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Jaya R. Smith
University of California, Davis, jayarsmith@gmail.com

Dirk H. Van Vuren
University of California, Davis, dhvanvuren@ucdavis.edu

Douglas A. Kelt
University of California, Davis, dakelt@ucdavis.edu

Michael L. Johnson
Univeristy of California, Davis, mbjohnson@ucdavis.edu

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SPATIAL ORGANIZATION OF NORTHERN FLYING SQUIRRELS, *GLAUCOMYS SABRINUS:* TERRITORIALITY IN FEMALES?

Jaya R. Smith[1,3], Dirk H. Van Vuren[1], Douglas A. Kelt[1], and Michael L. Johnson[2]

ABSTRACT.—We determined home-range overlap among northern flying squirrels (*Glaucomys sabrinus*) to assess their spatial organization. We found extensive home-range overlap among females, and though this overlap could reflect social behavior, we found no evidence of attraction among females, with only one instance of den sharing. Instead, our results suggest that females share foraging areas but may be territorial in portions of the home range, especially around den trees and during young-rearing. Home-range overlap could also result from the extrinsic effect of forest fragmentation due to timber harvest, which might impede dispersal and force squirrels to cluster on remaining fragments of suitable habitat.

RESUMEN.—Determinamos el sobrelapamiento del rango hogareño entre las ardillas voladoras del norte (*Glaucomys sabrinus*) para evaluar su organización espacial. Encontramos un extenso sobrelapamientos en los rangos hogareños entre las hembras; aunque esto podría reflejar su comportamiento social, no encontramos evidencia de atracción entre hembras, y en sólo un caso compartieron su guarida. Vienen su lugar, nuestros resultados sugieren que las hembras comparten áreas de forrajeo pero pueden ser territoriales en ciertas partes de su rango hogareño, particularmente cerca de los árboles donde tienen guaridas y cuando tienen cría. El sobrelapamiento del rango hogareño también podría ser el resultado del efecto extrínseco de la fragmentación forestal debido a la tala de madera, el cual podría impedir la dispersión y forzar a las ardillas a agruparse en fragmentos de hábitat adecuado que queden.

The northern flying squirrel (*Glaucomys sabrinus,* NFS) is a nocturnal and volant species found in coniferous and mixed conifer–hardwood forests across the northern part of North America, with southern extensions into mountainous regions of the United States, including California's Sierra Nevada. Despite its importance as (1) a member of a keystone complex in conifer forest communities (Carey 2009) and (2) the primary prey of spotted owls (*Strix occidentalis;* Zabel et al. 1995, Forsman et al. 2004, J. Keane personal communication), the NFS remains relatively understudied. In particular, its spatial organization is poorly understood. The species is considered social, but inferences about its social nature originate from accounts of multiple individuals cohabitating a single nest (e.g., Weigl 1974, Carey et al. 1997, Bakker and Hastings 2002). In the southern flying squirrel (*Glaucomys volans;* SFS), a better-known species, individuals den in larger groups than in the NFS (Layne and Raymond 1994). However, when female SFSs have dependent offspring, they isolate themselves, defend territories, and are aggressive toward conspecifics (Muul 1968, Madden 1974); females actively chase other SFS individuals away from dens containing young

(Muul 1968). After young are 2 months old, female SFSs terminate their defensive behavior and allow young to socialize with other squirrels (Muul 1968). Similar to female SFSs, female NFSs have been observed separating from conspecifics by establishing their own den during parturition and while offspring are dependent (Weigl 1978, Carey et al. 1997, Weigl et al. 1999). Whether female NFSs become aggressive and defend territories is unknown; however, one might expect them to defend at least some area around the den, as do SFSs (Madden 1974).

We investigated spacing behavior of the NFS in the northern Sierra Nevada by assessing home-range (HR) overlap among same-sex and opposite-sex dyads. Although most of our data are on females, we considered the available data on males as well. If the NFS were social, we would expect extensive spatial overlap among females. However, as with the SFS, social attraction may vary seasonally according to female reproductive status. Hence, we measured spatial overlap of females during 2 periods: (1) parturition and lactation (preweaning), and (2) after young were weaned and lactation had stopped but before winter (postweaning). We evaluated spatial segregation of den trees used by females

[1]Department of Wildlife, Fish and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616.
[2]John Muir Institute of the Environment, Aquatic Ecosystems Analysis Laboratory, University of California, Davis, One Shields Avenue, Davis, CA 95616.
[3]Present address: USGS Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk St., Boise, ID 83706. E-mail: jayar smith@gmail.com

to assess whether den sites were defended against conspecific females.

METHODS

We studied NFSs in the Plumas National Forest near Quincy, California, from May through October in 2006 and 2007. To maximize chances of capturing animals, we trapped along riparian areas (Meyer et al. 2005) and in areas that had yielded high trap success previously (Wilson et al. 2008). We used transects with 2 parallel trap lines that contained 10 trap stations each. Trap stations were centered on trees ≥30 cm dbh, and each station had 2 Tomahawk live traps (model 102; Tomahawk Live Trap Co., Tomahawk, WI) and 1 Sherman live trap (model XLK; H.B. Sherman Traps, Inc., Tallahassee, FL). One Tomahawk trap was mounted on the tree at approximately 1.5 m and the other 2 traps were placed on the ground within 5 m of the tree base. Adult flying squirrels (>100 g) were chemically immobilized and fitted with radio-transmitters (Model PD-2C, Holohil Systems Limited, Carp, Ontario, Canada) that were ≤4% of the animal's body mass (Kenward 2001). Animals were allowed to fully recover from anesthesia before release, and we deferred telemetry for 24 hours to allow time for full recovery from handling.

We tracked animals both diurnally and nocturnally using handheld 3-element Yagi antennas and a handheld receiver (Communications Specialists, Inc., Model R-1000, Orange, CA). A pair of observers took up to 4 observations per night on each animal 2–3 times per week. Observations were separated by ≥2 hours to reduce temporal autocorrelation between points (Swihart et al. 1988). A single observation included 4–6 bearings to the animal from known locations, all taken within 15 minutes. Locations were assessed with program Locate III (Nams 2006), and 95% fixed-kernel HR estimates (calculated using the reference smoothing parameter; Worton 1995) were constructed using program Ranges 6.1.2 (Kenward et al. 2003).

We assessed home-range overlap by quantifying both static and dynamic interactions (Macdonald et al. 1980, Powell 2000) of NFSs. Static interactions are estimated as the areal overlap between 2 home ranges over a specified time frame; we determined this both between and among sexes using program Ranges 6.1.2 (Kenward et al. 2003) and tested for significant differences using a oneway ANOVA in JMP®

version 7 (SAS Institute, Inc., Cary, NC, 1989–2007).

Dynamic interactions assess whether animals occur in greater or lesser proximity to each other relative to their known locations within their home ranges. These interactions typically are quantified by comparing simultaneous pairwise locations of 2 animals relative to that expected from the suite of possible locations, based on all locations where each animal was radiolocated. We summarized dynamic interactions for female–female (F–F) pairs using program Ranges 6.1.2 (Kenward et al. 2003) and quantified them with Jacobs' index values (Jacobs 1974), which ranks interactions on a scale from –1 (avoidance) to +1 (attraction; Jacobs 1974, Walls and Kenward 2001). We assessed whether Jacobs' index values were different from zero using Wilcoxon's signed-ranks test (Walls and Kenward 2001) in JMP® version 7 (SAS Institute Inc., Cary, NC, 1989–2007).

During the day, we tracked animals to den trees. Den-tree locations were recorded using a Trimble GPS device accurate to ±1 m (GeoXH handheld and backpack antenna; Trimble Navigation, Ltd., Sunnyvale, CA). Squirrels typically used multiple den trees, and we constructed 100% minimum convex polygons around all den-tree locations (hereafter den HR) of each female to assess overlap of female den locations.

Our observations indicated that female NFSs ceased lactating by the beginning of August, similar to the report of Carey et al. (1997). To assess whether NFSs at our study area were more territorial when caring for dependent offspring, we compared home-range overlap before and after August for reproductive females, a comparison that excluded only one pair of females. Three additional pairs could not be analyzed because one or both animals were not radiolocated prior to August; this left 4 female dyads for comparison, and 4 we could not compare. To determine if overlap was reduced simply because of an overall reduction in HR size in the preweaning period, we compared HR sizes between the pre- and postweaning periods using a paired *t* test. For dyads with sufficient data, we compared static overlap values for the 2 periods using a paired *t* test and dynamic interactions as described above.

For all parametric tests, we confirmed normality using the Shapiro–Wilks test. We tested for homoscedasticity using 4 tests (Bartlett's test, the Brown–Forsythe test, Levene's test, and
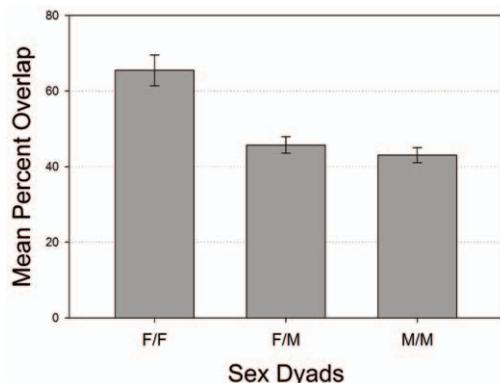
Fig. 1. Percent static home-range overlap of *Glaucomys sabrinus* by sex in northern California. Shown are female–female, female–male, and male–male overlaps (F–F, F–M, and M–M, respectively). Errors bars represent one standard error around the mean.

O'Brien's test) with mixed results. Because some tests indicated homoscedasticity but others did not, and because the parametric tests applied here are relatively robust to mild heteroscedasticity, we interpret parametric analyses conservatively.

RESULTS

Static overlap among females was greater than that among males or between sexes (one-way ANOVA: $F_{2,12} = 9.184$, $P = 0.0038$; Fig. 1). In contrast, dynamic interactions indicated neither attraction nor avoidance of F–F dyads (Wilcoxon's signed-ranks test: $P = 0.875$). Of the 8 dyads (10 females) that exhibited HR overlap, den HR of only 2 dyads (4 females) exhibited overlap, with values of 4% and 20%. If we assume the remaining 6 dyads did in fact have zero overlap, the mean percent overlap for all den HR dyads was 3% (SE = 2.4). Because measures of overlap are not independent (e.g., some females overlapped other females as well as males), we repeated the static-overlap analysis after removing these individuals. Results were not materially altered, overlap among females was still greater than overlap among males or between sexes.

Home-range area for reproductive females did not differ between the pre- and postweaning periods (9.3 ha [SE = 2.53] and 19.4 ha [SE = 4.79], respectively; paired t test: $t = 1.43$, $P = 0.11$, df = 4). Four F–F dyads in which at least one female exhibited signs of pregnancy or lacta-

tion showed an increase in home-range overlap from the prewean to postwean periods (42% [SE = 6.1] versus 63% [SE = 5.6]; paired t test: $t = 5.05$, $P = 0.015$, df = 3). One other F–F pair included reproductive females that showed no signs of having offspring, and these animals had very similar overlap before (49%) and after (48%) the weaning period. Dynamic interactions indicated neutrality ($P > 0.30$) in both pre- and postweaning periods.

DISCUSSION

Home ranges of northern flying squirrels in the northern Sierra Nevada overlap extensively, both within and between sexes, indicating the potential for sociality. Although this was especially pronounced for females, analysis of dynamic interactions indicated no evidence of attraction among females, contrary to what might be expected for a presumably social species. Moreover, home-range overlap among females decreased when they had dependent juveniles, and most females maintained areas of exclusive use around den trees. The only pair of females that shared a substantial area around dens (20% overlap) was also the only pair of females in which neither was reproductive. Our results suggest that NFSs share foraging areas but may be territorial in portions of the home range, especially around den trees. Evidence of territoriality was most pronounced for reproductive females, perhaps because of the threat of infanticide from conspecifics (Wolff and Peterson 1998).

Evidence of sociality in the NFS rests largely on reports of multiple individuals in the same nest (Weigl 1974, Carey et al. 1997, Bakker and Hastings 2002). In our study area, however, den sharing was rare. Although we recorded 91 different den trees used by a total of 22 squirrels over 2 years (Smith 2009), we observed only one instance of simultaneous den sharing (2 nonreproductive females). Our study was conducted primarily during the summer months, and we suppose den sharing may be more common in our study area during winter when thermal stress is greater (Carey et al. 1997).

Although obeservations reported here do not support extensive sociality in the NFS, available data do not allow us to assess the extent to which this reflects NFS ecology or the influence of extrinsic factors such as anthropogenic habitat fragmentation. Northern flying squirrels prefer

stands of large trees (Smith 2009), which are increasingly uncommon and fragmented in the northern Sierra Nevada because of the effects of 150 years of forestry practices (Millar 1996). Hence, extensive overlap of adult females may result from limited opportunities for dispersal, in turn resulting in small clusters of related females. The spatial organization of most tree squirrels is closely related to their mating system (Koprowski 1998). Both males and females require food resources, but males have the additional need to access multiple females; hence, males often have larger home ranges that overlap with those of multiple females (Ostfeld 1990, Koprowski 1998). Although the mating system for the NFS is unknown, studies elsewhere indicate that males have larger home ranges than females do (Martin and Anthony 1999, Weigl et al. 1999, Menzel et al. 2006, Hough and Dieter 2009), as is the case with most other tree squirrels (Koprowski 1998). In contrast, male and female home ranges in our study area are similar in size (Wilson et al. 2008, Smith 2009). Whether this home-range size similarity reflects regional variation in spacing patterns or the influence of habitat fragmentation is not clear. The high degree of overlap among females in our study suggests spatial clustering among females, which might be expected to select for male territoriality to maintain exclusive access. Nonetheless, limited available data show relatively high overlap among males (Fig. 1), suggesting that they were not territorial in our study area.

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