

Den use and selection by northern flying squirrels in fragmented landscapes

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We studied den use and den-habitat selection by the Prince of Wales Island flying squirrel (*Glaucomys sabrinus griseifrons*) at multiple spatial scales in fragmented temperate rain-forest habitats because of the role dens play in the distribution, reproduction, and population density of this endemic subspecies. We observed differences in spatial patterns associated with den use between juveniles and adults: juvenile core denning areas were almost an order of magnitude larger than those of adults, and juveniles used about one-half the number of dens per month as adults. Female juveniles exhibited both the largest mean and maximum movements between consecutive dens among all age and sex classes. At the microhabitat scale of den selection snags were not selected over live trees, but flying squirrels primarily used cavities in snags and live trees. Flying squirrels also selected dens in the largest diameter live trees and snags, in snags with intermediate levels of decay, in live trees with more conks and visible bole entries, and in western hemlock (*Tsuga heterophylla*). At the broader scale of den selection flying squirrels chose den locations in neighborhoods with higher-volume forests and lower levels of fragmentation, although not lower absolute amounts of edge, than was available across the landscape. Our results suggest that extensive modification of landscapes from clear-cut logging and the creation of an early-seral matrix appeared to influence spatial patterns of den use in flying squirrels and den selection at the broader scale. When compared to patterns in a more-intact landscape, den selection at the microhabitat scale did not relate to differences in landscape context, suggesting additional factors might play an important role in den use across the region. DOI: 00.0000/00-MAMM-X-000.1.

Key words: Alexander Archipelago, cavities, clear-cut logging, den use, fragmentation, matrix, Prince of Wales Island, Southeast Alaska, temperate rain forest

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The northern flying squirrel (*Glaucomys sabrinus*) is a common arboreal rodent of boreal and montane coniferous forests of North America (Wells-Gosling and Heaney 1984). The Prince of Wales Island flying squirrel (*G. s. griseifrons*) is an endemic of the Alexander Archipelago in southeastern Alaska, with a geographic range limited to Prince of Wales Island and smaller islands near its western shore (MacDonald and Cook 1996). The northern flying squirrel reputedly plays an essential role in the dynamics of coniferous forest ecosystems (Carey 2000a) because it disperses ectomycorrhizal fungi (Maser and Maser 1988) and because it is an important prey species for several predators (Carey et al. 1992; Forsman et al. 1984, 2001; Rosenberg et al. 2003; Wilson and Carey 1996). A fundamental forest and wildlife management issue pertaining to this species has been whether its habitat is

an emergent property of old-growth forest (Carey 2000a; Carey et al. 1999; Smith et al. 2005). With few exceptions (e.g., Rosenberg and Anthony 1992) the findings of several studies suggest that optimal conditions for the flying squirrel occur in mature forests (Carey 1995). More specifically, some structural attributes of older forest seem essential to meet northern flying squirrel life-history needs, especially locomotion (Scheibe et al. 2006, 2007), reproduction (Carey 2000a; Carey et al. 1997; Smith et al. 2004), and a highly mycophagous diet (Maser et al. 1986; Pyare and Longland 2002; Pyare et al. 2002). Forest management, especially



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extensive clear-cut logging, can create an expansive matrix of early-seral habitats that substantially reduce (Carey 1995, 2000b; Smith 2007; Smith et al. 2003) or isolate (Ford et al. 2004) flying squirrel populations. Such disturbances fragment populations into isolated patches that can lead to local extirpations (Smith and Person 2007) and ultimately the extinction of flying squirrels from an entire region (Hanski et al. 2000; Hokkanen et al. 1982).

Although the underlying mechanisms responsible for lower population densities in managed landscapes remain uncertain (Smith 2007; Smith et al. 2003), availability of dens, especially cavities (Carey et al. 1997; Witt 1991), is probably a limiting factor (Carey 2002; but see Ransome and Sullivan 2004). Cavities in large, live trees and snags are likely important for flying squirrel productivity (Smith et al. 2004) and have such important ecological functions as predator avoidance, food caching, and thermal regulation. Several investigators have reported a positive correlation between population density and large trees or large snags (Carey 1995; Gomez et al. 2005; Lehmkuhl et al. 2006; Smith et al. 2004). Furthermore, demographic studies and simulation models suggest that temperate rain-forest habitats with fewer large trees and snags had significantly lower densities of breeding females and acted as population sinks (Smith et al. 2004; Smith and Person 2007).

Den-site selection has been examined by numerous investigators across a large portion of this species' range and in a variety of land-use and ecological circumstances (Smith 2007). Northern flying squirrels use a variety of structures for denning in unmanaged and managed forests such as cavities in snags and live trees, burrows beneath tree roots and stumps, external nests such as drays (constructed nests), and witches' broom (Carey et al. 1997; Cotton and Parker 2000; Cowan 1936; Holloway and Malcolm 2007; Maser et al. 1981; Menzel et al. 2004; Meyer et al. 2005; Weigl and Osgood 1974). But there is relatively little information about den use of northern flying squirrels in highly fragmented landscapes composed of early-seral (<50-year-old) matrix and insular old-growth habitat patches. Clear-cuts and young growth provide fewer opportunities for denning (Carey et al. 1997; Witt 1991) and thus limit the utility of the landscape located between patches of old-growth forest (Selonen and Hanski 2003, 2004). Knowledge about patterns of den use in heavily modified landscapes is potentially important to understanding persistence of flying squirrels in managed forests (Smith and Person 2007).

The purpose of this study was to quantify patterns of den use and den-habitat selection by northern flying squirrels occupying small (<100-ha) old-growth fragments within a matrix of early-seral (<50-year-old) managed habitats. In addition, we wanted to compare our results to the findings of a similar nearby study in more-intact landscapes, from which we formulated specific hypotheses regarding den-related movement patterns and den selection at microhabitat (e.g., den-tree site) and landscape scales. Because of the pattern of clear-cut logging of high-volume stands in Southeast Alaska, we

expected the attributes of den trees and den use by northern flying squirrels in these managed (e.g., fragmented) landscapes to differ from those in largely unmanaged landscapes (Bakker and Hastings 2002). Specifically, we expected squirrels to use fewer den trees due to fewer options for movements between dens under these insular landscape conditions. Second, we expected distances between consecutive dens to be smaller; however, we also expected the maximum distance moved between dens to be greater due to occasional long-distance movements across an early-seral matrix. Third, we expected that squirrels would use external structures and smaller diameter trees relatively more frequently due to an overall reduction in cavity availability in managed landscapes. Last, we expected flying squirrels would den in the interior of remnant patches and in locales (den neighborhoods) that were composed of higher volume forests and were less fragmented than what was available on the landscape.

MATERIALS AND METHODS

Study area.—We selected a study area on Prince of Wales Island, the largest of >20,000 islands that comprise the Alexander Archipelago of southeastern Alaska (55.9 N, 133.2 W; Fig. 1). Fragmentation of natural forest habitats has increased substantially since the mid-20th century because of extensive clear-cut logging throughout the region (United States Department of Agriculture Forest Service 1997). West-central Prince of Wales Island experienced among the most intensive clear-cut logging in the region, resulting in a high-contrast landscape of early-seral and old-growth forests. The landscape of our study area was composed of 1% clear-cut, a dense concentration of residual timber slash mixed with shrubs and tree seedlings that grew rapidly within 5 years after overstory removal (Alaback 1982); 9% young (<25-year-old) 2nd-growth forest comprised of dense stands of Sitka spruce and western hemlock saplings that overgrew the shrub layer beginning 8–10 years after logging (Harris and Farr 1974); and 38% older (25- to 50-year-old) 2nd growth in which forest canopies close between 25 and 35 years postharvest and then remain even-aged for up to 300 years before gradually transitioning into an uneven-aged condition (Deal and Farr 1994; Harris and Farr 1974). Older (\bar{X} = 57–60 years) 2nd growth averaged 3,450–5,300 trees/ha with an overstory that is 25–30% Sitka spruce. Mean canopy height of nearby 19-year-old stands was 9–10 m, whereas the height of 58-year-old stands averaged 35–36 m (DeMars 2000). Only a minor portion (<10%) of 2nd-growth stands was thinned precommercially, but these stands differed markedly in structure and composition from other 2nd-growth stands, especially older 2nd growth, in which >70% of the regeneration was western hemlock to the exclusion of understory shrubs and herbs (Deal and Farr 1994). An additional 49% of our study area was old-growth forest, which is a combination of high-volume old-growth forest and more-mesic, peatland-scrub-mixed-conifer forest. Smith and Nichols (2003) describe these 2 forest types in greater detail. The remaining 3% of our study area was nonforested.

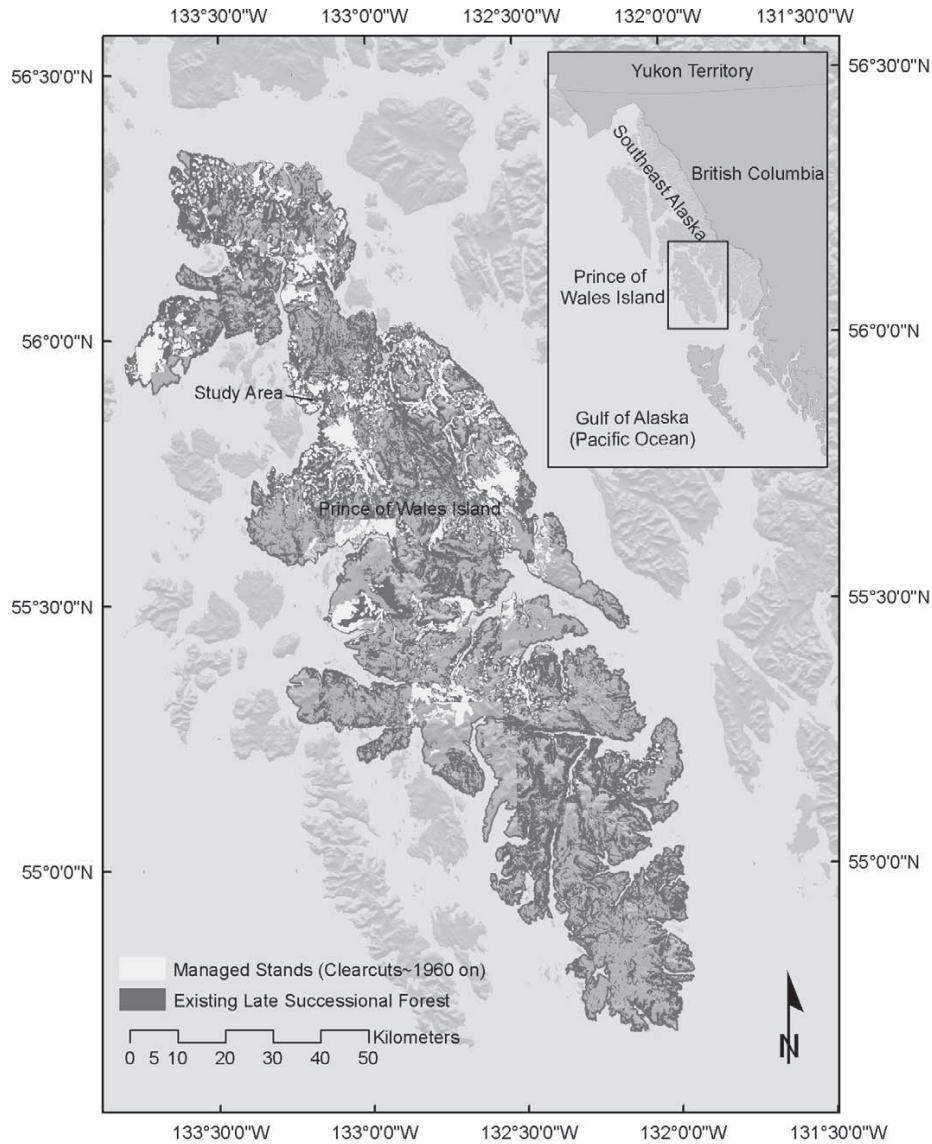


FIG. 1.—Study location on Prince of Wales Island, a landscape of extensively managed and fragmented coastal temperate rain-forest habitat of Southeast Alaska.

Animal capture.—To live capture animals we established 2 permanent grids composed of 30 trap stations distributed at 50-m spacing in patches of old-growth forest. Grids were 1.5 km apart (Euclidian distance) and were similar in age, structure, and composition (United States Department of Agriculture Forest Service 1997); each encompassed about 6 ha of relatively homogeneous forest. We followed the procedures of Smith and Nichols (2003) for livetrapping, handling, and processing northern flying squirrels. We conducted 16 livetrapping sessions annually for 3 years, 2003–2005. Sessions were distributed evenly across 2 seasonal periods lasting 3–4 months, February–May and August–October. Each session lasted 8–10 days with traps closed for

2–4 days between sessions. We released all flying squirrels near the capture site (recaptures) or near the center of the grid at a covered processing site (new captures). Livetrapping, handling, and processing procedures were approved by the University of Wyoming Institutional Animal Care and Use Committee and followed guidelines established by the American Society of Mammalogists (Gannon et al. 2007).

Radiotelemetry and animal movements.—We fitted adult and juvenile males and females with 3.0-g radiotransmitters (model PD-2C; 16- to 30-week life span; Holohil Systems, Carp, Ontario, Canada) during spring (March–May) and autumn (August–October). We subsequently relocated each radiocollared squirrel during diurnal and nocturnal radio-

tracking sessions weekly until the transmitter signal was no longer detected in both types of sessions. During diurnal sessions we located individual den trees through close-range triangulations. We distinguished den sites from other potential situations (e.g., mortalities and dropped transmitters) based on diurnal signals that indicated an animal was stationary but shifting in body position within a den, and by verifying that animals were active in nocturnal telemetry sessions. We labeled each den tree with flagging, assigned it a unique number, used a nondifferential global positioning system (accuracy ≤ 10 m) to obtain coordinates, and maintained a list of individual flying squirrels that used it. We included all individuals with ≥ 2 den locations to estimate interden movements or ≥ 3 den locations for space use (e.g., core den area). We averaged 6.5 den relocations per squirrel. Spatial error arising from global positioning system influenced final estimates of core den areas by 0.2–13.1%, and den movements by 1.5–8.1%, depending on age and sex class.

Den-site characteristics.—We generated a representative sampling pool of den sites to describe microhabitat attributes by including 1 den site per animal; however, a den site was not entirely an independent sample because it could have been used by multiple animals. We used indirect evidence to discern whether a flying squirrel was denning in a cavity or an external nest because we did not directly observe animals emerging from dens. We assigned den type as “cavity” if the den was in a snag without branches (often with visible entrance holes) or in a live tree without visible evidence of drays or stick nests. We assigned den type as “possibly external” when a flying squirrel was located in a live tree with stick nests or drays, or the presence of bark and branches obscured visibility of the upper bole.

We also recorded microhabitat characteristics using methods described in Bakker and Hastings (2002). We described those characteristics for each den tree and a paired sample ($n \leq 10$) of the nearest trees >45 -cm diameter at breast height (snags and live trees) within a 30-m plot centered at the den tree (Bakker and Hastings 2002). We also recorded 3 additional microhabitat variables: den height (estimated with a clinometer), distance to the nearest anthropogenic edge, and the adjacent landscape element (e.g., young growth or road corridor) that formed the edge boundary.

Habitat composition.—We used a geographic information system (ArcGIS version 9.1; ESRI, Inc., Redlands, California) to conduct a broader-scale analysis of den-site selection within the neighborhood of each trapping grid. To define a neighborhood we calculated distances from each den site to the center point of the trapping grid (i.e., centroid). These distances were used to calculate the standard distance deviations, which for our 2 study grids were 858 m and 1,307 m. Standard distance deviation is a spatial statistic analogous to a numerical standard deviation and thus represents the average variation in den-site distances from the center of each trapping grid (Wong and Lee 2001). We established a neighborhood for each grid (Fig. 2) by delineating a circle with a radius equal to 2 standard distance

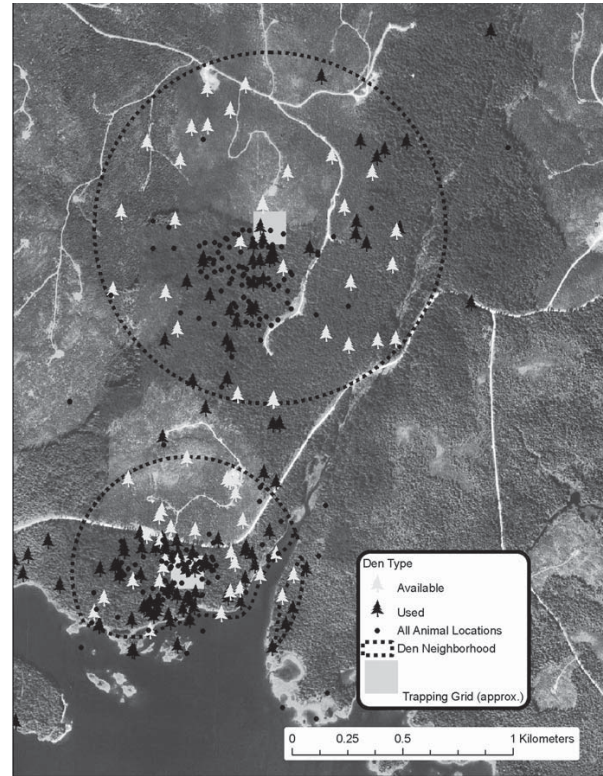


FIG. 2.—Den “neighborhoods,” 2 study grids, telemetry locations of radiocollared northern flying squirrels (*Glaucomys sabrinus*), and den (used) sites and random (available) sites within neighborhoods in a fragmented landscape of old-growth patches in a matrix of clear-cuts (<5 years old) and 2nd-growth forest, Prince of Wales Island, Alaska, 2004–2006.

deviations (theoretically encompassing 95% of the den sites), within which we established 30 random points to generate a data set of available habitat conditions. We justified using the grid centroid to delineate neighborhoods on the basis that radiolocations of dens were dispersed relatively uniformly throughout the grid (Fig. 2).

We described vegetation and landscape composition within 0.338-ha circular zones around each den and random location. We derived these zones using one-half the mean nearest-neighbor distance among den sites (65.6 m). We then calculated total areas and corresponding percentages of 13 vegetation classes within each zone. Vegetation classes included managed stands, subclasses of late-seral forests, unproductive forestlands, and nonforest lands (United States Department of Agriculture Forest Service 1997; Fig. 3). To further evaluate if flying squirrels selected dens in less-fragmented portions of neighborhoods, we also calculated 5 fragmentation indices (mean patch size, mean patch edge, perimeter/area ratio, mean shape index, and mean fractal dimension [FRAGSTATS software—McGarigal and Marks 1995]) in each zone using a geographic information system and the software V-LATE (University of Salzburg, Salzburg, Austria).

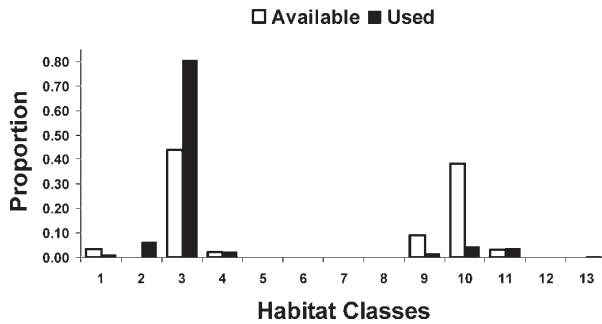


FIG. 3.—Proportions of vegetation classes (rain-forest volume classes or cover types) within 0.338-ha circular zones around den sites (used) and random (available) sites in highly modified landscapes of coastal temperate rain forest, Prince of Wales Island, Alaska, 2004–2006. Vegetation classes are as follows: 1 = productive old-growth, 184–294 m³/ha; 2 = productive old-growth, 166–187 m³/ha, >50% hydric soils; 3 = productive old-growth, 166–187 m³/ha, nonhydric soils; 4 = productive old-growth, 109–135 m³/ha, southerly aspect; 5 = productive old-growth, 109–135 m³/ha, northerly aspect; 6 = productive old-growth, 109–135 m³/ha, hydric soils; 7 = unproductive forest muskeg, <45 m³/ha; 8 = all other unproductive forests, <45 m³/ha; 9 = young growth (<25 years); 10 = 2nd growth (<25 years); 11 = water; 12 = nonforested muskeg; 13 = all other nonforest conditions.

Statistical analyses.—We used conditional logistic regression (Hosmer and Lemeshow 1989) to identify microhabitat attributes that best predicted den-site use by northern flying squirrels (Bakker and Hastings 2002). Conditional logistic regression facilitated a multivariate analysis of differences between treatment and control conditions that are spatially matched, an approach used by Bakker and Hastings (2002) to study den selection by this species in more-intact rain-forest landscapes. All variables were screened for collinearity using a pairwise correlation matrix with a removal threshold of $r > 0.7$. We ran conditional logistic regression in SPSS 12.0 (SPSS, Inc., Chicago, Illinois), using a forward stepwise selection with P (entry) = 0.05 and P (removal) = 0.1 (Bakker and Hastings 2002). We conducted 3 separate regressions: all den trees (i.e., internal and external den sites) versus all available trees (i.e., snag and live); snag den trees versus only available snags; and all live trees versus only available live trees. For each of the 3 final models we reran each model with all significant main terms and “distance to edge” interaction terms to determine if the microhabitat of dens varied relative to proximity to edge.

In modeling microhabitat selection we made at least 3 assumptions that potentially influenced our findings. We treated all den-site locations as independent observations, despite some locations being used by multiple individuals. Second, because sample sizes were inadequate to consider potentially different life-history needs that are specific to seasons or age or sex groups, we pooled den-use observations across seasons and years for all age and sex groups, effectively assuming that the denning needs of all flying squirrels are

similar year-round. We acknowledge this assumption is naïve, because previous studies have clearly illustrated that adult females have more stringent den requirements than males, especially during the spring (Carey et al. 1997; Holloway and Malcolm 2007; Smith 2007). Although pooling could have caused us to underestimate the importance of a microhabitat characteristic to a particular age class, sex class, or season, it is unlikely pooling inflated the importance of any characteristics we did find to be important: we pooled data from approximately equal ratios of sex classes, age classes, and seasons. Finally, we assumed that individuals were denning in cavities when no evidence of external nests in live trees was found. We acknowledge that instances of misclassification have occurred, especially if the presence of bark or branches obscured visibility of the upper bole. However, because of the criteria and categories used to classify dens, we believe that opportunities for misclassifying dens were few (only live trees).

To compare habitat composition between used and random sites at the broader spatial scale, we used a chi-square goodness-of-fit test to analyze overall differences and partial chi-square values to compare specific vegetation categories (Zar 1999). We used 1-way analysis of variance to contrast fragmentation indices between used and random sites. We accepted $P \leq 0.05$ as criterion for statistical significance. We present mean values with 95% confidence intervals (CIs) parenthetically, except in reference to diameter at breast height, for which we report median values to allow more direct comparison to median values reported for this variable in Bakker and Hastings (2002).

RESULTS

We instrumented and monitored 10 adult and 20 juvenile females and 22 adult and 12 juvenile males for a total of 118 den locations. Of these, 47 individuals had ≥ 2 den locations and were included in our analysis of space use and movements, which varied among age and sex groups (Table 1). Juvenile core den areas were almost an order of magnitude larger than those of adults, and males generally exhibited larger core den areas than females. Female juveniles exhibited both the largest mean and maximum movements between dens, with no other differences between other age and sex classes with respect to these 2 parameters. Juveniles averaged about half as many dens per month as adults, with no difference between sexes (Table 1).

Overall, we found indirect evidence that 93% of den locations were in cavities composed of either snags (51% of total) or live trees that lacked signs of external drays (42%); <5% of dens occurred in live trees with observable drays or in belowground locations (Fig. 4). Mean height of dens in snags was 11.3 ± 2.6 m (mean \pm 95% CI), whereas mean height in live trees was 19.7 ± 3.5 m. Western hemlock was the predominant species of live tree used, but western red cedar received much greater use than expected from its availability (Table 2).

TABLE 1.—Sex- and age-specific movement parameters associated with den use among radiocollared northern flying squirrels (*Glaucomys sabrinus griseifrons*) on Prince of Wales Island, Alaska, 2004–2006.

	Females		Males	
	Adult (n = 2)	Juvenile (n = 19)	Adult (n = 19)	Juvenile (n = 7)
Core den area (ha)				
\bar{X}	0.23	5.45	1.64	14.37
$\pm 95\%$ CI	0.44	4.49	0.97	16.28
Den movement (m)				
\bar{X}	116.94	367.16	195.80	118.32
$\pm 95\%$ CI	9.78	434.65	60.46	78.41
Maximum movement (m)				
\bar{X}	178.20	649.64	234.40	224.12
$\pm 95\%$ CI	129.85	867.56	71.73	176.45
Frequency (dens/month)				
\bar{X}	6.06	3.70	7.14	3.54
$\pm 95\%$ CI	1.19	1.03	3.45	1.43

All 3 microhabitat regression analyses produced significant models (Table 3). In the model that included all trees (live and snags), the presence of snags was not a significant selection variable, but diameter at breast height and prevalence of conks were positive correlates of den sites. Median diameter at breast height of den trees was approximately 20–30 cm greater than a random sample of trees in the same stands. About 30% of den trees had conks, whereas 11% of trees in the random sample had conks. In the snag model diameter at breast height and presence of decay (notably classes 1–) were positive correlates of snags selected as den sites. Median diameter at breast height of used snags was approximately 20 cm greater than a random sample. The greatest disparity in prevalence of decay between used and available snags occurred with decay classes 1 and 3 (Table 3). Diameter at breast height also was a positive correlate of live trees used as dens; the median diameter at breast height of live den trees was >30 cm greater than a random sample. A greater proportion of live den trees had bole entries than did available live trees (Table 3).

Distance from den trees to the nearest edge was not a significant factor in den-tree selection (Table 3); however, habitat composition at broader spatial scales did influence den selection (Fig. 3). Generally, habitat composition around den trees differed from what was available in the den neighborhood ($\chi^2_{12} = 96.00$, $P < 0.001$). Specifically, areas around den trees had a greater proportion of higher volume forest (hydric soils: $\chi^2_1 = 43.40$, $P < 0.001$; nonhydric soils: $\chi^2_1 = 12.60$, $P < 0.001$), and a smaller proportion of young ($\chi^2_1 = 7.00$, $P < 0.01$) and older ($\chi^2_1 = 31.10$, $P < 0.001$) 2nd growth than randomly chosen areas within the den neighborhood. Furthermore, areas around den trees differed significantly in degree of fragmentation than available areas in the den neighborhood (Table 4). Mean patch size was greater and perimeter/area ratio of patches was lower in areas around den trees than randomly chosen areas, although the mean length of

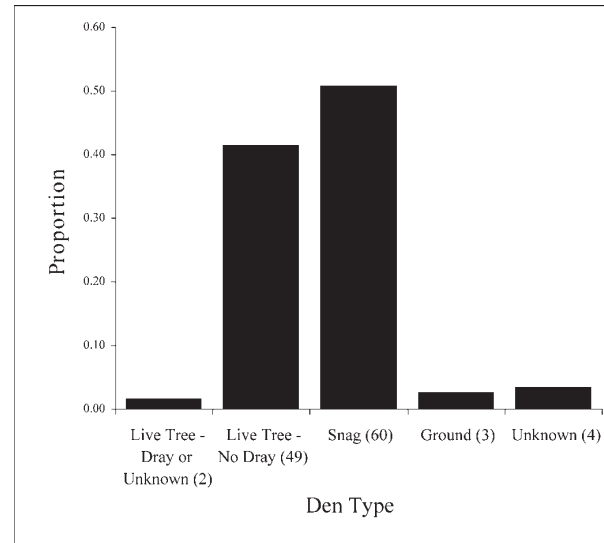


FIG. 4.—Proportion of different den types among all den locations ($n = 118$) of flying squirrels on Prince of Wales Island, Alaska, 2004–2006. Numbers in parentheses denote sample size.

edge between habitat and nonhabitat was higher in den areas. The 2 indices of shape complexity—shape index and fractal dimension—were both lower in areas around den trees than randomly chosen areas.

DISCUSSION

Our study is the 1st to examine den use by northern flying squirrels within insular habitat patches in a highly fragmented landscape (Smith 2007). Our predictions that mean distance and maximum distance between consecutive dens in highly modified landscapes would be smaller and larger, respectively, than in less-fragmented forests were not supported, at least for adults (Table 1). Furthermore, our results indicate that individuals in different age and sex groups varied significantly in den fidelity and movements among dens. Adult flying squirrels used more den trees, despite moving shorter distances between dens and occupying smaller core den areas, than juveniles. Females had smaller core den areas (Cotton and Parker 2000) and averaged shorter movements between consecutive dens than males. Typically, distance moved between dens is highly variable (Cotton and Parker 2000; Hackett and Pagels 2003), although usually smaller for females than males, and can be as great as 1 km (Carey et al. 1997; Meyer et al. 2005). In our study distance moved between dens fell within the range of values reported for adult northern flying squirrels in other portions of its range (Smith 2007). However, core den areas of adults were smaller and less varied than that reported for other portions of this species' range (Smith 2007). Although less striking, adult males had smaller core den areas (1.6 ha) than values elsewhere in western North America (e.g., Alberta, Canada, 2.7 ha [Cotton

TABLE 2.—Characteristics of 111 snag and live-tree dens and up to 10 available trees (≥ 45 -cm diameter at breast height) within a 30-m plot centered on the den tree, Prince of Wales Island, Alaska, 2004–2006 (dash denotes no data). 4

	Live trees		Snags	
	Den trees ($n = 51$)	Available trees ($n = 834$)	Den trees ($n = 60$)	Available trees ($n = 326$)
Median diameter, cm (95% CI) ^a	101 (86–113)	73 (72–77)	93 (80–108)	73 (70–78)
Species				
Western hemlock	53 (40–66)	48 (44–52)	—	—
Alaska-cedar	2 (0–5)	0.1 (0–2)	—	—
Western red cedar	36 (24–49)	14 (10–18)	—	—
Sitka spruce	9 (1–17)	8.9 (7–11)	—	—
Unknown	0	29 (26–32)	—	—
Other features				
Bole entries	—	—	61 (48–75)	47 (42–52)
Broken top	—	—	92 (84–100)	93 (90–96)
Conks	—	—	61 (48–75)	38 (33–43)
Scars	—	—	33 (20–46)	33 (28–38)
Dead top	13 (4–22)	—		
Epiphytes				
None	6 (0–11)	30 (27–34)		
Light	38 (25–50)	26 (22–30)		
Medium	36 (23–48)	30 (26–34)		
Heavy	20 (9–30)	14 (10–17)		
Mistletoe				
None	98 (92–100)	99 (97–99)		
Light	0	1 (1–2)		
Medium	2 (0–5)	0		
Heavy	0	0		
Decay class				
1 (least)			6 (0–9)	3 (1–5)
2			8 (0–16)	6 (4–9)
3			34 (19–45)	17 (13–21)
4			48 (34–62)	48 (42–53)
5 (most)			4 (0–9)	27 (22–32)

^a All values but median diameter are expressed as % (95% CI).

and Parker 2000]; and California, 2.2 ha [Meyer et al. 2005]). We included animals with fewer den-tree locations in our analysis of core den areas than Cotton and Parker (2000) and Meyer et al. (2005), who used only animals with ≥ 10

observations. However, it is unlikely that this explains the difference in core den area between studies because their studies were of shorter duration (<5 months) and occurred during periods of lower activity (e.g., winter).

TABLE 3.—Correlates of northern flying squirrel (*Glaucomys sabrinus griseifrons*) den trees ($n = 111$) using forward stepwise selection conditional logistic regression ($P = 0.05$ to enter and $P = 0.10$ to remove). $\text{Exp}(\beta)$ is the exponential of the regression coefficient; >1.0 means the odds of the response variable increases, and <1.0 means the odds decrease, with an increase in the variable. Tree attributes and sampling procedures followed Bakker and Hastings (2002).

Models and variables	β	SE	Wald statistic	<i>df.</i>	<i>P</i>	$\text{Exp}(\beta)$
All used relative to all available trees						
Diameter at breast height	0.03	0.00	58.74	1	<0.001	1.03
Conk	1.44	0.25	32.98	1	<0.001	4.22
Used relative to available snags						
Diameter at breast height	0.03	0.01	15.46	1	<0.001	1.03
Decay class			14.86	4	0.005	
1	4.82	1.41	11.67	1	0.001	123.50
2	2.48	1.09	5.18	1	0.023	11.87
3	2.94	0.89	10.88	1	0.001	18.91
4	2.91	0.87	11.13	1	0.001	18.29
Used relative to available live trees						
Diameter at breast height	0.02	0.00	30.49	1	<0.001	1.02
Bole	13.30	147.23	0.01	1	0.928	374.94

TABLE 4.—Mean (95% CI) fragmentation indices (McGarigal and Marks 1995) of used den ($n = 145$) and random ($n = 60$) locations on the landscape occurring in the study area. One-way analysis of variance was used to test for significant differences between location types.

Index	Used	Random	<i>F</i>	<i>df.</i>	<i>P</i>
Mean patch size (m ²)	56,254.39 (± 29,054.38)	41,464.69 (± 48,251.42)	26.22	1, 203	<0.00001
Mean patch edge (m)	910.45 (± 180.21)	815.41 (± 554.87)	12.99	1, 203	<0.0001
Perimeter/area ratio	0.02 (± 0.06)	0.04 (± 0.09)	25.98	1, 203	<0.0001
Mean shape index	1.11 (± 0.01)	1.28 (± 0.06)	39.65	1, 203	<0.00001
Mean fractal dimension	1.25 (0.20)	1.30 (0.20)	41.40	1, 203	<0.005

Conversely, juveniles (especially males) in our study had core den areas that were an order of magnitude larger than those of adults and larger than any sex-specific values reported for the species (Smith 2007). Core den areas of juvenile males in our study were larger than the average home-range (core den area + foraging areas) values reported for this species in many other portions of its range (Smith 2007). The cause of this striking difference between adults and juveniles is unclear, but we suspect it may be related to social interactions with adult residents or the exploratory behavior of young squirrels preparing for natal dispersal (Selonen and Hanski 2006). Nevertheless, despite moving greater distances encompassing larger areas, juveniles in our study used half as many den trees per month as adults (Table 1), suggesting that young squirrels undertook relatively long-distant forays into new areas but returned to familiar sites for denning. The extent to which this phenomenon was influenced by the highly modified nature of the habitat is uncertain, but warrants further investigation.

Mean number of den trees per month for adults in our study also was greater than typical values reported for the species across its range. Within a population number of nest trees used regularly by individuals can vary from 1 to 11 (Mowrey and Zasada 1984), but the mean number used per month (range 2.3–4.8) is similar between males and females, and differences throughout its range are relatively minor (Carey et al. 1997; Cotton and Parker 2000; Hackett and Pagels 2003; Menzel et al. 2004; Meyer et al. 2005; Smith 2007). Bakker and Hastings (2002) did not report mean number of dens used per month, but recorded 76 unique den sites with ≥ 1 den for 27 individuals, or a study-wide average of 2.8 dens per squirrel. Nonetheless, the evidence from our study suggests that adult northern flying squirrels in highly fragmented landscapes used more den trees, despite moving shorter distances between dens and occupying smaller den core areas. Whether this behavior is intended to reduce the risk to predation in circumstances where flying squirrels are restricted to relatively small habitat patches or a consequence of social interactions remains unclear but warrants further investigation because of the importance of suitable cavities to reproductive females (Carey et al. 1997) and the carrying capacity of managed forests (Smith 2007; Witt 1991).

Overall, 93% of dens were in snags or in live trees without obvious signs of external structures (i.e., drays), suggesting that flying squirrels in our study primarily used cavities. Because we relied on visual indicators of dray occurrence in live trees, it is possible that we missed smaller drays, drays near the bole, or drays in the extreme upper portion of the

>50-m canopy and consequently overestimated the use of cavities in live trees. However, the results of our logistic regression analyses indicated that flying squirrels selected not only the largest live trees but live trees with observable cavity entrances, further evidence that cavities were the preferred denning structure. Regardless, even a moderately high level of cavity use is counter to what we predicted. Because of the substantial overall reduction in large, old trees from 4 decades of logging, we anticipated that cavities would be much less available and flying squirrels would be forced to use external nests (Carey et al. 1997; Smith 2007). Rather, the undocumented use of external dens and lack of any apparent selection for snags (and associated cavities) suggest that cavities were readily available, even in the small and insular habitat fragments comprising our study area.

The general pattern of den use in our study was similar to that reported for populations in larger and less isolated stands of comparable habitat ~50 km north of our study area (Mitkof Island) where flying squirrels were more likely to use cavities as dens than external nests, and 60% of den locations (compared to 51% in our study) were in snags (Bakker and Hastings 2002). One striking difference was that Bakker and Hastings (2002) reported that 27% of dens might have been external structures, but only 2% of dens in our study were possibly external. The putative lower frequency of external nest use in our study can be explained partially by apparent differences in snag availability. The study area on Mitkof Island included a greater proportion of fens (forested peatlands), which occur on poorly drained sites (Neiland 1971) and in which snags are probably less common than in the closed-canopy old-growth habitats of our study area (DeMeo et al. 1992). Alternatively, red squirrels (*Tamiasciurus hudsonicus*), which were absent from our study area but common on Mitkof Island (W. P. Smith, pers. obs.) likely compete with flying squirrels for cavities. Red squirrels have been observed aggressively chasing flying squirrels in old-growth stands on Mitkof Island (V. Bakker, University of California Santa Cruz, pers. comm.), and Douglas's squirrels (*Tamiasciurus douglasii*) have displaced flying squirrels from cavities in similar habitat in Washington (T. Wilson, United States Forest Service, pers. comm.).

Flying squirrels that denned in live trees predominantly used western hemlock, a species that is widespread in Southeast Alaska. This also was true of flying squirrels on Mitkof Island, but to a much greater extent (73%—Bakker and Hastings 2002). That flying squirrels commonly used western hemlock for denning is not surprising because about 50% of

the old-growth trees are infected with decay-causing fungi that cause heartrot (Farr et al. 1976; Kimmey 1956), which increases the ease with which primary cavity-nesting species can excavate a bole entry. Why flying squirrels in our study used western hemlock nearly 33% less frequently than on Mitkof Island is less clear, but it might be related to the distribution of western red cedar, the 2nd-most frequently used and preferred (i.e., used more often than expected from availability) live tree species in our study area. The northern limit of western red cedar is reputedly south of the study area of Bakker and Hastings (2002) on Mitkof Island (Pojar and Mackinnon 1994). Another factor possibly contributing to the lower attractiveness of western hemlock on Prince of Wales Island is the decreasing incidence of heartrot with decreasing latitude (Farr et al. 1976). Nonetheless, we suspect that if western red cedar was available further north it would be used frequently for denning because $\geq 87\%$ of the old-growth trees are infected with heartrot (Kimmey 1956).

We also were surprised at one additional finding pertaining to den selection at the microhabitat level. Because our study area experienced extensive clear-cut logging for >50 years, we anticipated that the mean size of den trees would be smaller than in largely unmanaged landscapes. However, the median diameters of both live and snag den trees in our study were larger than those reported for flying squirrels on Mitkof Island (Bakker and Hastings 2002). Thus, for some reason other than availability, flying squirrels on Mitkof Island, many of which were captured in high-volume old growth, selected lower volume stands for denning (Bakker and Hastings 2002). It seems unlikely that this pattern is related to habitat differences in the abundance of cavities, because large tree and snag densities are substantially higher (order of magnitude) in old-growth stands as compared to lower-volume fens and mixed-conifer habitats (Smith et al. 2004). Alternatively, red squirrels, a highly territorial species (Smith et al. 2003), may aggressively displace flying squirrels from high-volume old-growth stands. High-volume old-growth reputedly is the primary habitat of red squirrels because of interlocking canopies and the codominance of Sitka spruce, the source of this species' likely staple food resource (Smith et al. 2003).

Because exposure to inclement weather (Concannon 1995) and predation pressure (Wilcove 1985) can be higher along edges, and because managed habitats along edges can limit access and reduce options for dispersal, foraging, or mate seeking, or a combination of these (Selonen and Hanski 2003, 2004, 2006), we expected that flying squirrels would den farther into the interior of forest patches. But the evidence from our study pertaining to the effects of fragmentation on den-site selection was mixed. Flying squirrels did choose to den in areas with larger habitat patches in which the proportion of interior forest habitat was relatively greater and forest cover was more continuous than typically occurs across this landscape. However, we found that distance to an edge was not a factor influencing selection of den microhabitat, and flying squirrels denned in areas with greater absolute amounts of edge than what was available across the landscape.

Ritchie (2006) reported that the distribution and abundance of flying squirrels at multiple spatial scales in fragmented landscapes were largely independent of landscape configuration. Likewise, Desrochers et al. (2003) found that nests of the Siberian flying squirrels (*Pteromys volans*) were closer to edges than expected. In our study area an apparent indifference to high-contrast elements also was reflected in the manner flying squirrels traveled across fragmented landscapes. Radiocollared individuals moved through linear old-growth remnants with a high edge-to-area ratio (e.g., 150-m-wide riparian buffers) at rates nearly equivalent to those in more-interior old-growth forest (S. Pyare, pers. obs.). Nonetheless, the consistent association of den sites with lower levels of fragmentation (excluding measures of absolute amounts of edge) suggests that the spatial configuration of habitats might affect den selection at broader scales and thus warrants further investigation.

Conservation implications.—The northern flying squirrel is an appropriate species to consider for landscape planning efforts and reserve design in coniferous forest ecosystems because several aspects of its life history are linked to forest structure and because it is susceptible to isolation in fragmented landscapes with a matrix of early-seral forests. The northern flying squirrel prefers large, old trees and snags for denning, and adult females depend on cavities for reproduction. Furthermore, because the probability of persisting in isolated old-growth fragments is not very high, the viability of flying squirrels in managed landscapes likely will depend upon a network of habitat patches with sufficient quality to support breeding individuals whose offspring can move freely through the matrix. Four decades of intensive clear-cut logging in Southeast Alaska has significantly altered the composition of productive temperate rain forest, removing about half of the low-elevation (<400 -m) old-forest vertical structure, dramatically decreasing the availability of suitable denning sites and food resources, and fragmenting most of the remaining habitat. Because less-accessible small fragments of high-volume old-growth forest are less attractive as sites for future timber sales, remnant patches of primary habitat potentially can play a crucial role in future conservation planning to sustain viable flying squirrel populations in highly fragmented landscapes. Our findings suggest that small patches of old-growth forests and individual legacy structures, even if dispersed, are occupied and used as den sites by *G. s. griseifrons*.

That northern flying squirrels in a heavily fragmented landscape were apparently all able to use cavities for denning is encouraging but underscores the importance of old-growth remnants in contributing essential habitat to populations in managed landscapes. Portions of the surrounding landscape that were clear-cut logged will require 200–300 years beyond canopy removal to develop old-forest structure, unless actively managed. Restoring old-forest structure, especially large trees or snags, is fundamental to sustaining female productivity and overall population density because of the reliance upon cavities as natal dens.

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