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Estimated persistence of northern flying squirrel populations in temperate rain forest fragments of Southeast Alaska

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ABSTRACT

Habitat reserves are a common strategy used to ensure viability of wildlife populations and communities. The efficacy of reserves, however, is rarely empirically evaluated. We examined the likelihood that small (650 ha), isolated habitat reserves composed of old-growth Sitka spruce (Picea sitchensis)–western hemlock (Tsuga heterophylla) rain forest (upland-OG) and mixed-conifer peatlands (peatland-MC) would sustain populations of northern flying squirrels (Glaucomys sabrinus) in the absence of immigration or emigration within the Tongass National Forest in Southeast Alaska. We used demographic data obtained from a study of flying squirrels on Prince of Wales Island in Southeast Alaska and litter size from flying squirrels in similar habitat to estimate per capita rate of increase (r) of flying squirrels in upland-OG ($r = 0.14$, SD = 0.42) and peatland-MC habitats ($r = 0.01$, SD = 0.39). Our results indicated that peatland-MC habitat was unlikely to sustain populations and that viability of flying squirrel populations in small habitat reserves largely depended on the upland-OG forest component. We subsequently estimated time to extinction (T_N) based on r, its variance (v), and the potential population ceiling (K). We used T_N to calculate the probabilities (P_t) that squirrel populations would persist in small reserves containing 100%, 50%, and 25% upland-OG habitat for 25, 50, and 100 years. In each scenario, we calculated T_N and P_t for 2 levels of v. For the best-case scenario (100% upland-OG forest, lowest variance, $t = 25$ years), T_N was 507 years and P_t was 0.95. For the worst-case scenario (25% upland-OG forest, highest variance, $t = 100$ years), T_N was 237 years and P_t was 0.66. Minimum patch size of upland-OG forest required for a high probability ($P_t = 0.95$) of sustaining a flying squirrel population in isolation with relatively low demographic variability ($v = 0.34$) for 25, 50, or 100 years was 578, 5077, and 78,935 ha, respectively. We concluded that it was unlikely that small isolated habitat reserves could sustain populations of flying squirrels for >25 years in the absence of immigration. Consequently, dispersal among small reserves is critical to ensure that they function to support metapopulations of northern flying squirrels.

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1. Introduction

Viability of wildlife populations and biological diversity are important land management issues for public (Thomas, 1991; Possingham et al., 1993; Marcot and Murphy, 1996; Iverson and Rene, 1997) and industrial lands (Smith and Pashley, 1994; Bullock and Wall, 1995; Lindenmayer and Possingham, 1996) because wildlife species are valued by many segments of society (Catton and Mighetto, 1998; Leopold, 1933; Naess, 1986), and because the persistence of wildlife at 'ecologically effective' densities (sensu Soulé et al., 2003, p. 1239) is a crucial component of healthy ecosystems (Gilbert, 1980; Petchey, 2000; Pimm, 1991; Pyare and Berger, 2003; Soulé et al., 2003). Fragmentation and loss of habitats are associated with the rapid decay of ecological and evolutionary diversity worldwide (Reed, 2004). Indeed, habitat loss has been implicated as a causal factor in declines of 83% and 89% of all threatened birds and mammals, respectively (Pereira et al., 2004). Undoubtedly, global demands for natural resources will increase and land managers will experience greater and more complex challenges to safeguarding biological diversity and ecosystem functions and services (Newton and Freyfogle, 2005a; Newton and Freyfogle, 2005b; Smith and Zollner, 2005).

The conservation of northern flying squirrel (Glaucomys sabrinus) populations in temperate rain forests of Southeast Alaska may represent one such challenge. The northern flying squirrel is a small (<200 g), forest dwelling, arboreal rodent that relies on gliding as its primary (and perhaps exclusive) means of travel (Wells-Gosling and Heaney, 1984; Scheibe et al., 2006). Flying squirrels are abundant and widely distributed within forested portions of the region (Smith, 2005). Smith and Nichols (2003) reported that spring population densities of squirrels on Prince of Wales Island averaged 1.80 squirrels/ha in upland old-growth forest and 1.15 squirrels/ha in peatland-scrub/mixed-conifer forest. Like flying squirrels elsewhere (e.g., Pteromys volans), G. sabrinus may be sensitive to industrial-scale harvesting of timber that eliminates mature forest across landscapes (Hanski et al., 2000; Hokkanen et al., 1982). Such disturbances fragment continuous populations into isolated patches (Gilpin, 1996) that, if unchecked, can ultimately lead to extirpation of flying squirrels from an entire region (Hokkanen et al., 1982).

Southeast Alaska (i.e., Alexander Archipelago and narrow mainland panhandle) contains the largest intact temperate rain forest in North America and one of the largest in the world. This region includes about 2.7 million ha of glaciers and rocky mountain peaks, 2 million ha of scrub forests and peatlands, and 2.0 million ha of commercially valuable old-growth forest (USDA Forest Service, 2003, pp. 3–43). The island topography naturally fragments much of the forest among >20,000 islands that range in size from 0.5 ha to 6700 km^2 (USDA Forest Service, 1997). Approximately 160,000 ha of the most productive forest stands have been clearcut logged (USDA Forest Service, 2003: 3–43), prompting concerns about the cumulative effects of timber harvests on forest plant and animal communities and sustainability of ecosystem functions and services (Everest et al., 1997; Shaw, 1999). To address those concerns, the US Forest Service revised the Tongass Land Management Plan (TLMP) in 1997 to include a conservation strategy designed to sustain terrestrial wildlife communities in an integrated system of large ($\geqslant$16,200 ha), medium ($\geqslant$4050 ha), and small ($\geqslant$650 ha) old-growth forest reserves (USDA Forest Service, 1997, K-1). The strategy includes 30.5 m wide riparian buffers, which if wind firm over the planning horizon, might provide some connectivity between old-growth reserves. Those reserves are expected to support viable populations of forest-dependent species either within individual reserves or among a collection of reserves that sustain a metapopulation structure (sensu Hanski and Gilpin, 1991; USDA Forest Service, 1997, N-16; Flynn et al., 2004).

To monitor the effectiveness of the OGR strategy, the northern flying squirrel was proposed as one of several management indicator species (Suring, 1993) because its abundance may reflect old-growth forest condition (Carey, 1989, 2000; Carey et al., 1999) and because of specific habitat requirements for efficient locomotion (Scheibe et al., 2006). Its small size and home range make it particularly well suited for evaluating the effectiveness of small OGRs. Our objective was to evaluate the potential of individual small OGRs to sustain breeding populations of flying squirrels. Two habitat types predominate in most OGRs: upland old-growth forest (upland-OG) and mixed-conifer peatlands (peatland-MC). Upland old-growth forest is ostensibly the primary habitat for flying squirrels; however, Smith and Nichols (2003) observed relatively high densities of squirrels in peatland-MC on Prince of Wales Island and concluded that peatland-MC habitat may be capable of sustaining flying squirrel populations. We evaluated the potential contribution of each of these habitats to population viability using demographic data obtained from live trapping studies in both habitats. We then estimated time to extinction (T_N) and probability of persistence (P_t) for flying squirrel populations occupying small OGRs composed of different proportions of upland-OG and peatland-MC habitats. Specifically, we addressed the following questions:

1. Can peatland-MC habitat support viable squirrel populations in isolation given demographic rates observed by Smith and Nichols (2003)?
2. Are flying squirrels likely to persist in isolation over periods of 25, 50, or 100 years in small OGRs composed of (a) exclusively upland-OG, (b) exclusively peatland-MC, (c) a mixture of upland-OG and peatland-MC consistent with TLMP guidelines for the 'preferred' habitat objective of small OGRs, or (d) a mixture of upland-OG and peatland-MC consistent with TLMP guidelines for the 'minimum' habitat objective of small OGRs?
3. How sensitive is 'persistence' of flying squirrel populations isolated in small OGRs to variance in r compared with population size?
4. What is the size and habitat composition of an isolated OGR needed to achieve 85%, 90%, and 95% probability of persistence (i.e., range of relatively high probabilities that land managers might consider regarding the risk of policy decisions) for periods of at least 25, 50, and 100 years?

Thus, our analysis modeled the dynamics of northern flying squirrel populations occupying isolated fragments in a matrix of unsuitable habitat.

2. Methods

2.1. Study area

The Tongass National Forest encompasses 6.8×10^6 ha of Southeast Alaska (USDA Forest Service, 1997). The region is unique with many naturally fragmented landscapes, a dynamic geological history (MacDonald and Cook, 1996), and coastal temperate rain forest (Alaback, 1982; Harris and Farr, 1974). It has a cool, wet (200–600 cm precipitation) maritime climate; mean monthly temperatures range from 13 °C in July to 1 °C in January (Searby, 1968). Coniferous rain forests are distributed among islands of the Alexander Archipelago and along the narrow mainland, which is essentially isolated from the interior of North America by mountains, glaciers, and ice fields. Topography, geology, climate, and other environmental features create a variety of isolated habitats on islands and the mainland; spatial heterogeneity occurs at multiple spatial scales in a manner rarely found elsewhere (MacDonald and Cook, 1996). The movement of non-volant vertebrates among islands or between the mainland and islands is uncommon and likely contributes to the nested structure and varied composition of mammal assemblages across the region (Conroy et al., 1999). Fragmentation of natural forest habitats has increased substantially since the mid-20th century because of extensive clearcut logging throughout the region (USDA Forest Service, 1997; USDA Forest Service, 2003).

We obtained demographic data from a study of flying squirrels located on north-central Prince of Wales Island (Smith and Nichols, 2003). Four decades of intensive logging in the study area created an ideal setting for examining the dynamics of *G. sabrinus* populations among old-growth forest remnants in a matrix of young (<50 years old) managed forest habitats. The study included sites that were largely in unmanaged patches within logged landscapes. These patches were composed of two common forest habitats that reflect the range of canopy and forest structure in temperate rain forests of Southeast Alaska: upland-OG and peatland-MC (Harris and Farr, 1974; Smith et al., 2005).

Upland-OG comprised several plant associations of Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forests (DeMeo et al., 1992) and to a lesser extent yellow cedar (*Chamaecyparis nootkatensis*) and red cedar (*Thuja plicata*). The *Tsuga-Picea* forest type constituted most of the closed-canopy forests in the region and included riparian forests as well as upland sites (Alaback, 1982; Harris and Farr, 1974). Typically, upland-OG had an uneven-aged multi-layered overstory, dominant trees >300 years old, and extensive structurally diverse understories with dense patches of *Vaccinium* (Alaback, 1982; DeMeo et al., 1992; Harris and Farr, 1974; Ver Hoef et al., 1988). Stands were spatially heterogeneous at a scale of <1 ha (Schoen et al., 1984), occurred on low elevation (<500 m), well-drained sites, often as a mosaic with muskegs (peatlands), and had a closed canopy of tall (>60 m), large (⩽2.5 m diameter) trees (Alaback, 1982; Harris and Farr, 1974).

Peatland-MC habitat differed markedly from upland-OG, especially the patchiness of dense forest canopy cover, which was a consequence of highly variable soil composition and moisture gradients (Neiland, 1971). It was heterogeneous at a scale of tens of meters – a complex of open- to sparsely-canopied muskegs intermixed with patches of mixed-conifer vegetation that occur on gently sloping, elevated accretions of better-drained, mineral soil (Neiland, 1971; DeMeo et al., 1992). Conifer vegetation included yellow cedar, red cedar, western hemlock, shore pine (*Pinus contorta* var. *contorta*) and mountain hemlock (*Tsuga mertensiana*). Understory vegetation varied considerably. Open areas with little overstory typically were comprised of a mixture of herbaceous and woody species, including sedges, grasses, skunk cabbage (*Lysichitum americanum*) and Labrador tea (*Ledum glandulosum*); blueberry dominated areas with well-developed overstories.

2.2. Habitat composition of small old-growth reserves

To meet biological objectives of the old-growth reserve strategy, TLMP stipulates that ⩾16% of the total acreage ($\bar{x} = 4050$ ha) in Visual Comparison Units (i.e., major watersheds) be retained in undeveloped condition, which on the Tongass National Forest averaged ≈650 ha (i.e., 0.16×4050 ha; USDA Forest Service, 1997). If not met by other prescriptions, then at least 16% of the watershed (i.e., 650 ha) must be set aside as a small OGR. The 'preferred' biological objective is for each small OGR to contain ⩾325 ha (i.e., 50% of small OGR) of contiguous, productive old growth (upland-OG with >27,000 board-feet/acre; Julin and Caouette, 1997). In watersheds <2025 ha reserves may contain a 'minimum' of 162.5 ha (i.e., 50% of 0.16×2025) of upland-OG (USDA Forest Service, 1997, K-2). Composition of the remaining acreage in each small OGR for preferred or minimum options is unspecified. We examined four scenarios of small OGR habitat composition: (a) 100% upland-OG forest; (b) 100% peatland-MC; (c) 50% upland-OG forest and 50% peatland-MC ('preferred' objective); and (d) 25% upland-OG forest and 75% peatland-MC ('minimum' objective).

2.3. Population dynamics and persistence in small old-growth reserves

To evaluate the potential for small OGRs to sustain populations independently, we estimated average per capita rates of increase (r) in the absence of immigration or emigration. We constructed a simple birth–death (b–d) process model for northern flying squirrel populations in both upland-OG and peatland-MC habitats:

$$r = b - d, \tag{1}$$

where b = percent females in population × percent females reproducing × average litter size, and d = percent of total population dying annually. We used live trapping data obtained between 1999 and 2001 from Prince of Wales Island (Smith and Nichols, 2003) to estimate means and standard deviations for annual proportions of females in the populations, proportions of females breeding, and rates of mortality for squirrels in each habitat type (Table 1). Smith and Nichols (2003) reported no differences between years in those rates, therefore

Table 1 – Parameter estimates used in Monte Carlo simulations of our birth–death model to estimate per capita rate of increase (r) for northern flying squirrels (Glaucomys sabrinus) occupying upland old-growth (upland-OG) and peatland-scrub/mixed-conifer (peatland-MC) rain forests, Southeast Alaska, USA, 1999–2001

Parameter	Habitat	
	Upland-OG $\bar{x}$ (SD)	Peatland-MC $\bar{x}$ (SD)
Litter size[a]	2 (1)	2 (1)
Percent females in the population[b]	0.45 (0.04)	0.37 (0.05)
Percent females reproductive[b]	0.76 (0.06)	0.76 (0.07)
Annual mortality rate[b]	0.53 (0.10)	0.54 (0.15)

a Villa et al. (1999).
b Smith and Nichols (2003).

Table 2 – Parameter estimates used in models to predict times to extinction for flying squirrels (Glaucomys sabrinus) in upland old-growth (upland-OG) and peatland-scrub/mixed-conifer (peatland-MC) rain forests, Southeast Alaska, USA

Parameter	Habitat	
	Upland-OG	Peatland-MC
r[a]	0.14	0.01
Low v[b]	0.34	0.22
High v[c]	0.39	0.39
Density (squirrels/ha) at carrying capacity (K)[b]	2.80	1.90

a Results from Monte Carlo simulations of birth–death model.
b Smith and Nichols (2003).
c Fryxell et al. (1998).

we pooled the data across years. Average litter size and its standard deviation were obtained from data (1993–1997) for northern flying squirrels in the Puget Trough of Washington (Villa et al., 1999) and used for flying squirrels in both habitats (Table 1). We simulated our birth–death model for northern flying squirrel populations in upland-OG and peatland-MC rain forests using Monte Carlo techniques where parameters were sampled repeatedly from normal distributions defined by their means and standard deviations. We performed 4000 simulations of the birth–death model to estimate the average value of r in each habitat.

Substantial empirical evidence indicates that northern flying squirrels exhibit density-dependent population growth (Fryxell et al., 1998; Lehmkuhl et al., 2006). Consequently, we estimated T_N using a model described by Foley (1994) that incorporates density-dependent population growth with respect to carrying capacity (K):

$$T_N \approx \frac{k^2}{v} * \left[1 + \frac{2}{3} * \left(\frac{k*r}{v} \right) \right] \quad \text{where } k$$
$$= \ln(K) \text{ and } v \text{ is variance in } r. \tag{2}$$

The model moderates population extremes compared with density-independent models of extinction (Goodman, 1987), and therefore, tends to predict longer times to extinction (Boyce et al., 2001). We used our simulated estimates of r for each habitat in Eq. (2) and estimated v from two different sources (Table 2). We estimated v for squirrels in upland-OG and peatland-MC habitats using data from a 3-year demographic study of northern flying squirrels on Prince of Wales Island (Smith and Nichols, 2003). Arguably, 3 years of demographic data usually will underestimate variance, especially in small mammal populations (Beissinger and Westphal, 1998). However, flying squirrel populations increased dramatically in both habitats between 1998 and 2001 (Smith and Nichols, 2003), and we likely captured a period of rapid growth similar to those described by Fryxell et al. (1998). Also, we used an estimate of v from a 43-year demographic study of northern flying squirrels in Ontario, Canada (Fryxell et al., 1998), which represented the longest time series for northern flying squirrel populations published in North America. We used that estimate of v to predict T_N for populations in both

habitats because the demographic data from Ontario were not habitat specific. Predictions of T_N were calculated for the two estimates of variance for each scenario of OGR composition. Effects of autocorrelation on r and v were not considered, but these effects are expected to be negligible compared to environmental stochasticity (Foley, 1994).

We estimated the population density of flying squirrels occupying each habitat within our hypothetical OGRs using mark-recapture estimates in spring within upland-OG and peatland-MC habitats (Smith and Nichols, 2003). In our analyses of time to extinction, we assumed N was equal to K, the population ceiling. Therefore, we used the highest population density reported by Smith and Nichols (2003) for each habitat type as our estimate of population density at K. For each scenario of OGR composition, we multiplied these estimates of maximum population density by the corresponding hectares of each habitat to calculate K within each habitat. Estimates of T_N were converted to probabilities of persistence (P_t) for a particular time horizon by assuming extinction was a rare event and followed a Poisson distribution (Boyce et al., 2001):

$$P_t = e^{(-t/T_N)}, \tag{3}$$

where t is the time horizon.

Lastly, to calculate the minimum area of habitat required (i.e., minimum size of an OGR) to sustain isolated flying squirrel populations, we used our extinction model to estimate the population of northern flying squirrels required to achieve 85%, 90% and 95% probabilities of persistence for 25, 50, and 100 years (see Appendix A for an example). We calculated projections for both estimates of variance in r. To estimate the minimum area required to sustain a population of flying squirrels, we divided population projections by the density of northern flying squirrels.
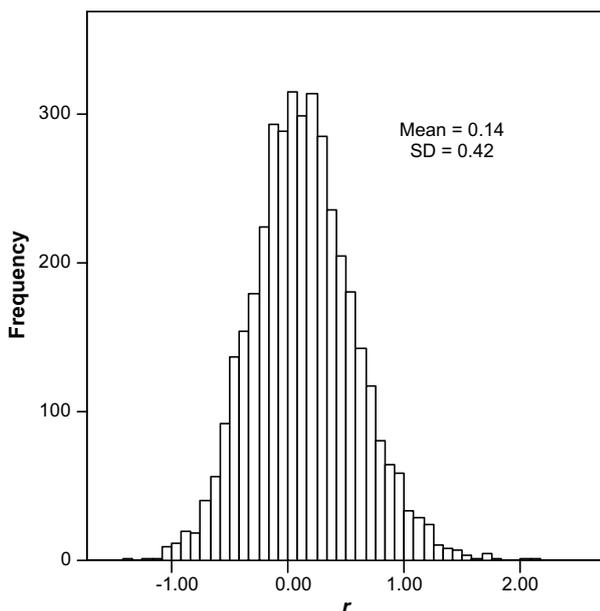
3. Results

Breeding density (number of resident adults during spring) of flying squirrels averaged across three replicate trapping grids in upland-OG varied annually from 1.6 (SE = 0.2) to 2.0 (SE = 0.4) squirrels/ha during 1998–2000. Breeding density averaged across all grids in peatland-MC ranged from 1.00

(SE = 0.5) to 1.30 (SE = 1.0) squirrels/ha during 1998–2000. The highest spring density recorded for all individual grids in upland-OG was 2.8 squirrels/ha and 1.9 squirrels/ha in peatland-MC.

Average population growth rate in upland-OG based on 4000 simulations of our birth–death model of population dynamics was 0.14 (SD = 0.42); 38.7% of the simulations resulted in $r < 0$ (Fig. 1). Our empirical estimate of v from spring live trapping data was 0.34. In peatland-MC, average population growth rate was 0.01 (SD = 0.39) with 51.0% of the simulated values <0 (Fig. 2). The difference in r between habitats was significant ($t = 12.5$, $n = 4000$, $P < 0.001$). In peatland-MC, v estimated from spring live trapping data was 0.22. Variance of r obtained from a long-term data set for flying squirrel populations in Ontario, Canada (Fryxell et al., 1998) was 0.39.

Maximum population sizes (K) in upland-OG under the minimum, preferred, and 100% upland-OG prescriptions were 454, 910, and 1820 flying squirrels, respectively (Table 3). The minimum value predicted for T_N was 237 years ($v = 0.39$, minimum prescription) and the maximum was 507 years ($v = 0.34$, 100% upland-OG, Table 3). Maximum population sizes (K) in peatland-MC under the minimum, preferred, and 100% upland-OG prescriptions were 927, 618, and 0 flying squirrels, respectively (Table 4). The minimum predicted T_N value was 118 years ($v = 0.39$, preferred prescription) and the maximum value was 156 years ($v = 0.34$, minimum prescription); if a small OGR was 100% peatland-MC, T_N was 173 years for $v = 0.34$ and 149 years for $v = 0.39$ (Table 4).

In the upland-OG forest component of OGRs, probabilities of persistence for 25 years ranged from 90% ($v = 0.39$, 25% upland-OG) to 95% ($v = 0.34$, 100% upland-OG, Table 3). For 50-year and 100-year time horizons those values ranged 81–

Fig. 1 – Frequency histogram illustrating results from Monte Carlo simulations ($n = 4000$) of birth–death model predicting intrinsic rate of population growth (r) for northern flying squirrels in upland old-growth forest habitat on Prince of Wales Island, Alaska, USA, 1999–2001.
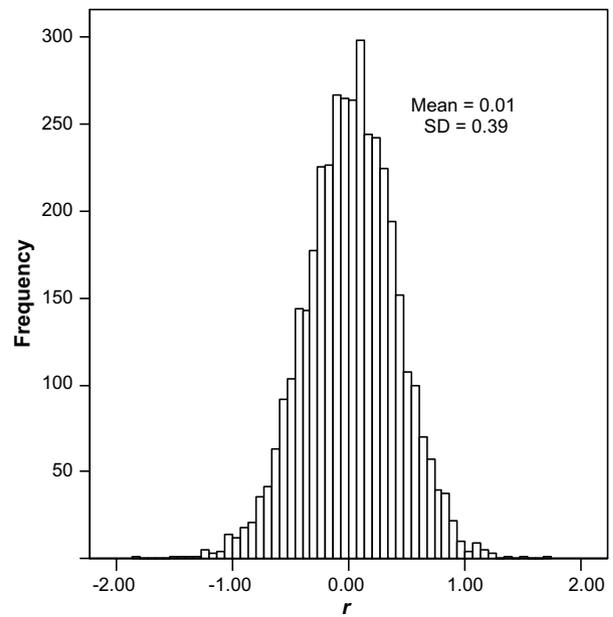
Fig. 2 – Frequency histogram illustrating results from Monte Carlo simulations ($n = 4000$) of birth–death model predicting intrinsic rate of population growth (r) for northern flying squirrels in peatland mixed-conifer habitat on Prince of Wales Island, Alaska, USA, 1999–2001.

Table 3 – Predicted times to extinction (T_N), and probabilities of persistence over 25 ($P_{t(25)}$), 50 ($P_{t(50)}$), and 100 years ($P_{t(100)}$) for northern flying squirrels within the upland-OG forest component of small old-growth forest reserves on Prince of Wales Island, Southeast Alaska, USA

	25%		50%		100%	
	$K = 454$		$K = 910$		$K = 1820$	
	v		v		v	
	0.34	0.39	0.34	0.39	0.34	0.39
T_N	295	237	392	313	507	404
$P_{t(25)}$	0.92	0.90	0.94	0.92	0.95	0.94
$P_{t(50)}$	0.84	0.81	0.88	0.85	0.91	0.88
$P_{t(100)}$	0.71	0.66	0.77	0.73	0.82	0.78

Predictions are based on an extinction model incorporating density-dependent population growth (Foley, 1994). Results are shown for three levels of K for squirrels occupying 650 ha reserves containing 25% (minimum), 50% (preferred), and 100% upland-OG forest habitat, and for two levels of variance (v) of per capita rate of growth ($r = 0.14$).

91% and 66–82%, respectively (Table 3). For flying squirrel populations in peatland–MC, probabilities of persistence for 25 years ranged from 81% ($v = 0.39$, 50% peatland-MC) to 87% ($v = 0.22$, 100% peatland-MC, Table 4). For 50-year and 100-year time horizons those values ranged 65–75% and 43–56%, respectively (Table 4).

We estimated only minimum areas for OGRs comprised of 100% upland-OG because the density of reproductive females in peatland-MC was substantially lower than in upland-OG, and because r for flying squirrel populations in peatland-MC

Table 4 – Predicted times to extinction (T_N), and probabilities of persistence over 25 ($P_{t(25)}$), 50 ($P_{t(50)}$), and 100 years ($P_{t(100)}$) for northern flying squirrels within the peatland-MC habitat component of small old-growth forest reserves on Prince of Wales Island, Southeast Alaska, USA

	50%		75%		100%	
	K = 618		K = 927		K = 1,235	
	v		v		v	
	0.22	0.39	0.22	0.39	0.22	0.39
T_N	137	118	156	134	173	149
$P_{t(25)}$	0.83	0.81	0.85	0.83	0.87	0.85
$P_{t(50)}$	0.69	0.65	0.73	0.69	0.75	0.71
$P_{t(100)}$	0.48	0.43	0.53	0.47	0.56	0.51

Predictions are based on an extinction model incorporating density-dependent population growth (Foley, 1994). Results are shown for three levels K for squirrels occupying 650 ha reserves containing 50% (preferred), 75% (minimum), and 100% peatland-MC habitat, and for two levels of variance (v) of per capita rate of growth ($r = 0.01$).

Table 5 – For two estimates of intrinsic variability in population growth (v), the minimum population ceiling (K) and minimum area (ha) of an old-growth reserve of contiguous upland-OG forest to support northern flying squirrels (Glaucomys sabrinus) with probabilities of persistence (P_t) of 0.85, 0.90, and 0.95, for periods of 25, 50, and 100 years

| V | 0.85 | | 0.90 | | 0.95 | |
	K	Area	K	Area	K	Area
25 years P_t						
0.34	116	41	277	99	1619	578
0.39	175	63	457	163	3156	1127
50 years P_t						
0.34	502	179	1516	542	14,214	5077
0.39	874	312	2927	1045	33,928	12,117
100 years P_t						
0.34	3181	1136	12,939	4621	221,018	78,935
0.39	6592	2354	30,607	10,931	684,880	244,600

during a period of increasing density was near zero. Over longer periods, populations in peatland-MC undoubtedly experience years with lower per capita growth rates, many of which would be negative. Indeed, r was negative in peatland-MC for the majority of our birth–death model simulations (Fig. 2). Consequently, areas composed solely of upland-OG habitat likely represent more realistic (albeit somewhat generous) estimates of minimum area for OGRs. The minimum area of an isolated OGR to achieve a specified P_t for 25, 50, and 100 years ranged widely (Table 5). For populations with lower variance of r, a 41-ha patch of upland-OG forest had an 85% probability of sustaining northern flying squirrels for 25 years. Populations with higher variance required 63 ha of upland-OG forest to achieve the same level of certainty. For P_t = 95% corresponding values were 578 and

1127 ha. For a time horizon of 100 years, 1136–2354 ha would be necessary to achieve an 85% probability of persistence, and 78,935–244,600 ha to achieve a 95% probability of persistence depending on v.

Nevertheless, for a planning horizon of 100 years, our simulations suggest that 650-ha OGRs are too small to assure a high probability of sustaining flying squirrel populations in the absence of immigration, regardless of habitat composition. For P_t = 0.95, small OGRs composed of 100% upland-OG would sustain a flying squirrel population for only 25 years. At P_t = 0.90, 650-ha OGRs composed of 100% upland-OG would sustain flying squirrels populations for 50 years only if v was low; however, the minimum OGR prescription likely would sustain squirrel populations for 25 years. For P_t = 0.85, the preferred OGR prescription would sustain squirrels for 50 years.

4. Discussion

4.1. Population dynamics and probability of persistence

We estimated T_N and P_t for each habitat type in isolation. Undoubtedly, flying squirrels within OGRs that contain a mix of upland-OG and peatland-MC components interact in ways that likely extend time to extinction of the total population beyond that predicted for each habitat independently. Modeling these interactions is beyond the scope of this paper. Nonetheless, the predicted intrinsic rate of growth was near zero for flying squirrels in peatland-MC habitat despite the fact that the demographic data used to estimate r were obtained during a period of rapid population increase. Consequently, peatland-MC habitat likely contributes little to the long-term persistence of northern flying squirrel populations in small OGRs. Rather, the demographics of northern flying squirrels occupying upland-OG have the principal influence on T_N and P_t. For this reason, predictions based solely on northern flying squirrels occupying the upland-OG component of an OGR represent lower limits of P_t. Likewise, our projections of T_N and P_t for small OGRs composed entirely of upland-OG forest define the upper limits of P_t regardless of prescription. Values of P_t from dynamic interactions of flying squirrels occupying OGRs with varying configurations of upland-OG and peatland-MC will lie between these limits.

Rates of growth estimated from simulations of our birth–death model were conservative when compared with rates measured directly from mark-recapture studies. For example, r estimated from changes in density of northern flying squirrels on Prince of Wales Island was 0.26 in peatland-MC and 0.22 in upland-OG habitats (Smith and Nichols, 2003). Lehmkuhl et al. (2006) reported rates of growth as high as 0.36 for flying squirrels in eastern Washington, USA. However, estimates of r from mark-recapture studies are based on changes in abundance across sampling grids that are not isolated populations and thus include contributions to population growth from immigration. Our simulations computed average intrinsic rates of growth only from rates of birth and death. Thus, these values represent potential growth rates of flying squirrel populations in isolation without influences of immigration or emigration and were more appropriate with respect to our objectives of evaluating the adequacy of individual small OGRs. Also, we acknowledge that maximum density likely

underestimates K because rarely do populations reach carrying capacity. However, *G. sabrinus* experiences little or no competition as it is the only small mammal on POW that is a forest habitat specialist (Smith et al., 2004). Furthermore, it apparently experiences relatively little predation pressure because of few large avian predators (Smith et al., 2001; Smith and Nichols, 2003), which likely is a consequence of a depauperate vertebrate fauna (Smith, 2005). Therefore, we believe *G. sabrinus* populations on POW are limited mostly by autecological factors (Smith and Nichols, 2003; Smith et al., 2004; Smith et al., 2005). Nonetheless, replacing our estimate of K with higher values should have relatively little effect on our projections because of the expected dampened influence of density-dependent population growth (Lehmkuhl et al., 2006).

Inferring habitat quality from population density can be misleading (Van Horne, 1983). Smith and Nichols (2003) observed relatively high densities of flying squirrels in peatland-MC habitat on Prince of Wales Island and concluded that habitat may sustain breeding populations of northern flying squirrels. In contrast, our birth–death model of population dynamics demonstrated that intrinsic population growth was effectively zero for flying squirrels in peatland-MC habitat. Smith and Nichols (2003) reported that the density of reproductive females in peatland-MC (2.1/grid) averaged about half that observed in upland-OG (3.9/grid). Smaller proportions of females in peatland-MC habitat may limit potential population growth. Indeed, flying squirrels occupying peatland-MC might in some years represent population sinks (Pulliam, 1988; Pulliam and Danielson, 1991) that are sustained by immigration; and the rapid increase of flying squirrels in peatland-MC habitat observed by Smith and Nichols (2003) probably resulted from frequent immigration from neighboring source habitat. This conclusion is further supported by a consistent pattern of more juvenile males captured in peatland-MC than upland-OG (Smith and Nichols, 2003) and invariably higher densities on the peatland-MC grid that was closest to upland-OG forest. Also, Smith et al. (2004) suggested that the density of reproductive females in peatland-MC might be limited by the abundance and distribution of large trees, which provide cavities for maternal dens (Carey et al., 1997). Flying squirrel densities in Southeast Alaska were strongly correlated ($r = 0.81$) with the density of large (>74 cm) trees, and capture sites in peatland-MC averaged twice the density of large trees than sites without captures. Furthermore, the mean density of large trees in peatland-MC (1.35, SE = 0.33) was an order of magnitude lower than that recorded in upland-OG (24.63, SE = 1.68; W.P. Smith, unpublished data) where densities of females were significantly higher.

The empirical data used in our analyses came from a 3-year study of northern flying squirrels that included three replicates of two habitats on a single, large (5800 km^2) island (Smith and Nichols, 2003). Ordinarily, such limited data would not capture intrinsic variation in growth rates of flying squirrels on a single island, much less across Southeast Alaska (Doak et al., 2005), where faunal assemblages and habitat vary among islands (Conroy et al., 1999; Smith and Nichols, 2003; Smith et al., 2005). However, the data were recorded during a period when flying squirrels were undergoing a surge in population growth and our empirical estimates of v were similar to that obtained from a 43-year study of flying squirrel population dynamics (Fryxell et al., 1998). Still, there was a chance that we underestimated demographic stochasticity for populations across Southeast Alaska, which would result in overestimates of P_t. Moreover, T_N was most sensitive to changes in v than population size. For example, our high estimate of v for upland-OG was about 15% larger than the low estimate, yet T_N for the lower estimate was 25% longer. By comparison, a 2-fold increase in K only increased T_N by 29%. Long-term studies are needed to capture variation in population growth (Beissinger and Westphal, 1998; Kendall and Fox, 2002) and to understand how northern flying squirrel populations respond to annual variation in weather, resource availability, and other ecological factors that influence population dynamics (Doak et al., 2005) and fitness (Reed, 2004). For Southeast Alaska, these should include studies of northern flying squirrel demography among other islands where vertebrate communities (especially potential competitors and predators) and perhaps habitat vary. Therefore, our findings should be generalized with caution.

We did not consider environmental or genetic stochasticity (Foley, 1994; Reed, 2004) or deleterious effects of inbreeding (Frankham, 2005; O'Grady et al., 2006). We assumed that over the time horizon the habitat available to flying squirrels remained unchanged, and there was no reduced fitness from inbreeding depression or genetic drift. However, Southeast Alaska periodically experiences severe catastrophic disturbances from windstorms, avalanches, and landslides that dramatically alter hundreds of hectares of forest during a single event (Mitchell, 1995; Nowacki and Kramer, 1998; Kramer et al., 2001). Furthermore, clearcut logging increases the chance of blowdown from windstorms in remaining old-growth forest and reduces the likelihood that patches in managed landscapes remain intact (Concannon, 1995; Mitchell, 1995). In addition, northern flying squirrel populations on Prince of Wales Island show severely reduced genetic variation, a likely consequence of descent from a single founder population (Demboski et al., 1998) that was isolated from mainland or near-shore island populations (Bidlack and Cook, 2001). The sensitivity of our predictions of T_N and P_t to changes in v emphasized the potential for additive genetic and environmental variance to increase the predicted probabilities of extinction within habitat patches or reserves.

We used mean litter sizes from populations in the Puget Trough for our birth–death modeling because data from Southeast Alaska were not available. Nonetheless, ratios of juveniles to adults during autumn in Southeast Alaska (Smith and Nichols, 2003) were about half that reported for the Puget Trough (Villa et al., 1999). It is uncertain if that difference was due to lower natality rates or higher juvenile mortality rates during summer in Southeast Alaska. Thus, we may have overestimated recruitment for flying squirrels in Southeast Alaska, and therefore, our results for time to extinction and probability of persistence may be optimistic. This is particularly important when considering the viability of flying squirrel populations in peatland-MC habitats. A slight decline in birth rate (or increase in mortality rate) is sufficient to reduce the intrinsic rate of population growth below sustainable levels in peatland-MC.

4.2. Implications for conservation planning

This study occurred within an island archipelago, where some factors influencing vertebrate distributions and community composition differ from most communities of continental land areas (MacArthur and Wilson, 1967). Specifically, colonization rates can be a major determinant of the distribution of individual species and the species richness of vertebrate assemblages among islands. In Southeast Alaska, differential colonization rates might have contributed to the highly nested structure in the mammal fauna (Conroy et al., 1999). Still, the diversity of vertebrate communities on islands is influenced significantly by extinctions rates that vary among species and vertebrate assemblages according to autecological factors and interspecific interactions such as competition and predation (Conroy et al., 1999; MacArthur and Wilson, 1967). This is especially true of populations occupying remote, large islands (MacArthur and Wilson, 1967). Extinction rate plays a greater role in determining species richness of vertebrate communities as island size and distance from source populations increases (MacArthur and Wilson, 1967). Also, extinctions are more likely among archipelagos (Burkey, 1995; Frankham, 1998) because total habitat and population sizes are smaller than continental land areas, with endemic taxa having higher extinction rates than nonendemic species because of greater inbreeding depression (Frankham, 1998). Because Prince of Wales Island is large ($\approx$5800 km^2), factors influencing the persistence of *G. sabrinus* populations occupying habitat reserves in a managed matrix are not unlike the ecological factors that determine the population dynamics of mainland populations under similar circumstances (e.g., Odom et al., 2001). For this reason, we believe the implications of our study, as well as its analytical approach, are relevant for conservation planning across managed landscapes of continental North America.

Land management plans such as TLMP, rely on systems of habitat reserves that presumably are sufficient in size and quality or adequately distributed and connected to assure viability of wildlife populations. Habitat reserves must either sustain individual insular populations or the matrix of managed lands between reserves must allow dispersal among reserves to maintain wildlife populations within a metapopulation structure. Testing the adequacy of a system of reserves for conservation of wildlife is a daunting task and requires long-term population monitoring and studies of animal movements. Nonetheless, we demonstrated that short-term evaluations of assumptions or expectations within a plan are possible using simple simulation modeling techniques.

Clearly, our study does not represent an evaluation of the overall conservation strategy employed in TLMP (or similar plans) with respect to northern flying squirrels, but we conclude that small OGRs do not have a high ($\geqslant$0.90) probability of supporting flying squirrel populations in isolation for long periods. Indeed, in the best case (100% upland-OG habitat) P_t ranged 78–82%, and under the preferred OGR prescription (50% upland-OG) specified in TLMP, P_t ranged 73–80%. We consistently predicted probabilities of persistence >90% only for a time horizon of 25 years regardless of habitat prescription. For a 50-year time horizon, only small OGRs composed of 100% upland-OG forest had >90% proba-bility of sustaining flying squirrel populations. Consequently, isolated individual small OGRs might not sustain squirrel populations for >25 years. To expect $\geqslant$90% probability of persistence in isolation for 50 and 100 years, the upland-OG component of an OGR would have to be about 1000 ha and 11,000 ha, respectively.

Those results and conclusion are based on a number of assumptions regarding the demographic data and analytical approach. We chose published models that were appropriate for our data and used in similar applications (Foley, 1994; Boyce et al., 2001). Furthermore, most of our assumptions contributed to more optimistic scenarios of persistence and minimum area. For those reasons, our findings underscore the importance of the capability of northern flying squirrels to disperse through the matrix of managed lands between small OGRs. Unfortunately, we know little about the ability of flying squirrels to move through a matrix of clearcuts and second-growth forest in Southeast Alaska. We are investigating several facets of flying squirrel dispersal in managed landscapes, including behavioral trials, translocations, and radio-telemetry of juveniles and adult males. Those data will be used to parameterize a GIS-based model of landscape connectivity to determine the extent to which OGRs are isolated. However, dispersal alone does not ensure a viable metapopulation. The Siberian flying squirrel (*Pteromys volans*) was extirpated from an entire region because industrial-scale logging fragmented continuous populations into isolated patches (Hokkanen et al., 1982). That occurred despite the ability of young flying squirrels to disperse long distances through a managed matrix that included residual trees and corridors connecting habitat patches (Selonen and Hanski, 2003).

Our simulations suggest that there is a high probability that large isolated OGRs containing >11,000 ha of upland-OG forest likely will support flying squirrels over the 100-year planning horizon of TLMP. Furthermore, the upland-OG component of a large OGR may not need to be contiguous because interspersed peatland-MC habitats clearly can support flying squirrels for a short time and likely facilitate dispersal between patches of upland-OG. However, the contribution of small OGRs to the TLMP conservation strategy for northern flying squirrels will depend on the degree of their isolation and functional connectivity with other large or small reserves. For this reason, conservation planning that explicitly considers the quality and spatial configuration of suitable habitat across highly modified landscapes (Fuller et al., 2006; Odom et al., 2001) will have a greater likelihood of sustaining viable metapopulations of flying squirrels (Hanski et al., 2000; Selonen and Hanski, 2003, 2004).

Acknowledgments

Appendix A

Example calculation to estimate minimum area of old-growth reserve to achieve an 85% probability of persistence over 25 years for a population of northern flying squirrels with $r = 0.14$ and $v = 0.34$.

Using the Poisson formula $[P_t = e^{(-t/T_N)}]$ for calculating the probability of a rare event, solve for flying squirrel population ceiling K that corresponds with time to extinction (T_N) for a specified probability of persistence (P_t). Divide K by density at carrying capacity to obtain minimum area.

For $P_t = 0.85$ and $t = 25$ years, (T_N) = 153.8 years yielding the equation

$$153.8 = \frac{x^2}{0.34}\left[1 + \frac{2 \times 0.14 \times x}{3 \times 0.34}\right], \quad \text{where } x = \ln(K).$$

This equation reduces algebraically to: $0.2745(x^3) + x^2 - 52.3 = 0$.

Solving the cubic equation yields $x = 4.76$, $K = e^x = 116$ squirrels; 116 squirrels/2.8 squirrels/ha (K) = 41 ha, the minimum area of primary habitat to achieve a probability of persistence of 85% for 25 years.

REFERENCES

Alaback, P.B., 1982. Dynamics of understory biomass in Sitka spruce–western hemlock forests of Southeast Alaska. Ecology 63, 1932–1948.

Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62, 821–841.

Bidlack, A.L., Cook, J.A., 2001. Reduced genetic variation in insular northern flying squirrels (Glaucomys sabrinus) along the North Pacific Coast. Animal Conservation 4, 283–290.

Boyce, M.S., Blanchard, B.M, Knight, R.R., Servheen, C., 2001. Population viability for grizzly bears: a critical review. Monograph Series No. 4, International Association for Bear Research and Management.

Bullock Jr., J.F., Wall, W.A., 1995. Proactive endangered species management: a partnership paradigm. Transactions of the North American Wildlife and Natural Resources Conference 60, 439–446.

Burkey, T.V., 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. Conservation Biology 9, 527–541.

Carey, A.B., 1989. Wildlife associated with old-growth forests in the Pacific Northwest. Natural Areas Journal 9, 151–162.

Carey, A.B., 2000. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. In: Goldingay, R.L., Scheibe, J.S. (Eds.), Biology of Gliding Mammals. Filander Verlag, Fürth, Germany, pp. 45–66.

Carey, A.B., Wilson, T., Maguire, C.C., Biswell, B.L., 1997. Dens of northern flying squirrels in the Pacific Northwest. Journal of Wildlife Management 61, 684–699.

Carey, A.B., Kershner, J., Biswell, B.L., Dominguez de Toledo, L., 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142, 1–71.

Catton, T., Mighetto, L., 1998. The fish and wildlife job on the National Forests: a century of game and fish conservation, habitat protection, and ecosystem management. USDA Forest Service, Washington, DC.

Concannon, J.A., 1995. Characterizing structure, microclimate, and decomposition of peatland, beachfront, and newly-logged forest edges in southeastern Alaska. PhD Dissertation, University of Washington.

Conroy, C.J., Demboski, J.R., Cook, J.A., 1999. Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. Journal of Biogeography 26, 343–352.

Demboski, J.R., Jacobsen, B.K., Cook, J.A., 1998. Implications of cytochrome b sequence variation for biogeography and conservation of the northern flying squirrels (Glaucomys sabrinus) of the Alexander Archipelago, Alaska. Canadian Journal of Zoology 76, 1771–1777.

DeMeo, T., Martin, J., West, R.A., 1992. Forest plant association guide: Ketchikan Area, Tongass National Forest. USDA Forest Service, Alaska Region R10-MB-210, Juneau.

Doak, D.F., Gross, K., Morris, W.F., 2005. Understanding and predicting the effects of sparse data on demographic analyses. Ecology 86, 1154–1163.

Everest, F.H., Swanston, D.N., Shaw III, C.G., Smith, W.P., Julin, K.R., Allen, S.D., 1997. Evaluation of the use of scientific information in developing the 1997 Forest Plan for the Tongass National Forest. USDA Forest Service General Technical Report PNW-GTR-415, Portland.

Flynn, R.W., Schumacher, T.V., Ben-David, M., 2004. Abundance, prey availability, and diets of American martens: implications for the design of old-growth reserves in Southeast Alaska. Final Report, US Fish and Wildlife Service Grant DCN 70181-1-G133. Alaska Department of Fish and Game, Douglas.

Foley, P., 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8, 124–137.

Frankham, R., 1998. Inbreeding and extinction: island populations. Conservation Biology 12, 665–675.

Frankham, R., 2005. Genetics and extinction. Biological Conservation 126, 131–140.

Fryxell, J.M., Falls, J.B., Falls, E.A., Brooks, R.J., 1998. Long-term dynamics of small-mammal populations in Ontario. Ecology 79, 213–225.

Fuller, T., Munguia, M., Mayfield, M., Sánchez-Cordero, V., Sarkar, S., 2006. Incorporating connectivity into conservation planning: a multi-criteria case study from Central Mexico. Biological Conservation 133, 131–142.

Gilbert, L.E., 1980. Food web organization and conservation of Neotropical diversity. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation Biology: An Evolutionary-Ecological Perspective. Sinauer Associates, Sunderland, pp. 11–33.

Gilpin, M., 1996. Metapopulations and wildlife conservation: approaches to modeling spatial structure. In: McCullough, D.R. (Ed.), Metapopulations and Wildlife Conservation. Island Press, Washington, DC, pp. 11–27.

Goodman, D., 1987. The demography of chance extinction. In: Soulé, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, New York, pp. 11–34.

Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42, 17–38.

Hanski, I.K., Mönkkönen, M., Reunanen, P., Stevens, P., 2000. Ecology of the Eurasian flying squirrel (Pteromys volans) in Finland. In: Goldingay, R.L., Scheibe, J.S. (Eds.), Biology of Gliding Mammals. Filander Verlag, Fürth, Germany, pp. 67–86.

Harris, A.S., Farr, W.A., 1974. The forest ecosystem of Southeast Alaska: 7. Forest ecology and timber management. USDA Forest Service General Technical Report PNW-25, Portland.

Hokkanen, H., Törmälä, T., Vuorinen, H., 1982. Decline of the flying squirrel (Pteromys volans L.) populations in Finland. Biological Conservation 23, 273–284.

Iverson, G.C., Rene, B., 1997. Conceptual approaches for maintaining well-distributed, viable wildlife populations: a resource assessment. In: Julin, K.R. (Comp.). Assessments of wildlife viability, old-growth timber volume estimates, forested wetlands, and slope stability. USDA Forest Service General Technical Report PNW-GTR-392, Portland, pp. 1–23.

Julin, K.R., Caouette, J.P., 1997. Options for defining old-growth timber volume strata: a resource assessment. In: Shaw III, C.G. (Tech. coord.), Assessments of wildlife viability, old-growth timber volume estimates, forested wetlands, and slope stability. USDA Forest Service General Technical Report PNW-GTR-392, Portland, pp. 24–37.

Kendall, B.E., Fox, G.A., 2002. Variation among individuals and reduced demographic stochasticity. Conservation Biology 16, 109–116.

Kramer, M.G., Hansen, A.J., Taper, M.L., Kissinger, E.J., 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in Southeast Alaska. Ecology 82, 2749–2768.

Lehmkuhl, J.F., Kistler, K.D., Begley, J.S., Boulanger, J., 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16, 584–600.

Leopold, A., 1933. Game Management. Charles Scribner's Sons, New York.

Lindenmayer, D.B., Possingham, H.P., 1996. Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using population viability analysis. Conservation Biology 10, 235–251.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Monographs in Population Biology, vol. 1. Princeton University Press, Princeton. pp. 1–203.

MacDonald, S.O., Cook, J.A., 1996. The land mammal fauna of southeast Alaska. Canadian Field-Naturalist 110, 571–598.

Marcot, B.G., Murphy, D.D., 1996. On population viability analysis and management. In: Szaro, R.C., Johnston, D.W. (Eds.), Biodiversity in Managed Landscapes. Oxford University Press, New York, pp. 58–76.

Mitchell, S.J., 1995. A synopsis of windthrow in British Columbia: occurrence, implications, assessment and management. In: Coutts, M.P., Grace, J. (Eds.), Wind and Trees. Cambridge University Press, Cambridge, UK, pp. 448–459.

Naess, A., 1986. Intrinsic value: will the defenders of nature please rise? In: Soulé, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, pp. 504–515.

Neiland, B.J., 1971. The forest bog complex of Southeast Alaska. Vegetatio 22, 1–63.

Newton, J.L., Freyfogle, E.T., 2005a. Sustainability: a dissent. Conservation Biology 19, 23–32.

Newton, J.L., Freyfogle, E.T., 2005b. All about nature. Conservation Biology 19, 42–44.

Nowacki, G.J., Kramer, M.G., 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. USDA Forest Service General Technical Report PNW-GTR-421, Portland.

Odom, R.H., Ford, W.M., Edwards, J.W., Stihler, C.W., Menzel, J.M., 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (Glaucomys sabrinus fuscus) in the Allegheny Mountains of West Virginia. Biological Conservation 99, 245–252.

O'Grady, J.J., Brook, B.W., Reed, D.H., Ballou, J.D., Tonkyn, D.W., Frankham, R., 2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. Biological Conservation 133, 42–51.

Pereira, H.M., Daily, G.C., Roughgarden, J., 2004. A framework for assessing the relative vulnerability of species to land-use change. Ecological Applications 14, 730–742.

Petchey, O.L., 2000. Species diversity, species extinction, and ecosystem function. American Naturalist 155, 696–702.

Pimm, S.L., 1991. The Balance of Nature? Ecological Issues in the Conservation of Species and Communities. University of Chicago Press, Chicago.

Possingham, H.P., Lindenmayer, D.B., Norton, T.W., 1993. A framework for improved management of threatened species based on population viability analysis (PVA). Pacific Conservation Biology 1, 39–45.

Pulliam, R.H., 1988. Sources, sinks, and population regulation. American Naturalist 132, 652–661.

Pulliam, R.H., Danielson, B.J., 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137 (Suppl.), S50–S66.

Pyare, S., Berger, J., 2003. Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. Biological Conservation 113, 63–73.

Reed, D.H., 2004. Extinction risk in fragmented habitats. Animal Conservation 7, 181–191.

Scheibe, J.S., Smith, W.P., Basham, J., Magness, D., 2006. Cost of transport in the northern flying squirrel, Glaucomys sabrinus. Acta Theriologica 51, 169–178.

Schoen, J.W., Kirchhoff, M.D., Wallmo, O.C., 1984. Sitka black-tailed deer/old-growth relationships in Southeast Alaska: implications for management. In: Meehan, W.R., Merrell, T.R., Hanley, T.A. (Eds.), Proceedings of a Symposium: Fish and Wildlife Relationships in Old-Growth Forests. American Institute of Fishery Research Biologists, Juneau, pp. 315–319.

Searby, H.W., 1968. Climate of Alaska. Climatography of the United States No. 60–49. Climates of the States, Alaska. US Department of Commerce, Environmental Science Service Administration, Environmental Data Service.

Selonen, V., Hanski, I.K., 2003. Movements of the flying squirrel Pteromys volans in corridors and in matrix habitat. Ecography 26, 641–651.

Selonen, V., Hanski, I.K., 2004. Young flying squirrels (Pteromys volans) dispersing in fragmented forests. Behavioral Ecology 15, 564–571.

Shaw III, C.G., 1999. Use of risk assessment panels during revision of the Tongass Land and Resource Management Plan. USDA Forest Service General Technical Report PNW-460, Portland.

Smith, W.P., 2005. Evolutionary diversity and ecology of endemic small mammals of southeastern Alaska with implications for land management planning. Landscape and Urban Planning 72, 135–155.

Smith, W.P., Nichols, J.V., 2003. Demography of the Prince of Wales flying squirrel: an endemic of Southeastern Alaska temperate rain forest. Journal of Mammalogy 84, 144–158.

Smith, W.P., Pashley, D.N. (Eds.), 1994. A workshop to resolve conflicts in the conservation of migratory landbirds of bottomland hardwood forests. USDA Forest Service General Technical Report GTR SO-114, New Orleans.

Smith, W.P., Zollner, P.A., 2005. Sustainable management of wildlife habitat and risk to extinction. Biological Conservation 125, 287–295.

Smith, W.P., Stotts, M.J., Andres, B.A., Melton, J.M., Garibaldi, A., Boggs, K., 2001. Bird, mammal, and vegetation community surveys on Research Natural Areas in the Tongass National Forest. USDA Forest Service Research Paper-PNW-RP-535, Portland.

Smith, W.P., Gende, S.M., Nichols, J.V., 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rain forest of southeastern Alaska. Journal of Mammalogy 85, 663–674.

Smith, W.P., Gende, S.M., Nichols, J.V., 2005. The northern flying squirrel as a management indicator species of north temperate rainforest: test of a hypothesis. Ecological Applications 15, 689–700.

Soulé, M.E., Estes, J.A., Berger, J., Martinez Del Rio, C., 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17, 1238–1250.

Suring, L.A. (compiler), 1993. Habitat capability models for wildlife in Southeast Alaska. USDA Forest Service, Alaska Region, Juneau [irregular pagination].

Thomas, J.W., 1991. Research on wildlife in old-growth forests: setting the stage. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.) (Tech. coords.), Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-285, Portland, pp. 1–4.

USDA Forest Service, 1997. Land and resource management plan: Tongass National Forest. USDA, Forest Service R10-MB-338dd. Juneau.

USDA Forest Service, 2003. Tongass land and resource management plan revision: final supplemental environmental impact statement (FSEIS). USDA Forest Service R10-MB-481a, Volume I: Final SEIS, Appendix A, B, D, E; Juneau.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47, 893–901.

Ver Hoef, J.M., Neiland, B.J., Glenn-Lewin, D.C., 1988. Vegetation gradient analysis of two sites in southeast Alaska. Northwest Science 62, 171–180.

Villa, L.J., Carey, A.B., Wilson, T.M., Glos, K.E., 1999. Maturation and reproduction in northern flying squirrels in pacific northwest forests. USDA Forest Service PNW-GTR-444, Portland.

Wells-Gosling, N., Heaney, L.R., 1984. *Glaucomys sabrinus*. Mammalian Species 229, 1–8.