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## Influences of mating strategy on space use of Arizona gray squirrels

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Space use frequently differs between sexes and may reflect differences in parental investment and limiting resources. We examined Arizona gray squirrels (*Sciurus arizonensis*) from April 2007 to December 2008 to determine effects of mating strategy on patterns of home-range size and overlap. Home ranges were large compared to those of congeners, suggesting an environment with low availability and predictability of resources, and differed by sex and season. Females maintained smaller home ranges overlapped more by males than females; overlap by male home ranges increased during the breeding season. Males had larger home ranges that overlapped females more than males; home-range size and overlap of both sexes increased during the breeding season. Additionally, male Arizona gray squirrels appear to respond to the distribution of females by enlarging home ranges to maximize proportion of females overlapped. Consequently, Arizona gray squirrels conform to theoretical predictions, with female space use influenced by access to food and male space use influenced by access to mates. DOI: 10.1644/09-MAMM-A-426.1.

Key words: Arizona, mating system, reproductive strategy, resource limitation, *Sciurus arizonensis*, sex differences, squirrel

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Parental investment frequently differs between sexes, which leads to sex-biased differences in fitness-limiting resources. In mammals, female parental investment is greater due to increased costs of pregnancy and lactation; therefore, food availability is commonly recognized as a key resource limiting female fitness. Conversely, males minimize parental investment, and fitness may instead be limited by access to mates (Clutton-Brock and Harvey 1978; Ostfeld 1985; Trivers 1972). These sex differences in limiting resources can be mirrored by differences in space use (Ims 1987; Ostfeld 1985).

Tree squirrels have substantial sex differences in life history and behavior. Females are receptive to mating for  $\leq 1$  day and often enter estrus only once annually (Gurnell 1987; Koprowski 1998), although populations can have multiple breeding peaks when resources are abundant (Gurnell 1983; Nixon and McClain 1975). The short estrus and high asynchrony of receptive females across a breeding season that can span most of the year (Gurnell 1987; Koprowski 1998) lead to a strongly skewed operational sex ratio (Emlen and Oring 1977; Koprowski 2007). Consequently, males tend to remain sexually active throughout the prolonged breeding season (Steele and Koprowski 2001). Competition among males for mating opportunities is intense, and  $>20$  males can participate in a mating chase during which males actively pursue a receptive female (Koprowski 2007; Steele and Koprowski 2001; Thompson 1977; Wauters et al. 1990). Male

success is likely determined by a linear dominance hierarchy in which a few dominant males attain the majority of copulations (Farentinos 1980; Koford 1982; Koprowski 1993; Pack et al. 1967; Thompson 1977; Wauters et al. 1990).

Territoriality is expected to evolve when resources are abundant and stable (Emlen and Oring 1977). Many tree squirrels inhabit environments where food availability is highly variable within and among years. Unlike *Tamiasciurus*, *Sciurus* does not larder hoard (Gurnell 1987) and therefore does not benefit from a stable, predictable larder during food-limited winter months. Scatter hoarding of mast crops provides a food store essential for overwinter survival (Gurnell 1987; Thompson and Thompson 1980; Vander Wall 1990); however, widely placed food stores make food defense uneconomical (Gurnell 1987). Consequently, spacing patterns are dominated by overlapping home ranges, commonly with exclusive female core areas (Gurnell 1987; Linders et al. 2004; Lurz et al. 2000; Wauters and Dhondt 1992).

Adult male squirrels typically enlarge home ranges and increase overlap of conspecifics in the breeding season (Gurnell 1987; Koprowski 2007); however, inter- and intraspecific variation occurs, likely based upon resource



distribution (Halloran and Bekoff 2000; Linders et al. 2004; Pasch and Koprowski 2006). We used patterns of home-range size and overlap to explore space use of Arizona gray squirrels (*Sciurus arizonensis*). Rainfall and food availability vary greatly (Brown 1984; Theobald 1983; N. L. Cudworth and J. L. Koprowski, pers. obs.) and could have large impacts on space use of both sexes, providing an excellent landscape in which to investigate trade-offs in home-range dynamics. We predicted home-range sizes of females to remain constant between breeding and nonbreeding seasons, because both seasons were expected to encompass highs and lows in food availability. Females are subordinate to males (Allen and Aspey 1986; Farentinos 1980; Pack et al. 1967) and in direct competition year-round with other females for food (Lurz et al. 2000; Ostfeld 1985; Wauters et al. 1994; Wauters and Dhondt 1992). Consequently, we predicted less overlap of female home ranges by other females than by males, especially during the energetically costly breeding and rearing season. However, males are limited by different resources throughout the year. We predicted enlarged male home ranges and increased overlap of females during the breeding season. During the nonbreeding season, females are no longer a limiting resource (Ostfeld 1985), and both sexes are likely limited by food availability (Erlinge and Sandell 1986). Therefore, because tree squirrels demonstrate little to no sexual dimorphism in body size (Best and Riedel 1995; Don 1983; Koprowski 1998), we predicted similar sizes of male and female home ranges. By examining home-range dynamics over the year we hoped to elucidate how mating strategy and food resources might influence space use.

## MATERIALS AND METHODS

*Study organism.*—Arizona gray squirrels are restricted to mountainous sky islands of the southwestern United States and northwestern Mexico (Hoffmeister 1986) at elevations above 1,120 m (Best and Riedel 1995) within riparian areas of deciduous or mixed forest. The Huachuca Mountains are believed to have among the highest densities (Brown 1984; Hoffmeister 1986). Despite a federal listing as threatened in Mexico due to habitat loss (Alvarez-Castañeda and Patton 1999), and sensitive by the United States Forest Service (*S. a. catalinae*—Best and Riedel 1995), little is known about the species, with only a single publication in the primary, ecological literature (Frey et al. 2008; Koprowski 2005). This dearth of data resulted in an *IUCN Red List* designation of Data Deficient (International Union for Conservation of Nature and Natural Resources 2009). No information is available on home-range dynamics.

*Study area.*—We investigated space use of Arizona gray squirrels on Ft. Huachuca Military Reservation in the northwestern Huachuca Mountains, Cochise County, Arizona, from April 2007 to December 2008. The Huachuca Mountains cover ~26,000 ha and span elevations from 1,500 to 2,880 m. We focused our study in ~150 ha of oak–juniper (*Quercus*–*Juniperus*) forests of lower Huachuca Canyon at 1,555–

1,860 m in an area with an ephemeral stream flowing from late summer through winter. Major tree species included Arizona white oak (*Quercus arizonica*), Emory oak (*Q. emoryi*), silverleaf oak (*Q. hypoleucoides*), alligator juniper (*Juniperus deppeana*), and Arizona sycamore (*Platanus wrightii*). Arizona walnut (*Juglans major*), Fremont cottonwood (*Populus fremonti*), piñon pine (*Pinus edulis*), manzanita (*Arctostaphylos pungens*), and Arizona madrone (*Arbutus arizonica*) were present in lower densities (Wallmo 1955).

*Trapping and telemetry.*—Between April 2007 and December 2008 we used Tomahawk live traps (model 104; Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter and peanuts to capture squirrels. We transferred all individuals to a cloth handling cone (Koprowski 2002) for examination, recorded sex, age class based upon mass (juvenile, subadult, or adult), and reproductive status, and marked individuals with unique combinations of metal ear tags and colored washers (1-cm model 1005-3 and model 1842, respectively; National Band and Tag Co., Newport, Kentucky). We radiocollared (<5% of body mass; model SOM 2380; Wildlife Materials, Inc., Murphysboro, Illinois) adult squirrels ( $\geq 540$  g) and released 48 individuals (21 females and 27 males) at the capture site. Based on behavioral observations ( $n = 1,626$ ) of marked and unmarked individuals during our study, we estimated >90% of our population was marked. Even during mating chases ( $n = 11$ ), when males were drawn from vast distances (Pasch and Koprowski 2006; Steele and Koprowski 2001), >60% of individuals were marked, providing an estimated density of 0.33–0.49 individuals/ha.

We used a yagi antenna (model F164-165-3FB; Wildlife Materials, Inc.) and receiver (model R-1000; Communications Specialists Inc., Orange, California) to locate collared individuals at >2-h intervals to avoid spatial autocorrelation (White and Garrott 1990), and recorded location with a global positioning system unit (eTrex Vista GPS unit; Garmin International, Inc., Olathe, Kansas); error associated with most locations was within  $\pm 6$  m. All telemetry locations included visual observations. Trapping and handling procedures were approved by Arizona Game and Fish Department and The University of Arizona Institutional Animal Care and Use Committee (IACUC protocol 08-025) and in accordance with guidelines of the American Society of Mammalogists (Gannon et al. 2007).

*Data analysis.*—We divided years into breeding (January–July) and nonbreeding (August–December) seasons based upon occurrence of scrotal males, lactating females, and emergence of litters. We used the Animal Movement extension to ArcView (Hooge and Eichenlaub 2000) with smoothing parameters calculated by least-squares cross-validation (Gitzen and Millspaugh 2003) to generate 50% core and 95% fixed-kernel home ranges. Home-range sizes tended to asymptote between 20 and 25 locations per individual during the breeding season; therefore, we generated home ranges for individuals with  $\geq 25$  data points. Mean ( $\pm SE$ ) number of telemetry locations obtained for individual radiocollared Arizona gray squirrels for which we were able to

calculate home ranges ( $n = 26$ ) was  $67.38 \pm 7.56$  points/individual throughout the study. Average number of telemetry locations did not differ between males ( $73.00 \pm 11.05$  points/individual) and females ( $62.57 \pm 10.56$  points/individual;  $t_{24} = 0.68$ ,  $P = 0.503$ ) or between breeding ( $40.76 \pm 6.93$  points individual<sup>-1</sup> season<sup>-1</sup>) and nonbreeding ( $38.06 \pm 6.97$  points individual<sup>-1</sup> season<sup>-1</sup>;  $t_{32} = 1.14$ ,  $P = 0.265$ ) seasons. We used a  $t$ -test to compare total home-range and core-area sizes of males and females and to compare male home-range and core-area sizes between years. We used a 2-factor analysis of variance (ANOVA) with sex, season, and their interaction to determine which variables best explain differences in home-range sizes; because some individuals were recorded for more than 1 season, we also included individual as a random variable. All home-range sizes were natural-log transformed to meet assumptions of normality.

We used the Overlap Matrix in Ranges 6 (Anatrack Ltd. 2003) to explore seasonal differences in patterns of overlap. We analyzed overlap differently depending on sex. For females, we determined the average percent of home ranges overlapped by males and females; for males, we determined the average percent of home ranges overlapping males and females. We used a  $t$ -test to compare male overlap of conspecific ranges between years. We analyzed overlap of 50% core areas and 95% home ranges with a 2-factor ANOVA with sex overlapped, season, and their interaction; because some individuals were recorded for more than 1 season, we also included individual as a random variable. We used logistic regression to explore the relationship between male home-range size and proportion of females within the population overlapped. Percentages of overlap were arcsine square-root transformed to meet assumptions of normality. Statistical analyses were conducted in JMP version 7 (SAS Institute Inc. 2007). We report means ( $\pm SE$ ) as untransformed values.

## RESULTS

*Does home-range size vary by sex and season?*—Arizona gray squirrels had large core areas ( $9.52 \pm 3.22$  ha) and home ranges ( $59.28 \pm 17.15$  ha) when sexes were combined. Male core areas ( $18.39 \pm 6.13$  ha,  $n = 12$ ) were  $>9$  times larger than female core areas ( $1.91 \pm 0.26$  ha,  $n = 14$ ;  $t_{24} = 5.23$ ,  $P < 0.001$ ), and male home ranges ( $112.52 \pm 31.07$  ha,  $n = 12$ ) were  $>8$  times larger than female home ranges ( $13.65 \pm 1.89$  ha,  $n = 14$ ;  $t_{24} = 5.65$ ,  $P < 0.001$ ). Male home-range sizes were similar in 2007 ( $n = 4$ ) and 2008 ( $n = 6$ ; core:  $t_8 = 1.79$ ,  $P = 0.111$ ; home range:  $t_8 = 1.92$ ,  $P = 0.091$ ); therefore, data were pooled. Males ( $n = 20$ ) had larger home ranges than females ( $n = 14$ ; core:  $F_{1,17.41} = 23.76$ ,  $P < 0.001$ ; home range:  $F_{1,17.75} = 25.32$ ,  $P < 0.001$ ), but we found little influence of season alone on home-range size (core:  $F_{1,18.88} = 3.11$ ,  $P = 0.094$ ; home range:  $F_{1,18.75} = 3.04$ ,  $P = 0.097$ ; Fig. 1), although the interaction of sex and season can make these single-factor effects more difficult to interpret. Effect of season tended to be influenced by sex, with male core areas and home ranges 17.0 and 12.5 times greater than

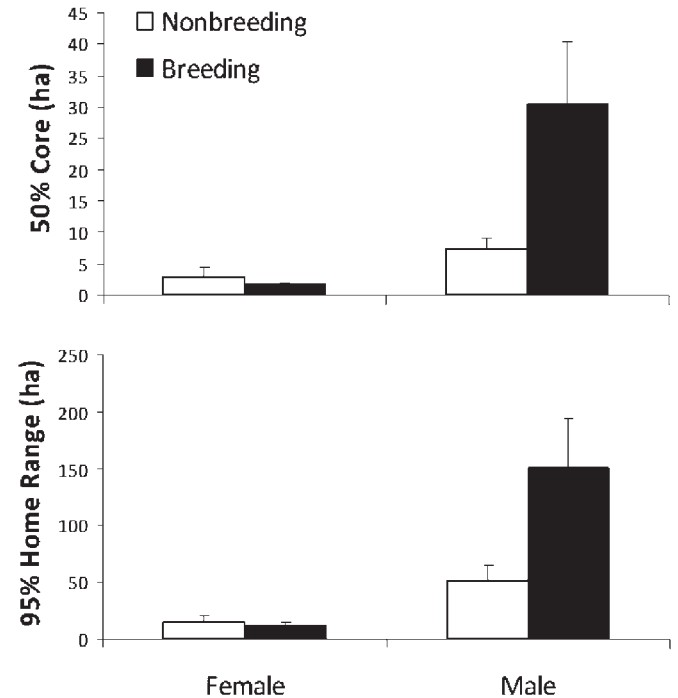


FIG. 1.—Mean ( $\pm SE$ ) 50% core and 95% home ranges of female and male Arizona gray squirrels (*Sciurus arizonensis*) for nonbreeding and breeding seasons, Huachuca Mountains, Arizona, August 2007–December 2008.

those of females during the breeding season, respectively (sex–season interaction; core:  $F_{1,18.88} = 3.87$ ,  $P = 0.064$ ; home range:  $F_{1,18.75} = 3.38$ ,  $P = 0.082$ ; Fig. 1).

*Does home-range overlap vary by sex and season?*—Overlap of female home ranges was influenced by sex; females were overlapped by males more than females (core:  $F_{1,15.16} = 19.53$ ,  $P = 0.001$ ; home range:  $F_{1,15.05} = 98.93$ ,  $P < 0.001$ ; Fig. 2). We detected no influence of season on overlap at the core area ( $F_{1,19.03} = 2.10$ ,  $P = 0.164$ ), but female home ranges were overlapped more during the breeding season ( $F_{1,16.6} = 9.77$ ,  $P = 0.006$ ), although the interaction of sex overlapping and season makes these single-factor effects more difficult to interpret. Effect of season was influenced by sex; females tended to be overlapped by males more during the breeding season for core areas (sex–season interaction,  $F_{1,15.16} = 4.13$ ,  $P = 0.060$ ) and were overlapped twice as much for home ranges (sex–season interaction,  $F_{1,15.05} = 13.16$ ,  $P = 0.003$ ; Fig. 2).

Male overlap of conspecific home ranges was similar between years (core:  $t_8 = 0.304$ ,  $P = 0.769$ ; home range:  $t_8 = 1.83$ ,  $P = 0.104$ ) so data were pooled. Patterns of male overlap were influenced by sex of the individual overlapped; males overlapped females nearly twice as much as males (core:  $F_{1,20.91} = 4.51$ ,  $P = 0.046$ ; home range:  $F_{1,21.29} = 4.57$ ,  $P = 0.044$ ; Fig. 3). Season also influenced overlap; males overlapped conspecifics 2.6–4.2 times more during the breeding season (core:  $F_{1,26.67} = 18.05$ ,  $P < 0.001$ ; home range:  $F_{1,26.84} = 12.32$ ,  $P = 0.002$ ). Effect of sex of the individual overlapped on amount of overlap did not vary by

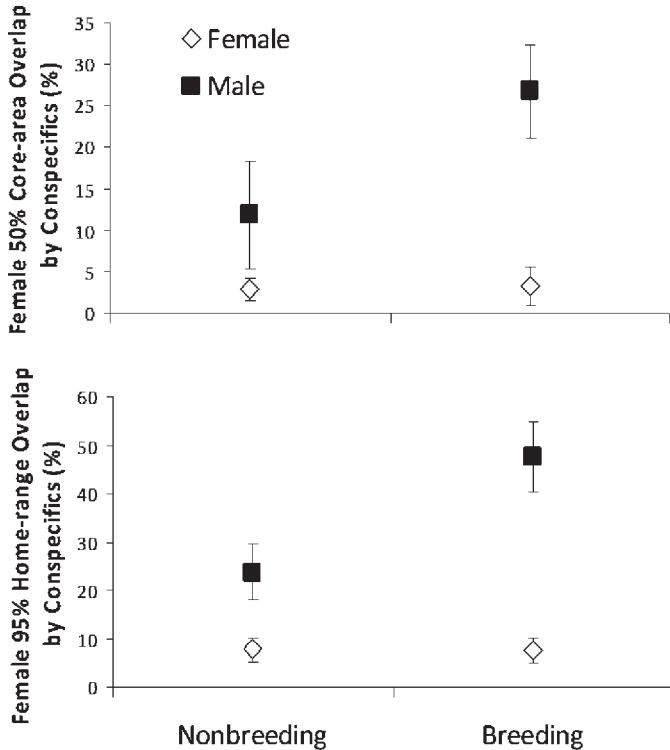


FIG. 2.—Mean ( $\pm SE$ ) percent of female 50% core and 95% home ranges overlapped by female and male conspecifics for Arizona gray squirrels (*Sciurus arizonensis*) during nonbreeding and breeding seasons, Huachuca Mountains, Arizona, August 2007–December 2008.

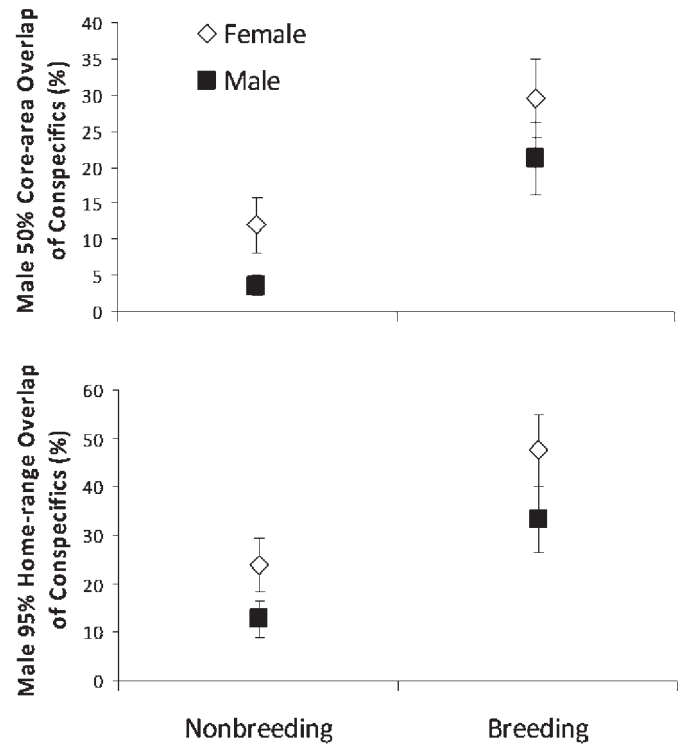


FIG. 3.—Mean ( $\pm SE$ ) percent of male 50% core and 95% home ranges overlapping female and male conspecifics for Arizona gray squirrels (*Sciurus arizonensis*) for nonbreeding and breeding seasons, Huachuca Mountains, Arizona, August 2007–December 2008.

season (sex–season interaction, 50% core:  $F_{1,20.91} = 0.36$ ,  $P = 0.557$ ; 95% home range:  $F_{1,21.29} < 0.01$ ,  $P = 0.956$ ; Fig. 3). However, male core-area and home-range size were positively related (marginally nonsignificantly so for core area) to the proportion of females in the population overlapped during the breeding season (core area:  $R^2 = 0.38$ ,  $F_{1,8} = 4.99$ ,  $P = 0.056$ ; home range:  $R^2 = 0.68$ ,  $F_{1,8} = 17.18$ ,  $P = 0.003$ ; Fig. 4).

### DISCUSSION

Home-range sizes decrease with increasing availability and predictability of food resources (Clutton-Brock and Harvey 1978; Lurz et al. 2000; Wauters and Dhondt 1992). Arizona gray squirrel home ranges are among the largest reported for tree squirrels (Carraway and Verts 1994; Koprowski 1994a, 1994b; Nash and Seaman 1977). Variation in food resources is suggested to affect home-range size of Sherman’s fox squirrels in Florida (*Sciurus niger shermani*—Kantola and Humphrey 1990), western gray squirrels in Washington (*S. griseus*—Linders et al. 2004), and closely related Chiricahua fox squirrels in Arizona (*S. nayaritensis*—Pasch and Koprowski 2006). The southwestern United States is an area of great spatial and temporal variation in rainfall that can have drastic impacts on food availability (Zlotin and Parmenter 2008; N. L. Cudworth and J. L. Koprowski, pers. obs.). Arizona gray

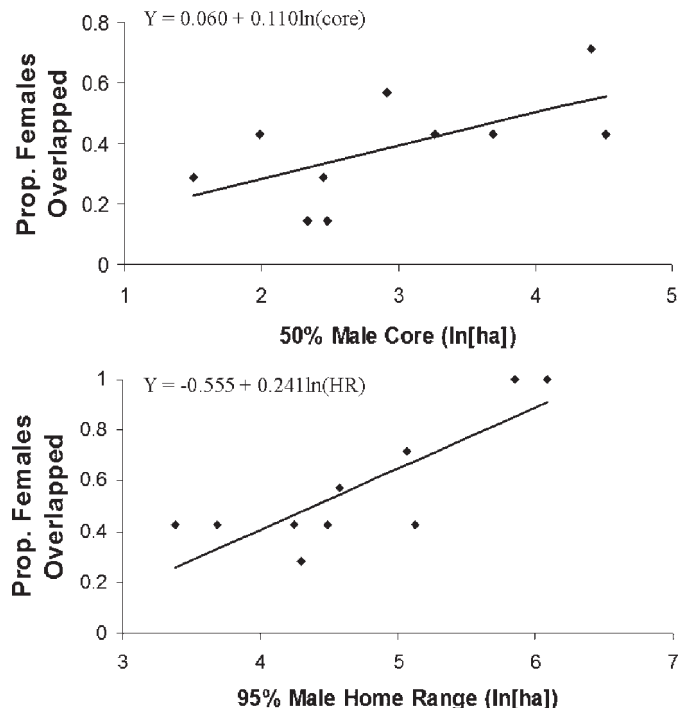


FIG. 4.—Proportion of females overlapped as a function of male 50% core and 95% home-range (HR) size for Arizona gray squirrels (*Sciurus arizonensis*) during breeding season in the Huachuca Mountains, Cochise County, Arizona, January–July 2008.



squirrels may respond to this variation by maintaining large home ranges.

Variation in availability of food can directly impact timing and success of female reproduction (Arlettaz et al. 2001; Becker 1993; Ben-David 1997; O'Donoghue and Krebs 1992). Female home ranges were large and did not change between seasons, consistent with the hypothesis of food as a limiting resource (Lurz et al. 2000; Wauters and Dhondt 1992). Additionally, female small mammals often increase intrasexual territoriality during the energetically costly breeding season due to competition for food (Lurz et al. 2000; Ostfeld 1985; Priotto et al. 2002; Wauters et al. 1994; Wauters and Dhondt 1992) or protection of pups (Wolff 1993). Female Arizona gray squirrels were overlapped less by females than males, as predicted by the intrasexual competition for resources hypothesis (Wauters and Dhondt 1992, 1993). Females maintained consistent patterns of intrasexual overlap but allowed increased overlap by males during the breeding season. Lack of exclusive home ranges during the breeding season was not due to a paucity of suitable cavities, because unused cavities were common. Instead, increased exclusivity during the breeding season might be uneconomical for females, because Arizona gray squirrels must already range widely to locate patchy food resources (Brown 1964; Emlen and Oring 1977; Ims 1987).

Large home ranges of male tree squirrels are commonly cited as a response to mate limitation (Edelman and Koprowski 2006; Gurnell et al. 2001; Linders et al. 2004; Lurz et al. 2000; Wauters et al. 1994; Wauters and Dhondt 1992). However, resources limiting male fitness can change throughout the year (Erlinge and Sandell 1986; Ostfeld 1985), from mate availability during the breeding season to food availability during the nonbreeding season. The trend toward enlarged home ranges of males in the breeding season supports this shift in limiting resources. Males often increase distances travelled during the breeding season (Pasch and Koprowski 2006) to maximize interactions with potentially receptive females (Steele and Koprowski 2001). As predicted, males increased home-range size, a pattern observed in other mammals, including voles (*Microtus*—Ostfeld 1985), grasshopper mice (*Onychomys torridus*—Frank and Heske 1992), badgers (*Taxidea taxus*—Minta 1993), kangaroo rats (*Dipodomys ingens*—Cooper and Randall 2007), and pygmy rabbits (*Brachylagus idahoensis*—Sanchez and Rachlow 2008), and also reptiles (*Lacerta monticola*—Aragón et al. 2001).

During the nonbreeding season both males and females are limited by food (Erlinge and Sandell 1986; Ostfeld 1985). Male home ranges decreased in size in the nonbreeding season but remained larger than female home ranges. Home ranges of eastern gray squirrels (*Sciurus carolinensis*) were influenced more by social pressures (population density) than food availability (Kenward 1985). Therefore, consistently large home ranges of male Arizona gray squirrels also might be due to social pressures, in this case temporal variation in female receptivity. Timing of male reproduction tracks timing of female reproduction (Emlen and Oring 1977), and timing and

proportion of females breeding differed between years of our study (N. L. Cudworth and J. L. Koprowski, pers. obs.). Because males should remain sexually active as long as females are in estrus (Bronson 1985; Emlen and Oring 1977; Steele and Koprowski 2001), slightly larger male home ranges during the nonbreeding season are likely a response to variability in female reproduction. Additionally, density in our population was low compared to mountain-wide surveys (0.74–1.89 individuals/ha—N. L. Cudworth and J. L. Koprowski, pers. obs.). Higher densities likely would result in smaller home ranges (Erlinge et al. 1990; Gurnell 1987; Jurczynszyn and Zgrabczynska 2007; Kenward 1985), although variable food resources still might maintain relatively large home ranges (Clutton-Brock and Harvey 1978; Lurz et al. 2000; Wauters and Dhondt 1992). Investigations of populations with different densities can help elucidate these interactions between social and environmental pressures on home-range dynamics. Therefore, we reject the hypothesis that food is the sole influence on male home-range size during the nonbreeding season.

Increasing total area covered is not the only strategy available to males to increase access to females. Male reproductive effort is often a trade-off between resource acquisition (access to females) and minimizing energy expenditure and risk (Bronson 1985; Cooper and Randall 2007; Don 1983; Gaulin and FitzGerald 1988). This can be especially important in populations already forced to travel widely to locate patchy and low-density resources (Fisher and Owens 2000). As predicted, males overlapped female home ranges more than male home ranges, and overlap of both sexes increased during the breeding season. However, increased overlap likely results from enlarged male home ranges during the breeding season, because overlap of male and female home ranges increased similarly. Large home ranges of males that overlap several, smaller home ranges of females are common among promiscuous mammals (Cooper and Randall 2007; Frank and Heske 1992; Hanski et al. 2000; Ribble and Stanley 1998; Tew and Macdonald 1994), and maintaining consistently large home ranges to maximize potential interactions with mates is a pattern observed for other tree squirrels (Linders et al. 2004; Lurz et al. 2000; Pasch and Koprowski 2006). However, males with larger home ranges also overlapped a greater proportion of females in the population, allowing for more potential encounters with females (Tew and Macdonald 1994). This suggests that males employ a strategy of home-range placement to maximize access to the greatest proportion of females. Consequently, Arizona gray squirrels conform to theoretical predictions whereby female space use is influenced by access to food resources and male space use is influenced by access to mates.

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