

## SEASONAL VARIABILITY IN THE USE OF SPACE BY WESTERN GRAY SQUIRRELS IN SOUTHCENTRAL WASHINGTON

MARY J. LINDERS,\* STEPHEN D. WEST, AND W. MATTHEW VANDER HAEGEN

Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501, USA (MJL, WMV)  
Wildlife Science Group, College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100, USA (SDW)

A lack of quantitative information on life history of the western gray squirrel (*Sciurus griseus*) has hampered conservation and management efforts across its range. We report on data from 21 squirrels radiotracked in Klickitat County, Washington, from 1998 to 1999 to examine the interaction between home-range size, sex, and season. Home-range estimates were calculated by using minimum convex polygon and fixed kernel methods. Only adult animals with  $\geq 40$  relocations were included in total home-range comparisons. Estimates of 95% minimum convex polygon home range in Washington averaged 73.0 ha for males ( $n = 9$ ) and 21.6 ha for females ( $n = 12$ ) for year-round use, significantly larger than those from Oregon and California. Differences in home-range size of males and females were significant. Fixed kernel and minimum convex polygon estimates were similar in size. We suggest that near the northern limit of the species' geographic range low species richness, low abundance, and a patchy distribution of mast-producing vegetation result in large male and female home ranges, low overlap of female home ranges, and a sparsely distributed squirrel population.

Key words: fixed kernel, home-range size, minimum convex polygon, *Sciurus griseus*, tree squirrels, Washington, western gray squirrel

Home range (Burt 1943) is sensitive to many ecological attributes including population density, distribution of resources, and spacing of individuals (Harris et al. 1990; Wauters and Dhondt 1992). Subadult squirrels lack a true home range; their association with the natal area changes (Don 1983; Gurnell 1987) in the search for an independent locale (Burt 1943). In contrast, movement patterns of adult squirrels are more stable over the annual cycle and across years (Cross 1969; Wauters and Dhondt 1998; Weigl et al. 1989) and provide a more reliable gauge of population parameters.

Home-range size also may vary by sex and season. Male tree squirrels may differ from females in size of their home range (Farentinos 1979; Ingles 1947; Wauters and Dhondt 1998; Weigl et al. 1989), although this is not always true (Cross 1969; Foster 1992; Halloran 1993). Tree squirrels are not sexually dimorphic with respect to body size. Instead, access to females by males and defense of maternal nest areas by females have been suggested to explain observed differences in home-range size (Don 1983; Gurnell 1987; Heaney 1984).

Don (1983) examined territoriality in tree squirrels and reported that home-range size is negatively correlated with population density in *Sciurus* but home-range overlap is similar at all densities. Species of *Sciurus* are associated with deciduous habitats where seed supplies vary spatially and temporally (Don 1983; Wauters and Dhondt 1992), conditions where costs of defending a territory outweigh resource benefits (Gurnell 1987). However, species of *Tamiasciurus* are territorial and associated with conifer habitats where cones can be cached and defended (Don 1983; Gurnell 1987).

Most studies that have examined home range for the western gray squirrel (*Sciurus griseus*) were based on few individuals and a single season, and nearly all reported small home-range sizes ( $< 5$  ha—Barnum 1975; Gilman 1986; Ingles 1947) relative to other species of *Sciurus* (Gurnell 1987; Weigl et al. 1989). Studies that reported larger home ranges (range 1–25 ha—Cross 1969; Foster 1992) lasted  $> 1$  season and used data derived from different techniques (i.e., trapping and telemetry).

The western gray squirrel is the largest native tree squirrel in its geographic range. Adults are 500–615 mm in total length and weigh 520–942 g (Carraway and Verts 1994). The species reaches its northern limit in Washington, where there are few species of pine and oak compared to Oregon and California (Brockman 1968; Peattie 1950). Surveys found that squirrels occur at low densities in Washington (Bayrakçı et al. 2001;

\* Correspondent: lindemjl@dfw.wa.gov

M. J. Linders, in litt.). Once abundant in some areas (Bowles 1921), the western gray squirrel is now restricted to 3 isolated parts of Washington and is listed as a state-threatened species (E. A. Rodrick, in litt.).

Like other *Sciurus* species, the western gray squirrel feeds primarily on mast and hypogeous fungi, supplementing its diet with green vegetation and insects (Gurnell 1987; Stienecker and Browning 1970). Pine nuts and acorns are critical winter foods that initiate lipogenesis and condition animals against colder weather (Stienecker and Browning 1970).

In 1998, we initiated a study in Klickitat County, Washington, to improve our knowledge of western gray squirrel ecology and factors that may limit its abundance and distribution. We hypothesized that a low diversity of mast-bearing trees would increase home-range size (Gurnell 1983; Heaney 1984; Weigl et al. 1989). We also predicted that males would move farther to gain access to females during the mating season and that females would remain closer to maternal nests (Don 1983; Gurnell 1987; Weigl et al. 1989). Based on patterns of home range and territoriality (Don 1983), we expected that a mixed oak–conifer habitat would result in limited home-range overlap and low population density.

## MATERIALS AND METHODS

**Study site.**—This study was conducted on the Klickitat Wildlife Area, a 5,600-ha reserve in Klickitat County, Washington (45°53'N, 121°3'W). The site was 518 ha with an elevation range of 488 to 560 m. Cool, wet winters and hot, dry summers are typical, with mean temperatures ranging from  $-5^{\circ}\text{C}$  in January to  $28^{\circ}\text{C}$  in July. Annual precipitation is about 63 cm, with an average snowfall of 108 cm (Western Regional Climate Center, <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?waglen>, <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wagol2>, accessed 16 April 1999). North-facing slopes are dominated by Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*), and south slopes are dominated by Oregon white oak (*Quercus garryana*), native forbs, and grasses (Franklin and Dyrness 1973).

**Procedure.**—Trapping of western gray squirrels occurred from August 1998 through August 1999. Sixty traps were set for a total of 2,731 trap days. We placed wire-mesh live traps (#105,  $18 \times 18 \times 61$  cm, and #205,  $23 \times 23 \times 66$  cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with whole English walnuts or hazelnuts near and between active nesting and foraging signs to establish continuous spatial coverage. Before the 1st session, traps were wired open during 6 days of prebaiting then opened for 3–5 days per week for 3 weeks. Because of radiocollar failures and high mortality, we trapped for 1–10 days every 2–3 months after 2 days of prebaiting. Traps were set before sunrise, checked at about 1100 h and 1600 h, and then closed for the night.

We anesthetized captured squirrels with isoflurane (Baxter Anaesthesia, Crowthorne, Berks, United Kingdom) and took standard measurements, including neck circumference to the nearest millimeter and weight to the nearest 5 g. We examined squirrels for ectoparasites and reproductive condition and applied numbered ear tags (model 1005-1, National Band and Tag Co., Newport, Kentucky). All squirrels  $\geq 675$  g were fitted with a 6.5-g or 12-g radiocollar (models RI-2Csp and SI-2C, Holohil Systems Ltd., Carp, Ontario, Canada).

We approached squirrels by homing in on telemetry signals and observed them with  $10 \times 40$  binoculars whenever possible. When

homing in, we discontinued tracking if signal strength decreased abruptly more than once during pursuit to avoid undue influence on animal movements. Between August 1998 and December 1999 we relocated squirrels several times weekly by radiotracking. Our minimum interval between fixes was 1 h, a period adequate for an animal to traverse its home range. The average time between consecutive fixes was  $98.8 \text{ h} \pm 17.6 \text{ SE}$  ( $n = 40$  animals). We relocated animals more frequently when they were in mating groups or during rare events such as long-distance movements and special foraging bouts. Thirty-eight such circumstances were recorded for 13 radiocollared animals. In most cases (29 of 38), 1 additional fix was obtained within the 1-h period. We distributed our relocation effort across the diurnal period to capture activity and resting periods for each individual. We used these methods to increase the likelihood of attaining independence of observations (Otis and White 1999; Swihart and Slade 1997; White and Garrott 1990). We located animals with a 2-element Yagi antenna, a Telonics TR-4 receiver (Telonics, Mesa, Arizona), and a Garmin-12 global positioning system receiver (Garmin International, Inc. Olathe, Kansas). We used real-time differential correction (RDS 3000 FM-receiver, Differential Corrections, Inc., Santa Clara, California) to achieve  $\leq 10$  m position accuracy. All locations were recorded as Universal Transverse Mercator coordinates and plotted on a 7.5" United States Geological Survey topographical map.

**Data analysis.**—Home-range size was estimated by using 100% and 95% minimum convex polygon (MCP; Mohr 1947) and 95% fixed kernel (Worton 1989) methods in the software program Ranges V (Kenward and Hodder 1995). We calculated 95% MCP estimates by omitting locations farthest from the arithmetic center. For the fixed kernel method, exploratory analysis was conducted by using least-squares cross validation to minimize smoothing. However, Ranges V rarely produced a minimal smoothing parameter for these data;  $h_{\text{ref}}$ , the program's default smoothing parameter, was used instead (see Seaman and Powell 1996). Although the default smoothing parameter produced contiguous home ranges in only 9 of 21 cases, it was not adjusted in the interest of minimizing both bias and variability of the estimates (Worton 1995). We used program default values for all other analysis options.

To conduct a planned comparison of home-range sizes from Washington with those from Oregon and California, we screened data from the literature. All western gray squirrel studies cited herein were conducted in rural, mixed oak–conifer landscapes. Data on all adult animals from studies in the literature were included in comparisons of home-range size, except where Cross (1969) reported that  $>50\%$  of an animal's relocations resulted from trapping. We used 100% MCP estimates for between-study comparisons of summer, winter, and total home-range size, because they were common to all studies. Total home range includes all movements for an individual. Summer and winter home ranges exclude extensive breeding movements and special feeding bouts to locally abundant, temporary food sources. Only adult animals with  $\geq 40$  relocations were included in total home-range comparisons to control for the effect of sampling intensity on home-range size (Boulanger and White 1990; Seaman and Powell 1996). In our study an asymptote was achieved at  $\leq 40$  relocations when individual home ranges were plotted against number of relocations; seasonal ranges reached an asymptote at 25 relocations. Mann–Whitney tests (Zar 1996) were used to compare home-range size between studies.

We derived home ranges for males and females separately. A reproductive female was dedicated to 1 nest for several weeks, and was later confirmed to be lactating or to have juvenile squirrels in close association with her or her nest. Within-study comparisons were conducted by using 95% MCP and fixed kernel estimates to reduce the

**TABLE 1.**—Comparison of total, winter, and summer 100% minimum convex polygon home-range estimates (ha) from Klickitat County, Washington (this study), versus Oregon and California. The *P*-values are from Mann–Whitney *U*-tests ( $\alpha = 0.05$ ).

	Washington		Oregon and California		<i>U</i>	<i>P</i>
	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>		
<b>Females</b>						
Total	31.6 $\pm$ 4.7	12	9.1 $\pm$ 3.3 <sup>a,b</sup>	6	6.0	<0.01
Winter	15.4 $\pm$ 3.2	7	1.8 $\pm$ 0.5 <sup>a</sup>	4	0.0	<0.01
Summer	19.5 $\pm$ 2.8	11	3.9 $\pm$ 1.1 <sup>a,c</sup>	7	2.0	<0.001
<b>Males</b>						
Total	115.9 $\pm$ 25.8	9	14.8 $\pm$ 2.8 <sup>a</sup>	5	2.0	<0.01
			4.4 $\pm$ 0.5 <sup>b</sup>	4	0.0	<0.01
Winter	30.2 $\pm$ 10.4	5	2.9 $\pm$ 0.3 <sup>a</sup>	3	1.0	0.07
Summer	37.8 $\pm$ 6.6	6	4.8 $\pm$ 0.6 <sup>a</sup>	6	0.0	<0.01
			2.9 $\pm$ 0.2 <sup>c</sup>	5	0.0	<0.01

<sup>a</sup> Cross (1969), Oregon.

<sup>b</sup> Foster (1992), Oregon.

<sup>c</sup> Gilman (1986), California.

influence of outlying points and to stabilize home-range estimates (Harris et al. 1990; White and Garrott 1990). We used a Mann–Whitney test to compare home-range size by sex.

To compare movement patterns throughout the annual cycle, we plotted frequency of consecutive interfix distances by month and defined the mating season as February through June. Only animals with >30 locations per season were included to ensure sound estimates and an adequate sample of animals. We used Mann–Whitney tests to compare interfix distances and interfix intervals between sexes. The Wilcoxon sign-rank test (Zar 1996) was used to compare home-range size between mating and nonmating seasons.

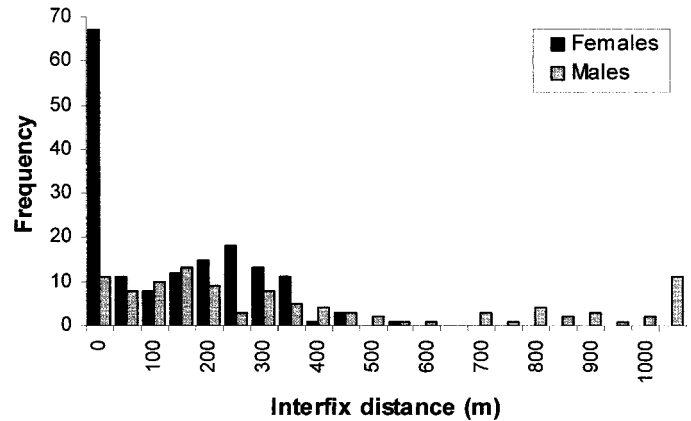
We compared overlap among individual home ranges by using 95% MCP and fixed kernel estimates. Percentage overlap was averaged by sex for mating and nonmating seasons. We used the Mann–Whitney test to assess differences in overlap by sex and Wilcoxon sign-rank test for seasonal comparisons.

Statistical tests were conducted at  $\alpha = 0.05$  by using Version 8.0 of SPSS software (SPSS 1997).

## RESULTS

We registered 2,731 trapping sessions (4 h each), capturing 25 female and 25 male western gray squirrels a total of 174 times. Between August 1998 and June 1999, 22 female and 18 male squirrels were fitted with radiotransmitters. Of 3,130 independent telemetry locations, 2,012 were of females and 1,118 were of males. Of the 3,130 total radiolocations noted, we saw squirrels in 32% (998), squirrels were concealed in a nest in 39% (1,210), and 29% (922) were telemetry fixes only. In all but 14 of the latter cases, accuracy of fixes was estimated at  $\leq 15$  m; we retained the 14 less-accurate locations because they represented movements outside the animal's normal use area. We obtained a sufficient number of locations to estimate home range for 12 female and 9 male squirrels. All locations were obtained between 0618 and 2030 h.

One hundred percent MCP home-range estimates from Washington were significantly larger than those from Oregon and California in seasonal and year-round comparisons (Table 1). Male home-range sizes were significantly different



**FIG. 1.**—Distances between radiotelemetry fixes, as shown by frequency distribution of interfix distances for 14 female and 10 male western gray squirrels in Klickitat County, Washington, during March 1999 (mating season).

among studies, so data were not combined as they were for females. Home-range sizes of males in winter were not different, which may reflect a small sample size and high variance.

We detected no significant difference between 95% MCP ( $\bar{X} = 21.6$  ha  $\pm$  3.3 *SE*) and 95% fixed kernel ( $\bar{X} = 22.1$   $\pm$  2.6 ha; Mann–Whitney *U*-statistic = 70.0, *P* = 0.91) estimates for 12 females. Mean home-range size for 9 males also did not differ between 95% MCP ( $\bar{X} = 73.0$   $\pm$  19.2 ha) and 95% fixed kernel ( $\bar{X} = 73.9$   $\pm$  16.9 ha, *U* = 40.0, *P* = 0.97) estimates. Mean number of fixes was not different for males ( $\bar{X} = 107$   $\pm$  19 *SE*) and females ( $\bar{X} = 144$   $\pm$  20; *U* = 41.0, *P* = 0.26).

When using 95% MCP estimates, 9 males ( $\bar{X} = 73.0$   $\pm$  19.2 ha) had larger home ranges than 12 females ( $\bar{X} = 21.6$   $\pm$  3.3 ha; *U* = 18.0, *P* < 0.01). Differences in home-range size between males ( $\bar{X} = 73.9$   $\pm$  16.9 ha) and females ( $\bar{X} = 21.9$   $\pm$  2.7 ha; *U* = 18.0, *P* < 0.01) also were reflected in 95% fixed kernel estimates.

Home-range size (95% MCP) for 4 males was not significantly different between mating ( $\bar{X} = 115.5$   $\pm$  36.2 ha) and nonmating seasons ( $\bar{X} = 36.9$   $\pm$  9.6 ha; *Z* =  $-1.5$ , *P* = 0.14), but sample size was low. Seven females with litters also showed no difference in 95% MCP home-range size between mating ( $\bar{X} = 17.4$   $\pm$  2.6 ha) and nonmating seasons ( $\bar{X} = 19.7$   $\pm$  3.0 ha; *Z* =  $-0.45$ , *P* = 0.40).

Females showed limited movement distances (Fig. 1) and high nest use (M. J. Linders, in litt.) during the mating season. For males, movement distances peaked at 150 m and again at >1,000 m (Fig. 1). Average distance between consecutive fixes was significantly greater for 5 males ( $\bar{X} = 359$  m  $\pm$  29 *SE*) than for 11 females ( $\bar{X} = 168$   $\pm$  17 m) during the mating season (*U* = 1.0, *P* < 0.01). Interfix distances from July to December of 1999 also were different (*U* = 11.0, *P* < 0.05) between males ( $\bar{X} = 277$   $\pm$  23 m, *n* = 6) and females ( $\bar{X} = 208$   $\pm$  21 m, *n* = 10); small sample size prevented a test of interfix distances in 1998. Interfix intervals did not differ for males ( $\bar{X} = 40.5$  h  $\pm$  4.3 *SE*) and females ( $\bar{X} = 33.5$   $\pm$  2.5 h) during the mating season (*U* = 17.0, *P* = 0.23) and the nonmating season

( $\bar{X} = 40.6 \pm 1.8$  h for males;  $\bar{X} = 44.4 \pm 2.9$  h for females;  $U = 23.0$ ,  $P = 0.45$ ).

Ninety-five percent MCP home-range overlap for all individuals averaged  $10.3\% \pm 2.4$  SE ( $n = 24$ ). Same-sex overlap was significantly lower ( $U = 30.5$ ,  $P < 0.05$ ) for females ( $\bar{X} = 3.5 \pm 0.7\%$ ,  $n = 14$ ) than for males ( $\bar{X} = 12.6 \pm 3.2\%$ ,  $n = 10$ ). Home ranges of males overlapped those of other squirrels (mating season,  $\bar{X} = 32.3 \pm 4.9\%$ ,  $n = 14$ ; nonmating season,  $\bar{X} = 14.0 \pm 2.0\%$ ,  $n = 16$ ) significantly more than home ranges of females overlapped those of other squirrels (mating season,  $\bar{X} = 5.6 \pm 1.2\%$ ,  $n = 14$ ; nonmating season,  $\bar{X} = 4.0 \pm 0.8\%$ ,  $n = 16$ ) during both mating ( $U = 28.0$ ,  $P < 0.001$ ) and nonmating seasons ( $U = 21.0$ ,  $P < 0.001$ ). Home ranges of males overlapped those of other squirrels significantly more in the mating season than in the nonmating season ( $Z = -2.4$ ,  $P < 0.05$ ). These patterns were similar for both home-range estimators.

## DISCUSSION

Home-range estimates for western gray squirrels in Washington were the largest yet reported for a North American tree squirrel (Flyger and Smith 1980; Halloran 1993; Heaney 1984; Koprowski 1994; Weigl et al. 1989; Wells-Gosling and Heaney 1984). Possible explanations for large home-range size include poor food resources (quality, quantity, or both) and low population density (intraspecific competition—Don 1983). The presence of few large-seeded, mast-producing tree species in Washington compared to Oregon and California (Gilman 1986; Ingles 1947; Stienecker and Browning 1970) may limit the availability of high-quality foods (Sanford 1985; Smith 1981). Where pine and oak are more diverse, mast failures are less likely to be concurrent, which may result in a more stable food supply (Gurnell 1983). Low abundance and a patchy distribution of mast are typical of low-diversity, open forests, a condition requiring seed-eating squirrels to travel extensively (Weigl et al. 1989). The diversity of trees on our site was similar to that in northern Oregon (Foster 1992) but lower than on sites farther south (Cross 1969; Gilman 1986; Hall 1979). Further studies of home range of western gray squirrels in northern Oregon may reveal similarities with Washington.

Home ranges of Eurasian red squirrels (*S. vulgaris*) in winter were not affected by food supply, and home-range size was more closely tied to population density (Wauters and Dhondt 1998). Other tree squirrel researchers (Cross 1969; Don 1983; Heaney 1984; Wauters and Dhondt 1998) have found that home ranges were larger in areas with low population density. Hall (1979) reported higher densities of western gray squirrels on sites with greater diversity of mast-producing trees.

The reproductive biology of tree squirrels offers insight into the large home-range size of males. Female squirrels are in estrus for only 1 day (Koprowski 1998), and 2–5 males were present in mating groups we observed. Large home ranges allow males to maximize their access to females during spring and early summer coincident with breeding (Don 1983; Gurnell 1987; this study). The distribution of females may reveal much about differences in home-range size of males. Food supply, population density, and nest preference all may play a role in

female spacing patterns (Cross 1969; Gurnell 1987; Wauters and Dhondt 1992; Weigl et al. 1989). Research on the autecology of female western gray squirrels could address these questions.

Other explanations for large home ranges of males include a dispersed food supply in spring and early summer when staple foods are depleted (Gurnell 1987; Weigl et al. 1989) and an avoidance of maternal nest territories that are defended against all other squirrels (Ingles 1947; Wauters and Dhondt 1992). Range shifts in Eurasian red squirrels, especially among males, were associated with availability of pine cones in June and July (Lurz and Garson 1998). Beginning in June, both males and females that we observed fed heavily on new, green pine cones, as previously reported (Barnum 1975; Stienecker and Browning 1970; Weigl et al. 1989). Weigl et al. (1989) reported that home-range size increased when cone supply was low and patchy.

Females with young have special nest requirements (Gurnell 1987). Western gray squirrels may locate maternal dens in oak cavities on open slopes hundreds of meters from core areas (Cross 1969; Linders 2000). However, females foraged in their core areas, which were dominated by large pines. Behaviors indicating defense of maternal dens (Gurnell 1987; Ingles 1947) were not detected even though males were observed in core areas of females. Dens may be isolated to protect young (Don 1983) rather than to guard food supplies (Cross 1969). Energy demands of lactation are high (Gurnell 1987; Knee 1983), and females with young may be unable to procure sufficient resources near maternal nests.

Mating season was distinguished from nonmating season by increased nest use and decreased distances moved by females and by more long-range movements by males. Don (1983) reported similar results for *S. carolinensis*. In our study, males increased the frequency of long-distance movements by 2–3 times during the mating season, resulting in greater variance but no difference in home-range size between mating and nonmating seasons. This suggests a dispersed use of the home range by males (Cross 1969; Gurnell 1987; Halloran 1993; Wauters and Dhondt 1992; Weigl et al. 1989).

The low home-range overlap we report relative to other studies (Gilman 1986; Ingles 1947; Halloran 1993 for *S. aberti*) was pronounced among females. *Tamiasciurus* species cache food and defend territories in coniferous habitat but exhibit overlapping home ranges in deciduous habitats (Don 1983; Gurnell 1987). Female tree squirrels have nearly exclusive home ranges (Gilman 1986; Gurnell 1987; Ingles 1947; this study). In Eurasian red squirrels, core areas of dominant females center on rich food resources that increase their reproductive fitness (Wauters and Dhondt 1992, 1995). In our study, as for female red squirrels in coniferous habitat (Wauters and Dhondt 1992), reproductive females held well-defined home ranges, which may indicate nearly exclusive use of high-quality core area habitat.

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