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Survival and population growth rate of the threatened Siberian flying squirrel (*Pteromys volans*) in a fragmented forest landscape[1]

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Abstract: Habitat loss is the major phenomenon threatening species in the boreal forests. One example of a threatened species affected by habitat loss is the Siberian flying squirrel (*Pteromys volans*). We used mark–recapture data from 1992 to 2004 for 3 flying squirrel populations to estimate the demographic parameters of these populations. Average adult survival was 0.43–0.53, and probability of surviving and staying near the natal territory through the first winter was 0.23–0.30 in different populations. These values are low compared to survival estimates presented in the literature for other Sciurid species. The estimated population growth rates indicated population decline in all areas. In one of the areas, we found a decline in adult survival and population growth rate during the study. This decline was demonstrated to be linked to ongoing habitat loss due to logging. Low survival and emigration probabilities suggest that these populations are likely to be sinks. This highlights the need to ensure dispersal between the remaining patches of suitable habitat for successful conservation of this and other species associated with old-growth forests. The situation is worrisome as the studied populations are situated in an area where flying squirrel population densities have traditionally been high.
Keywords: habitat loss, mark–recapture, source–sink.

Résumé : La perte d'habitat est la cause principale qui menace les espèces des forêts boréales. Un exemple d'une espèce menacée par la perte d'habitat est le polatouche de Sibérie, *Pteromys volans*. Nous avons utilisé des données de marquage-recapture de 1992 à 2004 pour 3 populations de polatouches afin d'évaluer les paramètres démographiques de ces populations. La survie moyenne des adultes était de 0.43–0.53 et la probabilité de survie et de présence près du territoire natal après le premier hiver était de 0.23–0.30 dans différentes populations. Ces valeurs sont faibles en comparaison avec les valeurs estimées présentées dans la littérature pour la survie d'autres espèces de sciuridés. Les taux de croissance démographique estimés indiquaient un déclin des populations dans tous les secteurs. Dans un des secteurs, nous avons trouvé une baisse de la survie des adultes et du taux de croissance démographique au cours de l'étude. Il a été démontré que ce déclin était lié à la perte d'habitat en cours causée par la coupe forestière. La faible survie et les probabilités d'émigration suggèrent que ces populations sont probablement des puits. Cela met en évidence la nécessité d'assurer la dispersion entre les parcelles restantes d'habitat approprié pour le succès de conservation de cette espèce ainsi que d'autres associées aux forêts anciennes. La situation est inquiétante puisque les populations étudiées sont situées dans un secteur où les densités de population de polatouches étaient traditionnellement élevées.
Mots-clés : marquage-recapture, perte d'habitat, source-puits.

Nomenclature: Latin binomials are those used by original authors.

Introduction

Loss, degradation, and fragmentation of habitats have major negative impacts on species worldwide, affecting almost 90% of threatened birds, mammals, and amphibians (Baillie, Hilton-Taylor & Stuart, 2004). In Finland forest structure and composition have changed dramatically due to modern forestry, which is the primary threat for one third of the endangered species in Finland (Rassi *et al*., 2001). Natural forests have for the most part been replaced by managed monoculture forests (Östlund, Zackrisson & Axelsson, 1997). Small and isolated good-quality habitat patches support only small populations that rapidly lose genetic variation and have a high extinction risk. Species adapted to connected landscape are less likely to persist in modern highly fragmented landscapes (Hanski, 2005). Predicting the impact of habitat loss or fragmentation requires information about the biology and habitat use of the species in question. The response to fragmentation may vary from no effect at all to considerable population decline, depending on species-specific dispersal ability and resource requirements (Wiegand, Revilla & Moloney, 2005). Nevertheless, the (meta)populations cannot be viable if the number of suitable patches in the landscape falls below a threshold, because colonization and extinction events are not balanced in the habitat patch network (Hanski, 2005). Populations of threatened species are typically small, which highlights the

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importance of demographic variance when assessing their viability (Shaffer, 1981; Morris & Doak, 2002). Inbreeding, Allee effect, and stochasticity together expose small populations to extinction more often than large ones. Acquiring information on demographic rates (survival, recruitment, and migration) and their variation is challenging, especially in rare species. Long time-series with individual data are needed to allow for the variance in population demography and environment (Lande, Engen & Sæther, 2003).

Estimates of apparent survival, reproductive rate, and movement can be used to determine the contribution of a local population to the larger population at the landscape level (Runge, Runge & Nichols, 2006). A population is a sink if mortality exceeds reproduction and immigration exceeds emigration. A source, on the other hand, is a population in which births exceed deaths and emigration exceeds immigration (Pulliam, 1988). Estimation of reproductive rate and apparent survival probability is fairly straightforward with mark–recapture methods, where individually marked animals are followed through time. Reliable estimates of emigration are considerably harder to get. However, excluding emigration when quantifying habitat quality will lead to biased results if all disappearing individuals are considered mortalities when in fact some are emigrants. Areas exporting a lot of individuals will be seen as sinks (Runge, Runge & Nichols, 2006). The effect of environmental deterioration is especially deleterious if source populations are turned into sinks (Hanski, 2005). When source populations are negatively affected, the effect spreads to sink populations (see for example Peery, Becker & Beissinger, 2006; Tittler, Fahrig & Villard, 2006). Classifying local populations is important in decision making. The number of individuals that the habitat is producing and exporting has to be estimated in order to direct management actions to the right areas.

In Finland, Siberian flying squirrel, *Pteromys volans* (hereafter flying squirrel), population censuses show a decline of about 50% from the 1950s to the 1980s (Hokkanen, Törmälä & Vuorinen, 1982). In a recent nationwide assessment the female population size was estimated to be 143 000, and the observed population decline was severe: 30–58% in 3 y (2003–2005; Hanski, 2006). The Finnish Ministry of Environment has classified the flying squirrel as an endangered species with IUCN threat category Vulnerable (Rassi *et al*., 2001). In addition, the European Union has included it in Habitats Directive Annexes II and IV, which include species requiring special areas for conservation (Anonymous, 1992). The decline of flying squirrels, as well as many other boreal forest species, is believed to be due to habitat loss associated to modern forestry practices (Hokkanen, Törmälä & Vuorinen, 1982; Rassi *et al.*, 2001). The flying squirrel habitats are of great interest to forest management and other land use, and there has been public debate over the conservation of the flying squirrel in Finland. Data on flying squirrel habitat use and movement patterns is already available. Occupied patches are generally larger in size, contain more deciduous trees, and are closer to other occupied patches than unoccupied ones (Hurme *et al.*, 2007). However, estimates of vital rates are practically lacking in the Siberian flying squirrel and most other flying squirrel species. Survival probabilities and reproductive success are essential in determining the sensitivity of population growth rate to changes in vital rates and assessing which individuals are affected most by the disturbance. For example, males are able to somewhat compensate for the effects of habitat fragmentation by expanding their home ranges to include more patches. The females, on the other hand, are more restricted to a single patch and may face greater difficulties trying to compensate for the habitat loss (Selonen, Hanski & Stevens, 2001).

The conservation of flying squirrels may prove to be beneficial for other taxa. Forests occupied by the flying squirrel are characterized by higher amounts of coarse woody debris, which are essential for one fourth of the forest-associated species in Finland (Siitonen, 2001). Many of these species (especially polypores, lichens, and beetles) are now endangered in Finland due to habitat loss (Rassi *et al*., 2001). Recently, Hurme *et al*. (2008) have suggested that the flying squirrel could indeed be used as an umbrella species in biodiversity conservation in Finland.

The objective of this paper is to provide estimates of adult survival probability, local recruitment, and population growth rate in 3 small populations of the flying squirrel. In light of the continuous population decline in the country, we suspect decline in these populations. We examine the negative effects of habitat loss on survival and population growth, with the expectation that the habitat loss in these populations has resulted in reduced survival, recruitment, and population growth. Furthermore, we evaluate the source–sink status of these populations.

Methods

The Siberian flying squirrel

The distribution of the flying squirrel ranges from Hokkaido, Japan to Estonia and Finland. Its range in Finland extends from the south coast to southern Lapland, where the distribution becomes patchy (Wilson & Reeder, 1993; Reunanen, 2001). The flying squirrel is a small nocturnal arboreal rodent that prefers mature mixed forests with deciduous trees for feeding and large Norway spruces (*Picea abies*) as cover from predators (Hanski, 1998). Tree cavities are preferred as nesting or roosting places, but flying squirrels accept nest boxes and twig dreys of the red squirrel (*Sciurus vulgaris*). Site fidelity of adult flying squirrels is high (Hanski *et al*., 2000). Natal dispersal distances are on average 2 km but can be up to 9 km (Selonen & Hanski, 2004).

Data collection and study areas

We studied flying squirrel populations in 3 areas (Figure 1). We classified 70–80-y-old and older mixed spruce-dominated forests as potentially suitable breeding habitat for flying squirrels (Reunanen, 2001). Nest boxes were placed in forest patches of various sizes (1–25 ha). Generally, the boxes were situated in sets of 3 and checked in June and August and once during the winter. To estimate annual survival, only the summer observations were used in this study. Clear-cuts destroyed some of the nest boxes, but in some cases the boxes were moved into a nearby forest after logging. Therefore, the total density of boxes increased

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somewhat during the study. Flying squirrels are willing to accept nest boxes in this area due to a lack of other cavities. Radio-tracking suggested that 90% of the females in the studied areas use nest boxes during the breeding season (R. Wistbacka, unpubl. data), while the males are less dependent on them.

Flying squirrels were captured in the nest boxes, sexed, weighed, and marked with gilded ear-tags (Hauptner 73850, Hauptner, Germany). Juveniles were captured while they were still with their mother. The handling of animals followed the ASM guidelines (Gannon *et al*., 2007) as well as the laws of Finland and was approved by the animal care and use committee in Finland.

The Mustasaari study area is in western Finland (Figure 1), southeast of the city of Vaasa. The total area is 375 ha, of which roughly 110 ha are covered by small forest patches suitable for the flying squirrel. The rest of the area consists of clear-cuts, thinned forests, fields, summer cottages, and water. During the study (1992–2004) the amount of flying squirrel habitat decreased by approximately 34% and the average patch size decreased from 7.7 ha (± 7.9 SD) to 4.9 ha (± 4.2). The data include capture–recapture histories of 59 females and 68 males (Figure 2). Altogether, 123 female and 125 male cubs were marked; annual numbers varied from 4 in 1996 to 38 in 2000.

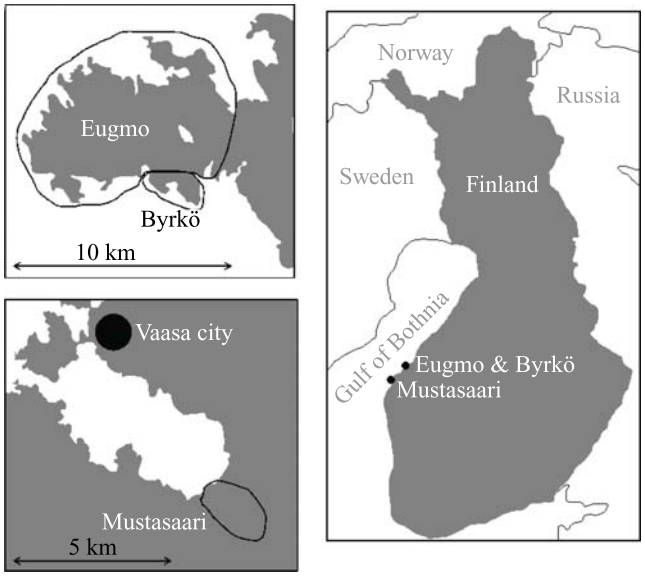


FIGURE 1. Study areas are situated on the west coast of Finland. Eugmo and Byrkö areas are situated on a peninsula.

Byrkö and Eugmo are on a peninsula about 100 km north of Mustasaari (Figure 1). The area was divided into a small (400 ha) intensively studied area (Byrkö) and a larger area of 4400 ha (Eugmo), where approximately 50–75% of the territory was consistently monitored through the years.

The more intensively studied Byrkö is located on the southern shore of the peninsula (Figure 1). When the study started in 1993 approximately 120 ha of the 400 ha were considered suitable habitat for flying squirrels. During the study the area of suitable habitat decreased by 31% and the average patch size decreased from 8.7 ha (± 6.0) to 5.7 ha (± 4.8). Despite the recent clear-cuts, the forest near the shoreline is intensely inhabited by flying squirrels. There were 20 sets of nest boxes. Fifty-one adult females and 55 males (Figure 2) were captured during the study (1993–2004). Altogether 120 female and 118 male cubs were marked in Byrkö. The lowest number of juveniles (9) was found in 2001 and the highest (31) in 2003. Byrkö is geographically adjacent to the larger Eugmo area. Byrkö and Eugmo are separated by 2 km of pine forest, open fields, and a road. There were only a few observations of flying squirrels moving between the areas: only 4 juveniles were successfully recruited from Byrkö to Eugmo during the study, and no adults were found to breed in both areas.

The main habitats in Eugmo are shoreline spruce-dominated mixed forest with summer cottages. Spruce-dominated forests are rapidly being replaced by cultivated Scots pine (*Pinus sylvestris*) forests. Thirty-five percent of the suitable habitat was lost from 1994 to 2004, and the average patch size decreased from 10.6 ha (± 7.0) to 8.1 ha (± 4.8). There were 31 sets of nest boxes in Eugmo. Seventy-five female and 102 male individuals were captured in Eugmo during 1994–2004 (Figure 2).

MODEL SELECTION

The most elegant way of analyzing the survival probabilities and population growth rate in relation to amount

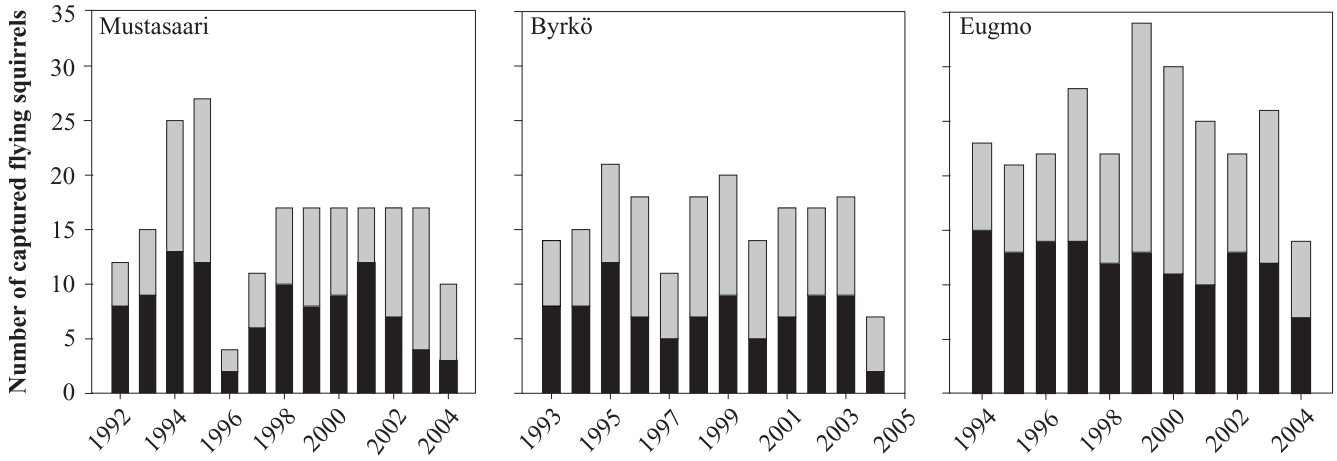


FIGURE 2. Annual numbers of captured flying squirrels. Black bars represent females and grey bars represent males.

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of suitable habitat would have been to pool the data from all the populations and explore the relationship between survival (or λ, *population growth rate*) and habitat by including the interaction term Population × Habitat in the models (Beissinger & Snyder, 2002). However, the study was initiated in different years in each area (1992 in Mustasaari, 1993 in Byrkö, and 1994 in Eugmo), and the effort of catching the animals was different in Eugmo than in the other areas. Pooling the areas together result in problems finding a suitable global model that would structurally fit the data and would not include too many parameters considering the sparse data. Thus, we modeled each population separately.

For model selection and parameter estimation we used the capture–mark–recapture methodology for open populations (Lebreton *et al*., 1992; Pradel, 1996). With the parametric bootstrap approach provided in MARK 5.1 (White & Burnham, 1999), we assessed the fit of the most highly parameterized model in the *a priori* chosen set of candidate models (the global model) and corrected for overdispersion and small sample size (Lebreton *et al.*, 1992). In all cases the estimated values were satisfactory, indicating that the global model structurally fitted the data (P = 0.17 – 0.51; $\hat{c}$ = 1.00 – 1.36). The overdispersion ($\hat{c}$) estimates for fully time-dependent models were used for Pradel's models as well. Model selection was based on Akaike's Information Criterion corrected for small samples and overdispersion ($QAIC_c$) and evidence ratios calculated with Akaike weights (w; the relative likelihood of model *i versus j*, which is identical to w_i/w_j; Burnham & Anderson, 2002). We used the total variance (σ^2_{total}) and the temporal process variance ($\sigma^2_{process}$) given by the program MARK to calculate the percentage of sampling variance ($1–\sigma^2_{process}/\sigma^2_{total}$).

Parameter estimation

We estimated the *apparent adult survival*, which refers to individuals that were at least 1 y old, survived through the winter, and stayed in the study area (Table I). We expected a decline in survival (or increased permanent emigration) due to increased clear-cutting in the study areas. Therefore, we fitted models with a linear trend in survival probabilities (Φ_{trend}, where year is indexed as a continuous covariate), and in other models the survival was constrained to be a function of the total amount of suitable habitat (hectares) in the study area ($\Phi_{habitat}$). For Mustasaari and Byrkö annual habitat estimates were available, but for Eugmo the data were only available from 1993, 2002, and 2004.

We simplified the global model by eliminating parameters one at the time, starting from the recapture parameter P. The global model for estimating adult survival included additive time and sex effect on survival and recapture probability. The sparse data would not support a high level of model complexity, and therefore we did not include interaction terms that would add several extra parameters to the model (Burnham & Anderson, 2002). We expected the recapture probability to depend on sex for 2 reasons: first, natal dispersal is female biased (Hanski *et al*., 2001), which may result in a lower recapture probability for females marked as juveniles. Second, breeding females seem to be more dependent on nest boxes than males, who spend a lot of time in the twig dreys of the red squirrel (R. Wistbacka, pers. observ.), and therefore females are more likely to be recaptured than males.

Local recruitment refers to individuals that were born in the study area, survived, and remained there through their first winter. Thus, this parameter is a function of first-year survival and site fidelity. To estimate local recruitment, data on newborn individuals marked in nest boxes were used (*i.e.*, animals of known age). We did not start with the fully time-dependent model because our data were sparse. Instead, the global model included 2 age classes (first-year and older animals), with sex and time effects on the first age class only. Adult survival was modeled as constant, and the recapture probability was different for males and females: $\Phi_{a0*t*s,\ a1+} P_s$ (a0 = juvenile; a1+ = adult, t = time, s = sex, * = interaction).

To estimate the *population growth rate* (λ) we used the reverse-time methodology of Pradel (1996). We pooled the data from both sexes to improve the precision of the estimates. The global model for estimating population growth rate was the fully time dependent model (Table I). During the first years of the study, the flying squirrels may not yet have located the nest boxes in the area. It also takes time for the field workers to establish the routine. Therefore, for estimating the population growth rate, we excluded the first 2 y in each data set (see Hines & Nichols, 2002; Rotella & Hines, 2005, and Williams, Nichols & Conroy, 2002 for discussion of the model assumptions). Based on our field observations, we believe that approximately 2% of the marked flying squirrels lost the ear tag, which should not have severely affected estimates of survival or growth rate as the recapture probabilities were satisfactory (Rotella & Hines, 2005).

Source–sink status of the populations

We wanted to assess if the populations were actually sink populations. Recently, Runge, Runge, and Nicols (2006) proposed a contribution metric (C^r) that "describes the proportional contribution a local population makes in

TABLE I. Models for estimating adult survival (1 – 9), and population growth rate (λ, 10 – 14). $\Delta QAIC_c$ = the difference between each model and the "best" model (lowest AIC_c); Φ = survival; P = recapture probability; c = constant; s = sex; t = time; trend = linear trend; habitat = area of suitable habitat; + = additive effect; 2 estimates = estimates for the first and the second half of the study period. Ps was used for models 1 – 7. The models with lowest AIC_c are indicated in bold.

	Model	$\Delta QAIC_c$ / AIC weight (shown when > 0.05)		
		Mustasaari	Byrkö	Eugmo
1	Φ_c	15.95	**0.00 / 0.33**	3.67 / 0.09
2	Φ_s	17.82	1.70 / 0.14	4.88 / 0.05
3	Φ_{trend}	16.15	2.07 / 0.12	**0.00 / 0.53**
4	$\Phi_{habitat}$	17.55	2.05 / 0.12	5.51
5	$\Phi_{s + trend}$	18.12	3.78 / 0.05	1.60 / 0.24
6	$\Phi_{s + habitat}$	17.55	3.78 / 0.05	6.77
7	Φ_t	**0.00 / 0.64**	2.02 / 0.12	5.73
8	$\Phi_{s + t\ P\ c}$	2.77 / 0.16	3.81 / 0.05	14.19
9	$\Phi_{s + t\ P\ s}$	2.32 / 0.20	6.15	7.89
		$\Phi_t\ P_c$	$\Phi_c\ P_c$	$\Phi_c\ P_c$
10	λ_c	10.81	**0.00 / 0.48**	3.98 / 0.06
11	$\lambda_{2\ estimates}$	12.75	2.09 / 0.17	1.52 / 0.21
12	λ_{trend}	12.75	2.06 / 0.17	1.03 / 0.27
13	$\lambda_{habitat}$	12.13	1.99 / 0.18	**0.00 / 0.45**
14	λ_t	**0.00 / 0.87**	12.42	8.12

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one time step to the metapopulation ….” C^r “integrates the processes of local recruitment, survival, site fidelity, and emigration, but assumes nothing about population equilibrium.” In many cases the data do not allow for an estimation of emigration probabilities. One solution is to solve C for the unknown emigration probabilities and to present a range of values where the population would be classified either as a source or as a sink (Runge, Runge & Nichols, 2006). We used this approach for Mustasaari, where emigration data were not available. For Byrkö we estimated emigration parameters using the observed emigrants from the Byrkö area found in the adjacent Eugmo area.

For solving emigration probabilities, we used the estimated mean adult survival and mean local recruitment for females for each population (see Runge, Runge & Nichols, 2006 for more details). For Eugmo, we used local recruitment estimates from Byrkö. The birth rate (female offspring per adult female) for Mustasaari was $\beta^M = 1.15$ and $\beta^B = 1.14$ for Byrkö.

Results

ADULT SURVIVAL AND LOCAL RECRUITMENT

The most parsimonious model for Mustasaari suggested time variation in survival and sex-dependent recapture probability (Model 7, Table I). It was 3.2 times better supported by the data than model 9, which included sex effects on survival. However, the actual difference in the sex-specific survival estimates was negligible. Adult survival was on average 0.43 (± 0.07 SE) over the years (Figure 3). The recapture probability was higher for female (0.95 ± 0.05) than for male (0.75 ± 0.12) flying squirrels. The temporal process variance ($\sigma^2_{process}$) in adult survival was 0.031 (CV = 0.42), and 35% of the total variance was due to sampling variance. The range of the annual estimates was wide, with fairly large standard errors (0.11 ± 0.06 – 0.92 ± 0.15). Models with constant survival, a linear trend, or amount of habitat were not well supported by the data (Table I).

In Byrkö the recapture probability was high and similar for both sexes (0.79 ± 0.06). Models 1–4 and 7 were almost equally supported by the data ($\Delta QAIC_c < 2.1$). Model 1 suggested constant survival over the years. Average adult survival was higher (0.53 ± 0.04) than in Mustasaari. Model 2 included the sex effect in survival, suggesting slightly higher survival for male (0.55 ± 0.05) than female (0.50 ± 0.06) flying squirrels. According to the time-dependent model (7), the lowest survival estimate (0.17 ± 0.10) was found in 1996-97 and the highest (0.79 ± 0.14) was observed in 2001-02 (Note however the large SE in Figure 3). Sampling variance accounted for 39.8% of the total variation.

Adult survival seems to have decreased in Eugmo during the study (Figure 3). Model 3, with a linear trend in survival estimates, was 2.2 times more likely to be the best model than model 5, which also included the declining trend in survival. Together the AIC weight for these models was 0.77. The estimated survival probabilities were 0.62 ± 0.07 for 1994-95 and 0.34 ± 0.07 for 2003-04. The survival estimates from model 5 were sex-specific and declining, and survival probability was higher for females than for males, starting at 0.63 ± 0.07 in females and 0.57 ± 0.09 in males in 1994-95 and declining to 0.36 ± 0.07 in females and 0.31 ± 0.07 in males in 2003-04. Model 1 suggested average constant survival of 0.48 (± 0.04), which was lower than in Byrkö but higher than in Mustasaari. The recapture probabilities were sex-dependent, females being much more likely to be recaptured (0.87 ± 0.06) than males (0.43 ± 0.09). This was expected, because in Eugmo the area was not intensively monitored. Males occasionally change to a different area or roost in red squirrel nests where they cannot be captured. It is not likely that the trend in survival was only an artifact due to heterogeneity in recapture rates, although it is possible that there was some negative bias in the last estimates. The slope estimates showed a very slight trend (from –0.64 to –0.13; Kéry, Madsen & Lebreton, 2006), and the GOF test did not indicate transience or trap-dependence in any of the groups. However, it is possible that the observed lower

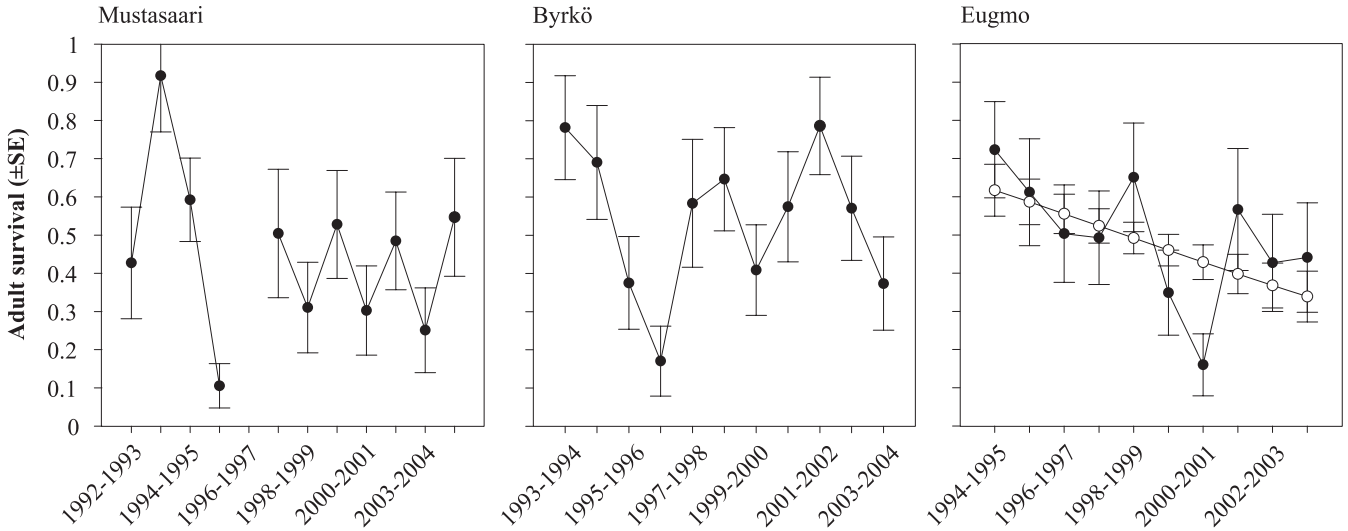


FIGURE 3. Annual adult survival estimates (± SE). For Eugmo, the filled symbols represent estimates from the time-dependent model and the open symbols represent estimates from the trend model.

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survival in males than in females was due to higher probability of permanent emigration or territory expansion as a response to habitat loss.

The estimates of local recruitment were fairly similar in both areas studied. In both cases, the Akaike weight for the best model was not large relative to the weight of the next best model. In Mustasaari, the most parsimonious model suggested a sex effect in local recruitment ($\Phi_{a0 * s, a1+} P_s$) with an evidence ratio of only 1.78 to the model with constant recruitment ($\Phi_{a0, a1+} P_s$). Models with year-dependent recruitment had no support, probably due to the small number of individuals. The average recruitment rate was 0.30 (± 0.06 SE) for males and 0.23 (± 0.05) for females. Contrary to our expectations, the recapture probability for juvenile females was higher (0.96 ± 0.05) than for males (0.74 ± 0.08). In Byrkö, the best model did not include sex effects ($\Phi_{a0, a1+} P_c$) in local recruitment or recapture probability. The estimated local recruitment was 0.27 (± 0.04), and recapture probability was 0.73 (± 0.08). The evidence ratio to the next best model ($\Phi_{a0 * s, a1+} P_s$) was 2.70.

Population growth rate

Models suggested substantial temporal variation in annual growth rates in Mustasaari, but not in the Byrkö or Eugmo populations (Table I). However, in all cases there was large uncertainty in annual estimates due to the small number of individuals. For Mustasaari, the annual estimates were so poor that they are not very informative and at best it can be concluded that there seems to have been substantial variation in λ. The estimated mean growth rate over the period 1994–2004 in Mustasaari was 0.96 (SE ± 0.12, $\sigma^2_{process} = 0.12$), and the coefficient of variation was 36%. Sampling variation accounted for 17% of the total variance (model 14). Models with constant population growth rates, trend, or amount of suitable habitat were not supported by the data ($\Delta QAIC_c > 10$).

Modeling population growth rate was also problematic for Byrkö due to sparse data. A model with a constant λ in Byrkö (10) had the highest support, followed by the habitat model (13), trend model (12), and the model with separate estimates for the first and the second half of the study period (11). The estimated mean λ from 1995 to 2004 was 0.96 (± 0.03, 95% CI: 0.82 – 0.99), indicating population decline during the period. Models 11 and 12 suggested that the growth rate may have slightly increased (*i.e.*, population decline slowed down) at the end of the study, but in all these models the population growth rate estimates were consistently below one.

The Eugmo population included the highest number of individuals, and the estimates of population growth for this population were more precise than for Mustasaari or Byrkö. The most parsimonious model of population growth in Eugmo (13) included a positive effect of the area of suitable habitat (β = 0.001, 95% CI: 0.0003 – 0.003). According to this model, estimated growth rate was high at the beginning (1.08 ± 0.06) but declined to as low as 0.78 (± 0.08). Models 11 and 12, which also indicated a decline in the population growth rate, were equally plausible given the data ($\Delta QAIC_c < 2.0$). Model 12 suggested a decreasing trend from 1.21 ± 0.13 to 0.79 ± 0.08. Models with time effect were not well supported ($\Delta QAIC_c > 8$).

Source–sink status of the populations

If $C^r > 1$ the population can be classified as a source. After solving for equation [1]

$$\phi_{a1}^{survival} + \phi_{a1}^{emigration} \times \beta \left(\phi_{a0}^{survival} + \phi_{a0}^{emigration} \right) > 1.0 \qquad [1]$$

the populations considered may be classified as sources if:

$$\text{In Mustasaari: } \phi_{a1}^{Ms} + 1.15\phi_{a0}^{Ms} \succ 0.316$$
$$\text{In Eugmo: } \phi_{a1}^{Bs} + 1.14\phi_{a0}^{Bs} \succ 0.319 \text{ and}$$
$$\text{In Byrkö: } \phi_{a1}^{Bs} + 1.14\phi_{a0}^{Bs} \succ 0.163$$

The range of values for classifying a sink is presented for each population in Figure 4. The area on the left side of the line represents values for emigration that produce a sink, whereas the area to the right of the line represents parameter values of a source. The results suggest that the Byrkö population has been a sink. We have no estimates for emigration from Mustasaari or Eugmo, but considering the even lower survival probabilities in these populations they are likely to have been sink populations as well. This can be seen from the figure 4 as the space covering values for sink populations is larger in Mustasaari and Eugmo than in Byrkö.

Discussion

Survival estimates

Estimated average survival probabilities were higher for adult flying squirrels in Byrkö (0.53) than in Eugmo (0.48) or Mustasaari (0.43). In Eugmo, formerly high survival rates appear to have crashed during the past decade. We did not expect the survival estimates to differ between the areas because all of them have suffered roughly 30% habitat loss. The difference in average survival may be due

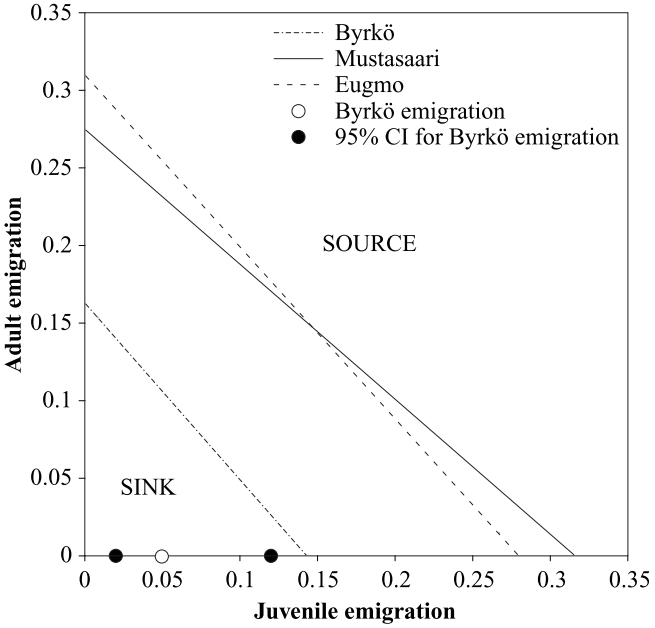


FIGURE 4. Classification of populations as source or sink depending on unknown adult ($\phi_{a1+}^{emigration}$) and juvenile emigration ($\phi_{a0}^{emigration}$). The open symbol represents the estimated average $\phi_{a0}^{emigration} = 0.05$ with the observed $\phi_{a1+}^{emigration} = 0$ from Byrkö, and the filled symbols represent the 95% confidence intervals for $\phi_{a0}^{emigration}$.

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to different fine-scale composition of the habitats, resulting in different predation pressure or emigration probabilities, but at present we can only speculate on such matters. The models supported time-dependence in adult survival in the Mustasaari population only. This does not indicate that there was no year-dependent variation in adult survival, only that this variation was relatively small in the sense of bias–variance tradeoff (Burnham & Anderson, 2002). Sparse data also affected the annual estimates, which had huge standard errors and consequently wide confidence intervals. Therefore, the annual survival estimates should be interpreted with caution.

Our estimates of local recruitment for the flying squirrel ranged from 0.23 to 0.30 depending on population and sex. As expected, the probability of surviving and staying near the natal territory through the first winter was lower than the probability of surviving subsequent winters. We have no data from other Siberian flying squirrel populations to judge whether our survival estimates are within the normal range for this species. However, the adult survival estimates are low compared to those reported for other Sciurid species. For example, average survival probability estimates are 0.85 for the northern flying squirrel (*Glaucomys sabrinus*) and 0.83 for the Douglas squirrel (*Tamiasciurus douglasii*) (Ransome & Sullivan, 2004) in British Columbia, Canada. Conner (2001) reported survival probabilities of 0.66 for female and 0.73 for male fox squirrels (*Sciurus niger*) in southwestern Georgia, USA.

The decline in Eugmo adult survival was linked to the area of suitable habitat. Observations of females disappearing immediately after logging within their home ranges suggested mortality due to clear-cuts. Permanent emigration is rare in adult flying squirrels (Hanski *et al*., 2000), but they may have been forced to leave their home range after the decimation. However, we find this unlikely because at least some of the emigrated females should have been found elsewhere. Despite the reduction of suitable habitat in all the populations, the effect of habitat loss on survival was evident only in Eugmo. The quality of forests that were lost due to clear-cuts may have varied between the areas. For example, the consequences of losing 31–35% of pine forests are quite different from those of losing spruce forests. We studied the effect of habitat loss on survival on a very coarse scale, using the total amount of suitable habitat in the whole study area. To further investigate the effect of habitat loss, detailed analyses of individual survival in territories of different quality are needed. Stochasticity in a seasonal environment may mask the negative effect of habitat loss. The causes and timing of death vary year to year depending on food availability, predation, and weather conditions during winter or the breeding season. These factors may have complex interactions with habitat loss that are difficult to model, especially with a small number of individuals. For example, logging or thinning of forest may enhance the effect of severe winter if a territory that was previously located in high-quality habitat does not provide enough food or shelter after the disturbance.

POPULATION GROWTH RATE

We observed a decline in all 3 populations and high temporal variation in Mustasaari. These results are in line with those of the censuses conducted since 1949, which consistently show a decline in flying squirrel populations in Finland. The same pattern was evident in the recent flying squirrel population inventory (Hanski, 2006). Forestry has been shown to have a negative effect on small mammals (*e.g*., Ecke *et al*., 2006) and birds (Lampila, Mönkkönen & Desrochers, 2005), but see Gomez, Anthony, and Hayes (2005) for different results. For example, southern flying squirrel (*Glaucomys volans*) densities declined and mortality increased in a logging experiment in Arkansas (Taulman, Smith & Thill, 1998), and northern flying squirrel densities in managed forests are generally 40–65% of those in old growth forests (Carey, 2000).

Flying squirrel density is highest in the western part of Finland and decreases towards the east. In western Finland (including our study areas) the number of females is $3.2 \cdot km^{-2}$ of forest land, whereas the average in Finland is 0.9 females$\cdot km^{-2}$ (Hanski, 2006). Our results indicate declines in areas that previously have been considered to be the stronghold for the flying squirrel populations in Finland. However, our estimates of population growth rate were quite imprecise. As in the survival models, the small number of individuals studied favoured constant models with fewer parameters. The low and variable adult survival and population growth rate with high variance in Mustasaari suggests that this population may be vulnerable to extinction due to stochastic events. In fact, this almost happened in 1996, when an eagle owl (*Bubo bubo*) was suspected of hunting flying squirrels in the area (Figure 2). In Eugmo the situation seems even worse: according to the models, the population growth rate severely declined during the study, possibly as a consequence of reduced adult survival. There was a positive relationship between the area of suitable habitat and the population growth rate in Eugmo, which implies that anthropogenic habitat loss has had a direct effect on the population size. Decrease in suitable habitat was likely the cause behind the decline in other populations as well. Compensating immigration to Eugmo from the surrounding area may have been lower than immigration to Mustasaari or Byrkö. This possibility is supported by microsatellite data that shows low genetic variation in Eugmo (Selonen, Painter & Hanski, 2005; Lampila *et al.*, 2009).

SOURCE–SINK DYNAMICS AND MOVEMENT

The contribution metric C calculated for Byrkö strongly suggested that the population at this site is a sink. In reality, however, in good years Byrkö may serve as a source and provide new individuals to Eugmo. Byrkö is a peninsula, and the majority of the individuals leaving Byrkö are forced to enter Eugmo. Evidence of low dispersal between these areas is provided by microsatellite markers that show significant genetic differentiation between the populations (Lampila *et al.*, 2009). We have probably underestimated dispersal. However, the recapture effort in Eugmo should have been sufficient to capture a notable number of juvenile dispersers from Byrkö. Altogether, only 4 juvenile individuals were observed to have been recruited from Byrkö to Eugmo and none in the opposite direction during the study. If Byrkö was a source in most years, the total emigration should have been at least 35 individuals. Marked

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underestimation of adult migration was not likely because our own observations and other studies (Hanski *et al*., 2000) suggest high site fidelity among adults. Adult individuals were not observed to successfully emigrate during the study, although it probably happens occasionally.

Occupancy of forest species is probably affected when some threshold in patch and landscape quality is reached. Numerous boreal forest species face the threat of diminishing habitat. Low colonization ability and narrow tolerance for different environmental conditions largely explain the decline of many forest species (Hanski, 2005). For example, the three-toed woodpecker (*Picoides tridactylus*) is associated with mature forests with dead trees (Pakkala, Hanski & Tomppo, 2002) and is listed in the IUCN category "near threatened" in Finland (Rassi *et al*., 2001). Pakkala, Hanski, and Tomppo (2002) found that three-toed woodpeckers occurred mainly in good-quality habitat fragments. They argued that parts of the studied population may inhabit regions where the total area of good habitat is under the landscape-level threshold required by the woodpecker. These populations represent source–sink dynamics. In our study area, the total amount of suitable habitat and the average size of forest patches have decreased in all the flying squirrel populations (see Methods), which has led to increasing isolation of the remaining patches. Andrén (1994) suggested that habitat fragmentation strongly increases the risk of extinction when the amount of suitable habitat falls below 20%. The studied populations are at or below this threshold. In Mustasaari and Eugmo only 10% and in Byrkö 21% of the total landscape area consists of forests suitable for the flying squirrel. Interestingly, adult survival estimates suggest that the Byrkö population may be more viable compared to the other studied populations. Even though the amount of good breeding habitat is the most important factor for the species' persistence, movement and population size could be enhanced more economically by adding poor-quality dispersal habitat (*i.e*., not good enough for breeding, but suitable for movement) to the landscape to facilitate movement and occupation of vacant home ranges (Wiegand, Revilla & Moloney, 2005). This seems reasonable in the case of the flying squirrel, since juvenile dispersers have been shown to use poor-quality habitat for temporary roosting, although they prefer breeding habitat when dispersing (Selonen & Hanski, 2004; 2006). The importance of securing dispersal habitat in addition to breeding habitats was highlighted also by Hurme *et al.* (2007).

To summarize, we conclude that habitat loss has had an effect on the viability of at least 1 of the studied populations. All the studied populations seem to have declined over the past decade and are likely to be sink populations. Reduced dispersal due to fragmentation may drive these already small populations into extinction. Fragmentation has been shown to affect movement among patches in grey-tailed voles (*Microtus canicaudus*) (Wolff, Schauber & Edge, 1997), and apparent lack of dispersal has been identified as a major issue in Delmarva fox squirrel (*Sciurus niger cinereus*) conservation (Hilderbrand *et al*., 2007). Furthermore, inbreeding and loss of genetic diversity in small populations may contribute to population decline (Frankham, 2005). As population size decreases demographic variance, variance in population size caused by differences in individual probabilities of death and reproduction increases (Engen, Sæther & Møller, 2001). This can create a phenomenon similar to the Allee effect, where most population trajectories below a certain threshold tend to decrease, causing rapid extinction (Lande, Engen & Sæther, 2003).

A population viability analysis with detailed modeling of the effects of habitat loss on individual survival will help to plan the conservation of these populations. The low estimates of population growth rates along with the overall, long-term decline of flying squirrels in Finland suggest that there is an urgent need to reconcile the conflicting ecological and economic goals in forestry in this country to ensure the persistence of the species. Although responses to habitat loss and fragmentation are species-specific, these results raise concern for other, less mobile boreal forest species facing the same problems of habitat isolation and destruction.

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Literature cited

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A Review. Oikos, 71: 355–366.

Anonymous, 1992. Council Directive 92/43/EEC. Official Journal of the European Communities, Luxembourg.

Baillie, J. E. M., C. Hilton-Taylor & S. N. Stuart (eds.), 2004. 2004 IUCN Red List of Threatened Species: A Global Species Assessment. IUCN, Gland and Cambridge.

Beissinger, S. R. & N. F. R. Snyder, 2002. Water levels affect nest success of the snail kite in Florida: AIC and the omission of relevant candidate models. Condor, 104: 208–215.

Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition. Springer, New York, New York.

Carey, A. B., 2000. Ecology of northern flying squirrels: Implications for ecosystem management in the Pacific Northwest, USA. Pages 45–66 *in* R. L. Goldingay & J. S. Scheibe (eds.). Biology of Gliding Mammals. Filander Verlag, Fürth.

Conner, L. M., 2001. Survival and cause-specific mortality of adult fox squirrels in southwestern Georgia. Journal of Wildlife Management, 65: 200–204.

Ecke, F., P. Christensen, P. Sandström & B. Hörnfeldt, 2006. Identification of landscape elements related to local declines of a boreal grey-sided vole population. Landscape Ecology, 21: 485–497.

Engen, S., B.-E. Sæther & A. P. Møller, 2001. Stochastic population dynamics and time to extinction of a declining population of barn swallows. Journal of Animal Ecology 70: 789–797.

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

Gannon, W. L., R. S. Sikes & The Animal Care and Use Committee of the American Society of Mammalogists, 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy, 88: 809–823.

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Gomez, D. M., R. G. Anthony & J. P. Hayes, 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. Journal of Wildlife Management, 69: 1670–1682.

Hanski, I., 2005. The Shrinking World: Ecological Consequences of Habitat Loss. Excellence in Ecology 14. International Ecology Institute, Oldendorf/Luhe.

Hanski, I. K., 1998. Home ranges and habitat use in the declining flying squirrel *Pteromys volans* in managed forests. Wildlife Biology, 4: 33–46.

Hanski, I. K., 2006. Liito-oravan *Pteromys volans* Suomen kannan koon arviointi. Loppuraportti. Luonnontieteellinen Keskusmuseo, Helsingin yliopisto.

Hanski, I. K., P. C. Stevens, P. Ihalempiä & V. Selonen, 2000. Home-range size, movements, and nest-site use in the Siberian flying squirrel, *Pteromys volans*. Journal of Mammalogy, 81: 798–809.

Hanski, I. K., H. Henttonen, U. Liukko, M. Meriluoto & A. Mäkelä, 2001. Biology and conservation of the Siberian flying squirrel (*Pteromys volans*) in Finland. Finnish Environment, 459. Finnish Ministry of Environment, Helsinki.

Hilderbrand, R. H., R. H. Gardner, M. J. Ratnaswamy & C. E. Keller, 2007. Evaluating population persistence of Delmarva fox squirrels and potential impacts of climate change. Biological Conservation, 137: 70–77.

Hines, J. E. & J. D. Nichols, 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture–recapture data. Journal of Applied Statistics, 29: 573–587.

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

Hurme, E., P. Reunanen, M. Mönkkönen, A. Nikula, V. Nivala & J. Oksanen, 2007. Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest. Ecography, 30: 277–287.

Hurme, E., M. Mönkkönen, A.-L. Sippola, H. Ylinen & M. Pentinsaari, 2008. Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. Ecological Indicators, 8: 246–255.

Kéry, M., J. Madsen & J. Lebreton, 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. Journal of Animal Ecology, 75: 1172–1181.

Lampila, P., M. Mönkkönen & A. Desrochers, 2005. Demographic responses by birds to forest fragmentation. Conservation Biology, 19: 1537–1546.

Lampila, S., L. Kvist, R. Wistbacka & M. Orell, 2009. Genetic diversity and population differentiation in the endangered Siberian flying squirrel (*Pteromys volans*) in a fragmented landscape. European Journal of Wildlife Research DOI 10.1007/s.10344-009-0259-2, in press.

Lande, R., S. Engen & B.-E. Sæther, 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford.

Lebreton, J.-D., K. P. Burnham, J. Clobert & D. R. Anderson, 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs, 62: 67–118.

Morris, W. F. & D. F. Doak, 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates Inc., Sunderland, Massachusetts.

Östlund, L., O. Zackrisson & A. L. Axelsson, 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research, 27: 1198–1206.

Pakkala, T., I. Hanski & E. Tomppo, 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. Silva Fennica, 36: 279–288.

Peery, M. Z., B. H. Becker & S. R. Beissinger, 2006. Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. Ecological Applications, 16: 1516–1528.

Pradel, R., 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics, 52: 703–709.

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

Ransome, D. B. & T. P. Sullivan, 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. Journal of Mammalogy, 85: 206–215.

Rassi, P., A. Alanen, T. Kanerva & I. Mannerkoski (eds.), 2001. Suomen lajien uhanalaisuus 2000. Ministry of the Environment, Helsinki.

Reunanen, P., 2001. Landscape responses of the Siberian flying squirrel (*Pteromys volans*) in northern Finland. M.Sc. thesis. Acta Universitas Ouluensis A 371.

Rotella, J. J. & J. E. Hines, 2005. Effects of tag loss on direct estimates of population growth rate. Ecology, 86: 821–827.

Runge, J. P., M. C. Runge & J. D. Nichols, 2006. The role of local populations within a landscape context: Defining and classifying sources and sinks. American Naturalist, 167: 925–938.

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

Selonen, V. & I. K. Hanski, 2006. Habitat exploration and use in dispersing juvenile flying squirrels. Journal of Animal Ecology, 75: 1440–1449.

Selonen, V., I. K. Hanski & P. C. Stevens, 2001. Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. Ecography, 24: 588–600.

Selonen, V., J. N. Painter & I. K. Hanski, 2005. Microsatellite variation in the Siberian flying squirrel in Finland. Annales Zoologici Fennici, 42: 505–511.

Shaffer, M. L., 1981. Minimum population sizes for species conservation. BioScience, 31: 131–134.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletin, 49: 11–41.

Taulman, J. F., K. G. Smith & R. E. Thill, 1998. Demographic and behavioral responses of southern flying squirrels to experimental logging in Arkansas. Ecological Applications, 8: 1144–1155.

Tittler, R., L. Fahrig & M. Villard, 2006. Evidence of large-scale source–sink dynamics and long distance dispersal among wood thrush populations. Ecology, 87: 3029–3036.

White, G. C. & K. P. Burnham, 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study, 46: 120–138.

Wiegand, T., E. Revilla & K. A. Moloney, 2005. Contributed papers: Effects of habitat loss and fragmentation on population dynamics. Conservation Biology, 19: 108–121.

Williams, B. K., J. D. Nichols & M. J. Conroy, 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California.

Wilson, D. D. & D. M. Reeder (eds.), 1993. Mammal Species of the World. Smithsonian Institute Press, Washington, DC.

Wolff, J. O., E. M. Schauber & W. D. Edge, 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conservation Biology, 11: 945–956.

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