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**Are habitat loss, predation risk and climate related to the drastic decline in a
Siberian flying squirrel population? A 15-year study**

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Abstract

To devise effective conservation actions, it is important to know which factors are associated with the population parameters of a declining population. Using mark-recapture methods, we estimated the annual population size, growth rate and survival probability of an ear-tagged flying squirrel population over a 15-year period in a 4,500 ha study area in western Finland. The species is considered vulnerable, but detailed knowledge concerning population sizes or trends is lacking. The population parameters and changes therein were regressed against habitat availability, an indicator of predation pressure, and mean winter temperature (an indicator of climate change), to reveal potential reasons for trends in the population. The best-fit models suggested the annual growth rate to be below one, and on average it was $0.93 (\pm 0.06; \text{SE})$ across the 15-year period. The survival probability was about $0.22 (\pm 0.03)$ for juveniles and $0.50 (\pm 0.03)$ for adults. The population size of adult flying squirrels decreased from $65 (\pm 11)$ individuals in 1995 to $29 (\pm 6)$ individuals in 2009. The number of flying squirrels was associated with the amount of available habitat, but the decline in population size was more rapid than the loss of habitat area. If the current decreasing trend in habitat availability continues, the population might become extinct by the year 2020. To halt the population decline, it is necessary to refrain from clear-cutting mature spruce stands until new suitable habitats develop from the maturation of younger forests.

Keywords: Alternative prey hypothesis · Landscape change · Mark-recapture analysis · Population regulation

Introduction

Ecology is a science that aims to understand species distribution and abundance. This task is particularly urgent for species that are declining or endangered. Caughley (1994) distinguished between two paradigms in conservation biology: the small-population paradigm and the declining-population paradigm. The small-population paradigm attempts to estimate the probability of extinction of a stochastically fluctuating population, and does not deal with the reasons why the population has become small. The declining-population paradigm aims to identify the underlying causes of the decline and to prevent further declines, and is thus the correct approach in conservation biology when trying to prevent a species from becoming seriously threatened (Caughley 1994). Studying a declining population over a long period of time enables trends and fluctuations in population parameters to be related to environmental variables, thereby gauging potential causes for them, which allows more effective conservation planning.

The Siberian flying squirrel (*Pteromys volans*, L. 1758) is classed as vulnerable in Finland by the IUCN (International Union for Conservation of Nature, 2010) classification (Rassi et al. 2010). The species is included in the Habitats Directive Annex IV of the European Union (92/43/EEC) and is therefore declared to be in need of strict protection. The species is considered to have declined in Finland since the mid-20th century (Hokkanen et al. 1982; Selonen et al. 2010). It has allegedly suffered from intensive forestry that has resulted in the reduction of optimal habitats, i.e., spruce-dominated old forests mixed with deciduous and cavity trees (Hokkanen et al. 1982; Hanski et al. 2001a). Habitat loss is considered the main reason for the endangered status of the species (Rassi et al. 2010). In addition to habitat loss, habitat fragmentation might limit the distribution of the flying squirrel in forest landscapes (Reunanen et al. 2000). Increased predation pressure from raptors has also been suggested to be related to the population decline (Hokkanen et al. 1982), although flying squirrels are not common in the diet of avian predators (Selonen et al. 2010). As a boreal forest

species, the flying squirrel might also be affected by climate change. For many boreal animals, winter conditions limit populations (Forsman and Mönkkönen 2003). At northern latitudes, winter temperatures will probably increase more due to climate change than summer temperatures (ACIA 2005), and thus, northern populations might face particularly altered winter temperatures, and increased winter temperatures as a consequence of climate change might improve flying squirrel survival. However, the long-term effects of climate change might be negative, because climate change in the southern boreal zone will probably create a suboptimal environment for Norway spruce (Kellomäki et al. 2008), resulting in lower habitat availability. To date, direct demonstration of population declines based on stringent population monitoring of marked individuals has been lacking (but see Lampila et al. (2009) for estimates of demographic parameters in three flying squirrel populations over 12 years). Therefore, there is no direct evidence for habitat alteration, predation or climate change as the cause of declines in flying squirrel populations.

In many ecosystems, predators are the driving force behind small mammal population cycles (Hanski et al. 2001b). The alternative prey hypothesis (Angelstam et al. 1984) suggests that generalist predators, including many owl and hawk species, switch to alternative prey when the number of main prey, which is voles, declines. If predation is a major limiting factor for flying squirrels, it is to be expected that in poor vole density years, particularly immediately following a vole population crash, flying squirrels would experience a stronger predation pressure than in a high density vole year (e.g., Korpimäki et al. 1990), resulting in lower survival and a population decline. If winter conditions are a limiting factor, a higher survival over time with an increase in mean winter temperature would be expected.

In this study, we estimated the annual population size, growth rate and survival probability of the flying squirrel over a 15-year time period in a 4,500 ha study area in western Finland. To address the role of human-induced landscape change, predation and climate, we regressed annual fluctuations in population parameters against variables reflecting habitat availability: an indicator of

potential predation pressure and an indicator of climate change. Usually, endangered species populations are only monitored for a short period of time and very little is known about the annual variation in population sizes. If considerable annual variation is evident, snap-shot studies might produce biased information on species abundance.

Material and methods

Study species

The Siberian flying squirrel is a nocturnal arboreal mammal that inhabits boreal forests from Siberia to western Finland and Baltic regions. It inhabits old spruce-dominated (*Picea abies*) forests with deciduous trees for food (Hanski et al. 2001a). Even though the species can feed in and move through younger forest stands (Selonen et al. 2001; Reunanen et al. 2004), it is highly dependent on mature forests. The species nests in tree cavities formed by great-spotted woodpeckers (*Dendrocopos major*), twig dreys of the red squirrel (*Sciurus vulgaris*), nest boxes or even buildings. Female flying squirrels give birth to usually two to three offspring once or twice a year (Hanski et al. 2001a). The sex ratio of juveniles is approximately 1:1. On average, juvenile males disperse 1.8 km and females 2.5 km away from their natal sites (Selonen et al. 2007). The flying squirrel is a territorial animal. According to Hanski et al. (2000) the mean sizes of male and female home-range (measured by 95% minimum convex polygons) are 40.0 ha and 5.7 ha, respectively. Both males and females show a high degree of site fidelity.

Study area and data collection

The data were collected during years 1995–2009 in Alavus, western Finland. The Alavus population breeds in nest boxes, which makes it possible to ear-tag and monitor nearly all

individuals in the population. Nest boxes were placed systematically in 1994 in suitable breeding habitats within an area of 4,500 ha ($5 \times 9 \text{ km}^2$; Mäkelä 1999, 2001). The coordinates of the SW-corner of our rectangular study area are $62^\circ 45' \text{N}$, $23^\circ 31' \text{E}$. All forest stands within the 10,000 ha study area, except for one small protected area ($<10 \text{ ha}$), are managed for timber production. As a consequence, even mature forests contain very little dead-wood or very few cavity trees. The number of boxes decreased almost every year because of the harvesting of suitable habitats (201 boxes in 1995; 124 boxes in 2009) and the density of nest boxes within suitable habitats decreased from 7.5 boxes/10 ha in 1995 to 5.2 boxes/10 ha in 2009. However, nest box densities were three-fold (in 1995) to six-fold (in 2005) higher than the density of flying squirrels (see results) and the number of nest boxes per individual flying squirrel increased slightly during the study (3.1 boxes/individual in 1995; 4.3 boxes/individual in 2009). Hanski et al. (2000) showed that over a year, a female flying squirrel uses five nests and a male eight nest sites on average, of which 36% are twig dreys and 64% are woodpecker cavities or nest boxes. Therefore, it is unlikely that the availability of nest boxes limited flying squirrel abundance.

Individuals were captured from nest boxes and were ear-tagged in June (during the first litter in the nest) and August (during the second litter) every year. The capture history of every individual was recorded so that an individual was noted as 'alive' if it was observed even once during a given year. New individuals were entered into the data by their tagging age, so that an individual born in the same year was marked as a juvenile and an individual born in previous years, as an adult. This allowed juvenile and adult population parameters to be distinguished from each other in the analysis. Data for both sexes were combined because the sample size did not allow an analysis of the effects of both sex and age and because age is a more important factor affecting population parameters than sex (Lampila et al. 2009).

Forest land covered about 70% of the 4,500 ha sized study area and included habitats from seedling to mature stands of all tree species. In 2009, about 7.5%, or 237 ha of the total forest area

was spruce-dominated mature forest and thus can be considered as a suitable breeding habitat for the species. The percentage habitat cover was evaluated during the data collection and was based on aerial photographs and maps. We used forestry files of the regional Forestry Centre for the township of Alavus to estimate the reduction in habitat area across the years.

Vole population abundance was determined by snap-trapping as described in Huitu et al. (2003). Trapping was carried out in both forest and field habitats at seven sites situated within a 70 km radius from Alavus. To obtain an index of vole population size for each site and trapping occasion, we pooled numbers of the three most numerous small rodent species caught within the area: the field vole *Microtus agrestis*, the sibling vole *M. levis* and the bank vole *Myodes glareolus*. The number of each species in both field and forest habitats was divided by the number of trap nights (number of traps set $\times$ number of nights they remained set), and was multiplied by 100. As an index for vole numbers at the flying squirrel study site, located centrally to the vole trapping sites, we calculated the mean of all site-specific indices for each trapping occasion. Predators exhibit very strong direct and delayed numerical responses to changes in vole numbers, typically lagging behind numbers of their vole prey by 0–4 months in late summer and 9–12 months in spring (Korpimäki et al. 1991, 2005; Korpimäki and Norrdahl 1991; Norrdahl and Korpimäki 1995, 2002; Sundell et al. 2004). Based on this, we used the autumn vole population size in the landscape as an indicator for predation pressure in the next reproductive season of the flying squirrel. Vole abundance data from years 1994–2008 were used for analyses, thus, the flying squirrel population size in a given year was regressed against the vole abundance in the previous autumn.

We included mean winter temperature into the models explaining flying squirrel population dynamics. Daily data from 1995 to 2008 for mean temperature, interpolated from measuring stations nearest to the town centre of Alavus (Venäläinen et al. 2005), about 15–20 km from the study area, were obtained from the Finnish Meteorological Institute. Daily means were used to calculate a mean winter temperature from November to February.

Statistical analyses

The modelling and parameter estimates were performed with the program MARK 5.0, which provides parameter estimates for open populations of marked animals (White and Burnham 1999). Before modelling, goodness-of-fit was tested using the program U-CARE 2.3 (Choquet et al. 2005), which tested the assumptions of the Cormack-Jolly-Seber model (CJS; Lebreton et al. 1992) used in this case. The testing was performed for the global model and separately for both marking age groups. To adjust the lack of fit, we calculated the variance inflation factor, $\hat{c}$ (Williams et al. 2002; Cooch and White 2009), which estimates the amount of overdispersion of the data for a given model (Lebreton et al. 1992). We then used this $\hat{c}$ ($= 1.2$) to adjust the AIC_c into a quasi-likelihood-adjusted $QAIC_c$ in MARK.

The data included 581 individuals (294 males and 287 females; 415 juveniles and 166 adults). We estimated the population size (N) and growth rate ($\lambda = N_{t+1}/N_t$) only for the adult population, because the models assume homogeneous survival and capture probabilities (Williams et al. 2002; Cooch and White 2009) and survival was expected (and observed; see results) to differ between juveniles and adults (Lampila et al 2009). The POPAN formulation was used to estimate population size and a Pradel model to estimate the growth rate (Cooch and White 2009). All possible different models with either constant or time-dependent parameters (population size or growth rate, survival and recapture probabilities) were tested.

We estimated survival and recapture rates with juveniles included in the analysis. Age was assumed to affect survival, because typically, juveniles survive less well than adults (Lampila et al. 2009). Furthermore, juveniles tend to disperse (Selonen and Hanski 2004), causing apparently lower survival rates, since dispersal often cannot be distinguished from death. Therefore, the survival and recapture probability models were allowed age-dependent estimates.

The model selection was based on Akaike's Information Criterion (AIC_c ; Hurvich and Tsai 1989), which was corrected for a small sample size. The best models with a ΔAIC_c value (i.e., the difference between AIC_c value of a model and the best model) less than four were selected to calculate weighted means of the estimates.

To study whether and how much the amount of habitat, predation pressure and winter temperature affect population size, a linear regression analysis was performed with SPSS Statistics 20.0. All three independent variables of habitat area, the abundance of voles in autumn and mean winter temperature, were entered into the model. In addition, population density was regressed against year, as was the annual growth rate of the population against the proportionate change in habitat area, abundance of voles and winter temperature.

Results

Population size and growth rate

The population size of adult flying squirrels decreased from 65 ± 11.0 ($N \pm SE$) individuals in 1995 to 29 ± 6.0 individuals in 2009 (Fig. 1). The lowest population size of 23 ± 4.9 adult individuals was estimated for 2005. Regression of the population size against year revealed a significant decline over time, with a reduction of 1.6 individuals per year ($F_{1,13} = 9.15$, $P = 0.010$); the predicted population size was 48.3 for 1995 and 25.9 for 2009, i.e., a 46 % decline. There were two outlier years when the population size was exceptionally high (1995 and 2006; Fig. 1), but even without these outliers, the decline was strong (1.3 individuals per year) and significant ($F_{1,11} = 12.5$, $P = 0.005$).

The regression model for population size against habitat area, vole abundance and winter temperatures explained 45.5% of the variation in population size. The area of suitable habitat was

the only variable that was significantly associated with the population size (Table 1). The regression coefficient for habitat area implies that each 10 ha reduction in habitat area was associated with a decline of about eight individuals from the population. The population size was related relatively linearly to habitat area (Fig. 2). However, the estimated density of individuals decreased from 1.8 to 1.1 per 10 ha during the study, which was statistically significant ($F_{1,13} = 5.35$, $P = 0.038$). If the density of individuals had remained constant, the decline in population size would have been modest (Fig. 2).

According to the best fit model, population growth rate varied with time. The geometric mean of growth rate in the best model was 0.93 ± 0.06 (geometric mean $\pm$ SE). However, two other models also gained some support (Table 2). These models suggest that the growth rate was constant over time and was significantly less than one: 0.96 ± 0.01 and 0.96 ± 0.02 ($\lambda \pm$ SE). Thus, all the best fit models suggest a significant population decline. Annual growth rate estimates varied between 0.71 ± 0.22 and 1.60 ± 0.65 (weighted mean $\pm$ SE; Fig. 3). In nine study years, the upper confidence limits of population growth were below or equalled one, so that in more than half of the years studied, the population declined or remained constant with a 95% probability. Habitat area, vole abundance and winter temperatures did not have a significant effect on population growth rates (Table 3).

Survival and recapture

The seven best fit models estimating survival and recapture probabilities included either age- (a) or both age- and marking age- (m) dependent survival parameters (Table 4). Age-dependent survival occurred in all seven models. Therefore, the models provide strong support that survival is affected by flying squirrel age. The weighted mean estimate of the seven best-fit models for the

survival probability of juveniles was less than half that of adults (Table 5). In contrast, modelling provided little support for the marking-age dependency of survival.

Two out of seven best fit models included a constant recapture estimate (Table 4). These models provide a summed weight for constant recapture of 0.49, which was much larger than expected by chance alone (0.13). We therefore conclude that the recapture rate did not vary among years and was not dependent on age or marking age. The weighted mean estimate suggested that about 60% of the individuals were recaptured at each trapping occasion (Table 5).

Discussion

The adult flying squirrel population approximately halved in 15 years. Of the measured variables, only habitat area was related to population size, indicating that population decline was related to habitat loss. Our results indicate that the reduction of 5.7 ha in habitat area (the mean size of the female flying squirrel home-range; Hanski et al. 2000), was associated with the loss of four to five flying squirrel individuals or, assuming that half of the adult individuals were females, with the loss of 2.4 females per loss of a home range. Furthermore, we observed a strong decrease in density, from 1.8 to 1.1 individuals per 10 ha over the 15-year period. Thus, the decline in flying squirrel numbers was faster than predicted by the loss of habitat area (compare the observed population trend with the predicted trend had the density remained constant in Fig. 2). Because habitat fragmentation tends to reduce population sizes more than expected based on habitat loss alone (Bender et al. 1998), our results imply but do not confirm, that fragmentation effects are involved in the population decline.

We found no support for the role of flying squirrels as an alternative prey for vole-eating predators. Population size was not a function of vole population size, nor was the flying squirrel population growth rate associated with the changes in vole population density. This might be

because of a very strong decline in the flying squirrel population with habitat area, masking any effects from other factors such as variation in predation pressure or in ambient conditions. Selonon et al. (2010) found that flying squirrels were consumed more frequently during years with a high vole number than during years with a low number, which also does not support the alternative prey hypothesis.

The estimates of annual growth rate varied between 0.71 and 1.60, with rather wide confidence intervals. Nevertheless, the geometric mean of the growth rate (0.93) of the best model and the growth rate estimates of the two next best models (0.96), indicate a significant overall decrease in population size. Lampila et al. (2009) studied three local flying squirrel populations in western Finland during 1992–2004, and found that in two of the populations, the mean growth rate was 0.96, and in one population it declined from more than one to less than 0.80. Thus, both our study and that of Lampila et al. (2009) suggest that local populations are decreasing. The growth rate of 0.93 across 10 years translates into a 52% reduction in population size, which corresponds to an endangered status according to IUCN criteria (IUCN 2001); correspondingly, a growth rate estimate of 0.96 for the two next-best models suggest a 34% decline over 10 years (classed as vulnerable). Thus, the present categorisation of the flying squirrel as vulnerable in Finland (Rassi et al. 2010), despite a rather large national population size is not too pessimistic. There is also evidence (Sulkava et al. 2008) that the national population is in fact smaller than that estimated by Hanski (2006).

We found adult survival (0.48–0.50) to be about twice as high as juvenile survival (0.22). This was expected because juveniles probably suffer from higher mortality and because juveniles also disperse while searching for a home range (Selonen and Hanski 2004) and might thus disappear from the study area and not be recaptured, lowering the apparent survival estimate. Lampila et al. (2009) found corresponding survival estimates in the three flying squirrel populations in Western Finland.

Even though the population size decreased over the 15-year study period, the models indicate a constant survival over time. This suggests that survival has been at a low level from the beginning of the study, resulting in growth rates below one and a decreasing population size. It is evident that the recruitment of new individuals into the population via reproduction or immigration is not large enough to compensate for mortality, and thus the population has declined.

The smaller the population is, the stronger are the effects of demographic and environmental stochasticity (Lande 1998). The population change we observed between consecutive years was large in some cases and, for example, between 1995–1996 and 2005–2007 population size changed at least by 30 percent. Our results suggest that short-term snapshots might provide seriously biased estimates of population size, even for populations that do not decline. It is evident that several years of data are needed to provide unbiased estimates of mean population size. Reliably detecting population trends requires an even longer time-series.

Based on this and previous studies (Mäkelä 1999, 2001), the future of the flying squirrel population in the Alavus study area does not appear hopeful. If the current decreasing trend in habitat availability continues, the population might become extinct by 2020. The problem of habitat loss is particularly severe because many of the cut spruce stands have been replanted with pine. Pine forests, even if old, are clearly suboptimal for the flying squirrel (Hanski 1998). Furthermore, in a simulation study, Kellomäki et al. (2008) predicted that climate change might substantially change the dynamics of managed boreal forests in northern Europe, and that in southern boreal forests, climate change will create a suboptimal environment for spruce, and that the dominance of Scots pine and birch will increase. This is likely to extirpate flying squirrel from its current strong holds in southern and western Finland if management does not maintain and favour spruce-dominated forests.

Because only a small fraction of the land area in southern Finland is protected (Finnish Statistical Year Book Forestry 2011), the persistence of species in general critically hinges on the

management of commercial forests. Our study area is very typical of southern Finland, therefore, we believe that our results of a sharply declining flying squirrel population can be generalised to the whole of southern Finland. Because clear-cutting even with green tree retention is detrimental to flying squirrel persistence (Santangeli et al. 2013), to halt the population decline it is necessary to refrain from clear-cutting mature spruce stands until new suitable habitats are developed by the maturation of younger forests. Alternative management regimes such as uneven-age management (Kuuluvainen et al. 2012), refraining from silvicultural thinning or applying extended forest rotations might provide an economically sustainable way to support flying squirrel persistence in commercial forest landscapes (M. Mönkkönen et al., unpublished data).

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References

- ACIA (2005) Arctic climate impact assessment. Cambridge University Press, Cambridge
- Angelstam P, Lindström E, Widén P (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199–208
- Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79:517–533
- Caughley G (1994) Directions in conservation biology. *J Anim Ecol* 63:215–244

- 343 Choquet R, Reboulet AM, Lebreton JD, Gimenez O, Pradel R (2005) U-CARE 2.2 User's manual.
344 CEFÉ, Montpellier
- 345 Cooch E, White G (eds) (2009) Program MARK: a gentle introduction. 7th Edition.
346 <http://www.phidot.org/software/mark/docs/book/>
- 347 Finnish Statistical Yearbook of Forestry (2011) Finnish Forest Research Institute, Vantaa
348 (<http://www.metla.fi/julkaisut/metsatilastollinenvsk/index-en.htm>)
- 349 Forsman JT, Mönkkönen M (2003) The role of climate in limiting European resident bird
350 populations. *J Biogeogr* 30:55–70
- 351 Hanski IK (1998) Home ranges and habitat use in the declining flying squirrel *Pteromys volans* in
352 managed forests. *Wildl Biol* 4:33–46
- 353 Hanski IK (2006) Liito-oravan *Pteromys volans* Suomen kannan koon arviointi. Loppuraportti.
354 Ympäristöministeriö, Helsinki (in Finnish with Swedish abstract)
- 355 Hanski IK, Stevens P, Ihalempiä P, Selonen V (2000) Home-range size, movements, and nest-site
356 use in the Siberian flying squirrel, *Pteromys volans*. *J Mammal* 81:798–809
- 357 Hanski IK, Henttonen H, Liukko U-M, Meriluoto M, Mäkelä A (2001a) Liito-oravan (*Pteromys*
358 *volans*) biologia ja suojelu Suomessa. Suomen ympäristö 459, Ympäristöministeriö, Helsinki
359 (in Finnish with Swedish abstract)
- 360 Hanski I, Henttonen H, Korpimäki E, Oksanen L, Turchin P (2001b) Small-rodent dynamics and
361 predation. *Ecology* 82:1505–1520
- 362 Hokkanen H, Törmälä T, Vuorinen H (1982) Decline of the flying squirrel *Pteromys volans* L.
363 populations in Finland. *Biol Conserv* 23:273–284
- 364 Huitu O, Norrdahl K, Korpimäki E (2003) Landscape effects on temporal and spatial properties of
365 vole population fluctuations. *Oecologia* 135:209–220
- 366 Hurvich CM, Tsai C-L (1989) Regression and time series model selection in small samples.
367 *Biometrika* 76:297–307

- 368 IUCN (2001) IUCN red list categories and criteria: version 3.1. IUCN species survival commission.
 369 IUCN, Gland, Switzerland and Cambridge, UK
- 370 Kellomäki S, Peltola H, Nuutinen T, Korhonen KT, Strandman H (2008) Sensitivity of managed
 371 boreal forests in Finland to climate change with implications for adaptive management. *Phil*
 372 *Trans R Soc B* 363:2341–2351
- 373 Korpimäki E, Norrdahl K (1991) Numerical and functional responses of kestrels, short-eared owls,
 374 and long-eared owls to vole densities. *Ecology* 72:814–826
- 375 Korpimäki E, Huhtala K, Sulkava S (1990) Does the year-to-year variation in the diet of eagle and
 376 Ural owls support the alternative prey hypothesis? *Oikos* 58:47–54
- 377 Korpimäki E, Norrdahl K, Rinta-Jaskari T (1991) Responses of stoats and least weasels to
 378 fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation?
 379 *Oecologia* 88:552–561
- 380 Korpimäki E, Norrdahl K, Huitu O, Klemola T (2005) Predator-induced synchrony in population
 381 oscillations of co-existing small mammal species. *Proc R Soc Lond B* 272:193–202
- 382 Kuuluvainen T, Tahvonen O, Aakala T (2012) Even-aged and uneven-aged forest management in
 383 boreal Fennoscandia: A review. *Ambio* 41:720–737
- 384 Lampila S, Wistbacka R, Mäkelä A, Orell M (2009) Survival and population growth rate of the
 385 threatened Siberian flying squirrel (*Pteromys volans*) in a fragmented forest landscape.
 386 *Ecoscience* 16:66–74
- 387 Lande R (1998) Anthropogenic, ecological and genetic factors in extinction and conservation. *Res*
 388 *Popul Ecol* 40:259–269
- 389 Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing
 390 biological hypotheses using marked animals: a unified approach with case studies. *Ecol*
 391 *Monogr* 62:67–118

- 392 Mäkelä A (1999) Liito-oravan elinalueet ja elinympäristön määrä Alavudella 1981 ja 1998.
 393 Luonnon Tutkija 2:56–57 (in Finnish)
- 394 Mäkelä A (2001) Liito-oravan (*Pteromys volans* L.) esiintyminen ja lajille sopivan elinympäristön
 395 määrä Alavuden Sulkavankylän tutkimusalueella vuosien 1981 ja 1998 inventointien
 396 perusteella. In: Hanski IK, Henttonen H, Liukko U-M, Meriluoto M, Mäkelä A (eds) Liito-
 397 oravan (*Pteromys volans*) biologia ja suojelu Suomessa. Suomen ympäristö 459,
 398 Ympäristöministeriö, Helsinki, pp 76–80 (in Finnish with Swedish abstract)
- 399 Norrdahl K, Korpimäki E (1995) Mortality factors in a cyclic vole population. *Proc R Soc Lond B*
 400 261:49–53
- 401 Norrdahl K, Korpimäki E (2002) Seasonal changes in the numerical responses of predators to cyclic
 402 vole populations. *Ecography* 25:428–438
- 403 Rassi P, Hyvärinen E, Juslén A, Mannerkoski I (eds) (2010) Suomen lajien uhanalaisuus – punainen
 404 kirja 2010. Ympäristöministeriö and Suomen ympäristökeskus, Helsinki (in Finnish with
 405 English summary)
- 406 Reunanen P, Mönkkönen M, Nikula A (2000) Managing boreal forest landscapes for flying
 407 squirrels. *Cons Biol* 14:218–226
- 408 Reunanen P, Mönkkönen M, Nikula A, Hurme E, Nivala V (2004) Assessing landscape thresholds
 409 for the Siberian flying squirrel. *Ecol Bull* 51:277–286
- 410 Santangeli A, Wistbacka R, Hanski IK, Laaksonen T (2013) Ineffective enforced legislation for
 411 nature conservation: A case study with Siberian flying squirrel and forestry in a boreal
 412 landscape. *Biol Cons* 157:237–244
- 413 Selonen V, Hanski IK (2004) Young flying squirrels (*Pteromys volans*) dispersing in fragmented
 414 forests. *Behav Ecol* 15:564–571
- 415 Selonen V, Hanski IK, Stevens PC (2001) Space use of the Siberian flying squirrel *Pteromys volans*
 416 in fragmented forest landscapes. *Ecography* 24:588–600

- 417 Selonen V, Hanski IK, Desrochers A (2007) Natal habitat-biased dispersal in the Siberian flying
418 squirrel. *Proc R Soc Lond B* 274:2063–2068
- 419 Selonen V, Sulkava P, Sulkava R, Sulkava S, Korpimäki E (2010) Decline of flying and red
420 squirrels in boreal forests revealed by long-term diet analyses of avian predators. *Anim Cons*
421 13:579–585
- 422 Sulkava R, Mäkelä A, Kotiaho JS, Mönkkönen M (2008) Difficulty of getting accurate and precise
423 estimates of population size: the case of the Siberian flying squirrel in Finland. *Ann Zool*
424 Fennici 45:521–526
- 425 Sundell J, Huitu O, Henttonen H, Kaikusalo A, Korpimäki E, Pietiäinen H, Saurola P, Hanski I
426 (2004) Large-scale spatial dynamics of vole populations in Finland revealed by the breeding
427 success of vole-eating avian predators. *J Anim Ecol* 73:167–178
- 428 Venäläinen A, Tuomenvirta H, Drebs A (2005) A basic Finnish climate data set 1961–2000:
429 description and illustrations. Finnish Meteorological Institute Reports 5
- 430 White GC, Burnham KP (1999) Program MARK: Survival estimation from populations of marked
431 animals. *Bird Study* 46:120–138
- 432 Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations.
433 Academic Press, San Diego
434

435 Table 1. ANOVA for the regression model of population size against the area of suitable habitat,
 436 vole abundance and winter temperature.

	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Regression	99.141	3	33.047	3.062	0.073
Residual	118.704	11	10.791		
	<i>B</i>	<i>SE</i>	<i>t</i>	<i>P</i>	
Habitat area	0.838	0.289	2.898	0.014	
Abundance of voles	0.260	0.251	1.036	0.323	
Winter temperature	0.633	1.232	0.130	0.618	
Intercept	-175.044	71.082	-2.463	0.032	

437

438

439 Table 2. The best-fit models ($\Delta AIC_c < 4$) for survival (ϕ), recapture (p) and growth rate (λ)
 440 (subscript a represents age-dependence, t for time-dependence and c for constant parameters) and
 441 their ΔAIC_c , AIC_c weights and numbers of parameters.

Model	ΔAIC_c	AIC_c weight	Number of parameters
$\phi_c p_c \lambda_t$	0.00	0.58	16
$\phi_c p_c \lambda_c$	1.84	0.23	3
$\phi_c p_t \lambda_c$	2.31	0.18	17

442

443

444 Table 3. ANOVA for the regression model of population growth rate against the area of suitable
 445 habitat, vole abundance and winter temperature.

	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Regression	0.091	3	0.030	0.510	0.684
Residual	0.594	10	0.059		
	<i>B</i>	<i>SE</i>	<i>t</i>	<i>P</i>	
Change in habitat area	10.913	52.028	0.210	0.838	
Change in abundance of voles	-0.059	0.050	-1.182	0.265	
Winter temperature	-0.002	0.035	-0.044	0.966	
Intercept	-9.746	51.665	-0.189	0.854	

446

447

448 Table 4. The best-fit models that estimate survival (φ) and recapture (p) (subscript a denotes age-
 449 dependence, m marking age-dependence and c constant parameters for age and marking-age
 450 groups) and their $\Delta QAIC_c$, $QAIC_c$ weights and numbers of parameters.

Model	$\Delta QAIC_c$	$QAIC_c$ weight	Number of parameters
$\varphi_a p_c$	0.00	0.33	3
$\varphi_a p_m$	1.28	0.18	4
$\varphi_{m,a} p_c$	1.56	0.15	4
$\varphi_a p_a$	1.83	0.13	4
$\varphi_{m,a} p_m$	3.01	0.07	5
$\varphi_{m,a} p_a$	3.15	0.07	5
$\varphi_a p_{m,a}$	3.31	0.06	5

451

452

453 Table 5. Weighted mean estimates of survival (ϕ) and recapture (p) and their standard errors and
 454 95% confidence intervals. ‘Marking age’ is the age of an individual when it was encountered for the
 455 first time and ‘Age’ is simply the age of an individual.

Parameter	Marking age	Age	Estimate	SE	95% CI	
survival	Juv	Juv	0.22	0.03	0.16	0.29
		Ad	0.48	0.04	0.40	0.57
	Ad	Ad	0.50	0.03	0.43	0.56
recapture	Juv	Juv	0.58	0.07	0.44	0.71
		Ad	0.59	0.07	0.45	0.72
	Ad	Ad	0.62	0.06	0.50	0.72

456

457

Figure legends

Figure 1. Annual population size estimates for the Alavus population with 95% confidence intervals.

Figure 2. The relationship between population size and habitat area. The first dot on the left represents the year 1995 and the last one represents the year 2009, i.e., habitat area on the x -axis is represented in descending order. The trend line with a slope of 0.84 is shown. The dashed line shows the population trend had the density of individuals remained at the 1995 level (1.8 individuals/10 ha).

Figure 3. The weighted mean estimates of the growth rates and their 95% confidence intervals of the three best-fit models (Table 2) over time.

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