

Master of Science Thesis

**The temporal variation in Siberian flying squirrel
(*Pteromys volans*) population size**

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ABSTRACT

Human land use causes declines of natural populations, for example, by loss of habitat area. Additionally, habitat fragmentation can cause the population size to decline more than is expected based on the area lost. Some ecological processes, such as demographic stochasticity and Allee effect, can expose already small populations to further decline. The endangered Siberian flying squirrel (*Pteromys volans*) has suffered from intensive forestry in Finland. In this thesis I estimated the size and growth rate of a local flying squirrel population living in nest boxes in Alavus using 15-year mark-recapture data. I regressed the estimated population size against habitat availability to detect relationships between the variables and also possible effects of fragmentation. The adult population size decreased from 65 to 29 in 1995–2009. The growth rate was less than one during the time period, also indicating a decline. The survival probability for adults was about 0.5 and for juveniles 0.22, both being constant in time and quite equal to another study in Finland. Population size declined with decreasing habitat area and the number of box sites, but no effect of fragmentation was seen, since the relationship between population size and habitat area was linear. There was also temporal variation in population size not caused by habitat availability but other reasons, for example demographic and environmental stochasticity or predator species. Therefore, the generalizability of single year census is not very good. Additionally, predicting the current or future population size only based on habitat availability is dangerous, which should be considered in the conservation of the flying squirrel populations. The availability of cavity and foraging trees is important for the persistence of the species. Maybe the conservation of the species also requires placing nest boxes to enable living in habitats of poor quality when preferred habitats are cut down. The nest boxes could have saved the population from extinction so far, but with similar forest cutting the population could go extinct in 15 years.

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TIIVISTELMÄ

Ihmisen maankäyttö, esimerkiksi elinympäristöjen häviämisen kautta, aiheuttaa luonnonpopulaatioiden pienenemistä. Lisäksi, elinympäristön pirstoutuminen voi pienentää populaatiota enemmän kuin pelkän pinta-alan vähenemisen perusteella voisi olettaa. Tietyt ekologiset prosessit, kuten demografinen stokastisuus ja Allee-efekti, voivat saada jo pienen populaation vielä jyrkempään laskuun. Uhanalainen liito-orava (*Pteromys volans*) on kärsinyt tehokkaasta metsätaloudesta Suomessa. Arvioin tässä tutkielmassa paikallisen liito-oravapopulaation kokoa ja kasvukerrointa käyttäen 15 vuoden merkintä-takaisinpyyntiaineistoa, joka on kerätty Alavudella pöntöissä asuvasta populaatiosta. Vertasin populaatiokokoa elinympäristön määrään löytääkseni yhteyksiä niiden väliltä sekä mahdollisen pirstoutumisen vaikutuksia. Populaatio pieneni 65 yksilöstä 29:ään vuosina 1995–2009. Kasvukerroin oli tutkimusajankohtana alle yksi, mikä myös merkitsee pienenemistä. Elossasäilyvyyden todennäköisyys oli 0,5 aikuisilla ja 0,22 poikasilla. Molemmat arvot pysyivät vakioina ja vastasivat erään toisen liito-oravatutkimuksen tuloksia. Populaatio pieneni elinympäristön ja pönttöpaikkojen vähetessä, mutta pirstoutumisen vaikutuksia ei todettu. Lisäksi, populaatiokoko vaihteli ajallisesti, mikä ei johtunut täysin elinympäristön määrästä, vaan esimerkiksi demografisesta stokastisuudesta, ympäristöolosuhteiden vaihtelusta tai pedoista. Siksi yhden vuoden arvio ei riitä populaatiokoon arvioimiseksi. Lisäksi, populaatiokoon ennustaminen elinympäristön määrään perustuen ei ole luotettavaa, mikä täytyisi ottaa huomioon liito-oravapopulaatioiden suojelussa. Kolo- ja ravintopuiden saatavuus on tärkeää suojelun kannalta. Suojelu voi lisäksi vaatia pesäpönttöjen lisäämistä, mikä mahdollistaisi lajin elämisen laadultaan huonommilla elinympäristöillä, kun sopivat elinympäristöt on hakattu. Pesäpöntöt ovat tähän asti saattaneet pelastaa populaation sukupuutolta, mutta hakkuiden jatkuessa samanlaisina populaatio voi hävitä 15 vuodessa.

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1. INTRODUCTION

Andrewartha & Birch (1984) defined ecology as the science that studies species' abundance and distribution. According to them, "*The expectation of life and the fecundity of the individual are reflected in the birth rate and death rate of the population, which is reflected in the distribution and abundance of species.*"

When studying the abundance and distribution of a species, the object is population (Andrewartha & Birch 1984). A population is defined as a group of individuals belonging to the same species in an area (Begon *et al.* 1996a). The boundaries of a population are sometimes artificial and depend on the study. The key parameter in population ecology is the population size (Williams *et al.* 2002). Four processes that affect population size are birth, death, immigration and emigration (Begon *et al.* 1996b). The management efforts of populations usually aim at changing the population size, for example, of a pest or an endangered species by affecting these processes (Williams *et al.* 2002).

Humans have a large impact on natural populations causing population declines and increasing extinction risk (Lande 1998). Land use, overexploitation, species introduction and pollution cause ecological and genetic effects that expose populations to extinction. Especially land use, i.e. clearing natural environment for human habitation, agriculture and industry, has transformed the planet's land surface greatly (Foley *et al.* 2005) and thereby caused habitat loss (Hanski 2005). Forestry, on the other hand, relates to habitat degradation, where original habitat is not totally lost but the quality of remaining habitat is lowered by human land-management practices (Hanski 2005).

Habitat is the environment where species live (Begon *et al.* 1996b). It is the most important requirement for populations to survive (Hanski 2005). Habitat loss includes loss of habitat area and habitat quality, often resulting in habitat fragmentation. Loss of habitat area reduces carrying capacity (Hanski 2005) which is the population size that environmental resources can maintain in an area (Begon *et al.* 1996a). It also reduces spatial variance of the habitat (Hanski 2005). Spatial variance buffers against temporal variation in environment. Hence reduction in habitat area increases the risk of extinction.

Habitat fragmentation usually accompanies habitat loss (Hanski 2005). It is a process where remaining habitat is subdivided into smaller and more isolated habitat patches. Carrying capacity decreases with patch size, and isolation may make it difficult for individuals to move between patches. Some species for natural reasons live in a fragmented habitat as a metapopulation (Hanski 1999) but not all species are adapted to it. Metapopulation consists of several local populations, some of which become extinct and new ones are established. Thus, the species in an area persists at metapopulation level in long-term (Hanski 1999).

Fragmentation causes the population size of some species to decline more than is expected based on the area lost (Bender *et al.* 1998). This results from patch size, isolation and edge effects. Because of fragmentation the relative area of edge increases in the landscape when the average patch size decreases (Hanski 2005). Environmental conditions can change and habitat quality may decline even inside patches (Lande 1998). Emigration is more probable from the edge than from the core of the patch, and thus, fragmentation increases emigration (Hanski 2005). Because of isolation emigrated individuals may spend more time between habitat patches, which can increase mortality rate and lower population size.

The effects of fragmentation on a population depend on the species' ecology (Bender *et al.* 1998). For example, migratory species tend to suffer less from fragmentation than

resident species, and generalist species suffer less than species specialised living in the interior of the patch. Edge species may even benefit from fragmentation.

Anthropogenic changes can decrease habitat quality, and the reduction in habitat quality (degradation) results also in reduced carrying capacity (Hanski 2005). In poor quality habitat, mortality and emigration rates are increased, with a simultaneous decrease of birth and immigration rates. In Finland forest is the most important habitat of endangered species (Rassi *et al.* 2001). The decline of decaying tree and changes in tree species composition and age structure together are one of the most significant reasons for species becoming endangered.

Some ecological processes can expose small populations to further decline (Lande 1998). Demographic stochasticity results from random individual variation in survivorship and reproduction. It causes fluctuations in population size, hence the smaller the population, the stronger the effect. The Allee effect, which is inverse density dependence at low density, causes reduced fitness for some species when population size is below a threshold (Allee *et al.* 1949). For example it is more difficult to find a mate or cooperate in a small than a large population. Demographic and environmental stochasticity and genetic processes, such as Allee effect, can reduce reproduction and increase mortality rate creating positive feedback loops which leads to even smaller population size (Gilpin & Soulé 1986). This process heading to extinction is called the extinction vortex. The minimum viable population size is a threshold where the population persists viable for a given time period despite those processes (Gilpin & Soulé 1986).

Populations can be studied because of pure science or conservation and management aims (MacKenzie *et al.* 2006). The interest can be just in understanding populations by discriminating between different hypotheses. When the aim is conservation (and management) of a population, management targets are set and their effects estimated. But to make conservation (and management) decisions, the current situation has to be known. In conservation biology, population size and population trajectories in time are of prime interest (Caughley 1994).

Caughley (1994) distinguished between two paradigms in conservation biology: the small-population paradigm and the declining-population paradigm. He argued that the small-population paradigm, being the more theoretical one, attempts to estimate the probability of extinction of a stochastically fluctuating population, when the more practical declining-population paradigm aims to identify the underlying causes of the decline and to prevent further declines. Both of the paradigms should be considered when practising effective conservation biology. In the case of endangered species, studying a population over a long period of time instead of conducting only single year census may achieve both targets. What is important to note is that decline can only be assessed when estimates of the population size are obtained for two or more years. Also, with enough data the population size can be correlated against other variables, for example habitat area, environmental conditions, predator or prey population size. Thus, the cause of the decline can be tracked down. When the relationship between population size and habitat area, predator population size or other factor is known and it can be predicted, the size of the target population can be projected forward and the extinction risk estimated.

Mathematical models can be used to understand and predict population dynamics. Modelling can be based on a sample, so that the whole population does not need to be studied. Thus, the population size or other population parameters can be estimated and also predicted more easily. The estimate of the population size of an endangered species must be accurate for effective conservation. The accuracy of an estimator is a combination of both bias and precision (Williams *et al.* 2002). Bias is the systematic difference between

the expected value of the estimator and the true value of the parameter. Precision is random variation and is measured by the variance of the estimator or standard error of the estimate.

The Siberian flying squirrel (*Pteromys volans*, L. 1758), the focal species in this thesis, is an endangered species which is defined as vulnerable by IUCN (The International Union for Conservation of Nature) classification in Finland (Rassi *et al.* 2001). The species is included in Habitats Directive Annex IV of European Union (92/43/EEC) and is, therefore, in need of strict protection. The destruction and deterioration of breeding sites and resting places used by the species in the Annex IV is prohibited on the basis of Finland's Nature Conservation Act (1096/1996). The species has been known to decline since the mid 20th century (Hokkanen *et al.* 1982).

The Siberian flying squirrel has suffered from intensive forestry (Hokkanen *et al.* 1982, Hanski *et al.* 2001). Changes in the composition of tree species and the decrease of cavity trees are the reasons for the species being endangered (Rassi *et al.* 2001). For example, the decrease of deciduous trees has affected the availability of food in winter (Mäkelä 1996c).

For the Siberian flying squirrel there has been differing estimates of the population size in Finland (Hanski 2006, Sulkava *et al.* 2008). A national survey of the flying squirrel in Finland was conducted based on faecal pellets and scent marks in a systematic sample grid (Hanski 2006). First, Southern Finland was divided in 10 km x 10 km squares. Second, within every other of these squares ten smaller (9 ha) squares were randomly positioned and surveyed. If traces of the flying squirrel were found, the square was marked as occupied. Every occupied square implied one female since their home-ranges were about the same size (Hanski *et al.* 2000) as the sample square. The result was 143 000 females in Finland.

Sulkava *et al.* (2008) compared the population estimates provided by the above method to estimates based on monitoring of ear-tagged individuals breeding in nest boxes in Alavus, western Finland. The latter method was assumed to give very accurate estimates because a great proportion of the population was caught and monitored. According to Sulkava *et al.* (2008) national survey may have overestimated the Finnish flying squirrel population size by a factor of two to three. Thus, the real number of flying squirrels in Finland might be less than half of the estimate given by the national survey. The bias of the national survey method was sensitive to the population size: the smaller the population the more biased the estimate. This is detrimental in the case of an endangered species. Therefore, a more accurate estimate of the flying squirrel population in Finland is needed.

In this thesis I estimated the essential population parameters of the flying squirrel population in Alavus using 15-year mark-recapture data. First, I estimated the local adult population size in each year and population growth rate (λ) for consecutive years. The population size and habitat area were expected to decrease during years 1995-2009 on the basis of previous studies (Mäkelä 1996a, 1999, 2001) of the same population. Second, I estimated annual survival in the population for adults and juveniles separately. These provide basic understanding of the population size and its trajectory in time. Inspecting the growth rate and survival in time provides information on potential causes of population changes. I also modelled the probability of recapture to control for the possibility that the potential changes in the population parameters are due to temporal variation in capturing individuals (e.g. variation in survey effort).

Finally, I regressed the estimated population size against habitat availability. If habitat availability is the reason for the observed population trajectory there should be a relationship between the two variables. If the relationship is linear, a certain amount of habitat loss causes always similar decline in population size. Possible fragmentation is

expected to decrease the population size more than habitat loss alone, and thus, the relationship between population size and habitat area would be expected to be non-linear, i.e. population decline becoming stronger with decreasing habitat area (Andrén 1994).

The results of this study provide a solid basis on which the conservation efforts of the local population of this endangered species can be based. Further, it provides novel biological knowledge on the population dynamics, survival and growth rates of the Siberian flying squirrel for a 15 year period. Usually, endangered species populations are only monitored for a short period of time and very little is known about the between-year variation in population size. If considerable annual variation is evident, snap-shot studies may give biased information on species abundance.

2. MATERIALS AND METHODS

2.1. Study species

The Siberian flying squirrel (*Pteromys volans*) is a nocturnal arboreal mammal (Hanski *et al.* 2000) living in boreal forests from Siberia to western Finland and Baltic regions (Nummi 1997). It inhabits old, spruce-dominated (*Picea abies*) forests with deciduous trees (Hanski *et al.* 2001). According to Reunanen *et al.* (2004) the minimum amount of spruce-dominated forest habitat required in the landscape is 12–16 %. Also younger forests will suffice if there are enough food and nest holes or boxes (Hanski *et al.* 2001). In the study of Hanski (1998) some flying squirrels were seen moving across and even feeding in open areas with scattered trees.

The flying squirrel feeds on leaves of aspen (*Populus tremula*), alder (*Alnus* spp.) and birch (*Betula* spp.) in summer (Mäkelä 1996c, Sulkava & Sulkava 1996). In winter it feeds on spruce sprouts and catkins of birch and alder which it stores, for example, on spruce branches. Spruce branches also provide protection from predators (Eronen 1996). Owls, goshawk (*Accipiter gentilis*), the European pine marten (*Martes martes*) and even domestic cat in close to human habitations prey on flying squirrel (Hokkanen *et al.* 1982, Koivisto 1983).

Siberian flying squirrels nest in tree cavities made by great-spotted woodpeckers (*Dendrocopos major*), twig dreys of the red squirrel (*Sciurus vulgaris*), birdhouses or even buildings. A flying squirrel has several nests within its home-range that it uses regularly for breeding, roosting, as storages and as backup nests (Eronen 1996, Hanski 1998, Hanski *et al.* 2001). Female squirrel gives birth to usually 2-3 cubs once or twice a year; from April to May and/or in June (Mäkelä 1996b). The sex ratio of juveniles is approximately 1:1. Young individuals disperse up to several kilometres while searching for own home-range (Mäkelä 1996b, Selonen & Hanski 2004). They reach maturity the next spring (Mäkelä 1996b).

The flying squirrel is a territorial animal. Hanski *et al.* (2000) studied home-ranges of flying squirrels. The average male and female home-range sizes (measured by 100 % minimum convex polygons) were 59.9 ha and 8.3 ha, respectively. Both males and females showed a high degree of site fidelity (Hanski *et al.* 2000), and females can use the same nests year after year (Mäkelä 1996b). Only males had overlapping home-ranges, and male home-ranges might have overlapped several female home-ranges. This indicates promiscuous or polygynous mating system (Hanski *et al.* 2000).

2.2. Study area and data collection

The data was collected by Antero Mäkelä during years 1995–2009 in Sulkavankylä which is a town in Alavus, western Finland (Figure 1). The population has been under intensive study since 1970s (Mäkelä 1996a, 1996b, 1996c, 1999, 2001). The study area was originally about 100 km² but it decreased because of logging so that when the nest boxes were placed systematically in 1994, there were suitable box sites only inside an area of 45 km², where most of the flying squirrels lived (Mäkelä, personal communication; Figure 1). A nest box site is an area containing several boxes used by one flying squirrel individual. As said above, nest boxes are for several purposes. The number of boxes and box sites decreased almost every year because of forest harvesting.

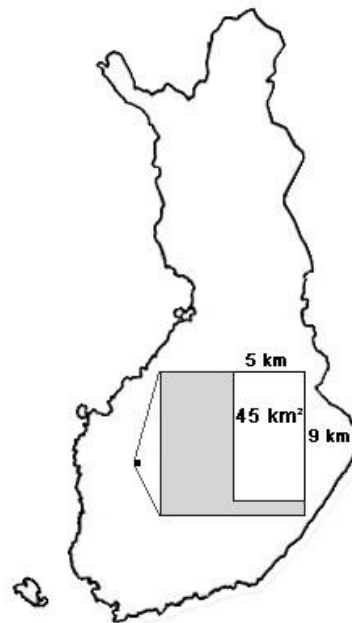


Figure 1. The location of the 100 km² study area (grey square) and the smaller (white) study area with nest boxes.

For this study I used the data on the flying squirrel population breeding in the boxes. Individuals were captured from nest boxes and ear-tagged in June (during the first litter in nest) and August (during the second litter in nest) every year. Additionally, in 1997–1999 and 2009 capturing and ear-tagging was carried out in April–May (before the first litter).

All the boxes were checked at least once a year. Both newborns and adults were ear-tagged, and individuals tagged in previous years were monitored at the same time. New squirrels were entered into the data by their tagging age so that an individual born in the same year as marked was a juvenile and individual born previous year was an adult. This allowed distinguishing juvenile and adult population parameters from each other in the analysis. Thus, there were two factors with every individual; age and marking age. ‘Age’ was the age of a squirrel at the given year which is either juvenile (less than one year old) or adult. ‘Marking age’ was the age at the first encounter and it is also either juvenile or adult. Age was assumed to affect survival because typically juveniles survive less well than adults. Further, juveniles tend to disperse causing apparently lower survival rates (see Lampila *et al.* 2009) because often dispersal cannot be discriminated from death. If a parameter was dependent on the age, it would have different values between juveniles and adults. If a parameter was dependent on the marking age, the age of an individual when it first was encountered and marked, would affect the value of the parameter. The data also

included the sex of the flying squirrels but it was not used in this study since the data was too small to use so many variables.

The capture history of every individual was pooled so that if an individual was seen even once during a year, it was marked 'seen' in that year. The data consists of capture histories of individually identified squirrels either seen ('1') or not seen ('0') in different years. For example capture history '000101100000000' means that the individual was seen only in years 1998, 2000 and 2001.

There were 19 tag losses during the monitoring years. Sometimes the squirrels manage to pull off their tags so that their ears are split. From these 19 individuals A. Mäkelä was able to identify six by making comparisons to the earlier data. The rest were removed from the data.

The number of nest box sites was counted in the study area every year. The habitat area was calculated from the forest cutting data for the town of Alavus. First I calculated the annual percentage of area logged in Alavus and then used this number to calculate the remaining forest habitat in the study area. The assumption was that the study area undergoes the same amount of forest cutting than the whole township. For years for which I did not have the forest cutting data, I used the average amount of forest cutting per year for years for which data was available.

2.3. Statistical analyses

2.3.1. Population size and growth rate

The modelling was performed with program MARK 5.0 which provides parameter estimates from open populations of marked animals (White & Burnham 1999). The data included 581 individuals. For the estimation of the population size (N) and growth rate (λ), I removed all the first encounters of the individuals which were marked as juveniles, after which all encountered individuals were adults. Therefore, the population size and growth rate were only estimated for the adult population. This was done because these models assume homogenous survival and capture probabilities (Williams *et al.* 2002, Cooch & White 2009) and survival was expected (and observed; see results) to differ between juveniles and adults.

I used the POPAN formulation (named after the computer package which is also a submodule of MARK) to estimate population size and a Pradel model to estimate the growth rate with MARK. In POPAN formulation MARK calculates a probability that an animal from the super-population enters the population between occasions i and $i + 1$ and survives to the occasion $i + 1$ (Cooch & White 2009). The hypothetical super-population consists of all animals ever been born to the population. Then MARK uses those probabilities to calculate the population sizes. Besides the growth rate or population size, these models estimate also survival and recapture probabilities in the population. Survival and recapture were estimated also separately from population size and growth rate (see below) to get more accurate estimates.

I started the modelling with the global (full) model which is the model with most parameters (Lebreton 1992, Burnham & Anderson 2002). In the case of the population size the global model included time-dependent survival ϕ_t , time-dependent recapture probability p_t and time-dependent population size N_t . In the case of the growth rate the full model included the terms ϕ_t , p_t and λ_t . In both cases I fitted eight different models with all possible combinations of parameters (survival, recapture and population size or growth rate being either constant or time-dependent).

The model selection was based on Akaike's Information Criterion (AIC). It was corrected for small samples (AIC_c) by MARK (Burnham & Anderson 2002, Williams *et al.* 2002, Cooch & White 2009). Best models with ΔAIC_c value (i.e. difference between AIC_c values of a model and the best model) less than 4 were selected to calculate weighted averages of the estimates. It means calculating estimates based on AIC_c weights (which sum to one) of the models (Burnham & Anderson 2002). This is done by multiplying the estimated parameter and the AIC_c weight of the respective model and summing the products of different models to get a weighted average. Therefore, every model contributes to the average estimate by its weight.

From eight models estimating the population size, only one satisfied the condition ($\Delta AIC_c < 4$). Thus, its AIC_c weight was 1.00. In the case of the growth rate, three of the eight models had $\Delta AIC_c < 4$ (Table 1) from which weighted average estimates were calculated. Also geometric mean of the growth rate was calculated from the best Pradel model where the growth rate was time dependent.

2.3.2. Survival and recapture

The survival and recapture parameters can be estimated by maximum likelihood estimation based on the data and the probability of every different capture history (Williams *et al.* 2002). For estimating survival and recapture probabilities, data on juveniles were included to allow age-dependent estimates. Twenty individuals were removed from the data because they were seen only during the last year, and thus, they did not give any information for the analysis of the survival and recapture parameters (and because MARK did not complete the modelling unless they were removed).

Before modelling, the goodness-of-fit testing was accomplished with program U-CARE 2.3 (Choquet *et al.* 2005) for the Cormack-Jolly-Seber (CJS) model in which survival and recapture parameters are time dependent (Williams *et al.* 2002). U-CARE tests the assumptions of CJS model which are: 1. Every marked animal present in the population at sampling period i has the same probability p_i of recapture. 2. Every marked animal in the population immediately after time i has the same probability ϕ_i of surviving to time $i + 1$. The other assumptions are: 3. Marks are not lost or missed. 4. All samples are instantaneous and animals are released immediately (Williams *et al.* 2002).

The goodness-of-fit testing was done for the global model and for both groups of different marking ages separately since at least survival was expected to depend on the age and juveniles were only in the other group (where marking age was juvenile). If the global model fits the data, also models derived from it with fewer parameters fit to the data (Burnham & Anderson 2002). For adults in which all individuals were marked as adults, the CJS model was fit (global test: quadratic $\chi^2 = 12.238$, $df = 33$, $P > 0.999$). For juveniles the CJS model was also fit (global test: quadratic $\chi^2 = 31.088$, $df = 27$, $P = 0.268$), but there was transience (TEST3.SR: $N(0,1)$ statistic for transient = 3.352, one-sided $P < 0.001$). This means that the second assumption was not met i.e. there was an excess of newly marked individuals that were never seen again (Choquet *et al.* 2005). This was expected because juveniles usually disperse before next capture occasion. Therefore, it was reasonable to take age into account during modelling and estimation of survival and recapture. To make this possible marking age also had to be considered since some of the individuals were marked as juveniles and the rest as adults, and these two groups had to be able to separate.

The third CJS assumption was not completely met since there was some tag loss and some of the individuals had to be removed from the data (see data collection). Also the

fourth assumption was not met. First, there were several sampling occasions during one year, and second, the number of those occasions varied between years.

To adjust the lack of fit I also calculated the variance inflation factor, \hat{c} , for the global model (Burnham & Anderson 2002) which in this case included marking age, age and time dependent survival ($\phi_{m, a, t}$) and recapture ($p_{m, a, t}$) parameters (several factors in a parameter means that there is an interaction between factors). The variance inflation factor estimates the amount of overdispersion of the data for a given model (Lebreton *et al.* 1992). I calculated \hat{c} for the global model by dividing the observed deviance (model deviance divided by the deviance degrees of freedom) by mean \hat{c} from bootstrapped simulations (Williams *et al.* 2002, Cooch & White 2009). Then I used this \hat{c} ($= 1.2$) to adjust the AIC_c for the lack of fit ($QAIC_c$) by editing the supposed \hat{c} in MARK.

All possible models nested within the global model (parameters from time, marking age and/or age dependent to constant; Appendix II) were run with MARK to provide estimates of survival and recapture parameters. Models with $\Delta QAIC_c$ less than 4 were selected to parameter estimation, and model averaging was done similarly as described above. From 64 models eight satisfied the condition (Table 1).

2.3.3. The effect of habitat availability on population size

To study if and how much the amount of habitat affects population size I performed two regression analyses using SPSS 15.0 (SPSS Inc.). The annual population size estimates were regressed against the number of nest box sites and its quadratic term. Linear relationship with an isometric slope would mean that the population size is determined by the availability of box sites, and every loss in box sites would result in a loss of a flying squirrel individual. I also regressed population size against the habitat area and its quadratic term which was not statistically significant.

All the assumptions of the regression analyses did not hold true. In the case of the box sites the residuals were autocorrelated (Durbin-Watson statistic $d = 2.958$) but normally distributed (Shapiro-Wilk statistic $W = 0.899$; $df = 15$; $P = 0.092$). In the case of the area the residuals were normally distributed ($W = 0.889$; $df = 15$; $P = 0.065$) and did not autocorrelate (Durbin-Watson statistic $d = 2.145$).

3. RESULTS

3.1. Population size and growth rate

The only fit model with $\Delta AIC_c < 4$ for population size suggested that survival and recapture parameters were constant in time but population size was time dependent (ϕ_c, p_c, N_t). According to this model the population size decreased from 65 ± 11 ($N \pm SE$) individuals to 29 ± 6 individuals in 1995-2009 (Figure 2, Appendix I). Lowest population size of 23 individuals was estimated for 2005.

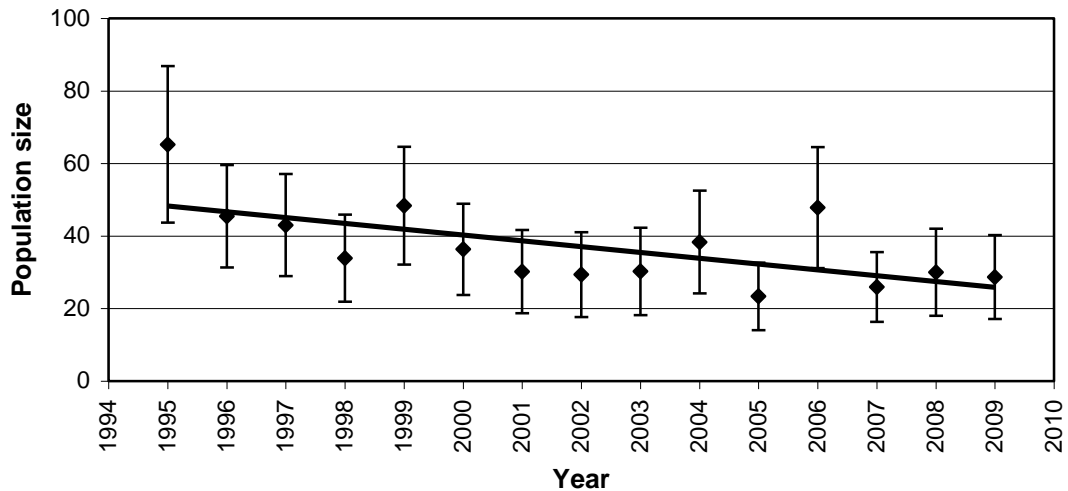


Figure 2. The annual population size estimates with 95 % confidence intervals and trend line with coefficient -1.604.

The best fit model showed that growth rate varied among years but survival and recapture probabilities were constant in time (Table 1). However, models where the growth rate was constant also got some support from the data as the ΔAIC_c values were less than four for these models (Table 1). The weighted average estimates of the growth rate were calculated from these three models. They varied between 0.71 ± 0.22 and 1.60 ± 0.65 (*WM*, *weighted mean* \pm *SE*) with quite wide 95 % confidence intervals, especially in 2005–2006 (Figure 3, Appendix I).

None of the lower confidence limits were above one so it can be said that the population did not for certain grow in any year. On the contrary, more than half of the upper limits were below or equalled one so at least in nine years the population decreased or remained constant with 95 % probability. The decrease can also be seen from the geometric mean of the best model which was 0.93 ± 0.06 (*GM* \pm *SE*). In the two next best models the growth rate was constant and also significantly less than one: 0.96 ± 0.01 and 0.96 ± 0.02 ($\lambda \pm SE$) for the second and third model in Table 1. Thus, all the best fit models suggest significant population decline.

Table 1. The best models ($\Delta AIC_c < 4$) which estimate survival (φ), recapture (p) and growth rate (λ) (*a* stands for age, *t* for time and *c* for constant) and their ΔAIC_c , AIC_c weights and numbers of parameters.

Model	ΔAIC_c	AIC_c w.	Par.
$\varphi_c p_c \lambda_t$	0.00	0.58	16
$\varphi_c p_c \lambda_c$	1.84	0.23	3
$\varphi_c p_t \lambda_c$	2.31	0.18	17

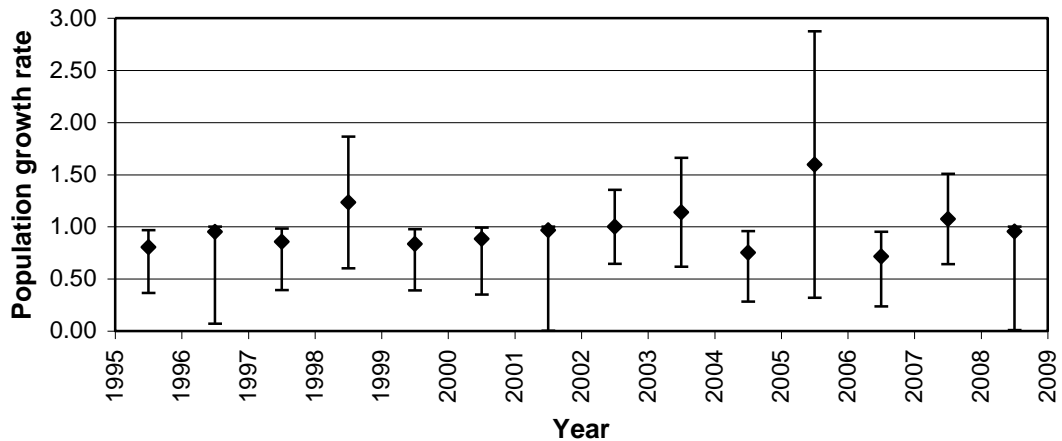


Figure 3. The weighted average estimates of the growth rates and their 95 % confidence intervals of three models between given years.

3.2. Survival and recapture

The eight best fit models for survival and recapture probabilities are shown in Table 2. Those models included either age (a) or both age and marking age (m) dependent survival parameters. Parameters estimating recapture were either constants or included marking age, age or both. None of the best fit models had time dependent parameters. The weighted average estimates of the eight fittest models for all marking ages and ages are shown in Table 3. Survival depended on the age, and the survival probability of juveniles was less than half of that of adults (Table 3). Recapture estimates did not differ markedly between ages or marking ages, and about 60 % of the individuals were captured (Table 3).

A total of 64 models were fitted with the data (Appendix II). Both parameters depending on a factor (marking age, age and/or time) appeared in 32 models, so their probabilities of being selected to the best model by chance alone were 0.5 for each parameter. Likewise the probability of a constant parameter to be selected by chance alone was 0.125 ($= 8/64$). These probabilities can be compared to sum of $QAIC_c$ weights of the best models for each parameter and factor (Table 4). Age-dependent survival occurred in all eight models so it was selected two times more than by chance alone. Therefore, survival was clearly affected by the age of the flying squirrels. Summed weight for constant recapture was 0.49 and much larger than the expected 0.125 by chance. This supports the conclusion that the recapture rate was not age, marking age or time dependent.

Table 2. The best models which estimates survival (φ) and recapture (p) (a stands for age, m for marking age and c for constant) and their $\Delta QAIC_c$, $QAIC_c$ weights and numbers of parameters.

Model	$\Delta QAIC_c$	$QAIC_c$ w.	Par.
$\varphi_a p_c$	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

Table 3. The weighted average estimates of survival (ϕ) and recapture (p) and their standard errors and 95 % confidence intervals. ‘Marking age’ is the age of an individual when it was encountered for the 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

Table 4. The survival (ϕ) and recapture (p) with different dependent factors (a stands for age, m for marking age and c for constant) and their sum of QAIC_c weights (calculated from Table 2) and the probability of being selected to the best models by chance alone.

Parameter	Sum of weights	Probability of occurrence
ϕ_a	1.00	0.50
ϕ_m	0.30	0.50
p_c	0.49	0.13
p_m	0.31	0.50
p_a	0.27	0.50

3.3. The effect of habitat availability on population size

The annual population size had a non-linear relationship with the number of nest box sites ($F = 11.406$, $df_1 = 2$, $df_2 = 12$, $P = 0.002$, $R^2 = 0.655$; Figure 4). The regression coefficients were -7.122 ± 0.171 ($a_1 \pm SE$; $t = -2.558$, $P = 0.025$) and 0.098 ± 1.055 ($a_2 \pm SE$; $t = -2.930$, $P = 0.013$) for the first- and the second-order term, respectively. The significance of the a_2 coefficient indicates that this model is significantly better than the one with linear effect only. However, the shape of the relationship is convex whereas fragmentation effects predict concave pattern where the decrease in population size would be particularly pronounced at low level of the number of box sites.

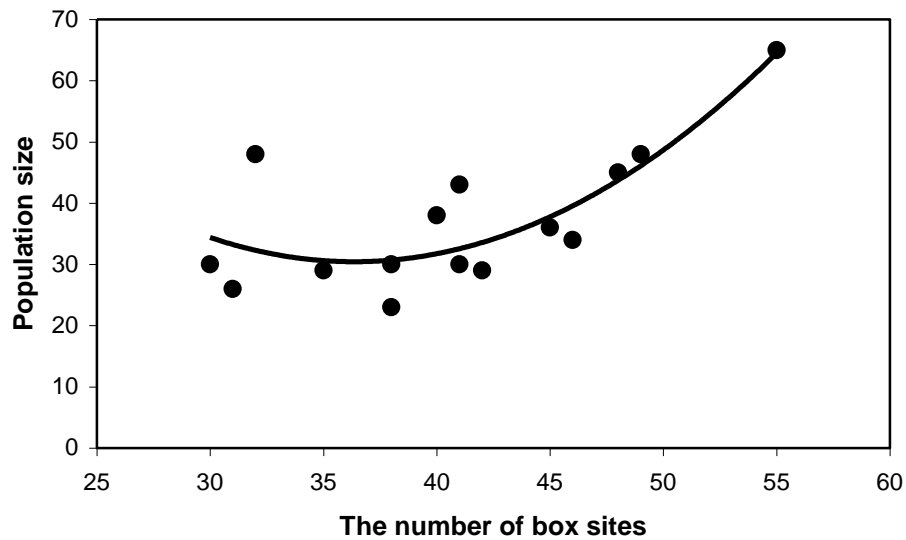


Figure 4. The quadratic relationship between population size and the number of box sites. The regression equation is population size = $0.098 * \text{number of box sites}^2 - 7.122 * \text{number of box sites} + 159.894$.

The population size was decreasing with decrease of the habitat area ($F = 9.156$, $df_1 = 1$, $df_2 = 13$, $P = 0.010$, $R^2 = 0.413$, Figure 5). The regression coefficient of area was 4.632 ($t = 3.026$, $P = 0.010$). This suggests that each 1 km^2 reduction in habitat area results in a loss of 5 individuals from the population.

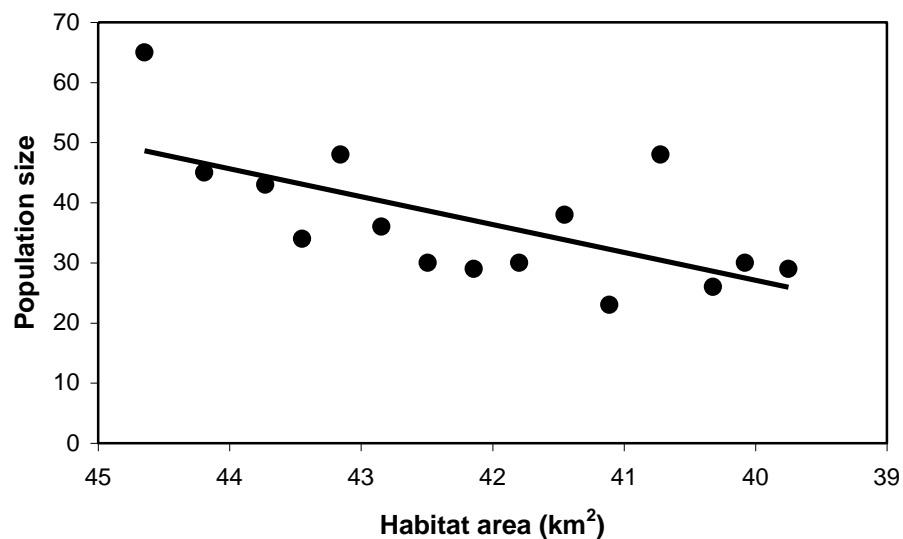


Figure 5. The linear relationship between population size and habitat area. The first dot from the left represents year 1995 and the last one represents year 2009. The regression equation is population size = $4.632 * \text{area (km}^2) - 158.203$.

4. DISCUSSION

The adult population declined from 65 (± 11) to 29 (± 6) ($N \pm SE$) individuals in 15 years (Appendix I). In Figure 2 an almost monotonic decline in population size can be seen with the exceptions of years 1999, 2004 and 2006 which may have been good years with plenty of food. Even though the population size estimates were not very precise, still a declining trend can be seen.

There are previous estimates of the population size in year 1998 (Mäkelä 1999, 2001, Sulkava *et al.* 2008) which were 28-37 females, while in this study the estimate was 34 (± 6) adults of which about a half are assumed to be females (Mäkelä 1999). The previous studies however were completed in the larger study area of 100 km² which is about twice the size in this study. That still does not completely explain the difference in the estimates since most of the flying squirrels lived in the smaller (45 km²) area where the boxes were placed. In addition to the marked individuals, the earlier studies include the individuals that were not caught but observed based on faecal pellets. Even though the marked individuals do not constitute the whole population living in the study area, they still give a good picture of the trend in the population size in last 15 years.

Since there was temporal variation in the population size caused not only by the number of nest box sites or habitat area, the generalizability of the population size estimate only in one year is not very good, especially, if this population fluctuation is not considered. In some years there was great variation in the population size compared to previous year. For example, in 1995-1996 and 2005-2007 the population size estimates changed at least by 30 percent. By censusing the flying squirrels only in 2006 would have given too optimistic picture of the population's situation. Maybe three or four consecutive years would give a rather good estimate. But a longer study period is needed to estimate the long-term trend in population size.

The growth rate estimates varied between 0.71 (± 0.22) and 1.60 (± 0.65) (Figure 3, Appendix I). Some of the estimates were imprecise since their confidence intervals were so wide, as for the largest growth rate. The best model's geometric mean of the growth rate (0.93) and the constant growth rate estimates of the two next best models (0.96) revealed also a decrease in the population size during 1995–2009. With the growth rate of 0.96 a population would decline 44 % from the initial size and with the growth rate of 0.93 it would decline 64 % from the initial size in 15 years. In fact, the decline from 65 to 29 individuals is between these two numbers (accurately 55 %). According to IUCN Red List criteria this single population would be determined as threatened, almost endangered (Rassi *et al.* 2001).

Lampila *et al.* (2009) studied three flying squirrel populations in Western Finland during 1992–2004. In two of the populations the mean growth rate during the time interval was also 0.96 and in one population it declined from more than one to less than 0.80.

The age affected survival probability (Tables 3 and 4), and it was for adults (0.48–0.50) about twice as big as for juveniles (0.22). This was expected since juveniles disperse while searching for own box site (Selonen & Hanski 2004) and can disappear from the study area never to be recaptured again, which lowers the survival parameter. Therefore, the survival probability of juveniles is the probability of surviving and staying in the study area over the first winter. The adult survival equalled to the average adult survivals (0.43–0.53) of three flying squirrel populations in Western Finland (Lampila *et al.* 2009). The probabilities of a juvenile to survive and stay in the study area through the first winter were 0.23–0.30 which are little higher than in this study. The juvenile survival should be studied more to recognise the effect of dispersal.

Even though the population size decreased, the survival remained constant through time, which means that mortality rate did not increase with time. That means that the same proportion of adults stay alive year after year despite of the loss of box sites and habitat area. Instead, breeding success may have decreased. Maybe, despite of the habitat loss, adult individuals stayed in their home-ranges, but the habitat patches possibly became too isolated and small to draw young dispersing individuals (Hanski *et al.* 2001). Another possibility is that either the survival or the breeding success or both, possibly being constant, were just too low, so that the recruitment of new individuals did not compensate the mortality rate, and that is partly why the population declined.

The recapture estimate did not significantly vary between ages and marking ages (0.58–0.62, Table 3). The recapture probability was on average lower than in abovementioned three Western populations, in which it was 0.43–0.79 for males and 0.79–0.96 for females (Lampila *et al.* 2009). Time did not seem to have an effect on recapture parameter. This suggests that the estimated population size or other parameters were not affected by the number of capture efforts. Even though survival and recapture parameters could have truly been and probably were varying in time, the sample size was probably too small to reveal such a variation (Burnham & Anderson 2002).

The number of box sites and population size had a non-linear relationship (Figure 4). When the number of box sites varies between 30 and 55, the population size, according to the regression formulation, varies between 31 and 64, being lowest when the number of box sites is around 36. At the same time the number of flying squirrels per box site varies around one (0.80–1.18), and it is lowest around 40 box sites. So, according to the regression formulation, when the number of box sites increases from 30 to 36, the population size decreases, and after 36 box sites the population starts to grow increasingly. There is no logical explanation for this. However, the second-order term and the whole regression model were not significant when the highest data point (in Figure 4) were left out. This was also true for the linear regression model. Without this data point, the relationship between the number of box sites and population size is statistically not significant.

Logging affected population size linearly (Figure 5). A loss of about 1 km² reduces the population, roughly, by five individuals. The limit size where the population size turns into a positive number is about 35 km² (based on the regression equation). During the time period there were 60–110 ha unlogged forest area per flying squirrel, which sounds large since average home-range size was 59.9 ha for male and 8.3 ha for female in the study of Hanski *et al.* (2000). The true home-range sizes were probably smaller, since every hectare in the study area is not used by the flying squirrel.

The linear relationship between the population size and the habitat area suggests that the population does not suffer from habitat fragmentation, only from the reduction of the habitat area. Otherwise the relationship would have been curved downwards with small habitat areas. A quadratic relationship was also tested but the second-order term was not significant, which supports the linear relationship. This does not mean that there has not been any habitat fragmentation. Study area may have been fragmented but it is not yet seen in population size. For example, male flying squirrels are able to expand their home-ranges to compensate fragmentation by moving between several patches that include younger forests (Selonen *et al.* 2001, Hanski *et al.* 2001). For females, which have smaller home-ranges, the habitat patches may have remained large enough in spite of the forest cutting. Actually, Reunanen *et al.* (2004) found that the flying squirrel is not very sensitive to fragmentation because it can disperse long distances and use various habitats.

Unlike male flying squirrels, females usually lived only within one habitat patch surrounded by less suitable habitat in the study of Selonen *et al.* (2001). More important than the area of a single patch may be the amount of deciduous trees for food, at least in the case of females. On the other hand, breeding might require a patch of minimum area (Selonen *et al.* 2001). Further habitat loss and possible fragmentation is especially a threat to female flying squirrels since they are more dependent on one habitat patch.

The coefficient of determination (R^2) of regression analyses between population size and habitat area and number of box sites was about 0.41 and 0.66, respectively. The number of box sites and habitat area explains a large proportion of the variation in the population size. A multiple regression analysis would have been more effective to detect which factor affects more on the population size but it was not performed because of the collinearity between the habitat area and the number of box sites.

All the CJS assumptions were not met. Because of tag loss 13 individuals had to be removed from the data. This could have affected results, especially if those individuals were present last years when the population size was smaller. There is uncertainty also because capture effort varied between years. In 1997–1999 and 2009 there were three sampling occasions whereas there were only two occasions in other years. It is not, however, seen in the results when compared to years with only two sampling occasions (Figure 2). It is difficult to distinguish the effects of temporal variation and the number of sampling occasions. As said above, the time independent recapture probabilities suggest that the number of capture efforts did not affect the recapture probabilities. But of course a third sampling occasion in every year would have provided more reliable results.

The estimation of habitat area was not very confident because it was calculated from the forest cutting data of town Alavus and it was not available for some years. Since there was (or was assumed to be) some forest cutting every year, the study area was assumed to have decreased every year. This might have been possible, but the forest cutting data of Alavus maybe does not reflect the logging in the study area. Even though, it is clear that the population declined at least partly due to habitat loss.

The existence of the flying squirrel should be considered when planning the future forest cutting in the area. The availability of food and nest cavities is an important requirement for a home-range (Hanski *et al.* 2001, Selonen *et al.* 2001). Therefore, deciduous and extant or possible future cavity trees with buffer zones should be saved. Unfortunately this particular population is probably dependent on the nest boxes since cavity trees are scarce. The boxes might have saved the population from extinction this far.

Additionally, some tree corridors should be left to enable moving across cut forest stands (Hanski *et al.* 2001). Though, the loss of preferred habitat may be more important reason for the decline of the Finnish flying squirrel population than the lack of connectivity between habitats (Selonen *et al.* 2001). This is because flying squirrel can use less preferred habitat to move between habitats (Hanski 1998, Selonen *et al.* 2001), although it is more prone to predation (Hokkanen *et al.* 1982, Eronen 1996). Of course the best option would be to leave the forests completely unlogged.

With similar forest cutting as so far the population would become extinct in about 2025 (based on the regression equation of population size and habitat area). There might be a time lag between habitat loss and its effects on the population. Showing a high degree of site fidelity, a flying squirrel individual may stay in its home-range when it is partly cut down (Hanski *et al.* 2001). When the individual dies and the home-range becomes free, it may not be good enough for a new individual because of its low quality and small area. Thus, the habitat loss may not seem to immediately affect the population. On the other hand, some factors can accelerate the decline.

As said above, the population size was not solely affected by habitat size or the number of box sites, but there was temporal variation caused by other reasons, for example, demographic and environmental stochasticity or predator species. The smaller the population is, the stronger the effects of demographic stochasticity and pure chance are (Lande 1998). Also, the Allee effect and the possible effects of fragmentation could contribute to the population extinction. Thus, predicting the current or future population size only based on habitat availability is dangerous. This should also be taken into account when planning the conservation of the (or any other flying squirrel) population. The areas of optimum habitat should be kept large enough to sustain a viable population. This population could already be below its viable population size.

Based on this and previous studies of the population (Mäkelä 1996a, 1999, 2001), its future does not seem so bright. Flying squirrels have been able to escape from clear cuts to other forest patches, also of less preferred habitat, thanks to nest boxes (Mäkelä 1996a). Maybe, in the future, the conservation of the species would require placing nest boxes to enable living in habitats of poor quality when preferred habitats are cut down. A proportion of the flying squirrels could then live in waterside forests and forests surrounding fields and other marginal areas which are saved from logging.

Since the study area is used for normal forestry, it is expected that the trend is similar or even worse (if nest boxes are unavailable) in other flying squirrel populations living in silvicultural forests. We still do not know if the current conservation actions can at some point halt the decline of the Finnish flying squirrel population or if the species should already be classified as endangered.

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APPENDIX I

The estimates of the annual population size and their standard errors and 95 % confidence intervals. N-hat is the hypothetical super-population that consists of all animals ever been born to the population. The results are based on the one fit model in which survival and recapture parameters were constant and population size was time dependent (φ_c, p_c, N_t).

Year	Estimate	SE	95 % CI	
1995	65	11.01	43.69	86.84
1996	45	7.22	31.30	59.60
1997	43	7.17	28.96	57.08
1998	34	6.12	21.88	45.87
1999	48	8.27	32.15	64.59
2000	36	6.43	23.74	48.94
2001	30	5.83	18.75	41.62
2002	29	5.96	17.67	41.02
2003	30	6.15	18.18	42.30
2004	38	7.23	24.19	52.51
2005	23	4.75	14.04	32.65
2006	48	8.50	31.19	64.53
2007	26	4.90	16.36	35.57
2008	30	6.12	18.04	42.04
2009	29	5.90	17.11	40.23
N-hat	299	18.21	270.97	344.07

The estimates of the annual population growth rates and their standard errors and 95 % confidence intervals. The results are based on three models from which weighted average estimates were calculated. One of the models had time-dependent growth rate and the other two had constant growth rates.

Year	Estim.	SE	95 % CI	
1995-1996	0.80	0.16	0.37	0.97
1996-1997	0.95	0.13	0.07	1.00
1997-1998	0.86	0.14	0.39	0.98
1998-1999	1.23	0.32	0.60	1.86
1999-2000	0.84	0.15	0.39	0.98
2000-2001	0.88	0.14	0.35	0.99
2001-2002	0.97	0.16	0.00	1.00
2002-2003	1.00	0.18	0.65	1.36
2003-2004	1.14	0.27	0.62	1.66
2004-2005	0.75	0.19	0.28	0.96
2005-2006	1.60	0.65	0.32	2.87
2006-2007	0.71	0.22	0.24	0.95
2007-2008	1.07	0.22	0.64	1.51
2008-2009	0.96	0.16	0.01	1.00

APPENDIX II

All the models that estimate survival and recapture. There are 64 possible combinations of the two parameters either depending on marking age (m), age (a), and time (t) or being constant (c). The eight best fit models are shown in bold font.

Survival	Recapture	Survival	Recapture
<i>m, a, t</i>	<i>m, a, t</i>	<i>m</i>	<i>m, a, t</i>
<i>m, a, t</i>	<i>m, a</i>	<i>m</i>	<i>m, a</i>
<i>m, a, t</i>	<i>m, t</i>	<i>m</i>	<i>m, t</i>
<i>m, a, t</i>	<i>a, t</i>	<i>m</i>	<i>a, t</i>
<i>m, a, t</i>	<i>m</i>	<i>m</i>	<i>m</i>
<i>m, a, t</i>	<i>a</i>	<i>m</i>	<i>a</i>
<i>m, a, t</i>	<i>t</i>	<i>m</i>	<i>t</i>
<i>m, a, t</i>	<i>c</i>	<i>m</i>	<i>c</i>
<i>m, a</i>	<i>m, a, t</i>	<i>a</i>	<i>m, a, t</i>
<i>m, a</i>	<i>m, a</i>	<i>a</i>	<i>m, a</i>
<i>m, a</i>	<i>m, t</i>	<i>a</i>	<i>m, t</i>
<i>m, a</i>	<i>a, t</i>	<i>a</i>	<i>a, t</i>
<i>m, a</i>	<i>m</i>	<i>a</i>	<i>m</i>
<i>m, a</i>	<i>a</i>	<i>a</i>	<i>a</i>
<i>m, a</i>	<i>t</i>	<i>a</i>	<i>t</i>
<i>m, a</i>	<i>c</i>	<i>a</i>	<i>c</i>
<i>m, t</i>	<i>m, a, t</i>	<i>t</i>	<i>m, a, t</i>
<i>m, t</i>	<i>m, a</i>	<i>t</i>	<i>m, a</i>
<i>m, t</i>	<i>m, t</i>	<i>t</i>	<i>m, t</i>
<i>m, t</i>	<i>a, t</i>	<i>t</i>	<i>a, t</i>
<i>m, t</i>	<i>m</i>	<i>t</i>	<i>m</i>
<i>m, t</i>	<i>a</i>	<i>t</i>	<i>a</i>
<i>m, t</i>	<i>t</i>	<i>t</i>	<i>t</i>
<i>m, t</i>	<i>c</i>	<i>t</i>	<i>c</i>
<i>a, t</i>	<i>m, a, t</i>	<i>c</i>	<i>m, a, t</i>
<i>a, t</i>	<i>m, a</i>	<i>c</i>	<i>m, a</i>
<i>a, t</i>	<i>m, t</i>	<i>c</i>	<i>m, t</i>
<i>a, t</i>	<i>a, t</i>	<i>c</i>	<i>a, t</i>
<i>a, t</i>	<i>m</i>	<i>c</i>	<i>m</i>
<i>a, t</i>	<i>a</i>	<i>c</i>	<i>a</i>
<i>a, t</i>	<i>t</i>	<i>c</i>	<i>t</i>
<i>a, t</i>	<i>c</i>	<i>c</i>	<i>c</i>