Spatial Organization, Habitat Preference, and Management of Northern Flying Squirrels, *Glaucomys sabrinus*, in the Northern Sierra Nevada.

By

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THESIS

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Squirrels, *Glaucomys sabrinus*, in the Northern Sierra Nevada.

ABSTRACT

The northern flying squirrel (*Glaucomys sabrinus*) is an important member of

forest ecosystems because of its role both in consuming and dispersing truffles,

and as a prey item. Through these roles it aids forest regeneration and provides

food to mammalian and avian predators, especially the spotted owl (*Strix

occidentalis*). The work presented here provides home range estimates and den

selection data for 22 northern flying squirrels using data collected via

radiotelemtetry in 2006 and 2007. Northern flying squirrels had home ranges

8.56 ± 1.36 (SE) ha in size, and there was no difference between males and

females. These home range data provide the foundation for habitat assessment,

management recommendations, and insight into northern flying squirrel spatial

arrangement. Using compositional analysis we determined that flying squirrels

disproportionately selected large mixed-conifer stands at two spatial scales, and

they preferred to den in hardwood trees over conifers. Consequently, forest

managers should retain these features when managing for northern flying

squirrels. We also assessed home range overlap and found some evidence of

sociality. However, females became territorial around den trees and during the

time of year that they had offspring. Due to limitations associated with

fragmented habitat, males of this species may also be constrained to smaller home

ranges, thereby limiting opportunities for polygyny.

INTRODUCTION

The northern flying squirrel (NFS; *Glaucomys sabrinus*) is an arboreal species

that occurs in coniferous forests throughout much of northern North America,

including the Sierra Nevada and northern Rocky Mountains, with disjunct

populations in the Appalachians and the southern Rocky Mountains (Wells-

Gosling and Heaney 1984, Smith 2007). It is an animal that is somewhat

understudied because of its nocturnal and volant nature. However, in the Pacific

Northwest, it has been recognized as a keystone species (Carey 2000, Smith 2007)

or part of a keystone complex (e.g., spotted owls, NFS, ectomycorrhizal fungi,

Douglas fir; Carey 2009), which has piqued the interest of researchers and led to a

modest increase in publications on the animal in the last decade or two.

Additionally, the NFS is a key prey item to spotted owls (*Strix occidentalis*) in

areas where the two species overlap (Carey et al. 1992). Because of this

relationship, forest managers are keenly interested in incorporating plans to

accommodate NFS populations into management plans (Lehmkuhl et al. 2006).

To properly do so, forest managers need to understand areal requirements for NFS

in addition to those for spotted owls. Additionally, forest managers can infer

habitat requirements of NFS based on where they are found in the forest. In the

first chapter of this thesis I report on this topic with the intention of informing

forest managers about the areal and habitat needs of northern flying squirrels.

This builds on preliminary work by Wilson et al. (2008) and provides greater

sample sizes both in number of animals and number of observations per animal.

The second chapter of this thesis addresses the spatial organization of NFS.

While in other areas of its range the NFS appears to nest communally to facilitate

social interactions (Carey et al. 1997, Bakker and Hastings 2002), communal

nesting apparently was very uncommon in this study area. Communal nesting

may be a facultative strategy to alleviate thermal stress, in which case I predict

this should be more prevalent in winter. Additionally, observations in Oregon

suggest that females isolate themselves when caring for dependent young (Carey

et. al 1997), indicating a potential for territoriality. I use home range data to test

for sociality and to determine if there is a temporal component to NFS

territoriality.

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Chapter I

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Running Head: SMITH ET AL—H.R. AND HABITAT OF *G SABRINUS*

Home range, habitat preference, and management of northern flying squirrels, *Glaucomys sabrinus*, in the northern Sierra Nevada.

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Northern flying squirrels (*Glaucomys sabrinus*) are important to forest managers in the western United States because they are key prey for threatened spotted owls (*Strix occidentalis*), and thought to be keystone dispersers of mycorrhizal fungal spores in the Pacific Northwest. We quantified home range size for 22 northern flying squirrels over 2 years in the northern Sierra Nevada using radiotelemetry. We applied compositional analysis to assess habitat preferences at 2 spatial scales, and to quantify den tree selection. Home ranges were 8.56 ± 1.36 (SE) ha., and did not differ between sexes or across years. Habitat selection was scale-independent: home ranges included disproportionate cover by large mixed-conifer stands, and habitat use within home ranges also favored use of areas with large mixed-conifer stands. Squirrels selected large conifers and hardwoods for den sites preferentially over smaller conifers and saplings. These results suggest that forest managers should retain stands of large mixed conifers as well as hardwoods to maintain viable populations of this key prey species.

Key words: den selection; *Glaucomys sabrinus*; habitat preference; home range; northern flying squirrel.

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Northern flying squirrels (*Glaucomys sabrinus*; NFS hereafter) are ecologically and politically important mammals in western North America because of their

numerous ecological roles. Perhaps most salient, they are trophic specialists foraging on subterranean fungi (truffles), many of which develop mycorrhizal associations with conifers, and they are key prey for northern and California spotted owls (*Strix occidentalis caurina* and *S. o. occidentalis*, respectively). Northern spotted owls are threatened under the US Endangered Species Act, and California spotted owls are listed as Species of Special Concern by the state of California. Consequently, understanding the ecology of western forests requires an understanding of the biology of NFS, and management of these forests implicitly mandates management for this important prey species.

Because NFS are nocturnal gliding mammals, they are logistically challenging to study, especially in terms of spatial behavior. Consequently, estimates of home range size are limited (Table 1). Research on NFS has been greatest in the Pacific Northwest (e.g., Carey 2000 and references therein), with more restricted efforts in Alaska (e.g., Bakker and Hastings 2002, Pyare et al. 2002), the eastern United States (Weigl et al. 1999, Menzel et al. 2006), and the Sierra Nevada (e.g., Meyer et al. 2005, Wilson et al. 2008).

We studied NFS over 2 years in the northern Sierra Nevada (Fig. 1) to characterize home ranges with greater resolution than previously available. We built on preliminary work by Wilson et al. (2008) in the northern Sierra Nevada by studying a larger number of squirrels from multiple sites and obtaining more observations per individual. Additionally, we determined habitat preferences at 2 spatial scales and we characterized den trees used by flying squirrels relative to available trees. Finally, we apply this information to give recommendations to

forest managers for large-scale management decisions. This study provides the most comprehensive treatments of home range size for this species, thereby allowing greater resolution of habitat associations.

MATERIALS AND METHODS

Our study sites were in the Plumas National Forest near Quincy, California (Figure 1). We studied flying squirrels at four sites with an elevation range of about 1100-2000 meters in managed second-growth forest composed of mixed conifers from June through October of 2006 and 2007. We established trapping transects (Carey et al. 1991) along riparian corridors and in areas known to yield high trap success (Wilson et al. 2008) to maximize chances of flying squirrel capture (Meyer et al. 2005). Each transect comprised 2 parallel trap lines each with 10 trap stations at approximately 40-50 m intervals and with trap stations centered on a tree ≥30 cm dbh. We placed 2 Tomahawk traps and 1 Sherman trap at each trap station; 1 Tomahawk trap was fitted on a tree at approximately 1.5 m height, and the other 2 traps were located within 5 m of the tree base. Traps were baited with a mixture of oats, peanut butter, molasses, and raisins, and lined with polyester insulation and milk cartons to protect animals from the elements (trapping methods modified from Carey et al. 1991).

Telemetry—Flying squirrels captured at sites suitable for telemetry were fitted with a radiotransmitter. Suitable sites were those with road access to facilitate nocturnal telemetry, and moderate topography to facilitate accurate

reception of radio signals. Consequently, our samples do not represent a fully random selection of available habitat or of NFS in this region, but such a selection was not logistically feasible. Adult animals (based on pelage and body mass >100g) were chemically restrained with a low dose of ketamine and xylazine (1.4 mg ketamine, 0.06 mg xylazine, in 0.10 ml saline solution), then fitted with a 4.0 g radiotransmitter (Model PD-2C; Holohil Systems Limited; Carp, Ontario, Canada) that weighed ≤4% of the animal's body mass (Kenward 2001). Individuals were allowed to fully recover before release, and we deferred telemetry for ≥24 hr to allow animals to adjust to their collars. All methods were approved by the University of California Institutional Animal Care and Use Committee and meet guidelines published by the American Society of Mammalogists (Gannon et al. 2007).

We located animals during nocturnal activity periods using triangulation. Field efforts were initiated just after dusk and ended before dawn, and were conducted across the entire field season (May - October). To ensure independence between readings and to reduce temporal autocorrelation, we accepted only those locations separated by ≥2 hr (Swihart et al. 1988). In 2006 we took a minimum of 4 bearings to determine each location, but in 2007 greater efficiency and observer skill allowed us to increase this to 6 bearings. Bearings were taken simultaneously by 2 observers in radio contact, and all bearings for a single observation were taken within a period of 15 minutes. If large movements were detected between the initiation and termination of an observation, a second observation was taken, and the first was excluded.

We quantified observer error with dummy collars that were placed at the field sites at random locations. These collars were moved weekly and observers were not aware of collar location in advance. Mean bearing error was 8.9 ± 0.6 (SE) degrees at a mean distance of 166 ± 1.51 m; although we recognize that this is somewhat high, it reflects the topographically complex environment that characterized our study area.

Reflecting this topography, signal "bounce" was a concern during data collection. We therefore employed 3 precautions to reduce error and remove erroneous bearings. First, observers scored their confidence in bearings on a scale from 1-3 (poor, good, excellent); all "poor" bearings were subsequently excluded (Haskell and Ballard 2007, Innes et al. 2009). Second, if we still had >4 bearings, we discarded up to the 2 most divergent bearings (leaving a minimum of 4 bearings per location). Finally, we discarded all locations >1 km from observers to minimize the influence of bearing error.

Home Range Analysis—We applied incremental area analysis (IAA; Kenward 2001) to all animals to ensure that sample sizes were sufficient to estimate home ranges. Asymptotes were reached after a mean of 34 locations, and we analyzed data only for animals with >34 locations and an IAA graph exhibiting an asymptote. We eliminated 8 animals from subsequent calculations. Home ranges were delineated using Ranges 6.1.2 (Kenward et al. 2003). We estimated home ranges and core areas using 95% and 50% fixed kernel (FK95 and FK50, respectively; Silverman 1986). We used the reference smoothing

parameter or bandwidth to smooth kernels (Worton 1995), as this allows for comparison across studies (R. Kenward, personal communication, November 2008); we did not use least-squared cross-validation because it has been shown to be inconsistent with <100 locations, and because it is influenced by the distribution of data points, creating home ranges with small patches of disjunct areas surrounding small clusters of locations (Hemson et al. 2005, R. Kenward, personal communication, November 2008) that might not be biologically meaningful. We used fixed rather than adaptive kernels because the latter can overestimate home range area (Seaman and Powell 1996). For comparison with previous studies we also present 95% minimum convex polygons (MCP). Because we only captured female squirrels in 2006, we compared female home ranges and core areas across years using a 2-tailed *t*-test; we then applied 2-tailed *t*-tests to compare home ranges and core areas in males vs. females.

Habitat Selection and Den Trees—Available habitat was obtained from high-resolution aerial mapping of the Plumas National Forest available in a GIS format. We quantified habitat selection at 2 spatial scales. We compared the proportion of selected habitat types in an animal's home range relative to that available in the study area (2nd order selection; Aebischer et al. 1993) defined by a 2 km buffer around 95% home ranges; we used a 2 km buffer as this is the mean dispersal distance of NFS (W. P. Smith, personal communication, November 2008). Additionally, we compared the use of habitat within an animal's home range relative to the available habitat (3rd order selection; Aebischer et al. 1993).

At both scales we used compositional analysis (Compos-Analysis 6.2 plus, Smith Ecology Ltd., Wales, UK) to quantify habitat selection. Compositional analysis incorporates Multivariate Analysis of Variance (MANOVA) to rank and test for disproportionate use of habitats relative to their availability (Aebischer et al. 1993, Smith 2004).

After determining important habitat types in the 2nd order analysis, we combined 3 categories in the 3rd order analysis (see "Missing habitat types" in Aebischer et al. 1993). In addition, because NFS is a forest-dwelling animal that is positively associated with old-growth (Waters and Zabel 1995), we combined chaparral, small Sierra mixed-conifer, and monocultures into a single habitat category.

We located den trees by homing in on telemetry signals during the day, 1-2 times per week in 2006, and weekly in 2007. Den sites were marked with labeled flagging for later identification, and UTM coordinates were recorded using a GPS device accurate to ± 1m (GeoXH handheld and backpack antenna; Trimble Navigation, Limited; Sunnyvale, CA). We applied compositional analysis to compare den trees with all trees available in an 18 m radius around the den tree.

We characterized these trees initially as hardwood or conifer. Conifers were further characterized as saplings (0-10 cm diameter breast height), poletimber (10-27.9 cm dbh), small sawtimber (28-53.3 cm dbh), or large sawtimber (>53.3 cm dbh). Hardwoods were characterized as small or large (< 33 cm dbh vs. ≥ 33 cm dbh) based on increased mast production in the larger size class (Innes et al. 2007).

RESULTS

Home Range Analysis—We captured and collared 30 individuals, 22 of

which (7 in 2006, 15 in 2007) yielded sufficient data for further analysis (e.g., >34

locations and a clear asymptote on an IAA graph; Appendix 1). All animals

tracked in 2006 were females; mean home range area for females did not differ

across years ($t = 1.04$, *d.f.* $= 15$, $P = 0.31$) so these were combined for comparison

with males. In addition, core areas for females did not differ across years ($t =$

0.90, *d.f.* $= 7$, $P = 0.40$) and were also combined for comparison with males.

Fixed kernel (FK95) home range estimates did not differ for males and females

(Table 1; $t = 0.49$, *d.f.* $= 7$, $P = 0.64$). Mean FK95 home range size across all

individuals was 8.56 ± 1.36 SE ha. Home range size using 95% MCP was $8.95 \pm$

2.46 ha and 9.23 ± 1.44 ha for males and females, respectively. As with home

ranges, core areas (FK50) did not differ for males and females (3.38 ± 1.00 ha and

4.80 ± 1.09, respectively; $t = 0.69$, *d.f.* $= 19$, $P = 0.49$).

Habitat Selection—Habitat selection was remarkably similar at both

spatial scales studied, with significant preference for medium and large Sierra

mixed-conifer (e.g., SC1, SC2; Fig. 2a and 2b, Table 2). Following SC1 and SC2

was montane riparian habitat, which in turn was favored over all remaining

habitat types.

Within home ranges (3rd order selection), we combined monocultures, montane

chaparral, and small Sierra mixed-conifer as a composite habitat type because of

very low availability and a limited number of squirrels with these habitats in their

home ranges. Consequently, 3rd order selection compared use vs. availability of only 3 habitat categories. Results reflected 2nd order analysis, however, with medium and large Sierra mixed conifer favored (albeit not significantly) over the other habitat types.

Den Trees—We located 91 den trees, of which 26 were in white fir (*Abies concolor*), 25 in black oak (*Quercus kelloggii*), 12 in Douglas fir (*Pseudotsuga menzeisii*), 11 in red fir (*Abies magnifica*), 7 in incense cedar (*Calocedrus decurrens*), 5 in bigleaf maple (*Acer macrophyllum*), and 5 in various pines (*Pinus* spp.). Although 59% of trees in the vicinity of documented den trees were saplings, no dens occurred in saplings (Fig. 3). In contrast, large trees were clearly preferred; large sawtimber comprised only 6% of available trees but nearly 41% of den trees, and large hardwoods comprised <0.5% of available trees, but nearly 16% of den trees. Compositional analysis confirmed these preferences, indicating a tendency for large hardwoods to be favored over large sawtimber, in turn over small hardwoods; as a group these categories are favored over small sawtimber, which is favored over poletimber, and in turn over saplings (Table 2).

DISCUSSION

The NFS is considered to be a keystone species (Carey 2000, Smith 2007), and recently has been treated as a core member of a keystone complex (e.g., spotted owls, NFS, ectomycorrhizal fungi, Douglas fir; Carey 2009). Additionally, flying squirrels are associated with old-growth or mature forests, typically occurring at

lower densities in more recently logged stands (Rosenberg and Anthony 1992; Waters and Zabel 1995). These squirrels select relatively large diameter trees for den sites (Martin 1994, Carey et al. 1997, Meyer et al. 2005, this study), presumably because these are more likely to have woodpecker or fungal cavities, or other decay features that could provide internal dens for NFS, and thereby offer protection from predation and environmental extremes (Carey 2000).

Perhaps reflecting challenges associated with telemetry on a nocturnal volant animal, there are few published estimates of home range size for northern flying squirrels; however, the range of sizes in the available data is notable (Table 1). Some of these studies were limited by certain factors. Some were constrained by technology and used short-lived collar batteries (Urban 1988, Weigl et al. 1999), others (Witt 1992) combined telemetry and trap data and possibly provided biased estimates (see discussion in Kenward 2001 and Wheatley and Larsen 2008), while others yet were constrained by a lower number of observations per animal (Wilson et al. 2008, Hugh and Dieter 2009). We tried to avoid these pitfalls as best we could, and therefore believe that data presented here represent an accurate and useful model of NFS home range, especially in the Sierra Nevada.

In NFS as in other tree squirrels, the home range of males is larger than females, as males try to overlap home ranges of as many females as possible to increase fitness (Martin and Anthony 1999, Menzel et al. 2006, Hough and Dieter 2009). A unique finding from our research indicates that males and females do not have different home range sizes (Table 1). This could be because of individual behavioral plasticity that varies with resource availability (Koprowski 1998). For

instance, we found that the NFS in this area are preferentially choosing stands of large mixed conifers over other available habitat types. If habitat availability is determining their distribution, then the NFS may be adjusting their HR to fit into the fragmented landscape. Even small differences in the landscape could have a large impact on how these squirrels are distributed, and possibly lead to home range sizes constrained to available habitat in this managed landscape. As a final explanation for this, we also found female flying squirrels with a high degree of HR overlap (Smith et al. 2009). In this instance, males would not need large home ranges to overlap multiple females.

Males and females together had home range sizes of 8.56 ± 1.36 ha. in this study. This is a significantly smaller mean home range size than reported previously at these sights (Wilson et al. 2008), reflecting either yearly variation or differences because of sample sizes. However, although the mean HR size we report is well within the limits for NFS (Table 1), the mean sizes for females are higher than the 'typical' size for female NFS (<5ha; Smith 2007; also see discussion above).

One female NFS in our study (# 27; Fig. 4) had a very different home range in the 2 years of study. This animal used approximately 25 ha in 2006, but only 4.3 ha in 2007. When data from 2006 are divided into early, mid, and late season, however, they indicate that this animal shifted her activities from east to west across a large home range; she returned to the eastern portion of this area the following year (Fig. 4). During this second year that she had a smaller home-range, trap data indicate the female had mangy fur with missing patches of hair and small wounds, which suggest she was in poor condition. Additionally, she

was nursing young in early 2006, but not later in the season, and her home range

might have seasonally shifted and expanded westward subsequent to dispersal of

young during that year. During the second year, she has a smaller home range

perhaps due to intraspecific exclusion and resulting in her poor condition.

Regardless of the cause, no other animals exhibited dramatic changes across

years, and inclusion or exclusion of animal 27 does not materially alter our

results.

Conservation and Management Implications—Forest managers frequently

are faced with the difficult task of balancing pressures for logging and wildfire

reduction with responsibility to meet needs for wildlife species. This is further

complicated when threatened or endangered species are involved. In such cases,

understanding basic ecological requirements is critical for establishing

management objectives and strategies. Such information includes the habitat and

dietary needs of threatened species, although such information may be sparse

even for charismatic species in otherwise well-studied regions.

Our data on habitat preferences have direct implications for management. At both

spatial scales analyzed, squirrels clearly exhibit a preference for large and

medium-sized trees, although this is less apparent within home ranges (3rd order).

Interestingly, squirrels favor hardwoods as much as they do large conifers when

selecting sites for den sites (Fig. 3). While mature coniferous stands are thought

to harbor flying squirrels because of increased den availability (Carey 1991) and

different fungal species composition relative to nearby recently logged areas

(Waters et al. 2000), the apparent importance of hardwoods to NFS appears to be

a novel conclusion of this study. This preference could reflect greater susceptibility of hardwoods to rot and consequently greater likelihood of having cavities at a younger age than conifers (Bunnell et al. 1999). Of interest to managers, preference for hardwoods is not unique to flying squirrels (e.g., Campbell 2004, Innes et al. 2008).

These observations lead to several recommendations for forest managers. First, the clear preference for stands of large mixed conifers indicates that management against monocultures and for diverse species assemblages will benefit NFS. Additionally, tree size is important, as our squirrels preferentially chose stands of large Sierra mixed-conifers (Table 2), indicating retention of mature stands would aid NFS persistence. Second, medium- and large-sized hardwoods share an important role with large conifers as preferred den sites. This is especially the case with black oak, which comprised 83.3% of hardwood dens documented, but also bigleaf maple in riparian areas. Because hardwoods grow more slowly than conifers, active retention of the former in logging activities might favor NFS during forest re-growth, in addition to mature stands.

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FIGURE LEGENDS

Fig. 1.—Map of the study area in the northern Sierra Nevada, California. Boxes indicate location of study areas. Inset shows location of Plumas National Forest within California.

Fig 2.—Percentage of used and available habitat types for northern flying squirrels (*Glaucomys sabrinus*) at 2 spatial scales: a) home range relative to that available in a 2 km buffer around the home range (e.g., Aebischer's (1993) 2nd order), and b) use of habitats within the home range relative to that available (e.g., Aebischer's (1993) 3rd order). BAR=barren, MCP=montane chaparral, MON=monoculture, MRI=montane riparian, SC0=small Sierra mixed conifer, SC1= medium Sierra mixed conifer, SC2=large Sierra mixed conifer, WAT=water, WTM=wet meadow.

Fig. 3.—Distribution of available (*n*=11,602) and used (*n*=91) den trees of northern flying squirrel (*Glaucomys sabrinus*) in the northern Sierra Nevada, classified by tree type (hardwood vs. softwood) and size (in cm dbh; Sapling=0-10, poletimber=conifers 10-27.9, small sawtimber=conifers 28-53.3, large sawtimber=conifer≥53.4, small hardwood=10-33, large hardwood>33) . Available trees are those trees within a 0.1 ha circle centered on den tree. Used trees are den trees.

Fig. 4.—Two 95% fixed kernel home ranges from animal #27, generated in consecutive years, 2006 (grey) and 2007 (hatched). Points from 2006 were divided into equal thirds and displayed, showing movement across the home range throughout the 2006 season.
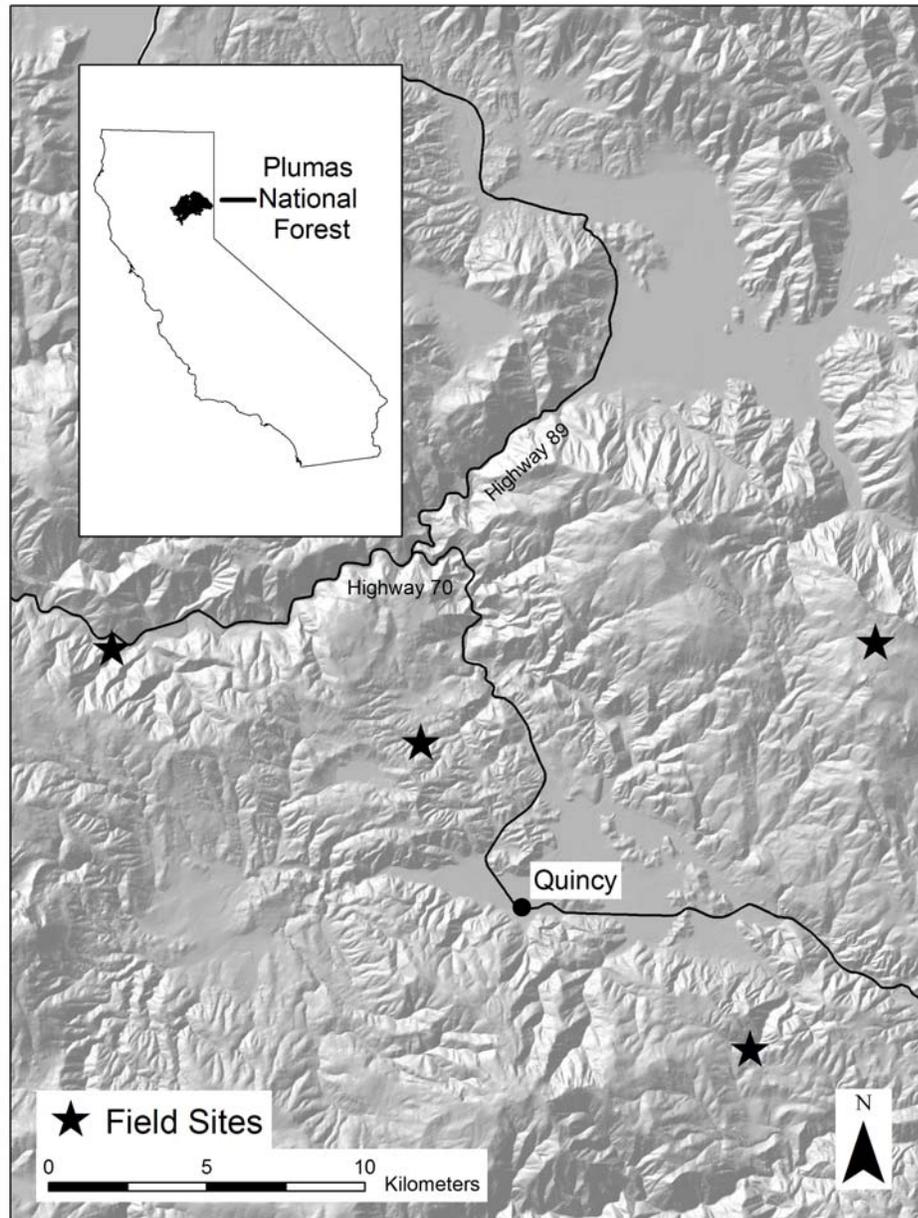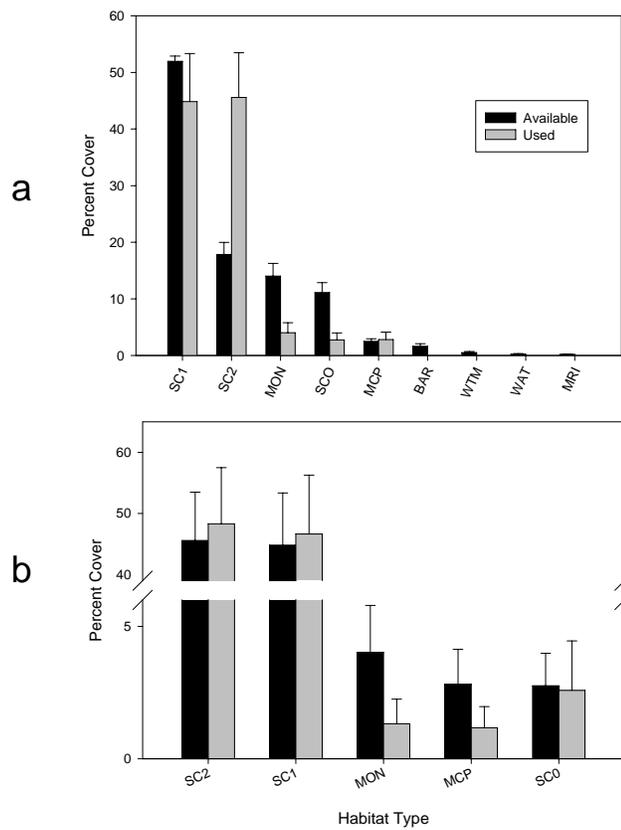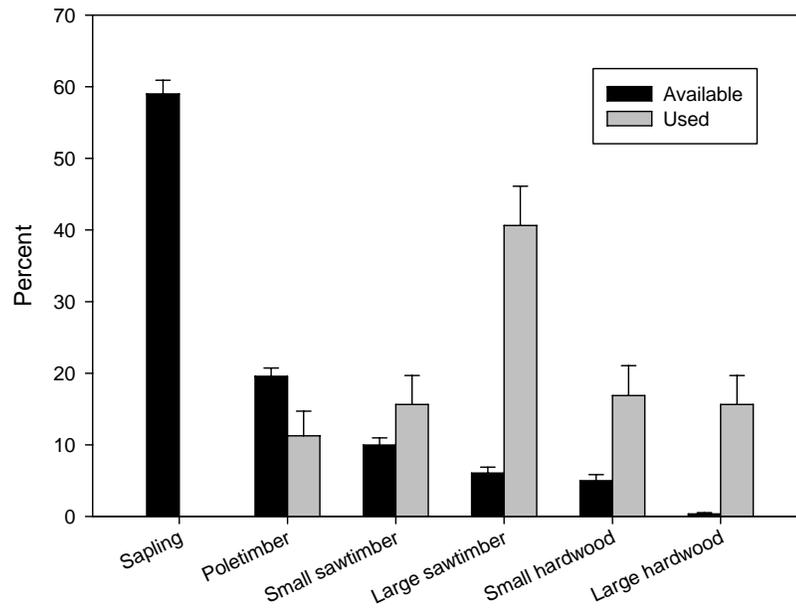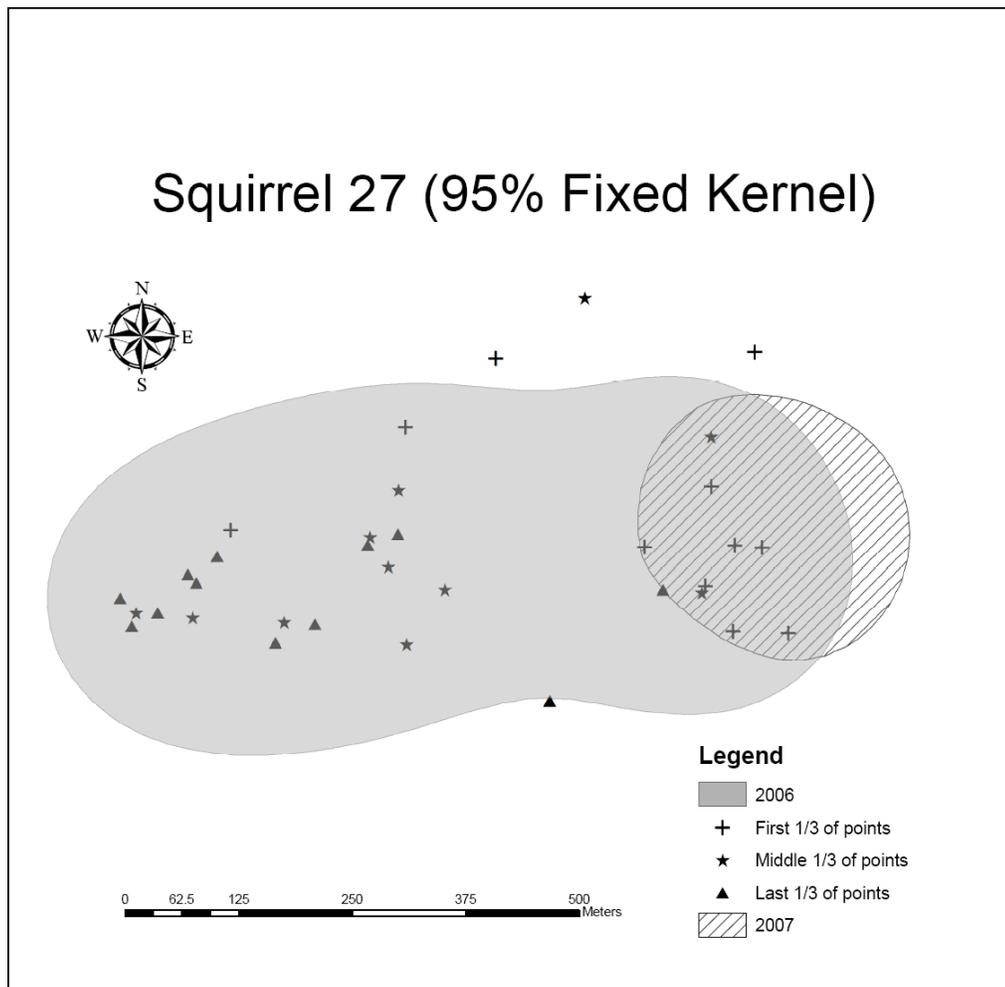
Figures

Figure 1

Figure 2

Figure 3

Figure 4

Squirrel 27 (95% Fixed Kernel)

Legend
2006
+ First 1/3 of points
★ Middle 1/3 of points
▲ Last 1/3 of points
2007

0   62.5   125   250   375   500
Meters

TABLES

Table 1. Home ranges (SE) reported for northern flying squirrels (*Glaucomys sabrinus*). Home ranges at our study site lie between the extremely large home ranges reported from West Virginia (Menzel et al. 2006), and the small home ranges first reported with a relatively low sample size (Urban 1988). The home ranges reported here are significantly smaller than those reported earlier from this region (Wilson et al. 2008).

Source(s)	Sex	Mean Home Range Area (ha; MCP; SE in parentheses)	Mean Home Range Area (ha; Fixed kernel unless otherwise noted; SE in parentheses)	Location
Urban 1988	Male (n=3)	5.2 (1.1)	-	West Virginia
Witt 1992	Unknown (n=5)	3.7 (0.5)	-	Oregon
Martin and Anthony 1999	Male (n=20)	-	5.9 (0.8)**	Western Oregon
	Female (n=19)	-	3.9 (0.4)**	
Weigl et al. 1999	Male (n=6)	10.1 (3.3)	-	North Carolina/ Tennessee
	Female (n=4)	6.9 (2.4)	-	
Weigl et al. 2002	Male (n=5)	20.3 (8.5)	-	North Carolina/ Tennessee
	Female (n=2)	4.9 (0.1)	-	
Menzel et al. 2006	Male (n=4)	59.8 (23.5)	54.2 (18.4)**	West Virginia
	Female (n=8)	15.9 (8.7)	15.3 (7.1)**	
Holloway and Malcolm 2007	Male (n=7)	11.2 (3.4)	14.6 (4.0)	Ontario
	Female (n=7)	3.8 (0.6)	5.7 (1.3)	
Wilson et al. 2008	Male (n=9)	28.6 (9.3)	25.5 (4.0)**	Sierra Nevada, CA
	Female (n=4)	23.8 (5.7)	35.8 (10.4)**	
Hugh and Dieter 2009	Male (n=30)	11.2 (1.4)	-	Black Hills, SD
	Female (n=19)	6.9 (0.9)	-	
This paper	Male (n=5)	9.0 (2.8)	7.35 (2.8)	Sierra Nevada, CA
	Female (n=17)	8.9 (1.6)	8.92 (1.6)	

** - Adaptive kernel

Table 2. Ranking of habitat types at 3 scales of analysis using compositional analysis. The 2nd order reflects disproportionate cover by "preferred" habitats within home ranges relative to that available in a 2 km buffer around each home range. The 3rd order reflects differential use of habitat types within home ranges (based on telemetry locations) relative to their distribution within the home range. The den tree analysis compares trees used for diurnal nests relative to those available within 18 m of each den tree. Habitat types as in Fig. 2a and 2b. Sizes of den trees are given in Fig. 3. Habitats are ordered from left to right in decreasing order of selection; > reflects preference that is not statistically significant, whereas >>> represents statistically significant differences between adjacent variables.

Habitat Type Ranking	
2nd order	SC2>SC1>>>MRI>>>MCP>SC0=BAR=WTM>MON
3rd order	SC2>SC1>(SC0+MON+MCP)
Den trees	LgHardwood>LgSawtimber>SmHardwood >>>SmSawtimber>>>Poletimber>>>Sapling

Appendix 1. Home range data with the number of locations from the 7 animals monitored in 2006 and the 15 in 2007. Animal 27, a female from 2006 had the largest home range (24.90 ha; see Fig. 4 for discussion), while animal 7 from 2007 (also a female) had the smallest home range (1.52 ha).

ID	# locations	95% MCP (ha)	95% Fixed Kernel (ha)	year
Females				
2	36	13.97	11.2	2006
27*	37	20.05	24.9	2006
26	41	3.2	4.47	2006
8	50	3.55	1.82	2006
6	51	10.92	9.51	2006
1	53	20.44	22.43	2006
7	60	1.9	1.99	2006
27	34	2.61	4.3	2007
20	50	12.95	11.11	2007
19	53	12.74	12.3	2007
7	56	2.25	1.52	2007
22	56	7.81	5.69	2007
16	57	13.27	11.05	2007
17	57	11.55	8.45	2007
18	59	5.32	7.37	2007
6	66	9.48	9.64	2007
12	69	4.83	3.84	2007
Males				
24	50	7.1	4.33	2007
21	56	14.57	9.83	2007
23	61	2.82	2.05	2007
15	62	5.36	3.5	2007
25	62	14.9	17.05	2007

Chapter II

Spatial organization of northern flying squirrels, *Glaucomys sabrinus*

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ABSTRACT

We determined home range overlap among northern flying squirrels (*Glaucomys sabrinus*) to assess their spatial organization. We found limited evidence of sociality, with only 1 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 when raising young. Forest fragmentation from timber harvest may have influenced the spatial organization of this species by limiting opportunities for dispersal, and the mating system by constraining males from establishing large home ranges to include multiple females.

Keywords: spatial organization, home range, northern flying squirrel, *Glaucomys sabrinus*, territoriality, overlap

INTRODUCTION

The northern flying squirrel (NFS; *Glaucomys sabrinus*) 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 a member of a keystone complex in conifer forest communities (Carey 2009) and the primary prey of spotted owls (*Strix occidentalis*; Zabel et al. 1995, Forsman et al. 2004, J. Keane, pers. com.), 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 a better studied species, the southern flying squirrel (SFS; *G. volans*), individuals den in larger groups than in NFS (Layne and Raymond 1994). However, female SFS isolate themselves, defend territories, and are aggressive toward conspecifics seasonally, when they have dependant offspring (Muul 1968, Madden 1974); females actively chase other SFS individuals away from dens containing young (Muul 1968). After young are 2 months of age, female SFS terminate defensive behavior and allow young to socialize with other squirrels (Muul 1968). Similar to SFS, female NFS have been observed separating from conspecifics by establishing their own den

during parturition and while offspring are dependent (Weigl 1978, Weigl et al. 1999, Carey et al. 1997). Whether they become aggressive and defend territories is unknown, although one might expect that at least some area around the den would be defended, as in SFS (Madden 1974).

We investigated spacing behavior in NFS in the northern Sierra Nevada by assessing home range (HR) overlap among same-sex and opposite-sex dyads. If NFS are social, we would expect extensive spatial overlap among females. However, as with SFS, social attraction may vary seasonally according to female reproductive status. Hence, we measured spatial overlap of females during two periods: 1) during parturition and lactation (pre-weaning), and 2) after the young were weaned and lactation had stopped, but before winter (post-weaning). To assess whether den sites were defended against conspecific females, we evaluated spatial segregation of den trees used by females.

MATERIALS AND METHODS

We studied NFS in the Plumas National Forest near Quincy, California from May to 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 in previous years (Wilson et al. 2008). We used trap transects with 2 parallel trap lines that contained 10 trap stations each. Trap stations were centered on trees ≥30 cm dbh with 2 Tomahawk (model 102; Tomahawk Live Traps, Tomahawk, WI) live traps and 1 Sherman (model XLK; HB Sherman Traps, Inc., Tallahassee, FL) live trap at each station. One Tomahawk trap was

mounted on the tree at ca. 1.5 m and the other 2 traps were placed within 5 m of

the tree base. Adult flying squirrels (>100 g) were chemically immobilized and

fitted with radiotransmitters (Model PD-2C; Holohil Systems Limited; Carp,

Ontario, Canada) that were ≤4% of the animal's body mass (per Kenward 2001).

Animals were allowed to fully recover from anesthesia before being released, and

we deferred telemetry for 24 hours to allow time for full recovery from handling.

We tracked animals both diurnally and nocturnally using hand-held 3-element

Yagi antennas and a hand-held receiver (Communications Specialists Model R-

1000, Orange, California). 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 from known locations on an animal taken

within 15 min. Locations were assessed with program Locate III (Nams 2003),

and 95% fixed kernel HR estimates with 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 NFS. 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 using a 1-way analysis of variance (ANOVA) in

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

Dynamic interactions assess whether animals occurred in greater or lesser proximity to each other relative to their known locations within their home ranges, and typically are quantified by comparing simultaneous pair-wise 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 F-F pairs using program Ranges 6.1.2 (Kenward et al. 2003), and quantified this 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 a Wilcoxon-signed-rank test (as per 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 ± 1m (GeoXH handheld and backpack antenna; Trimble Navigation, Limited; Sunnyvale, CA). Squirrels typically used multiple den trees, and we constructed 100% minimum convex polygons around all den tree locations of each female to assess overlap of female den locations. Our observations indicated that female NFS ceased lactating by the beginning of August, similar to that reported by Carey et al. (1997). To assess whether NFS at our study area were more territorial when caring for dependent offspring, we compared home range overlap before vs. after this date for reproductive females, which excluded 1 pair of females. Three additional pairs could not be analyzed because 1 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 pre-weaning

period, we compared HR sizes between the pre- and post-weaning periods using a

paired *t*-test. For dyads for which we had sufficient data, we compared static

overlap values for the 2 periods using a paired *t*-test, and dynamic interactions as

above.

For all parametric tests we confirmed normality using the Shapiro-Wilks test. We

tested for homoscedasticity using 4 tests (Bartlett tests, Brown-Forsythe test,

Levine test, O'Brien test) with mixed results. Because some tests indicated

homoscedasticity but others did not, and since 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 (1-way ANOVA, $F = 9.184$, df $= 2, 12$, $p = 0.0038$; Fig. 2-1). In contrast,

dynamic interactions indicated neither attraction nor avoidance of F-F dyads

(Wilcoxon signed-rank test, $p = 0.875$). Of the 8 dyads (10 females) that

exhibited HR overlap, 100% MCP "den tree areas" of only 2 dyads (4 females)

exhibited overlap, with values of 4% and 20%; including zero values for the

remaining 6 dyads, the mean percent overlap for all dyads was 3 ± 2.4 SE%.

Because measures of overlap are not independent (e.g., some females overlapped

other females as well as with males), we repeated the static overlap analysis after

removing these individuals. Results were not materially altered and females still exhibited greater overlap than males or across sexes.

Home range area for reproductive females did not differ between the pre- and post-weaning periods (9.3 ± 2.53SE and 19.4 ± 4.79SE ha; 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 lactation also showed an increase in home range overlap from the pre-wean to post-wean periods (42 ± 6.1SE % vs. 63 ± 5.6SE%; 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 post-wean 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

northern flying squirrels 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 northern flying squirrels rests largely on reports of multiple individuals in the same nest (Weigl 1974, Carey et al. 1997, Bakker and Hastings 2002). However, den-sharing was rare in our study area; although we recorded 91 different den trees used by a total of 22 squirrels over 2 years (Smith 2009), we observed only 1 instance of simultaneous den-sharing. Our study was conducted primarily during the summer months, however, and den-sharing may be more common in our study area during winter when thermal stress is greater (Carey et al. 1997).

The spatial organization and mating system of northern flying squirrels in our area may be influenced by forest management. 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 requirement of access to 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 northern flying squirrels is unknown, studies elsewhere indicate that males have larger home ranges than females (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), perhaps because habitat fragmentation constrained the opportunities for polygyny. Nonetheless, the high degree of overlap among females in our study suggests female clusters that provide the opportunity for male territoriality to maintain exclusive access. However, a relatively high degree of overlap among males (Fig. 2-1) suggests that they were not territorial.

ACKNOWLEDGEMENTS

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Fig. 2-1.—Static home range overlap (percentage ± SE) of *Glaucomys sabrinus* by sex in northern California. Shown are female-female, female-male, and male-male overlap (F-F, F-M, and M-M, respectively).

Figure 2-1