Journal of Mammalogy, 87(2):380–386, 2006

SEX DIFFERENCES IN SPACE USE OF CHIRICAHUA FOX SQUIRRELS

BRET PASCH* AND JOHN L. KOPROWSKI

Wildlife Conservation and Management, School of Natural Resources,
The University of Arizona, Tucson, AZ 85721, USA

Sex differences in reproductive investment influence space use patterns of many animals. In polygynous mammals, male space use reflects distribution of females and female space use reflects relative distribution of food. We used radiotelemetry to examine seasonal patterns of home-range size, overlap, and distance traveled by male and female Chiricahua fox squirrels (*Sciurus nayaritensis chiricahuae*) from 2002 to 2003. Male and female home-range and core-area size varied little between nonmating and mating seasons. Female core areas had a greater percentage overlap by males than by females during mating and nonmating seasons. Males traveled farther in the mating season and females showed little variation between seasons. Extreme spatial and temporal fluctuations of food experienced by Chiricahua fox squirrels may result in space use patterns that differ from those of tree squirrels living in forests with a greater abundance of food.

Key words: Arizona, mating system, reproductive strategy, *Sciurus nayaritensis*

Sex differences in space use often represent unequal investments of energy into reproduction by males and females (Emlen and Oring 1977; Trivers 1972). Differential reproductive investment is pronounced in polygynous mammals that lack male parental care (Gittleman and Thompson 1988) and results in divergent strategies to maximize reproductive success (Clutton-Brock and Harvey 1978). Male reproductive success is limited by number of mates, whereas female reproductive success is limited by conversion of available energy into offspring (Davies 1991). Consequently, distribution of fitness-limiting resources influences space use by the sexes differentially (Clutton-Brock 1989). Male space use reflects distribution of females, whereas female space use reflects distribution and abundance of food (Ims 1987).

Sex differences in space use are pronounced in nonterritorial tree squirrels (e.g., genus *Sciurus*) because females are receptive for only 8 h of the mating season (Goodrum 1961; Koprowski 1998; Thompson 1977) and operational sex ratios are heavily male-biased (5:1 to 20:1—Steele and Koprowski 2001). Mate competition is high and a limited period of female receptivity requires males to closely monitor females in estrus to reduce costs due to missed mating opportunities. Accordingly, males travel long distances in mornings during the mating season to locate and determine the stage of female receptivity (Steele and Koprowski 2001). Consequently, male home-range size and overlap of female home ranges typically increases during the mating season (Koprowski 1998). Conversely, female home-range size and degree of overlap with other females varies little between mating and nonmating seasons (Koprowski 1998). Females do not actively search for mates and instead flee from ≤ 30 males that aggressively pursue copulations on her single day of estrus (Koprowski 1993; Thompson 1977). Lack of sexual dimorphism in tree squirrels (Gurnell 1987) suggests that resource requirements should be similar between the sexes during the nonmating season. Thus, males and females are expected to maintain home ranges of similar size as food distribution becomes the primary fitness-limiting resource.

Chiricahua fox squirrels (*Sciurus nayaritensis chiricahuae*) are large-bodied (700 to 800 g) tree squirrels endemic to the Chiricahua Mountains of southeastern Arizona (Best 1995). Basic information on the ecology of the species is restricted to scant field notes of early naturalists (Cahalane 1939; Goldman 1933) and recent natural history observations (Brown 1984; Hoffmeister 1986; Kneeland et al. 1995; Koprowski and Corse 2001). However, Chiricahua fox squirrels are excellent organisms to test hypotheses related to space use because low densities of mates (Pasch and Koprowski 2005) are expected to magnify sex differences. We used radiotelemetry to examine seasonal patterns of home-range size, overlap, and distance traveled by male and female Chiricahua fox squirrels. We predicted a large increase in male home-range size and distance traveled during the mating season to locate widely dispersed females, but little variation in female home-range size and

---

* *Correspondent: bpasch@u.arizona.edu*

Table 1.—Multifactor analysis of variance estimating effects of year, season, and sex on Chiricahua fox squirrel home-range and core-area sizes in the Chiricahua Mountains, Arizona, May 2002 to September 2003.

		50% core area		85% core area		95% home range	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Year	1	2.81	0.106	6.45	0.018	5.73	0.024
Season	1	1.43	0.243	1.75	0.197	1.23	0.277
Sex	1	9.41	0.005	11.64	0.002	12.35	0.002
Season × sex	1	0.004	0.951	0.06	0.805	0.02	0.902

distance traveled between seasons. We also predicted similar overlap of male and female home ranges by females between seasons but increased overlap of male and female home ranges by males during the mating season.

Materials and Methods

Study area.—Chiricahua National Monument (elevation 1,573–2,228 m) is located along the northwestern terminus of the Chiricahua Mountains (37,000 ha, maximum elevation 2,986 m) in extreme southeastern Cochise County, Arizona. Rhyolite pillars and rocky outcroppings covered by chaparral (*Arctostaphylos pungens*, *Quercus toumeyi*, and *Pinus cembroides*) dominate the 5,000-ha preserve. Squirrels live in canyons dominated by pines (*Pinus engelmanni*, *P. leiophylla*, and *P. ponderosa*), oaks (principally *Quercus arizonica*, *Q. emoryi*, *Q. hypoleucoides*, and *Q. rugosa*), alligator juniper (*Juniperus deppeana*), and Arizona cypress (*Cupressus arizonica*—Brown 1984; Cahalane 1939; Hoffmeister 1986).

Trapping and radiotelemetry.—We captured 43 squirrels (15 females and 28 males) in live traps (model 104, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter between May 2002 and September 2003. We marked squirrels with numbered metal ear tags and colored washers (1-cm model 1005-3 and model 1842, respectively, National Band and Tag Co., Newport, Kentucky). We assessed sex, age class, reproductive condition, and body mass of all squirrels in a cloth handling cone (Koprowski 2002) and radio-collared adults (those > 670 g; model SOM 2380, <3% of body mass, Wildlife Materials, Inc., Carbondale, Illinois). Trapping and handling were conducted in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and with approval from The University of Arizona Institutional Animal Care and Use Committee and permits from Arizona Game and Fish Department and the National Park Service.

We mapped (eTrex Vista GPS unit, Garmin International, Inc., Olathe, Kansas) 126 locations and 63 nest sites (dreys) to use as telemetry stations. We located squirrels using the intersection of 2 strong signals (25% of locations—White and Garrot 1990) and homing (75% of locations). Relative indifference to human presence (Cahalane 1939; Kneeland et al. 1995) facilitated homing on squirrel locations without influencing movement patterns (Kenward 1987). Upon sighting a squirrel, we used the nearest telemetry station to record a bearing and distance to animals and calculated locations with Distance/Azimuth Tools (Jenness 2003). Narrow canyons allowed observers to collect all bearings <150 m from squirrels. We obtained successive locations at ≥120-min intervals to ensure spatial and temporal independence (White and Garrot 1990). We used LOAS version 2.10 (Ecological Software Solutions, www.ecostats.com) to calculate squirrel locations from bearings.

Error estimates.—We obtained locations evenly throughout periods of squirrel activity by prudent scheduling. Numbers of radiolocations were similar between mating (37.9 fixes ± 6.0 *SE*) and nonmating (48.3 ± 6.1 fixes) seasons ($t = 1.21$, $d.f. = 31$, $P = 0.24$). We acquired consecutive bearings on focal animals ≤8 min apart (Cochran 1980) and used interbearing angles of ≥70° and ≤110° to reduce geometric error (White and Garrot 1990). We affixed collars on road-killed Chiricahua fox squirrels at ambient temperature to simulate absorption of radiosignals (Withey et al. 2001) and placed specimens on tree limbs to imitate natural squirrel locations. Researchers blind to actual collar locations obtained bearings on hidden transmitters. Bearing error between estimated and actual locations was unbiased ($\bar{X} = -0.78° \pm 1.1$ *SE*, 1-sample $t = -0.71$, $d.f. = 49$, 2-sided $P = 0.48$) and precise ($SD = 2.9$). Mean linear error (17.4 m ± 3.1 *SE*, 1-sample $t = 5.63$, $d.f. = 24$, 2-sided $P < 0.0001$) was adequate for our objectives. Researchers also estimated distances to selected points in the forest to calculate linear error associated with homing of animals. Estimated distances were <1 m of actual locations ($\bar{X} = 0.25$ m ± 0.31 *SE*, 1-sample $t = 0.82$, $d.f. = 39$, $P = 0.42$).

Data analysis.—Area–observation curves reached an asymptote at 30–35 locations (Kernohan et al. 2001). Thus, data analyses included animals with ≥30 locations ($\bar{X} = 33.2 \pm 0.52$, $n = 20$) per season. We included locations of squirrels within dreys only once per squirrel to avoid artificial clustering of fixes (Gurnell et al. 2001). We determined duration of seasons (nonmating: mid-June through mid-December; mating: mid-December through mid-June) from data on reproductive condition, mating chases, and emergence of offspring.

We used Animal Movement Analysis extension (Hooge and Eichenlaub 1997) of ArcView (ESRI 1996) to calculate 50%, 85%, and 95% fixed-kernel estimates (Worton 1989) and selected least-squares cross-validation to create the smoothing parameter (Gitzen and Millspaugh 2003). The 85% level represents the core area (Wray et al. 1992) and was selected based on examination of the utilization distribution in Ranges 6 (Anatrack Ltd. 2003). The 50% and 95% levels provide additional descriptors of finer- and broader-scale space use habits and permit comparisons with other studies.

We used XTools (DeLaune 2000) to determine overlap characteristics among squirrels between seasons. We calculated overlap by measuring total percentage of an animal's 85% core area overlapped by squirrels of same and opposite sex and determined number of squirrels that overlapped an individual's core area per season.

We quantified morning distance traveled by randomly selecting 3 days per season when animals were located 3 times between 0500 and 1100 h. We calculated total linear distance traveled between 3 successive fixes over the 6-h morning period. Average distance traveled over 3 days served as an index of daily movement. Such methods allowed us to incorporate 2 animals that were depredated or disappeared before we obtained 30 locations.

We conducted all statistical analyses in JMP (SAS Institute Inc. 2002). We log-transformed home-range size, percentage core-area overlap, and distance traveled to meet assumptions of normality and homogeneity of variance (Ramsey and Schafer 2002). We used multifactor analyses of variance with a sex–season interaction to determine how space use parameters differed between sexes and seasons. We report means (± *SE*) as untransformed values.

Results

Home-range and core-area size during a season had no interaction with sex of squirrels (Table 1). Both male and female home-range and core-area size varied little from nonmating to mating seasons (Fig. 1). Home ranges of males were

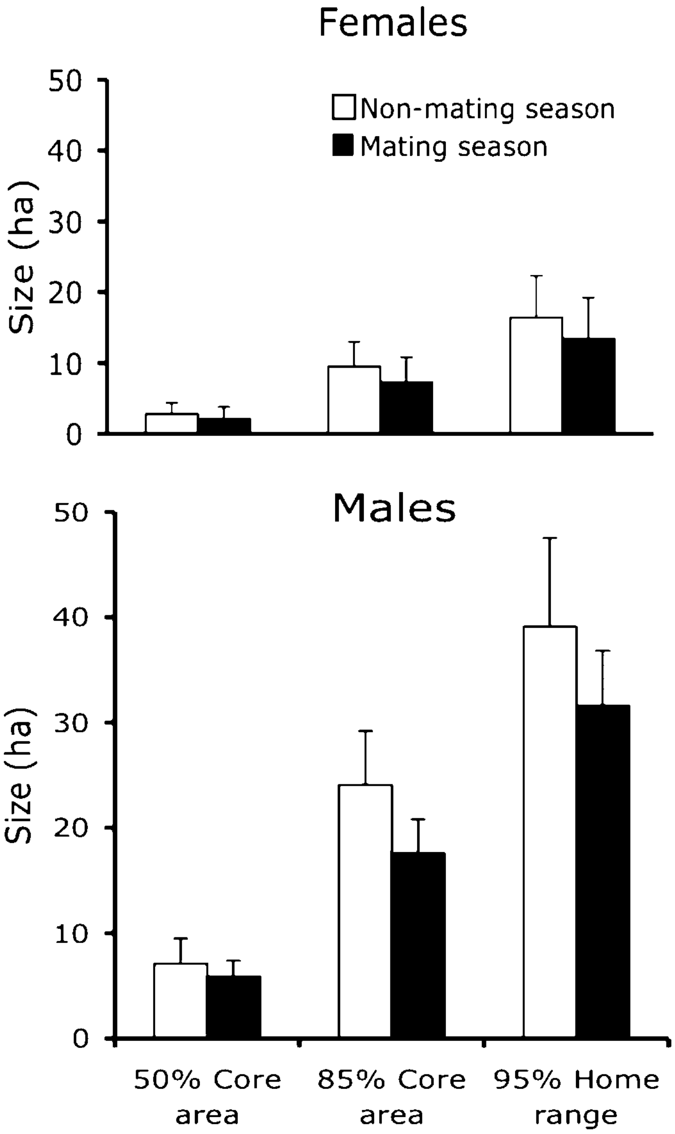

Fig. 1.—Sizes of seasonal home ranges (95%) and core areas (85% and 50%) of female and male Chiricahua fox squirrels in the Chiricahua Mountains, Arizona, May 2002 to September 2003. Error bars are *SE*.

10.0 ± 3.0 ha larger and core areas were 6.0 ± 1.9 ha larger than those of females, regardless of year and season (Fig. 1). Males increased home ranges by 12.4 ± 5.9 ha and core areas by 8.2 ± 3.4 ha from 2002 to 2003. Similarly, females increased home ranges by 2.7 ± 2.1 ha and core areas by 1.7 ± 1.4 ha from 2002 to 2003.

Percentage overlap of female core areas by conspecifics did not differ between seasons but was affected by sex (Table 2). Female core areas were overlapped more by males (69.2% ± 8.9%) than by females (26.1% ± 6.6%) during all seasons (Fig. 2). Percentage overlap of male core areas by conspecifics did not differ between seasons or sex (Table 2). Males (40.8% ± 8.3%) and females (42.6% ± 6.8%) overlapped male core areas similarly during both seasons (Fig. 2).

Total number of squirrels overlapping female core areas did not differ between seasons but was influenced by sex (Table 2).

Table 2.—Multifactor analysis of variance estimating effects of season and sex on 85% core area overlap characteristics of Chiricahua fox squirrels in the Chiricahua Mountains, Arizona, May 2002 to September 2003.

		Females				Males			
		% Overlap		No. individuals		% Overlap		No. individuals	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Season	1	0.009	0.992	0.048	0.826	0.002	0.959	0.071	0.791
Sex	1	15.19	0.004	8.43	0.006	0.028	0.867	0.28	0.597
Season × sex	1	0.0002	0.988	0.30	0.589	0.19	0.662	1.13	0.293

More males (1.8 ± 0.4 animals) than females (0.7 ± 0.1 animals) overlapped the core areas of females in both seasons (Fig. 3). Total number of squirrels that overlapped male core areas did not differ between seasons or sex (Table 2). Males had 1.9 ± 0.4 males and 1.7 ± 0.2 females overlapping their core area during both seasons (Fig. 3).

Morning distance traveled by squirrels did not vary between 2002 and 2003, regardless of sex and season ($F = 0.57$, *d.f.* = 1, 47, $P = 0.45$). Morning distance traveled during a season was influenced by sex of squirrels (sex–season interaction, $F = 10.27$, *d.f.* = 1, 48, $P = 0.0024$). As expected, males traveled farther during the mating season and females showed little variation between seasons (Fig. 4).

Discussion

Female space use.—Relative stability of female home ranges and core areas between seasons parallels space use patterns of other nonterritorial tree squirrels (Gurnell 1987) and polygynous mammals in general (Ostfeld 1985). During the mating season, females must procure sufficient energy stores to endure costs associated with gestation and lactation (Knee 1983). For example, lactating eastern fox squirrels (*Sciurus niger*) require >150% more energy than nonreproductive females (Havera and Nixon 1979). During nonmating seasons, females attempt to recover energy stores lost through lactation to increase overwinter survival and maximize future reproductive success (Havera and Nixon 1980). Accordingly, female space use patterns reflect distribution and abundance of food (Ostfeld 1990). Female eastern gray squirrels (*S. carolinensis*) and Eurasian red squirrels (*S. vulgaris*) exhibit stable home ranges between seasons when food resources are constant (Kenward 1985; Thompson 1978; Wauters and Dhondt 1992).

The slight increase in home range and distance traveled during the nonmating season is likely due to decreased food availability in late spring and early summer (Koprowski 1991). Summer diet of Chiricahua fox squirrels is more diverse than winter diet and includes twice as many food species (Koprowski and Corse 2001). Such dietary diversity likely translates into an increase in home range to locate seasonally fruiting trees. Indeed, 1 female regularly traveled >1 km to forage on Arizona walnuts (*Juglans major*) in August 2002 and 2003.

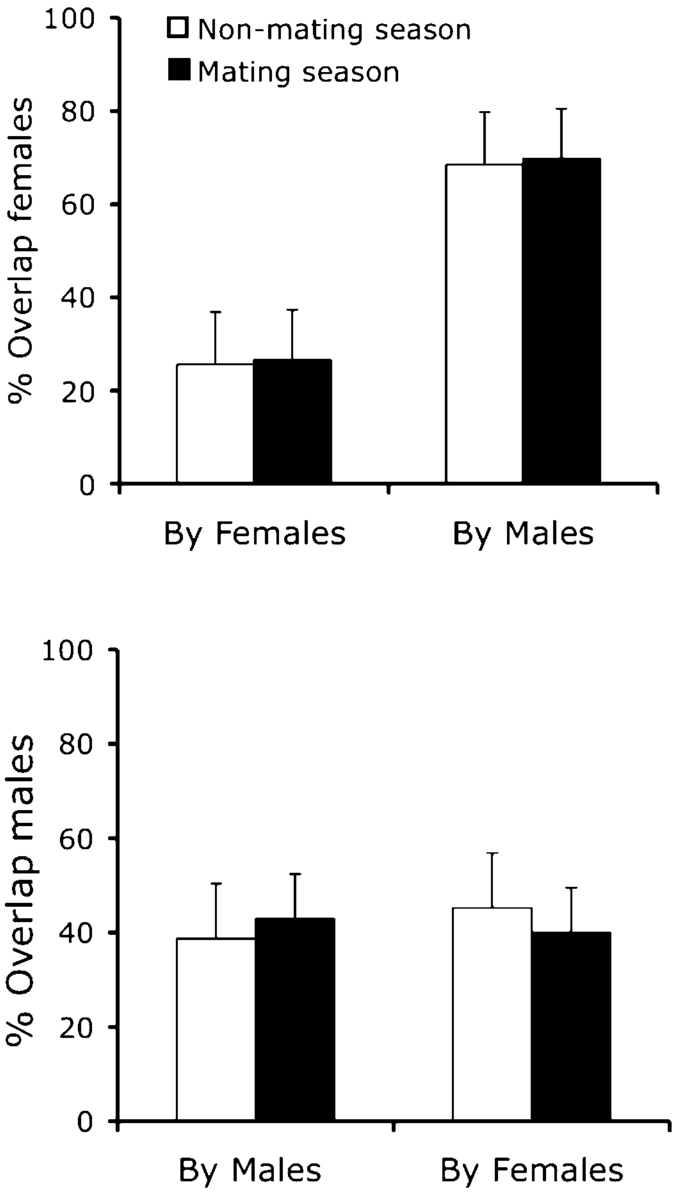

FIG. 2.—Percentage overlap of Chiricahua fox squirrel 85% core areas by male and female conspecifics in the Chiricahua Mountains, Arizona, May 2002 to September 2003. Female core areas were overlapped more by males than by females during both seasons ($P \leq 0.005$). Error bars are *SE*.

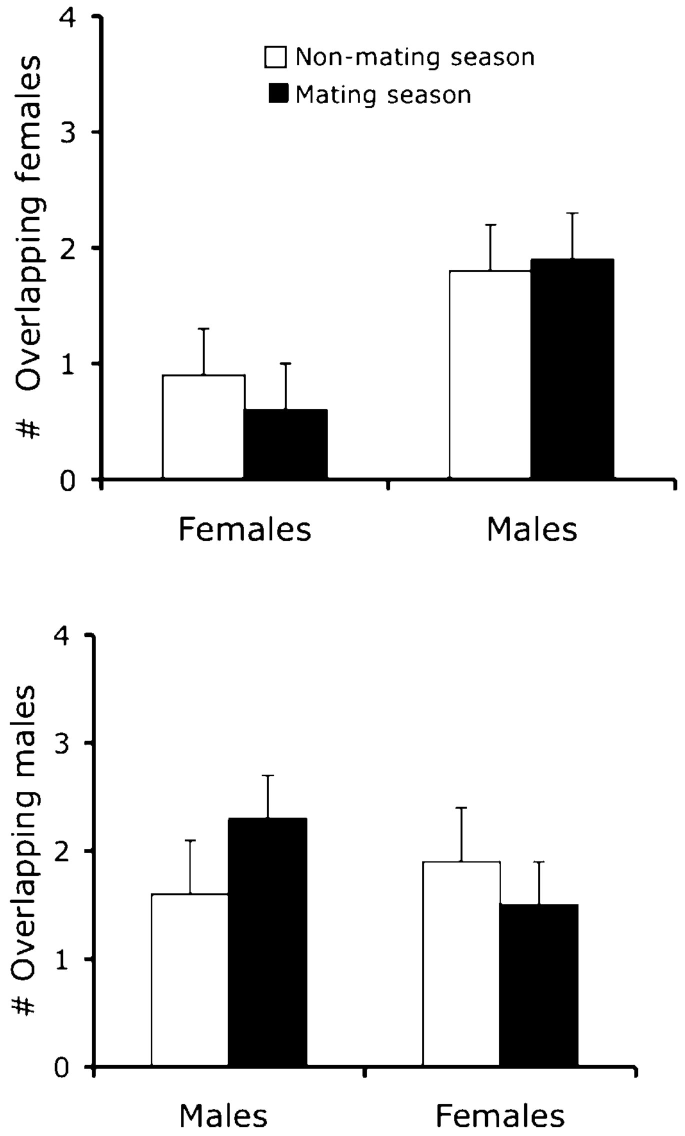

FIG. 3.—Total number of conspecifics overlapping male and female Chiricahua fox squirrel 85% core areas in the Chiricahua Mountains, Arizona, May 2002 to September 2003. More males than females overlapped core areas of females in both seasons ($P \leq 0.01$). Error bars are *SE*.

Incomplete overlap of core areas among females is consistent with observations from other tree squirrels (Gilman 1986; Gurnell 1987). Holarctic tree squirrels are generally nonterritorial and exhibit overlapping home ranges (Gurnell 1987; Steele and Koprowski 2001). However, females maintain exclusive areas and expel other females during the mating season to ensure sufficient energy stores (*S. griseus*—Gilman 1986; *S. niger*—Havera and Nixon 1978; *S. carolinensis*—Kenward 1985; *S. vulgaris*—Wauters and Dhondt 1992). Slight intrasexual overlap suggests that females rarely interact (Gurnell 1987). Furthermore, low density of Chiricahua fox squirrels (Pasch and Koprowski 2005) may account for the extreme spacing of females in our study. Overlap among females is extremely minor in low-density populations of western gray squirrels (*S. griseus*) where patchy resources result in a highly dispersed population (Linders et al. 2004).

Male space use.—Male home ranges typically enlarge during the mating season to increase the probability of encountering estrous females (Koprowski 1998). In eastern gray squirrels, male home ranges increased dramatically when female density was reduced experimentally (Kenward 1985). Conversely, the nonmating season is devoted to recovering fat reserves lost to reproduction (Steele and Koprowski 2001; Thompson 1977) and is characterized by reduction in home-range size in many polygynous species (Lagarde et al. 2003). Because Chiricahua fox squirrels occur at low densities, we expected a large increase in home-range size during the mating season. However, males demonstrated no such enlargement and held home ranges and core areas large and constant. Male Abert's squirrels (*S. aberti*—Halloran and Bekoff 2000), western gray squirrels (Linders et al. 2004), and some populations of eastern gray squirrels (Gurnell et al. 2001) exhibit seasonal stability in home-range size and maintain larger home ranges than do females in both seasons (also see Table 1 in Koprowski 1998:34). Chiricahua fox squirrels appear to use a similar strategy; male home ranges and core areas were much larger than those of females throughout the year. Such stability may enable males to overlap multiple females in the mating season and encompass richer feeding patches in the nonmating season to recover energy stores lost during the mating season (Wauters and Dhondt 1998).

Despite the relative stability of home-range and core-area size between seasons, male Chiricahua fox squirrels exhibited a typical pattern of long-distance movements during the mating season (Gurnell 1987). An increase in distance traveled but not in home-range size appears to be characteristic of populations of tree squirrels in western North America. Male western gray squirrels increase the frequency of long-distance movements during the mating season, resulting in a greater variance but no difference in home-range size between seasons (Linders et al. 2004). Such space use patterns explain why males do not overlap more females yet slightly increase overlap with other males through the mating season; males overlap other males as a by-product of their extensive travels to monitor female receptivity (Heaney 1984; Steele and Koprowski 2001). However, in low-density populations, male home ranges may overlap those of most females in the nonmating season, thus negating the need to increase home-range size during the mating season (Halloran and Bekoff 2000).

Conclusions.—Tree squirrel home-range size is negatively correlated with population density (Heaney 1984; Wauters and Dhondt 1998) and population density is affected by quality and quantity of food resources (Don 1983). In general, tree squirrels living in forests with seasonally abundant and predictable resources have smaller home ranges than populations where food supplies are limited (Gurnell 1987). The large home-range size and low density of Chiricahua fox squirrels is matched only by western gray squirrels in Washington (Linders et al. 2004), Abert's squirrels in Colorado (Halloran and Bekoff 2000), and Sherman's fox squirrel (*S. niger shermani*) in Florida (Kantola and Humphrey 1990). Food distribution and abundance are highly variable within the drought-prone Chiricahua Mountains, where trees depend on snowmelt and monsoonal precipitation for production of cone crops (Earl and Bash 1996; Pase 1969; Vogl et al. 1977). The tremendous increase in home-range size in 2003 concomitant with a record low in precipitation ($\bar{X}_{2003} = 19.6$ cm, $\bar{X}_{1909–2002} = 48.8 \pm 0.8$ cm) demonstrates the squirrels' response to such variability. Additionally, the diverse diet (22 food items) of Chiricahua fox squirrels is attributed to living in forests with great spatial and temporal variation of mast (Koprowski and Corse 2001). Low food availability requires that squirrels have large home ranges to meet energy requirements (Ford 1983; Weigl et al. 1989). Consequently, great variation in food distribution and abundance appears to influence space use patterns of tree squirrels in forests of western North America differently than species living in forests with more abundant food resources.

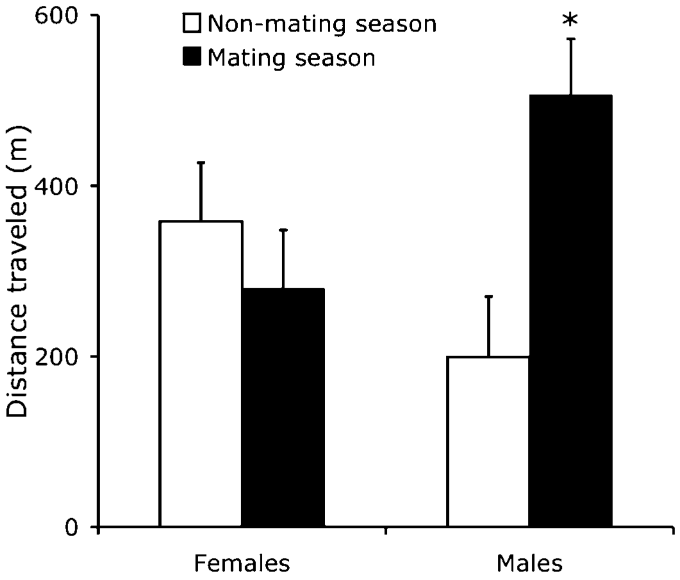

FIG. 4.—Morning distance traveled by male and female Chiricahua fox squirrels during mating and nonmating seasons in the Chiricahua

ACKNOWLEDGMENTS

A. Whalon, C. Dennett, and R. Olsen at Chiricahua National Monument provided admirable logistical support. We thank S. Estrada-Villegas, C. Kottschade, S. Ranly, K. Smetak, J. Lynch, T. Vandervote, and D. Wood for assistance in data collection. The Desert Southwest–Cooperative Ecosystems Studies Unit, Arizona Agricultural Experiment Station, T&E, Inc. Conservation Biology Grant, and the Southwestern Association of Naturalists Howard McCarley Student Research Grant graciously provided funding. Two anonymous referees provided insightful comments to improve the manuscript.

LITERATURE CITED

ANATRACK LTD. 2003. Ranges 6, version 1.208. Anatrack Ltd., Wareham, United Kingdom.

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

BEST, T. L. 1995. *Sciurus nayaritensis*. Mammalian Species 492:1–5.

BROWN, D. E. 1984. Arizona's tree squirrels. Arizona Game and Fish Department, Phoenix.

CAHALANE, V. H. 1939. Mammals of the Chiricahua Mountains, Cochise County, Arizona. Journal of Mammalogy 20:418–440.

CLUTTON-BROCK, T. H. 1989. Mammalian mating systems. Proceedings of the Royal Society of London, B. Biological Sciences 236:339–372.

CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1978. Mammals, resources, and reproductive strategies. Nature 273:191–195.

COCHRAN, W. W. 1980. Wildlife telemetry. Pp. 507–520 in Wildlife management techniques manual (S. D. Schemnitz, ed.). 4th ed. Wildlife Society, Washington, D.C.

DAVIES, N. B. 1991. Mating systems. Pp 263–294 in Behavioral ecology: an evolutionary approach (J. R. Krebs and N. B. Davies, eds.). Blackwell, Oxford, United Kingdom.

DeLaune, M. G. 2000. XTools ArcView extension, version 10/18/2000. Oregon Department of Forestry, Salem.

Don, B. A. C. 1983. Home-range characteristics and correlates in tree squirrels. Mammal Review 13:123–132.

Earl, R. A., and D. L. Bash. 1996. Response of alligator juniper (*Juniperus deppeana* Pinaceae) to historic environmental variability. Southwestern Naturalist 41:227–238.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

ESRI. 1996. ArcView, version 3.2. Environmental Systems Research Institute, Redlands, California.

Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23:315–326.

Gilman, K. N. 1986. The western gray squirrel (*Sciurus griseus*), its summer home range, activity times, and habitat usage in northern California. M.S. thesis, California State University, Sacramento.

Gittleman, J. L., and S. D. Thompson. 1988. Energy allocation in mammalian reproduction. American Zoologist 28:863–875.

Gitzen, R. A., and J. J. Millspaugh. 2003. Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. Wildlife Society Bulletin 31:823–831.

Goldman, E. A. 1933. Five new rodents from Arizona and New Mexico. Proceedings of the Biological Society of Washington 46:71–77.

Goodrum, P. D. 1961. The gray squirrel in Texas. Texas Parks and Wildlife Department Bulletin 42:1–43.

Gurnell, J. 1987. The natural history of squirrels. Facts on File, New York.

Gurnell, J., L. A. Wauters, D. Preatoni, and G. Tosi. 2001. Spacing behaviour, kinship, and population dynamics of grey squirrels in a newly colonized broadleaf woodland in Italy. Canadian Journal of Zoology 79:1533–1543.

Halloran, M. E., and M. Bekoff. 2000. Home range use by Abert squirrels: a comparative analysis. Southwestern Naturalist 45: 253–257.

Havera, S. P., and C. M. Nixon. 1978. Interaction among adult female fox squirrels during their winter breeding season. Transactions of the Illinois State Academy of Sciences 71:24–38.

Havera, S. P., and C. M. Nixon. 1979. Energy and nutrient cost of lactation in fox squirrels. Journal of Wildlife Management 43: 958–965.

Havera, S. P., and C. M. Nixon. 1980. Winter feeding of fox and gray squirrel populations. Journal of Wildlife Management 44: 41–55.

Heaney, L. R. 1984. Climatic influences on the life-history tactics and behavior of North American tree squirrels. Pp. 43–78 in The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.

Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to Arcview, version 1.1. Alaska Science Center–Biological Science Office, United States Geological Survey, Anchorage.

Ims, R. A. 1987. Male spacing systems in microtine rodents. American Naturalist 130:475–484.

Jenness, J. 2003. Distance/Azimuth Tools, version 1.4e. Jenness Enterprises, Flagstaff, Arizona.

Kantola, A. T., and S. R. Humphrey. 1990. Habitat use by Sherman's fox squirrel (*Sciurus niger shermani*) in Florida. Journal of Mammalogy 71:411–419.

Kenward, R. 1985. Ranging behaviour and population dynamics in grey squirrels. Symposia of the British Ecological Society 25:319–330.

Kenward, R. 1987. Wildlife radiotagging: equipment, field techniques and data analysis. Academic Press, London, United Kingdom.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 125–166 in Radio tracking and animal population (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, New York.

Knee, C. 1983. Squirrel energetics. Mammal Review 13:113–122.

Kneeland, M. C., J. L. Koprowski, and M. C. Corse. 1995. Potential predators of Chiricahua fox squirrels. Southwestern Naturalist 40: 340–342.

Koprowski, J. L. 1991. Response of fox squirrels and gray squirrels to a late spring–early summer food shortage. Journal of Mammalogy 72:367–372.

Koprowski, J. L. 1993. Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job." Behavioral Ecology 4:165–171.

Koprowski, J. L. 1998. Conflict between the sexes: a review of social and mating systems of the tree squirrels. Pp. 33–41 in Ecology and evolutionary biology of tree squirrels (M. A. Steele, J. F. Merritt, and D. A. Zegers, eds.). Virginia Museum of Natural History, Martinsville.

Koprowski, J. L. 2002. Handling tree squirrels with an efficient and safe restraint. Wildlife Society Bulletin 30:101–103.

Koprowski, J. L., and M. C. Corse. 2001. Food habits of the Chiricahua fox squirrel (*Sciurus nayaritensis chiricahuae*). Southwestern Naturalist 46:62–65.

Lagarde, F., et al. 2003. Sex divergence in space utilisation in the steppe tortoise (*Testudo horsfieldi*). Canadian Journal of Zoology 81:380–387.

Linders, M. J., S. D. West, and M. Vander Haegen. 2004. Seasonal variability in the use of space by western gray squirrels in southcentral Washington. Journal of Mammalogy 85: 511–516.

Ostfeld, R. S. 1985. Limiting resources and territoriality in microtine rodents. American Naturalist 126:1–15.

Ostfeld, R. S. 1990. The ecology of territoriality in small mammals. Trends in Ecology and Evolution 5:411–415.

Pasch, B., and J. L. Koprowski. 2005. Correlates of vulnerability in Chiricahua fox squirrels. Pp. 426–428 in Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II. Proceedings RMRS-P-36 (G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. Edminster, eds.). United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Pase, C. P. 1969. Survival of *Quercus turbinella* and *Q. emoryi* seedlings in an Arizona chaparral community. Southwestern Naturalist 14:149–156.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth, a course in methods of data analysis. 2nd ed. Duxbury Press, Belmont, California.

SAS Institute Inc. 2002. JMP, version 5. SAS Institute Inc., Cary, North Carolina.

Steele, M. A., and J. L. Koprowski. 2001. North American tree squirrels. Smithsonian Institution Press, Washington, D.C.

Thompson, D. C. 1977. Reproductive behavior of the grey squirrel. Canadian Journal of Zoology 55:1176–1184.

Thompson, D. C. 1978. Regulation of a northern grey squirrel (*Sciurus carolinensis*) population. Ecology 59:708–715.

Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 in Sexual selection and the descent of man, 1871–1971 (B. Campbell, ed.). Aldine, Chicago, Illinois.

Vogl, R. J., W. P. Armstrong, K. L. White, and K. L. Cole. 1977. The closed-cone pines and cypress. Pp. 295–358 in Terrestrial vegetation of California (M. G. Barbour and J. Major, eds.). John Wiley & Sons, Inc., New York.

Wauters, L. A., and A. A. Dhondt. 1992. Spacing behaviour of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. Animal Behaviour 43:297–311.

Wauters, L. A., and A. A. Dhondt. 1998. Variation in spacing behavior of Eurasian red squirrels, *Sciurus vulgaris*, in winter: effects of density and food abundance. Pp. 71–77 in Ecology and evolutionary biology of tree squirrels (M. A. Steele, J. F. Merritt, and D. A. Zegers, eds.). Virginia Museum of Natural History, Martinsville.

Weigl, P. D., M. A. Steele, L. J. Sherman, and J. C. Ha. 1989. The ecology of the fox squirrel (*Sciurus niger*) in North Carolina: implications for survival in the southeast. Bulletin of Tall Timbers Research Station 24:1–93.

White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.

Withey, J. C., T. B. Bloxton, and J. M. Marzluff. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. Pp. 43–75 in Radio tracking and animal population (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, New York.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Wray, S., W. J. Cresswell, P. C. L. White, and S. Harris. 1992. What, if anything, is a core area? An analysis of the problems of describing internal range configurations. Pp. 256–271 in Wildlife telemetry: remote monitoring and tracking of animals (I. G. Priede and S. M. Swift, eds.). Ellis Horwood, Chichester, United Kingdom.

Submitted 11 April 2005. Accepted 27 July 2005.

Associate Editor was Craig L. Frank.