado <sup>b</sup> |          | Arizona <sup>c</sup> |          |
|                          | 95% MCP <sup>a</sup> | 95% Fixed kernel |          | 95% MCP               | <i>n</i> | 95% Fixed kernel     | <i>n</i> |
| <b>Mating season</b>     |                      |                  |          |                       |          |                      |          |
| Male                     | 20.3                 | 25.4             | 9        | 19.3                  | 5        | 25.0                 | 10       |
| Female                   | 7.0                  | 5.4              | 5        | 10.4                  | 5        | 8.3                  | 6        |
| <b>Non-mating season</b> |                      |                  |          |                       |          |                      |          |
| Male                     | 6.3                  | 6.4              | 8        | 15.9                  | 5        | 21.9                 | 10       |
| Female                   | 8.6                  | 8.8              | 8        | 15.3                  | 5        | 15.4                 | 6        |

<sup>a</sup>Minimum convex polygon.

<sup>b</sup>Data from Halloran and Bekoff 2000.

<sup>c</sup>Data from Lema 2001.

**Fig. 4.** Number of viable conifer seeds (Douglas-fir, southwestern white pine, and ponderosa pine) per area (mean + SE) in mixed-conifer forests of the Pinaleno Mountains, Arizona, from 1993 to 2004. Seed numbers were estimated from seed fall collected in wire traps (Shearer 1976) at forested, random sites (3 seed traps / site). Nine and 8 sites were monitored during 1993–1996 and 1997–2004, respectively.



#### Home ranges in mixed-conifer vs. ponderosa pine forests

Compared with studies on Abert's squirrels in ponderosa pine forests (Halloran and Bekoff 2000; Lema 2001), males in our study in mixed-conifer forest had the most dramatic change in home-range size between non-mating and mating seasons (Table 1). Furthermore, while male home-range size during the mating season was almost identical between previous studies and ours, males in our study averaged home ranges over 2.5 times smaller during the non-mating season than males in ponderosa pine forests. Females in our study averaged smaller home ranges (1.5–1.8 times) than females in ponderosa pine forests (Halloran and Bekoff 2000; Lema 2001) during both non-mating and mating seasons (Table 1).

Home-range size in tree squirrels decreases significantly with food supplementation (Koprowski 1998). Thus, the small home ranges exhibited by individuals in our study may reflect a higher abundance and (or) quality of resources in mixed-conifer forests than in ponderosa pine forests. Mixed-conifer forests have higher conifer species richness than monotypic ponderosa pine forests (Brown 1982), which could provide increased abundance or stability in food resources. A larger than usual conifer seed crop during our study might also account for the smaller home ranges in mixed-conifer forests. However, the estimated seed crop (J.L. Koprowski, unpublished data) of the three conifer species most frequently eaten by Abert's squirrels in our study area (Douglas-fir, southwestern white pine, and ponderosa

pine; Edelman and Koprowski 2005) did not differ between 2002 and all other years from 1993 to 2004, except in 2001 (Tukey–Kramer test,  $P < 0.05$ ; Fig. 4).

A possible alternative explanation for the small home ranges in mixed-conifer forests is that competition with endemic Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis* (J.A. Allen, 1894)) results in reduced home ranges for Abert's squirrels. Red squirrels are territorial (Steele 1998) and appear to be dominant over Abert's squirrels in inter-specific encounters (Hutton et al. 2003). Unlike in ponderosa pine forests, both of these species co-occur in close proximity in our study site. Therefore, red squirrels may be able to exclude Abert's squirrels from their territories and into smaller areas. However, Abert's squirrels in our population do not appear to be negatively affected by small home-range size because they were able to establish residence, survive, and reproduce (Edelman and Koprowski 2006).

If Abert's squirrels are able to subsist on smaller home ranges in mixed-conifer forests, then their dependence on ponderosa pine may not be as strong as previously reported. Other factors such as interspecific competition with sympatric tree squirrel species or harsh winter climate may prevent Abert's squirrels from extensively using non-ponderosa-pine forests in their natural range (Ferner 1974; Edelman and Koprowski 2006). Further research is needed to determine whether food resources are greater in mixed-conifer than in ponderosa pine forests or if interspecific competition with red squirrels results in Abert's squirrels occupying small home ranges.

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