

Source–sinks, metapopulations, and forest reserves: conserving northern flying squirrels in the temperate rainforests of Southeast Alaska

Summary

Reserves are a common strategy used to ensure the viability of wildlife populations, but their effectiveness is rarely empirically evaluated. The Tongass National Forest implemented a conservation plan (TLMP) in 1997 to maintain biological diversity across Southeast Alaska, the cornerstone of which was an integrated system of large, medium, and small old-growth reserves (OGRs). Small OGRs were intended to facilitate functional connectivity between larger reserves and ensure well-distributed populations of forest-dependent wildlife. The northern flying squirrel (*Glaucomys sabrinus*) was selected as an indicator of wildlife communities that operate at small spatial scales because its abundance has been correlated with old-growth forest structure and processes and because of specific habitat requirements for efficient locomotion. Previous research predicted that small OGRs were unlikely to support flying squirrels over a 100-year time horizon. Consequently, the presence and persistence of flying squirrels in small OGRs depended on dispersal from larger reserves. Using data from telemetry experiments, we determined effective distances immigrants could move through landscapes composed of old-growth and managed forests. Effective distance accounted for the resistance of habitats such as clearcuts that are difficult for flying squirrels to traverse. We used findings of previous studies to parameterize a logistic population growth model incorporating dispersal to determine the number of dispersers necessary to enable a flying squirrel population in a small OGR to persist for 25 and 100 years. We combined that information with a function relating the probability

of successful dispersal with effective distance to estimate the maximum effective distances between OGRs that would ensure flying squirrels colonize and persist in small OGRs for 25 and 100 years. Our findings underscore the essential role of immigration in sustaining sinks and facilitating metapopulation viability among unsustainable fragmented populations (i.e., sinks). They also demonstrate the extent to which permeability of landscape elements can influence the probability of dispersal and functional connectivity of subpopulations in a managed matrix.

Introduction

Habitat loss and fragmentation are widely regarded as major threats to the viability of wildlife populations (Wilcove *et al.* 1986; Rolstad 1991; Fahrig and Merriam 1994; Wiens 1995; Reed 2004). Along the northwestern Pacific coast, for example, habitat loss and fragmentation from timber harvests have threatened wildlife species that rely on late-seral forests (Richards *et al.* 2002). Of particular concern is maintaining the minimum population size (i.e., “ecologically effective” density, *sensu* Soulé *et al.* 2003: 1239) of essential species to fulfill their critical roles in ecosystem processes (Carey 2000). For many species, fragmentation can cause population declines beyond what would be expected solely from the total amount of habitat loss (Schumaker 1996) because of critical thresholds in their responses to landscape structure (With and Crist 1995).

A consequence of habitat fragmentation can be the fracturing of wildlife populations into subpopulations distributed among residual habitat patches. Disjunct population segments may take on the characteristics of patchily distributed populations, metapopulations (i.e., groups of separate but functionally connected subpopulations), source–sinks, or insular populations depending on the size and quality of patches or the dispersal and connectivity between patches. Empirical evidence suggests that the population dynamics of a wide range of wildlife species in fragmented landscapes resembles a pattern of stochastic local extinctions and recolonizations (Opdam *et al.* 1985; Opdam 1991; Hanski 1994). Thus, for wildlife populations to persist in heterogeneous landscapes, individual habitat patches must be large enough to provide for viable subpopulations (e.g., Hanski 1994; Smith and Person 2007), or the juxtaposition of suitable habitat must allow for interpatch migration to colonize patches that become vacant from localized extinctions (Burkey 1989; Bender *et al.* 1998). Nonetheless, habitat fragmentation may create an uneven distribution with respect to size and quality of patches and source–sink dynamics may arise in which unsustainable subpopulations in small or poor-quality habitat fragments (sinks) are maintained by frequent dispersal from larger source populations (Pulliam 1988). Under those circumstances, landscape connectivity (the

degree to which landscape facilitates or impedes movement between resource patches; see Taylor *et al.* 1993) is a critical feature largely determining species' distributions (Verbeylen *et al.* 2003) and persistence (Fahrig and Merriam 1985; Beier 1993; Ferreras 2001; Richards *et al.* 2002).

Establishing habitat reserves is a common strategy used to increase the probability that wildlife populations remain viable and well distributed in developed and fragmented landscapes (FEMAT 1993; USDA Forest Service 1997). Depending on size and habitat quality, some reserves sustain viable populations that produce a surplus of offspring (i.e., source populations), many of which disperse to other habitat patches. Smaller or poorer-quality reserves are less likely to sustain viable populations (Smith and Person 2007), in which case they function as sinks that are subsidized by the surplus of emigrants from source populations (Pulliam 1988). Nevertheless, sinks can play a key role in sustaining viable metapopulations by serving as breeding habitat for females (thereby contributing to the overall population) and by functioning as stepping-stones that facilitate dispersal among subpopulations (Pulliam 1988; Pearson and Fraterriigo, Chapter 6, this volume). Unfortunately, the efficacy of reserves to sustain wildlife populations is rarely empirically evaluated, even for individual species (Ferreras 2001; Richards *et al.* 2002; Carroll *et al.* 2003). Because metapopulation or source–sink dynamics may occur in populations distributed among habitat reserves (Hansen, Chapter 16, this volume), conservation strategies that rely on reserves must consider not only the amounts of habitat to be retained, but also the spatial configurations of habitat across landscapes (Schumaker 1996), the characteristics of the intervening matrix (Wiens *et al.* 1993; Ferreras 2001), and temporal dynamics (Leroux *et al.* 2007).

A provocative example of land use planning incorporating habitat reserves at a large scale is the conservation strategy for the Tongass National Forest in southeast Alaska (USDA Forest Service 1997). Southeast Alaska, which comprises the Alexander Archipelago and a narrow mainland strip, is almost entirely national forest, encompassing ~6.8 million hectares. The island topography divides much of the forest among thousands of islands that range in area from 0.5 ha to 6,700 km² (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 impacts of timber harvests on forest plant and animal communities and the 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. The 1997 TLMP was recently amended (USDA Forest Service 2008), but the underlying framework for the conservation strategy remains fundamentally unchanged.

A cornerstone of the TLMP strategy was an integrated system of large ($\geq 16,200$ ha), medium ($\geq 4,050$ ha and $< 16,200$ ha), and small (≥ 650 ha and $< 4,050$ ha) old-growth forest reserves (OGR; USDA Forest Service 1997: K-1), which – together with other non-development lands – was expected to sustain viable populations without demographic contributions from the matrix. That is, the conservation strategy explicitly assumed that wildlife species that were intended to be conserved through the reserve system occurred exclusively within old-growth forests. Medium and large reserves were established across landscapes at intervals of ≤ 12.9 km and ≤ 32.2 km, respectively. The old-growth tracts were expected to support viable populations of forest-dependent species either within individual reserves (e.g., small mammals, mustelids) or among a collection of reserves (e.g., wolves, bears) that sustain a metapopulation structure (*sensu* Hanski and Gilpin 1991; USDA Forest Service 1997: N-16; Flynn *et al.* 2004). A small OGR comprising $\geq 16\%$ of national forest lands was established in each Value Comparison Unit (i.e., management unit) and was intended to provide functional habitat for animals dispersing between large and medium reserves and to ensure that the species of concern have a relatively high likelihood of occurring in each watershed $> 4,000$ ha (USDA Forest Service 1997: N-21). This implies that small OGRs must support populations of focal species of sufficient size and persistence (low risk of extinction) to ensure a high probability of dispersal from reserves as well as a high probability that populations will be present within individual watersheds (i.e., well distributed). Consequently, small OGRs must sustain populations for long enough to produce a sufficient number of dispersers to ensure successful emigration to neighboring reserves, or the distances separating small OGRs from larger OGRs must be sufficiently small to ensure a steady flow of immigrants and emigrants to and from small OGRs. Resistance of the landscape to movement by focal species and size and quality of small OGRs will likely determine the success of either strategy.

To monitor the effectiveness of the OGR strategy, the northern flying squirrel (*Glaucomys sabrinus*) was proposed as one of several management indicator species (Suring 1993) because its abundance may be correlated with old-growth forest structure and processes (Carey 2000) and because of specific habitat requirements for efficient locomotion (Scheibe *et al.* 2006). Its small size and home range (< 5 ha; Smith 2007) make it particularly well suited for evaluating the effectiveness of small OGRs (Smith *et al.* 2005). Previously, Smith and Person (2007) modeled the population dynamics of northern flying squirrels to determine the minimum patch size and habitat composition to sustain flying squirrel populations over the 100-year planning horizon. Their simulations indicated that flying squirrels had a low probability (0.66–0.73) of persisting in isolated small OGRs; furthermore, the minimum patch size to

sustain populations with a high probability (≥ 0.95) of persistence was an order of magnitude larger than the “preferred” prescription of 650 ha reserves with a composition of $\geq 50\%$ productive old-growth forest (USDA Forest Service 1997: Appendix K). Consequently, small OGRs specified by TLMP may function as sinks or metapopulation segments dependent on recolonization from larger reserves. Because dispersal by flying squirrels may be critical for the viability of flying squirrel populations within small – and possibly larger – OGRs, S. Pyare and W. P. Smith, in related studies, used field behavioral trials, radio-telemetry, and landscape analysis to quantify landscape connectivity in highly modified landscapes (Pyare and Smith 2005), and Flaherty *et al.* (2008) studied behavioral and energetic aspects of dispersal in managed landscapes. We combine results from Pyare and Smith (2005) and results from population modeling described by Smith and Person (2007) to evaluate the efficacy of small OGRs as a functionally connected network of reserves that provide temporary functional habitat for animals dispersing between large and medium OGRs. Our specific objectives were

1. to determine the number of immigrants required for flying squirrel populations in small OGRs to persist for 25 and 100 years;
2. to determine the maximum landscape resistance that could exist between small and larger reserves and still ensure the required number of immigrants.

We used those results to assess the value of small OGRs specified by TLMP for the conservation of northern flying squirrels within the Tongass National Forest. Because the conservation strategy assumed that viability of northern flying squirrels depended solely on old-growth forest reserves, our analysis excluded any contribution of the matrix to population viability except in considering landscape permeability and the probability of dispersal among old-growth reserves. The results of our analyses are useful in establishing general guidelines for designing a network of functionally connected reserves. We offer specific recommendations for the distribution of reserves to improve the likelihood of viable northern flying squirrel populations in managed landscapes of Southeast Alaska.

Study area

Southeast Alaska is unique because of many naturally fragmented landscapes, a dynamic geological history (MacDonald and Cook 1996), and its expansive coastal temperate rainforest (Harris and Farr 1974; Alaback 1982). 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 rainforests occur at lower elevations (<600 m) throughout the region. Fragmentation of old-growth forest habitats has increased substantially since the mid-twentieth century because of extensive clearcut logging throughout the region (USDA Forest Service 1997, 2003).

Smith and Nichols (2003) provide more detail about the region and the two major forest types that represent the ends of a continuum of forest canopy and a range of soil conditions in this region. High-volume old-growth stands (Julin and Caouette 1997) are primarily Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) forests (DeMeo *et al.* 1992) with a dense canopy of tall (>60 m), large (<2.5 m diameter) trees (Harris and Farr 1974; Alaback 1982) interspersed with small openings created by windthrow. Old-growth forests have not experienced any logging or anthropogenic disturbance and can vary in age from 300 to more than 500 years old, depending on exposure and natural disturbance. Secondary forests typically do not develop old-forest characteristics until 350 years following catastrophic disturbance (Nowacki and Kramer 1998). This is the primary habitat of the Prince of Wales flying squirrel, *Glaucomys sabrinus griseifrons* (Smith and Nichols 2003; Smith *et al.* 2004) and supports the highest mean densities recorded for the species (Smith *et al.* 2003; Smith 2007). In contrast, peatland-scrub/mixed-conifer forests typically have a sparse canopy, and understory vegetation varies from thick patches of shrubs to open peatland heaths. Flying squirrels can be abundant in this habitat (Smith and Nichols 2003; Smith *et al.* 2003; Smith 2007), but sex ratios in those populations are skewed toward males and the habitat probably does not sustain populations without immigration (Smith and Person 2007).

We used data from study sites located on Prince of Wales Island (55.9° N, 133.2° W; Fig. 19.1) to conduct our evaluation of small OGRs. Prince of Wales is the largest island in the Alexander Archipelago, a group of more than 20,000 islands that – together with a narrow mainland strip – comprise Southeast Alaska. Four decades of intensive logging in the study area has created an ideal setting for studying functional connectivity and the population dynamics of northern flying squirrels in managed landscapes. The landscape surrounding our study sites were composed of about 1% clearcut, 9% young (<25-year-old) second-growth, 38% older (25–50-year-old) second-growth, and 49% old-growth forests, including lower-volume peatland-scrub/mixed-conifer forests. The remaining 3% was non-forested, which included open peatland heaths.

In clearcuts, residual shrubs and tree seedlings grow rapidly within 5 years after canopy removal (Alaback 1982). A shrub community dominates the vegetation initially, but Sitka spruce and western hemlock seedlings, which become established at about the same time, overtop the shrub layer within 8–10 years after logging (Harris and Farr 1974). Shrubs and herbs are effectively eliminated after the forest canopies close, between 25 and 35 years post-harvest and

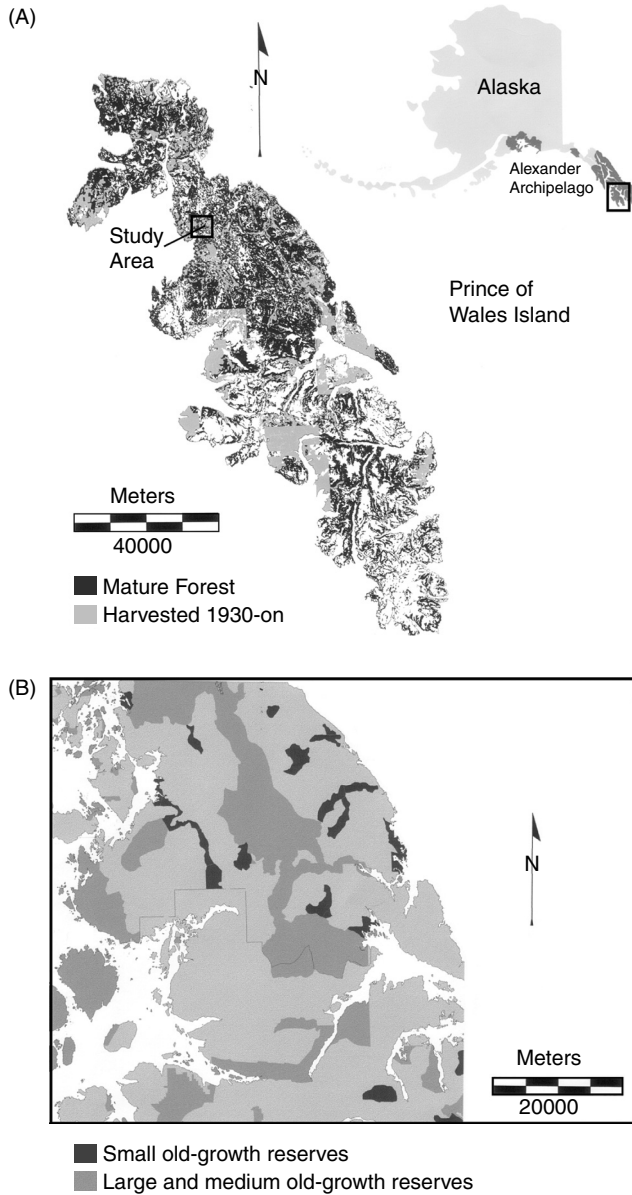


FIGURE 19.1.

(a) Study area, an extensively managed landscape of coastal temperate rainforest, Prince of Wales Island, Alexander Archipelago, Southeast Alaska. (b) Boundaries of old-growth reserves prescribed in the 1997 Tongass Land Management Plan (USDA Forest Service 1997) for northern Prince of Wales Island. Additional information regarding land use designations for the Tongass National Forest, including size and placement of old-growth reserves, can be found at <http://steffenrasile.com/staging/tetrattech/tongass/implementation-maps.php>.

usually do not become re-established until the stand age approaches 150 years (Alaback 1982). Secondary forests remain even-aged for up to 300 years before gradually transitioning into an uneven-aged condition (Harris and Farr 1974). Mean stem density in unthinned young ($\bar{x}$ = 19 years) second-growth stands ranges around 3,300–5,300 trees/ha, with the composition of spruce being 31–52%. Older ($\bar{x}$ = 57–60 years) second growth averages 3,450–5,300 trees/ha and an overstory composition that is 29–42% Sitka spruce (Deal and Farr 1994). Average 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). The sparse understory and lower abundance of preferred food items (Flaherty *et al.* 2008) render older second-growth stands unsuitable as habitat for northern flying squirrels; the structure of unthinned second-growth stands likely precludes their use as travel corridors. Indeed, small old-growth fragments (<50 ha) surrounded by second growth can become isolated and the local flying squirrel population extirpated (E. A. Flaherty and M. Ben-David, unpublished data).

The ability of northern flying squirrels to move through managed landscapes is significantly influenced by forest structure, and factors to take into consideration include perceptual range and fine-scale movements (Flaherty *et al.* 2008), cost of transport (Scheibe *et al.* 2006), and effective movement rates (Pyare and Smith 2005). Generally, the average length of straight-line movement increases and cost of transport decreases as forest canopy increases in height and stem density decreases. Friction (i.e., resistance to movement), and presumably risk of predation, is higher in clearcuts than mature forests; unthinned second-growth stands obstruct visibility and impede gliding.

Methods

We tested the functionality of small OGRs in two ways. First, we estimated the number of juvenile immigrants required for a flying squirrel population that had been reduced to a breeding pair within a small OGR to persist for short (25-year) and long (100-year) time periods. We excluded adult dispersal because our focus was evaluating the role of immigration in facilitating demographic rescue. We assumed that persistence over 25 years would represent the role of small OGRs as stepping-stones between larger reserves or as population sinks; whereas persistence for 100 years, which was the planning horizon in the 1997 TLMP, would also imply greater population stability in small OGRs contributing to metapopulation dynamics. We related the achievement of those persistence goals to dispersal rates from source populations and to the probability of successful dispersal as a function of habitat composition and distance between reserves. We assumed that source populations were supported solely by primary habitat because peatland-scrub/mixed-conifer forests depended

on immigration to sustain flying squirrel populations and likely produced few emigrants (Smith and Person 2007), and second growth was unsuitable (Smith and Nichols 2003; Flaherty *et al.* 2008).

The second way in which we examined functionality of small OGRs was to predict the number of immigrants necessary to ensure that a vacant reserve would be colonized by a breeding pair (i.e., dispersers included ≥ 1 member of each sex) given distance from a source population and the habitat composition of the landscape separating the reserves.

Emigration rate and dispersal probability

We used the proportion of radio-marked juvenile northern flying squirrels that left their natal area during autumn to estimate emigration rate. To distinguish juvenile movements as emigration, Pyare *et al.* (2010) computed the mean $\pm$ 95% confidence interval (CI) of Euclidean distances between natal dens and all subsequent den locations (67 dens among 21 juveniles). Permanent relocations with a displacement distance greater than the upper 95% CI were classified as emigrations.

Pyare and Smith (2005) estimated the probability of successful juvenile dispersal as a function of distance and habitat type. They used experimental translocations to measure the elapsed time and distance moved by flying squirrels coursing through different habitats: the ratio of distance traveled to elapsed time (effective movement rate) became a surrogate for landscape resistance. Specifically, they derived habitat-specific “effective distance” estimates to represent the effective travel distance of moving through a habitat patch after explicitly taking into account its landscape resistance. For example, because travel times were about 16 times greater in recent clearcuts than in intact old-growth forest, the effective distance of a clearcut crossing was relatively 16 $\times$ greater than moving a similar distance through uninterrupted old-growth forest. Effective distance estimates were derived experimentally for a subset of common habitats in the study area and subsequently modeled as a function of vertical forest height (Table 19.1). To estimate cumulative landscape resistance, the total effective distance was calculated by adding the effective distance of all habitats encountered during a specific dispersal event. Thus, dispersing through 1 km of continuous old-growth forest was equivalent to dispersing through 0.1 km of a recent clearcut; intermediate effective distances result from flying squirrels moving across a combination of habitats (Table 19.1). Because the exact pathway of dispersal events was not known, Pyare and Smith (2005) used minimum effective distances between points of origin and dispersal in all subsequent analyses. To estimate the dispersal probability of juveniles, the total effective distance of each juvenile that dispersed from the natal

TABLE 19.1. *Habitat-specific estimates of effective distance, which represents the distance that animals can effectively move through a patch after considering its resistance, i.e., the degree to which the habitat facilitates or impedes movement. Estimates were initially derived from a series of translocation experiments in a related study (Pyare and Smith 2005) and then subsequently modeled as a function of the vertical height of vegetation.*

Habitat type	Effective distance (m-equivalent)
Late successional conifer	1.00
Mesic conifer–peatland	1.00
Regenerating conifer stands (6–80 years)	1.00–15.58
Open peatland	5.34
Brush	5.34
Recent clearcuts (≤ 5 years)	15.58
Open other (alpine/development)	15.58
Major roads	15.58
Minor roads	15.58
Minor streams	15.58
Minor freshwater bodies	15.58
Saltwater crossings	999.000
Major freshwater bodies	999.000
Major streams/rivers	999.000

den to a new den was calculated, and the resulting proportions of the juvenile sample that dispersed over a range of observed effective distances was then used to derive the following dispersal probability function (Fig. 19.2):

$$P = -0.4559 * \ln [\text{effective distance, ft}] + 3.7644. \quad (19.1)$$

Probability of persistence

We followed the procedures of Smith and Person (2007) to compute probability of persistence (P_t) from predictions of time to extinction (T_e) using the following equation:

$$P_t = e^{-t/T_e} \quad (19.2)$$

where t is the time period for which P_t is calculated. Rearranging Eq. (19.1), we computed T_e for $P_t = 0.95$ and $t = 25$ years (comparable to the time horizon of the revised TLMP conservation strategy; USDA Forest Service 2008) and $t = 100$ years (time horizon of 1997 TLMP and typical of viability analyses of vertebrate populations). Time to extinction for 95% probability of persistence over a period of 25 years was 490 years; for a time horizon of 100 years, T_e was

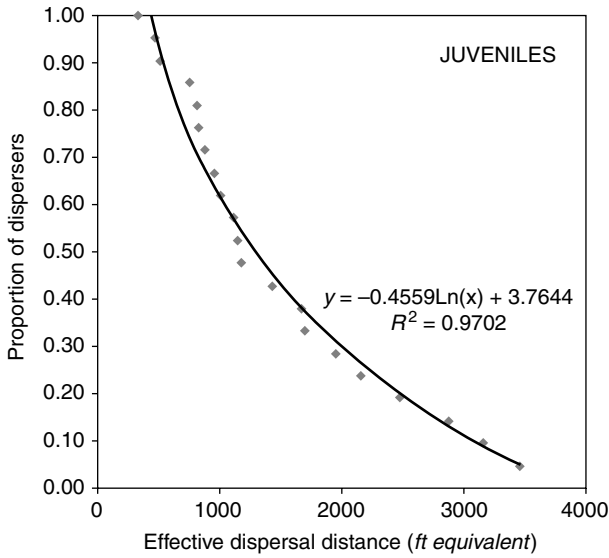


FIGURE 19.2.

Proportion of juvenile northern flying squirrels (*Glaucomys sabrinus*) that dispersed in managed landscapes of Southeast Alaska relative to effective distance (ft-equivalent), which was calculated by adding the effective distance (i.e., resistance or permeability) of different landscape elements, from Pyare and Smith (2005).

1,950 years. Smith and Person (2007) used a model described by Foley (1994) to estimate time to extinction (T_e) for northern flying squirrels in isolated small (650 ha) old-growth reserves:

$$T_e = \frac{k^2}{v} \left[1 + \frac{2}{3} \left(\frac{kr}{v} \right) \right]; \quad (19.3)$$

where k is the natural log of the population carrying capacity (K) of the reserve, r is the per capita rate of increase when the population is at low density relative to K , and v is the variance of r . The model incorporates density-dependent population growth, which dampens large fluctuations in population growth and increases the predictions of T_e compared with results from models that ignore density-dependent population growth. We rearranged terms in Eq. (19.3) to compute r , given T_e , K and v :

$$r = \left(\frac{3v}{2k} \right) \left[\left(\frac{T_e v}{k^2} \right) - 1 \right]. \quad (19.4)$$

We chose $v = 0.39$ because it was based on the variance in r reported for a 43-year population study of northern flying squirrels (Fryxell *et al.* 1998); the longest time series of population data in the literature for this species. Carrying capacity (K) was estimated for the two prescriptions of habitat composition for small old-growth reserves specified in TLMP (USDA Forest Service 1997) and

for a third scenario in which the entire reserve was composed of primary habitat for flying squirrels (Smith and Person 2007). For the “minimum” prescription in which $\geq 25\%$ of the habitat within the reserve was primary habitat, $K = 454$ squirrels. For the “preferred” prescription in which $\geq 50\%$ of a small OGR was primary habitat, $K = 910$ squirrels. If the entire reserve was primary habitat, $K = 1,820$ squirrels. We computed r for each value of K and for T_c equal to 490 and 1,950 years. This procedure generated estimates of r (for each value of K) necessary at low densities of flying squirrels to achieve a 95% probability of populations in small OGRs persisting for 25 and 100 years.

Smith and Person (2007) estimated an intrinsic value of $r = 0.14$ for flying squirrels that were undergoing rapid population growth at low density. Their value was estimated directly from birth and death rates and thus it represented intrinsic growth for a closed population (i.e., in the absence of immigration) well below carrying capacity. We compared their value with r calculated using Eq. (19.4) and assumed that the difference in values represented the contribution to population growth required from immigration to achieve 95% probability of persistence within small OGRs for 25 and 100 years.

To convert the difference in r to an annual number of dispersers, we constructed a simple logistic population growth model:

$$N_{t+1} = N_t + N_t r_i \left(1 - \frac{N_t}{K}\right) + d \quad (19.5)$$

where N_t is the population at time t , r_i is intrinsic r in the absence of immigration, K is carrying capacity of the reserve, and d is the number of dispersers per year. We assumed that the sex ratio of dispersers was 50:50. We began the simulation with a single breeding pair of flying squirrels and calculated N_t for three time steps that represented population growth at low density relative to K . For each simulation, we added a constant number of dispersers (d) and estimated average per capita rate of growth ($\bar{r}$) over the three time steps. We continued to increase d until the estimate of $\bar{r}$ equaled r predicted from Eq. (19.4). We used the estimate of $r_i = 0.14$ from Smith and Person (2007) and repeated simulations for $K = 454, 910$, and $1,820$ flying squirrels. Our procedure enabled us to predict the number of immigrant dispersers needed annually to achieve our stated goals for persistence of flying squirrel populations in small OGRs, given three different carrying capacities.

We modeled juvenile dispersal within hypothetical landscapes in which a small OGR was positioned between two medium OGRs ($\sim 4,000$ ha of $\geq 50\%$ primary habitat; USDA Forest Service 1997). That configuration was consistent with the intended purpose of small OGRs to function as stepping-stones between larger reserves or as components in a source-sink or metapopulation structure. We selected medium OGRs because they represented the smallest

reserve with a relatively high (0.85) probability of persisting in isolation for 100 years (Smith and Person 2007). To simulate dispersal from two medium OGRs to a connecting small OGR, we estimated the number of available dispersers by multiplying the average proportion of juveniles occupying primary habitat (0.193, SE = 0.395, $n = 254$; Smith and Nichols 2003) within the medium reserve multiplied by the average autumn population size (i.e., average population density $\times$ habitat acreage) in primary habitat (Smith and Person 2007). The number of available juveniles in the medium OGRs was multiplied by the proportion of radio-collared juveniles that emigrated (Pyare and Smith 2005) and was doubled to simulate dispersers emigrating from two source populations (i.e., one on each side). We used this information and output from the logistic growth model to estimate the maximum effective distance that could exist between small OGRs and medium OGRs and still meet demographic requirements in six scenarios that varied in habitat composition and time horizon. To calculate effective distance for each scenario, we substituted the proportion of juveniles needed into Eq. (19.1) (Pyare and Smith 2005).

To estimate the number of dispersers required to recolonize a vacant small OGR, we estimated the number of juvenile emigrants needed to establish a breeding pair, regardless of patch size, habitat composition, or time horizon. The probability that n dispersers are all one sex depends on the sex ratio of the source population and is estimated as $p^n + q^n$ for females (p) or males (q), respectively (Zar 1999: 517). We assumed that the source population did not depart from a 50:50 sex ratio (Smith and Nichols 2003) and calculated the number of juvenile dispersers (d) for a 0.95 probability of at least one immigrant being the opposite sex. As above, we used Eq. (19.1) to estimate the maximum effective distance between small and medium OGRs (Pyare and Smith 2005).

Results

The values of per capita growth rate needed for low populations to persist with a 0.95 probability ranged from 0.19 to 0.39 for populations to persist for 25 years, and from 0.97 to 1.85 for populations to persist for 100 years (Table 19.2). The number of annual dispersers needed to prevent flying squirrels from becoming extirpated for ≥ 25 years averaged one every 5 years for populations in small OGRs with 100% primary habitat and one per year for small OGRs with a "minimum" (25% primary habitat) prescription. An estimated 162 dispersers per year were needed to sustain populations for 100 years in small OGRs comprising 25% primary habitat (Table 19.3). For small OGRs in which flying squirrel populations are extirpated, ≥ 6 juvenile dispersers per year were needed in order to have a 0.95 probability that a breeding pair would reach the patch.

TABLE 19.2. *Number of annual dispersers (d) needed to achieve an average intrinsic rate of population growth (r) sufficient to achieve time to extinction (T_e) for time horizons of 25 and 100 years ($P_t = 0.95$; Smith and Person 2007) in reserves with three different carrying capacities (K) and populations that reach a low population density (at least one breeding pair) relative to K.*

Years	K	T_e	Average r	Ψ^a	d
25	454	490	0.39	2.8	1
25	910	490	0.27	1.9	0.5
25	1,820	490	0.19	1.4	0.2
100	454	1,950	1.85	13.2	162
100	910	1,950	1.32	9.4	30
100	1,820	1,950	0.97	6.9	10

^a The ratio of average r and intrinsic rate of growth of the study population (0.14), with a variance in $r_i = 0.39$ (Smith and Person 2007).

TABLE 19.3. *For scenarios that vary in habitat composition (K) and time horizons (Years), maximum effective distances between a small OGR serving as a functional stepping-stone and two medium OGRs for flying squirrels (Glaucomys sabrinus) to persist with 0.95 probability. Maximum effective distance (m – equivalents) delimits landscape connectivity that facilitates a minimum level of immigration for flying squirrel populations to persist with 0.95 probability (distance_{*i*}) or colonize a vacant reserve (distance_{*c*}).*

Scenario	Years	K	Maximum effective distance _{<i>i</i>} (m)	Maximum effective distance _{<i>c</i>} (m)
1	25	454	1,172	1,161
2	25	910	1,174	1,161
3	25	1,820	1,174	1,161
4	100	454	844	1,161
5	100	910	1,105	1,161
6	100	1,820	1,151	1,161

Maximum effective distances for 0.95 probability persistence over 100 years ranged from 844 m for small OGRs with 25% primary habitat to 1,151 m for small OGRs comprised of 100% primary habitat (Table 19.3). Corresponding values for persistence in small OGRs over a 25-year time horizon were 1,172 m and 1,174 m. Maximum effective distance to establish a breeding pair in vacant small OGRs was 0.1% less than in circumstances when dispersal supplemented

r_i during 25-year time horizons (Table 19.3). For a 100-year horizon, the maximum effective distance to establish a breeding pair in a vacant small OGR was 38% greater than in circumstances when dispersal augmented populations in small OGRs composed of 25% primary habitat; the difference was <0.1% for small OGRs composed of 100% primary habitat (Table 19.3).

Discussion

Our study makes at least three contributions to the science and application of conservation. First, it demonstrates the value of linking applied ecological research to a sound theoretical foundation. A thorough understanding of source–sink dynamics is fundamental to evaluating the effectiveness of habitat reserves in sustaining viable metapopulations across fragmented landscapes. Also, our study illustrates that achieving a greater understanding of the spatially explicit dynamics of source and sink populations in fragmented landscapes can guide conservation planning toward sustainability. Lastly, our study illustrates the need, feasibility, and value of evaluating the assumptions of conservation plans. The 1997 TLMP reserve network has a sound theoretical framework. Without empirical evidence to support the underlying assumptions, its effectiveness in sustaining well-distributed and viable wildlife populations and the utility of habitat reserve networks remain uncertain.

Probability of dispersal and functional connectivity

We explicitly defined and quantified landscape resistance with empirical data, used those empirical data to parameterize models of functional connectivity, and generated model output that is meaningful for land use planning and conservation of biological diversity (Schumaker 1996; Ruckelshaus *et al.* 1997; Tischendorf and Fahrig 2000; Richards *et al.* 2002). Specifically, we combined results of population modeling (Smith and Person 2007) with logistic growth modeling and simulations of natal dispersal in hypothetical landscapes in order to determine the number of immigrants required for northern flying squirrel populations in small OGRs to function as sinks sustained through immigration from nearby source populations (short term), or to be components of a metapopulation structure that sustains viable populations (long term). We found that the number of dispersers needed per year to achieve an intrinsic rate of population growth to avoid extinction over the short term was well within the range of what source populations can produce annually (Smith and Nichols 2003). The maximum effective distance between small OGRs and source populations required to achieve persistence was not much more than a kilometer. For small OGRs to contribute to metapopulation viability, the number of

required dispersers ranged 1–2 orders of magnitude greater than that needed for small OGRs to be sustained in the short term. Moreover, maximum effective distances for the long-term horizon were shorter than short-term scenarios, especially for small OGRs that meet the Tongass Land Management Plan (TLMP) minimum habitat prescription.

For population enhancement, the range of maximum effective distances was relatively narrow and the distribution was skewed toward the maximum value, especially among scenarios with a 25-year horizon. Even the maximum value of 1,174 m falls well within the distance that juveniles can move through intact landscapes (~7 km) over relatively short time periods (48 hours; W. P. Smith, unpublished data). Unfortunately, fewer than half the small OGRs prescribed in the 1997 TLMP for northern Prince of Wales Island were functionally connected to a source population (Pyare and Smith 2005). Since the initial drafting of this manuscript, some revisions have been made to the configuration of small OGRs across the landscapes we analyzed in this chapter (USDA Forest Service 2008). However, revisions have been relatively minor and further analysis revealed that functional connectivity may have been reduced rather than improved (S. Pyare and W. P. Smith, unpublished data). For 51 small OGRs that on average comprised 64% primary habitat, effective distances to large tracts ($\geq 4,000$ ha) of protected old-growth forest (i.e., medium or large OGRs) were such that only 20 reserves were located in landscapes where juvenile dispersal would be likely to occur, and these were essentially contiguous (S. Pyare and W. P. Smith, unpublished data). Therefore, the probability of juvenile dispersal between small OGRs and large tracts of old-growth in our study area was either 1 or approached zero.

Because flying squirrel populations are unlikely to persist over the long term in isolated small OGRs (Smith and Person 2007), the role of small reserves within the TLMP conservation framework is to function as stepping-stones connecting larger reserves, i.e., sinks that support ephemeral populations that are frequently replaced and enhance the distribution of flying squirrel populations (i.e., functional components within a metapopulation). Our findings underscore the essential role of immigration in sustaining sinks or facilitating metapopulation viability among unsustainable fragmented populations (i.e., sinks) and the extent to which permeability of landscape elements can influence the probability of dispersal and functional connectivity of subpopulations in a managed matrix (With and Crist 1995; Schumaker 1996; Richards *et al.* 2002; Verbeylen *et al.* 2003; Baum *et al.* 2004; Pyare and Smith 2005; Smith and Person 2007).

Assumptions and limitations

We considered only juvenile emigrants because our goal was to assess the potential for small OGRs to facilitate demographic rescue. Adult males

often undertake long forays (4–5 km) during spring in search of estrous females, but it is juvenile squirrels vacating their natal areas that provide a pool of emigrants to supplement existing populations or colonize vacant patches (Wilson 2003, 2010). Also, we limited our simulations to scenarios in which dispersal occurred between two medium OGRs and a single small OGR because the assumption in the 1997 TLMP was that small reserves would serve as “stepping-stones” between larger reserves. For the purpose of this chapter, the consequences of limiting our analysis to those scenarios are probably negligible. When we varied the probability of emigrants selecting a target small OGR (i.e., a situation with multiple small OGRs within the dispersal distance of medium OGRs) the maximum effective distance changed little (<1%). Exceptions did occur for scenarios with the lowest K over a 100-year time horizon, which are unlikely to persist and produce dispersers (Smith and Person 2007).

Most of our modeling assumptions resulted in more optimistic scenarios of dispersal and persistence. For example, our estimates of per capita rate of growth (0.14) and available dispersers (juvenile proportion $\times$ population size) are generous given the mean recruitment rate of juveniles into the breeding population (i.e., the proportion of juveniles in the autumn population) incorporated no overwinter mortality (Smith and Person 2007). Furthermore, we assumed that all natal dispersers successfully established home ranges and contributed to the breeding population of reserves; a liberal assumption given expected energetic constraints while dispersing in managed landscapes (Flaherty *et al.* 2008) and added risk of predation. Also, our predictions of persistence in small OGRs and our assumption that medium OGRs function as source populations are probably optimistic (Smith and Person 2007).

We did not consider environmental or genetic stochasticity (Foley 1994; Reed 2004), deleterious effects of inbreeding (Frankham 1998; O’Grady *et al.* 2006), or potential Allee effects (Allee *et al.* 1949). Also, we assumed that habitat available to flying squirrels remained unchanged over the time horizon, 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 nearshore island populations (Bidlack and Cook 2001). The sensitivity of predictions of T_c and P_t to changes

in v (Smith and Person 2007) underscores the potential for additional environmental and genetic variability to increase predicted probabilities of extinction in reserves.

Implications for conservation planning

Land management plans such as TLMP rely on systems of habitat reserves that are sufficient in size and quality, or are adequately distributed and connected, to ensure the viability of wildlife populations (Smith and Zollner 2005). Habitat reserves must either sustain individual insular populations, or the managed matrix between reserves must allow dispersal among reserves to maintain wildlife populations within a metapopulation structure. In Southeast Alaska, the primary habitat component of large old-growth patches may not need to be contiguous because interspersed habitats (e.g., fens, peatland mixed-conifer forests) can clearly support flying squirrels for a short time or facilitate dispersal (Smith and Nichols 2003; Pyare and Smith 2005). 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 larger or other small reserves. For this reason, conservation planning that explicitly considers the quality and spatial configuration of habitat across highly modified landscapes (Odom *et al.* 2001; Fuller *et al.* 2006) will have a greater likelihood of sustaining viable metapopulations of flying squirrels (Hanski *et al.* 2000; Selonen and Hanski 2003, 2004).

We estimated the maximum effective distance between larger reserves and a small OGR that would achieve an immigration rate sufficient to persist for 25 or 100 years or colonization by a breeding pair. Maximum effective distance, which accounts for the landscape resistance of different habitats, is dependent upon forest structure (Pyare and Smith 2005). In our study, maximum effective distance for supplementing populations and establishing a breeding pair were essentially the same for $P_t = 25$ (1.1 km). Thus, spacing small OGRs at an effective distance of one kilometer across old-growth habitat would probably facilitate both recolonization of vacant reserves and supplementation of existing populations. For $P_t = 100$ years, the maximum effective distance for supplementing populations was less than the effective distance for recolonization. Small OGRs that meet the TLMP minimum prescription of 25% productive old-growth (POG) should probably be <850 m from other reserves; small OGRs comprised of $\geq 50\%$ primary habitat (i.e., POG) can probably be spaced at 1-km intervals in landscapes composed of old-growth forests. We suggest the smaller of those distances be used as a guideline for the spacing

of reserves, conditional on the time horizon for persistence and the carrying capacity of the reserve.

Clearly, our study does not represent an evaluation of the overall conservation strategy implemented in TLMP with respect to northern flying squirrels. Still, we conclude that most small OGRs on Prince of Wales Island (as described in the 1997 TLMP; USDA Forest Service 1997) were not functionally connected. Maximum effective dispersal distance for northern flying squirrels was ≤ 1 km, whereas the mean expected distance between small OGRs to achieve well-distributed populations (USDA Forest Service 1997) was ≥ 5 km (i.e., the radius of circular watersheds, which averaged 7,700 ha). Consequently, the extent of functional connectivity among reserves or between small OGRs and larger patches of primary habitat require fundamental changes in reserve design if metapopulations of flying squirrels are expected to have a high probability (i.e., ≥ 0.95) of persisting in managed landscapes. Even then, a system of functionally connected reserves does not ensure a viable metapopulation in managed landscapes. 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). Furthermore, as landscapes become increasingly fragmented, a threshold point is reached where metapopulations are limited solely by production in the source habitats (Davis and Howe 1992).

Sustaining viable populations of the northern flying squirrel (and the ecological communities it represents) in Southeast Alaska may require adaptive management, i.e., an iterative process of revising conservation plans and further study. Admittedly, testing the adequacy of a system of reserves for conservation of wildlife can be a daunting task, requiring long-term (decades) population monitoring and studies of animal behavior and demography. However, we demonstrated that short-term evaluations of a plan are possible using empirical data to parameterize simple simulation models designed to evaluate the underlying assumptions.

Nevertheless, we believe the system of small OGRs implemented in the 1997 TLMP would have a substantially higher probability of sustaining metapopulations of flying squirrels if the composition of primary habitat in small OGRs was increased to levels that will provide a relatively high probability of sustaining reserves without immigration (Smith and Person 2007), or if the permeability of habitat comprising the matrix was improved through active management to resemble old-growth. For example, pre-commercial and commercial thinning of second-growth stands, which are less permeable to

northern flying squirrels (E. A. Flaherty and M. Ben-David, unpublished data), will increase canopy height and create more open space in the midstory, both of which facilitate efficient gliding (Vernes 2001; Scheibe *et al.* 2006). In any case, active management of second-growth stands will likely hasten succession toward achieving stand conditions that will support additional breeding populations of northern flying squirrels, potentially adding stepping-stones and migrants to a network of old-growth reserves.

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