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THE CAUSES AND CONSEQUENCES OF POPULATION DECLINES OF TWO BOREAL FOREST SPECIES

THE CASE OF THE WILLOW TIT (PARUS MONTANUS) AND THE SIBERIAN FLYING SQUIRREL (PTEROMYS VOLANS)

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Abstract

I used individual-based capture-mark-recapture data and genetic markers to gain understanding of the demographic and genetic processes operating in small and declining populations of two different species, the willow tit *Parus montanus* and the Siberian flying squirrel *Pteromys volans*. Both species have declined in Finland and the flying squirrel has been considered to be vulnerable. The willow tit study was conducted in northern Finland, near city of Oulu. The population size in the studied area has on average been stable during the past decade. Adult survival in the willow tit was high and fairly stable and was positively correlated with recruitment. Adult survival has been the most influential vital rate to the population growth rate. Local recruitment and immigration have high variation, inducing variation in the population growth rate. Female willow tits use extrapair copulations to maximise offspring heterozygosity. Heterozygous individuals are supposedly of higher quality than homozygous ones. I found weak negative association between individual homozygosity and recruitment probability. The flying squirrel populations have declined during the past ten years. Furthermore, adult survival has declined in one of the populations, most likely due to habitat loss and fragmentation that decrease the adult survival and limit dispersal. The flying squirrel populations were studied in western Finland. The flying squirrel densities in the studied areas are the highest in Finland and therefore these areas have been regarded as favourable for the flying squirrel. My results question this view. Microsatellite analyses strengthen the view of populations doing poorly, because the heterozygosities in all the populations and particularly in the most isolated one were rather low. High F_{ST} values indicate low dispersal even between adjacent populations. Following work should investigate the spatial variation in individual performance and the dispersal processes in these populations. For the flying squirrel it is vital to determine the size and quality of the patches that can support flying squirrels and the ones that apparently can not. Present estimates of survival and genetic diversity can be used to reconstruct a meaningful PVA and projections for these populations.

Keywords: demography, local recruitment, mark-recapture, microsatellite, survival

To my mom and dad

Acknowledgements

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I   Lampila S, Orell M, Belda E & Koivula K (2006) Importance of adult survival, local recruitment and immigration in a declining boreal forest passerine, the willow tit *Parus montanus*. Oecologia 148: 405–413.
II Lampila S, Orell M & Kvist L (2009) Female willow tits Parus montanus gain from promiscuous behaviour. Manuscript.
III Lampila S, Wistbacka R, Mäkelä A & Orell M (2009) Survival and population growth rate of the threatened Siberian flying squirrel *Pteromys volans* in a fragmented forest landscape. Écoscience 16(1). In press.
IV Lampila S, Kvist L, Wistbacka R & Orell M (2009) Genetic diversity and population differentiation in the endangered Siberian flying squirrel *Pteromys volans* in fragmented landscape. European Journal of Wildlife research. DOI: 10.1007/s10344-009-0259-2.

Contents

1 Introduction

The dramatically increased anthropogenic impacts have accelerated the rate of extinctions in the 20th century (Pimm *et al.* 2006). The presently observed extinction rates exceed the extinction rates in fossil record by up to 500 times (Baillie *et al.* 2004), and the sixth mass extinction may already be on its way (Pimm & Brooks 2000). Loss, degradation and fragmentation of habitats have major negative impact on species worldwide, affecting almost 90% of threatened birds, mammals and amphibians (Baillie *et al.* 2004). Habitat loss means changes in landscape composition that cause a proportional loss of individuals from the landscape whereas habitat fragmentation refers to additional effects resulting from the reduction of patch size, edge effects, and isolation of habitat patches (Andrén 1994, Fahrig 1997).

1.1 The changing world

1217 bird species (12% of known species) are globally threatened and another 12% have extremely small geographical ranges in areas where human actions rapidly destroy their habitats (Pimm & Brooks 2000). In Europe, 13% of the bird species are threatened. However, long before a species even becomes threatened the majority of its local populations are already extinct. Many common and widespread bird species are currently declining at an alarming rate. For example, in Europe the common farmland birds have declined by 44% and common forest birds have declined by 9% from 1980 to 2005. Contrary to common farmland birds that have declined across Europe, the populations of common forest birds have been stable in Western and Eastern Europe and decreased in Northern and Southern Europe. Two common forest species that declined the most were the lesser spotted woodpecker *Dendrocopos minor* and the willow tit *Parus montanus* (PECBMS 2007). Of mammals, 22% (1094) of all the evaluated species are threatened by extinction. In Europe, 15% of the mammal species are threatened and an additional 9% almost qualify to the threatened status (Near Threatened by the IUCN criteria). About one third (27%) of all European mammal populations are declining (IUCN 2007a).

Habitats have changed in their amount, quality and composition. Most of the natural ecosystems on Earth have been replaced with artificial environments or have become fragmented (Pimm *et al.* 2006). In Finland the forest structure and composition have changed dramatically due to modern forestry. Natural forests

have for the most part been replaced by managed monoculture forests and pristine forests are virtually nonexistent (Östlund *et al.* 1997). In Finland old semi-natural forests are nowadays mainly found in scattered fragments close to the eastern border (Kouki & Väänänen 2000). The landscape changes in different ways with different human usage. When a forest is converted to an urban area or agricultural use, the resulting landscape is static with mostly sharp edges. On the other hand, forestry practises lead to dynamic landscapes with varying edges. These are in most parts covered with forest, while undergoing changes in composition and age structure (Schmiegelow & Mönkkönen 2002).

Species adapted to connected landscapes are less likely to persist in the modern highly fragmented landscapes (Hanski 2005). Small and isolated patches of remaining natural habitat can only support small populations that rapidly loose genetic variation and have high extinction risk due to deterministic changes in the vital rates or stochastic factors (Lande 2002). Depending for example, on a species' dispersal ability, its response to fragmentation may vary from no effect at all to considerable population decline (Wiegand *et al.* 2005). Ims *et al.* (1993) recognised three patterns of space use responses in individuals (Fig. 1): the fusion response, fission response and the expansion response, which has been found in the flying squirrel males (Selonen *et al.* 2001). Different costs may be involved in each of these responses. Hanski (2002) highlights the importance of building models and predictions for relatively common species. If current trends in habitat loss and fragmentation continue many species not yet threatened will become endangered in the future. Modelling the viability of highly endangered species' populations is hard because the data are often insufficient to properly estimate population parameters and their variance (Hanski 2002). Thus, lack of detailed population data is the major limitation to the application of population viability analysis (PVA, Shaffer *et al.* 2002).

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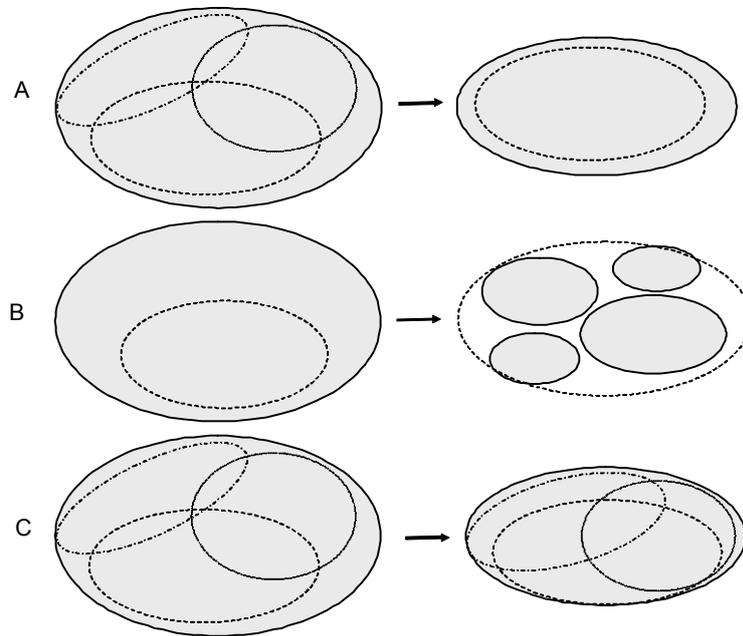
Fig. 1. The different space-use responses of individuals to fragmentation. The grey ovals represent habitat patches and the dashed lines individual home ranges. A) The fission response is expected for territorial animals. The overlap between the home ranges decrease as surplus individuals are expelled from fragments of limiting size. B) The expansion response. As patch size diminishes individuals expand their home range to include several patches and they frequently move between patches. C) The fusion response is expected for social animals that tolerate more overlap in the home ranges as the patch size decreases. Overlap between the home ranges increases (Andreassen *et al.* 1998).

1.1.1 Processes of population decline

Population decline or extinction is a process involving both stochastic and deterministic components. Most endangered species are originally threatened by deterministic human impacts, such as habitat destruction and overexploitation. Once the populations have diminished in size stochastic components contribute to the extinction risk. They not only cause extinctions by chance, but have cumulative deterministic tendency to decrease population size (Lande 2002).

Demographic stochasticity, the intrinsic variability caused by small population size, arises from variation in reproduction and survival between individuals within a season (Shaffer 1981, Morris & Doak 2002) and is usually the major stochastic component when the population size is on the order of 100 individuals or smaller (Lande 1993) Demographic stochasticity produces a deterministic reduction in the growth rate that is inversely proportional to population size (Lande 2002). The effect of individual variation tends to average out in large populations where environmental stochasticity, the extrinsic variation in the biotic and abiotic factors, is the major source of uncertainty (Lande 1993, Sæther *et al.* 1998). Environmental stochasticity is the variation in the vital rates caused by unpredictable changes in the environment, but not seasonal patterns or consistent trends, and its impact does not depend on population size (Lande *et al.* 2003). Extreme cases of environmental stochasticity are catastrophes or bonanzas. The vital rates may be correlated both within and between years. In many species there is positive correlation between survival and reproduction. For example persistent environmental conditions can result in autocorrelation, where adjacent years tend to be similar. These correlations add variability to the population growth rate (Morris & Doak 2002). Stochasticity decreases the long-term population growth rate because the annual growth is a stochastic multiplicative process for which the "average" result is given by *geometric*, not arithmetic mean of the multiplier. The geometric mean is always less or equal to the arithmetic mean of a set of numbers and the difference between two grows with increasing variance in the numbers (Morris & Doak 2002).

Genetic processes can play an important role in determining the population viability in fragmented landscape (Frankham *et al.* 2002). Stochastic genetic processes affecting small populations include genetic drift, effective population size, inbreeding and fixation of mildly deleterious mutations (Lande 2002).

1.1.2 Sources and sinks

Once demographic data are acquired, they can be used in determining the contribution of a local population to the whole larger population at the landscape level (Runge *et al.* 2006). A population is a sink if mortality exceeds reproduction and immigration exceeds emigration and a source if the opposite is true (Pulliam 1988). A way of describing the source-sink dynamics is to define the population by its intrinsic growth rate (r), which indicates whether the population is in decline (r < 0) or on the increase (r > 0, Hanski 2005). More specifically, when

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the environmental stochasticity (σ_e^2) is taken into account, the stochastic growth rate is given as:

$$r_0 = r - \sigma_e^2 / 2.$$

A population with $r_0 < 0$ is an absolute sink, whereas a viable population that appears to be a sink because immigration exceeds emigration, but with $r_0 > 0$ is a pseudo-sink (Watkinson & Sutherland 1995). Immigration from the other populations may rescue a sink population. Therefore, a species can be found in habitats where it actually should not be able to persist (Hanski 2005). Because of the environmental stochasticity, the metapopulation may persist in the long term even when all the local populations are sinks, if the local populations behave independently and migration evens out the growth in local populations (Hanski 2005). The consequences of habitat alteration to populations are especially devastating if source populations are turned into sink populations. If the changes in the environment are slow and gradual, the response of long-lived species may appear after considerable time-lag (Hanski 2005). Classification of local populations to sources and sinks is important in decision making for habitat management, when considering whether to protect areas with source or with sink populations.

1.2 Population fluctuation

Variation in animal population size can be immense or seemingly nonexistent. Fluctuation in population size is connected to the life history traits of species. Births, deaths, immigration and emigration are the fundamental factors of population fluctuations. Since these life history traits vary over space and time, it is essential to quantify this variation for understanding population dynamics and for developing conservation strategies. In general, species can be placed into a slow – fast continuum according to their life history (Saether *et al.* 1996). Species with long life span, low adult mortality and long pre-reproductive period can be called survivor species, or 'slow' life history species. The populations of such species are fairly stable and they are vulnerable to decrease in adult survival and recover slowly after population decline. Species that mature early, have high reproductive output, and high adult mortality are 'highly reproductive species' (Sæther & Bakke 2000), or species with 'fast' life history. These species typically have variable population sizes and they recover rapidly after a disturbance. Also

body size is related to the life history. At the slow end of the continuum the species are on average large and at the fast end they tend to be small. Birds are more long-lived than mammals compared to their size, but the reason for this is still unknown.

1.2.1 Estimates of population variation

Explaining variation in population size has attracted increased attention in studies of natural populations. Advances in methodology have been substantial in the past 20 years or so (Lebreton *et al.* 1992, Pradel 1996, White & Burnham 1999, Nichols *et al.* 2000, Nichols & Hines 2002). Traditionally, estimates of survival and fecundity have been used in prospective matrix projection models (Caswell 2001) to produce estimates of future population growth rate (projected λ) and population viability (Beissinger & McCullough 2002). Development of reverse-time capture-recapture models for open populations (Pradel 1996, Nichols *et al.* 2000) provides retrospective methods to directly estimate the (realized) λ with variance and standard error, without having to estimate the population size. These two parameters describing population growth, projected λ and realized λ, are the same only if the population is in stable age distribution (White & Burnham 1999). Reverse-time capture-recapture approach enables direct estimation of relative contributions ("seniority parameter", γ_i) of adult survival, local recruitment and immigration to population growth rate (Nichols *et al.* 2000). These parameters are analogous to the traditional matrix-model based concept of elasticity (Caswell 2001), although they are retrospective and traditional elasticities are prospective in nature (Nichols *et al.* 2000). Furthermore, these contributions are applicable to a specific time interval whereas the asymptotic matrix based elasticities present a mean over longer period of time (Nichols & Hines 2002).

Traditional sensitivities and elasticities obtained from matrix models are not especially useful in populations with transient dynamics or high temporal variance or if movement is an important contributor to population dynamics (Nichols *et al.* 2000). Direct estimation of γ_i enables estimating temporal variation in relative contributions of demographic parameters. This is relevant for analysis of population viability (Nichols & Hines 2002, White *et al.* 2002).

1.3   Genetics and small populations

Although demographic and environmental stochasticities are important factors in population extinctions, most populations are not driven to extinction before genetic factors have started to affect them (Frankham 2005). If genetic factors are ignored in conservation ecology, extinction risk will be underestimated and conservation actions could be inappropriate (Frankham 2005). Population decline leads to reduced genetic variation due to inbreeding and random genetic drift (Frankham 1996, Garza & Williamson 2001). Low genetic variability affects the ability of the species to evolve in the changing environment and most threatened taxa already suffer from reduced ability to evolve, elevated inbreeding and reduced reproductive fitness (Reed & Frankham 2003).

Inbreeding depression affects negatively e. g. disease resistance, immune response (Reid *et al.* 2007, Spielman *et al.* 2004, Whiteman *et al.* 2006), sperm production, mating ability, female fecundity, juvenile survival, recruitment (Jensen *et al.* 2007), maternal care, age at maturity and adult survival (Frankham 2005). Effects of inbreeding depression are higher in the wild than in captivity (Crnokrak & Roff 1999) and more deleterious under stressful conditions (e. g. Coltman *et al.* 1999). Jensen *et al.* (2007) found a negative relationship between individual inbreeding coefficient (F) and standardized multilocus heterozygosity (H) in sparrows *Passer domesticus* (Jensen *et al.* 2007). However, correlation between inbreeding and heterozygosity has often been weaker than expected (e.g. Overall *et al.* 2005, Bensch *et al.* 2006).

Factors other than inbreeding are also important in small populations. Loss of genetic diversity in small populations increases extinction risk by adversely affecting the ability to evolve (Frankham 2005). As populations go through a bottleneck the allelic diversity is lost more rapidly than heterozygosity. In small populations drift may lead to fixation of mildly deleterious mutations (in nuclear or mitochondrial DNA) that may decrease population growth (Frankham 2005).

1.4   Aims of this study

In this thesis I examined various aspects of population ecology and population genetics using a declining bird (willow tit *Parus montanus*) and a threatened mammal species (Siberian flying squirrel *Pteromys volans*) as study objects. I carried out research on the effects of demographic, environmental, and genetic stochasticities to population fluctuation in the two species that have different life

histories and conservation status but are facing the same threats in the modern world. The willow tit and the Siberian flying squirrel are only two of many species suffering from habitat loss. In Finland 1505 species are considered threatened, out of which 522 are suffering in one way or another from modern forestry (Rassi *et al.* 2001).

First, I used extensive long-term data to explore the realized growth rate (λ), its variation and relative contributions of vital rates (adult survival, local recruitment and immigration) to the growth rate of an open population of the willow tit (I). I discuss the importance of variation in adult survival, local recruitment and immigration, especially in relation to continuous forest fragmentation in boreal areas. Second, I aimed at deeper understanding of individual level population genetics by studying the heterozygosity – fitness correlations, patterns of female mate choice and frequency of extra-pair paternity in the willow tit broods (II) with microsatellite markers. Females are expected to maximise the genetic and phenotypic quality of their progeny. Heterozygous individuals are considered to be of better quality than individuals with more homozygous alleles and the genetic quality of individual genotypes has an impact on population dynamics (Reed *et al.* 2007). Mostly, heterozygosity – fitness correlations have been studied in small, somewhat isolated or inbred populations (see e. g. Bensch *et al.* 2006, Brouwer *et al.* 2007, Randall *et al.* 2007), but here I studied the local recruitment in relation to individual heterozygosity in a polymorphic and panmictic population of the willow tit.

Third, I studied the basic vital rates (local recruitment and adult survival) of the Siberian flying squirrel in western Finland. The area has traditionally held high flying squirrel density, but habitat loss and fragmentation raise a concern about the viability of populations in the changing landscape. I determined the adult survival probability, local recruitment, and realized population growth rate (λ) in three populations (III). Furthermore, I explored the genetic structure and differentiation of these populations, to see if microsatellite markers reveal population isolation, bottleneck effects, or low genetic variability (IV).

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2 Methods

2.1 The study species

The distribution of the willow tit ranges through central and northern Europe and Russian Taiga from north-eastern France to the Pacific coast (Cramp & Perrins 1993). The willow tit is globally classified as a least concern species according to the IUCN criteria (IUCN 2007b). However, based on line-transect and winter bird censuses in Finland, it has declined in numbers by about 60% during 1940–1980, and about 15% from 1983 to 2004 (Väisänen *et al.* 1998, Väisänen 2005). The decline has been especially dramatic in south-western Finland (Lehikoinen *et al.* 2003).

Willow tit is a small, socially monogamous and sexually monomorphic passerine. It prefers coniferous boreal forest habitats. The willow tit is highly sedentary, spending its entire life in a home range, which is established after natal dispersal (Koivula & Orell 1988). Generally, it produces one brood per year (Orell & Ojanen 1983). The birds breed in holes that they excavate in decaying stumps (Orell *et al.* 1996). The cavities are mainly found in birch *Betula* sp. stumps in the study area. Willow tits spend the winter in a social flock of 3–6 non-related individuals that maintain exclusive territories. Winter ranges are formed by September and they are defended against conspecific flocks (Ekman 1979). Intensive hoarding of animal and plant food takes place in the autumn (September–October) until the snow comes. In addition to this peak hoarding period, willow tits can cache food at any time of the year if excess food sources are available (Brodin *et al.* 1996).

The distribution of the Siberian flying squirrel (hereafter the *flying squirrel*) ranges from Hokkaido, Japan through Siberia to Estonia and Finland. It is considered extinct in Latvia (Hanski 2006). Its range in Finland extends from the south coast to southern Lapland where its distribution becomes patchy (Wilson & Reeder 1993), (Reunanen 2001). The flying squirrel is globally considered near threatened (NT, IUCN 2007b). In Finland flying squirrel populations have declined about 50% from the 1950's to the 1980's (Hokkanen *et al.* 1982). During the past 10–20 years the decline has been 30–58% in different populations (Hanski *et al.* 2001a, Hanski 2006). At present, the number of females in Finland is approximately 143000 (Hanski 2006). Due to the population decline in Finland the flying squirrel is considered endangered with status vulnerable (VU, Rassi *et*

al. 2001). Furthermore, the flying squirrel is listed on Appendix II of the Bern Convention, and on Annexes II and IV of the EU Habitats & Species Directive (Anonymous 1992). The decrease of flying squirrel numbers in Finland is associated to habitat loss due to modern forestry practices (Hokkanen *et al.* 1982, Rassi *et al.* 2001).

The flying squirrel is a small, nocturnal, and arboreal rodent, that prefers mature mixed forests with deciduous trees (especially aspen *Populus tremula*) and large Norway spruces *Picea abies* (Hanski 1998). Tree cavities are preferred as breeding or roosting places, but they accept nest boxes and use twig dreys of the red squirrel *Sciurus vulgaris* for roosting. The flying squirrel also occurs in cultural environments in southern Finland (Wistbacka *et al.* 1996) and may breed in outbuildings such as warehouses. The flying squirrel is herbivorous, eating leaves, catkins and buds from deciduous trees (Mäkelä 1996). Flying squirrels occupy large home ranges for their body mass. Females have smaller territories than males (average 8.3 hectares vs. 60 ha, Hanski *et al.* 2000) and one male territory can overlap several female territories. Adult flying squirrels are highly site tenacious (Hanski *et al.* 2000). Natal dispersal distances are highly variable: females usually disperse further (0.7–8.7 km) than males (0.5–6.5 km, Hanski *et al.* 2001b).

2.1.1 Data collection

The willow tit study area is located in the Oulu (65°N, 25°30´E) area, Northern Finland (Fig. 2). The breeding population in this area has been studied already since 1975 e.g. (Orell & Ojanen 1983) and more intensively from 1986 (Orell & Koivula 1988). The study area was gradually increased during 1986 – 1991 and has stayed fairly constant since then (22 km^2). Therefore, I included data collected from 1991 and onwards. The area consists of fragmented forests of different ages, including clear cuts, young forest stands, bogs, two small lakes and a small river (see e. g. Orell & Koivula 1988, Siffczyk *et al.* 2003 for further details).

In the first paper (I) the capture – recapture histories of willow tits were used (N = 1230). The data consist of individuals that were first captured as adults or fledglings and later identified from colour ring combinations inside the study area (Orell *et al.* 1994). During the summer nestlings are ringed with aluminium ring. Colour ringing of immigrants and local recruits takes place in late autumn after the juvenile dispersal period is over. Unmarked adults found during the breeding season are captured and marked with colour rings. Each year in the beginning of

the breeding season the majority of the breeding population (ca. 90–95%) is previously marked (Orell & Koivula 1988). If tag loss was suspected (or the colour of the plastic rings faded and become difficult to see), identity of an individual was verified by capturing the bird and reading the aluminium ring. There is no evidence that losses of colour rings may have biased the data. Despite the intensive search for the willow tit nests, it is possible that some nests (1−3 broods) were undiscovered annually (Orell *et al.* 1999a). Thus, few residents without a ring may later have been misclassified as immigrants. Handling mortality of birds was very low (0−3 individuals / season).

Collecting DNA samples from all the living nestlings started 2001. The nestlings were sampled by plucking the growing feathers that contain DNA. From the year 2002 onwards DNA was collected also from adult birds upon capture. From the adults a blood sample was taken by puncturing the brachial vein. In paper II the data from eight microsatellite markers and capture histories of the sampled individuals were combined (N = 231 adults, 1498 nestlings).
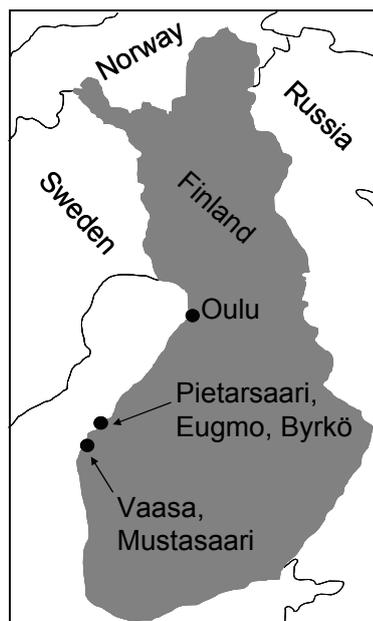
Fig. 2. The study areas. The willow tit study was conducted in Oulu area, and the Siberian flying squirrel study in Pietarsaari, Eugmo, Byrkö, Vaasa, and Mustasaari.

The flying squirrel data were collected in the coastal area of western Finland (Fig. 2) in 1992–2002. We classified 70–80 years old spruce-dominated forests as potentially suitable habitat for flying squirrels (Reunanen 2001). In all the study areas the amount of suitable habitat decreased about 30% during the past ten years. Flying squirrels were captured from nest boxes that were in spruce trees. The boxes were mostly situated in sets of three. The nest boxes were checked in June and August and once in wintertime. When captured, the animals were sexed, weighed and ear-tagged. DNA-samples were taken since 2002 by puncturing the ear lobe. The field procedure was similar in all study areas.

The set of populations differed somewhat in papers III and IV Long-term capture-recapture data from *Eugmo* (N = 177 adults), *Byrkö* (N = 106 ad, 238 juveniles) and *Mustasaari* (N= 127 ad, 248 juv) were used in determining the vital rates in paper III . Byrkö is connected to Eugmo in the north and the animals can move between these areas, although it seems to happen infrequently. The microsatellite data used in paper IV was collected in Eugmo (N = 23 individuals), Byrkö (N = 33), *Pietarsaari* (N = 5), and *Vaasa* (N = 67). Vaasa area includes the small Mustasaari population studied in the demography paper (III).

Detailed descriptions of the study areas are presented in the respective papers. In general, the flying squirrel habitats are spruce-dominated mixed forest. Spruce dominated woods are rapidly vanishing because of Scots pine *Pinus sylvestris* cultivation. The forest areas consist of small patches surrounded by fields, summer cottages, clear-cuts, thinned forests, and water.

2.2   Analyses of the capture-mark-recapture data

2.2.1 "All models are wrong, but some are useful."

An information-theory approach was used in the estimation of survival, local recruitment and population growth rate. Rather than testing for a specified hypothesis with fixed α-levels and the associated p-values, the information-theory approach starts with the careful *a priori* construction of a set of biologically meaningful model set and ends with multimodel inference. The model set starts with the so called *global model*, which has many parameters, includes all potentially relevant effects and reflects the causal mechanisms thought likely. Other models in the *a priori* model set are simplifications of the global model and contain fewer parameters. The fit of the global model to the data is investigated

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with appropriate goodness-of-fit tests and the model is used only if it adequately fits the data. Possible overdispersion is estimated from the global model. The amount of candidate models should be kept relatively small to avoid overfitting. On the other hand all the carefully considered, potentially good models should be taken into consideration to avoid underfitting. Burnham and Anderson (2002) suggest that in many cases sets of 4–20 candidate models should suffice. Large data sets can justify considering larger number of models than small data sets. There is no guarantee that the "true model" is included in the candidate model set. In fact, the true model of complex biological systems is seldom possible or meaningful to construct. Instead, modelling aims at finding a best approximation of reality (Burnham & Anderson 2002).

An important concept in information-theory approach is the principle of parsimony (known also as Occam's razor), which in statistical terms is called bias versus variance trade-off. This means that as more parameters are introduced to the model, the fit of the model increases and the precision of the model estimates decreases. The most parsimonious model is the one that with as few parameters as possible adequately describes the data. There is often uncertainty which model in the a priori chosen set is the "best" approximating model and then multi-model inference can be used. AIC (Akaike's information criterion) with its corrections (AICc for small samples and QAIC for correcting overdispersion) has become a widely-used approach in selecting the best approximating model in capture-recapture studies. Smallest AIC is given to the model that is estimated to be "closest" to the unknown reality that generated the data, from among the candidate models considered. The absolute size of AIC value is not important: it is the differences in AIC between the compared models (ΔAIC) that are used in model ranking. Here, the maximum likelihood method was used in obtaining the parameter estimates and their standard errors from the best approximating model (or models) (Burnham & Anderson 2002).

2.2.2 Estimates of survival and population growth

Demographic analyses were carried out with capture-mark-recapture (CMR) models for open populations (see Lebreton *et al.* 1992, Pradel 1996 and Nichols *et al.* 2000). The analyses were performed with program MARK (White & Burnham 1999) and the goodness-of-fit tests (GOF) were done with parametric bootstrap approach implemented in MARK or with program U-CARE (Choquet *et al.* 2005).

The corrected quasi-Akaike Information Criterion (QAICc) was used for ranking the fit of models to the data (Burnham & Anderson 2002). We used the overdispersion factor ($\hat{c}$) and model averaging when appropriate (Burnham & Anderson 1998). A component of variation analysis with the mean model was used (Burnham *et al.* 1987, Gould and Nichols 1998). The variance components procedure of program MARK was used to estimate the means, process variances, and the 95% confidence intervals for parameters of interest.

We estimated the apparent adult survival (Φ_{a1+}) and local recruitment (Φ_{a0}) probabilities for the willow tit (I) and the flying squirrel (III). *Adult survival* refers to the individuals that are at least one year old, survive through the winter, and stay within the study area. *Local recruitment* refers to animals that were born in the study area, survived through their first winter and remained in the area. Thus, the local recruitment is a function of first-year survival and site fidelity. It is important to notice that the estimated apparent survival differs from the so called return rate (the proportion of marked animals observed alive in the next sampling occasion), which does not take into account the encounter probability of an individual. The return rate is actually a product of two probabilities: the true survival and the encounter probability, and it underestimates survival probability to an unknown degree. The realized *population growth rate* (λ) was estimated applying Pradel's (1996) reverse-time approach where the capture histories are read backwards. Pradel's approach to estimate the population growth rate has advantages compared to simply calculating the ratio of successive population abundances (N_{t+1} / N_t). Population abundance is very difficult to estimate with reasonable precision, and Pradel's approach enables the calculation of confidence intervals on the population growth estimates (White and Burnham 1999). In the case of the willow tit, the recapture rate was high, but varied from 1.00 to 0.87 (II). Using the observed population sizes to estimate the λ would lead to underestimation of population growth in the years when the recapture rate has been low. For example, if the population size remained constant, but the recapture rate declined, the ratio N_{t+1} / N_t would falsely indicate population decline.

Population growth rate was unfolded into different components to estimate the relative importance of demographic parameters in paper I. Capture-recapture framework is needed to account for the recapture probabilities of individuals in different demographic states. Nichols *et al.* (2000) proposed a reverse-time multi-state approach for directly estimating the relative contributions of demographic parameters to population growth. The transition parameter estimated from the flipped encounter history is the seniority parameter (γ), which is the conditional

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probability that if alive and in the population at time *i*, the individual was alive and in the population at time *i* − 1. This parameter reflects the magnitude of demographic contribution to population growth (Nichols *et al.* 2000). With reverse-time multi-state modelling, the relative contributions of demographic parameters to λ were estimated as the probability that adults in population at time i + 1 were in the population 1) *as adults at time i*, 2) *as juveniles at time i*, or 3) *as immigrants entering the population between i and i + 1*. This approach allows for the assessment of temporal variation in the relative contributions and direct estimation of sampling variances and covariances (Nichols *et al.* 2000).

In paper I the mean λ and its variance were used to generate population projections for 10, 20 and 50 years. Then the product of 10 (20, 50) randomly generated values of λ were used to estimate the composite change after 11 (21, 51) years. The frequency of simulated values below 1.0 gave the probability of population decline in the future. The procedure was replicated 1000 times to calculate the 95% confidence intervals (CI).

2.2.3 CMR model assumptions

Survival estimates are generally robust to violations of model assumptions (Williams *et al.* 2002). However, this is not necessarily true for estimating the population growth rate. In general, the trap-response in capture probabilities is of greater concern than heterogeneous capture probabilities (Hines & Nichols 2002). The trap-response may be trap-happiness, if the animal learns to go into the trap in hope of food, or trap-shyness if the animal learns to avoid the uncomfortable experience of being caught. A temporal trend in λ may be generated by violations of the assumption of equal capture probabilities. Nichols *et al.* (2000) suggested avoiding modelling temporal trend in λ. In time-dependent models the first estimate of λ should be viewed with caution as the bias in this estimate is likely to be larger than in other estimates. The trap-response may also be a result of researcher action. This may happen during the first years of the study as the researcher learns to be more effective. In our case this is not a problem because the willow tit study was started long before these data were used and in the case of the flying squirrel we excluded the first two years when estimating λ to avoid trap-response. Losses on capture may result in substantial bias (Nichols *et al.* 2000), but if losses due to handling mortality are rare (as in our case with both species), the bias in λ is negligible. Estimates of λ are robust to homogenous tag loss, but not to heterogeneous rates of tag loss (e. g. rate of loss is related to tag

age, Rotella & Hines 2005). However, as the recapture probabilities were satisfactory and tag loss insignificant in our data, the possible bias in estimates of λ should be negligible.

2.2.4 Source-sink calculations

The source-sink status of the flying squirrel populations (III) was evaluated using the approach of Runge *et al.* (2006), which uses a contribution metric (C^r) to integrate the local recruitment, site fidelity and emigration probabilities. Patterns of combined adult survival/emigration and juvenile survival/emigration were used in assessing the relative likelihoods of these populations being a source or a sink. These patterns can be studied by using the equation:

$$\Phi_{a1+}^{rr} + \Phi_{a1+}^{rs} * \beta^r (\Phi_{a0}^{rr} + \Phi_{a0}^{rs}) \succ 1.0,$$

where Φ_{a1+}^{rr} is the adult survival of population r, Φ_{a1+}^{rs} is the emigration probability of adults from r to population s (conditional of surviving), β^r is the birth rate in population r, Φ_{a0}^{rr} is the local recruitment probability and Φ_{a0}^{rs} is the emigration probability of juveniles (conditional on survival) from r to s. (Runge *et al.* 2006.)

2.3   Microsatellite analyses

The detailed descriptions of the methods are provided in the papers in question and a brief summary is given here. In paper II samples from willow tit nestlings ringed during 2001–2003 (N = 1498) and adult birds from the years 2002 and 2003 (N = 231) were included in the analyses. The sample size for the flying squirrel in 2002–2006 was 128 individuals in four locations (IV).

We analysed eight microsatellite loci from the willow tit and six loci from the flying squirrel. The DNA extraction followed traditional phenol-clorophorm method for blood and tissue (Sanbrook & Russell 2001) and the lysis method for feathers (Lillandt *et al.* 2001). The PCR products were run on ABI 377 or ABI 3730 (Applied Biosystems) for the willow tit and ABI 3730 for the flying squirrel.

The statistical methods in population genetics tend to involve wide variety of software and the computer programs used are mentioned in detail in each paper. In both studies, the first step was to recognise the possible scoring errors, null alleles, stuttering or large allele dropouts. Other routine procedures were the

testing of the Hardy – Weinberg equilibrium (HWE), linkage disequilibrium (LD) and calculation of the inbreeding coefficient (F_{IS})

The Hardy – Weinberg principle describes the relation between the allele frequencies and the genotype frequencies under the assumption that the allele frequencies do not change from one generation to the next because of mutation, natural selection, or migration. Furthermore, the population size is large enough for genetic drift to be ignored. Ergo, the HWE is a reference model for a situation where no evolutionary forces are at work (Hartl & Clark 1997). If mating is random, the alleles of a gene are combined at random into genotypes according to frequencies given by the HW proportions. Genes that are not in random association with each other are in linkage disequilibrium (Hartl & Clark 1997). LD in local populations can be caused by LD in the founding population, by admixture of populations with differing gametic frequencies, or by natural selection that favours differentially some genotypes over others (Hartl & Clark 1997). LD is measured as D, the classical linkage disequilibrium coefficient:

$$D_{ij} = p_{ij} - p_i * p_j,$$

where p_{ij} is the frequency of the haplotype having allele i at the first locus and allele j at the second locus, and p_i and p_j are the frequencies of alleles i and j. (Excoffier et $al.$ 2005).

In small populations a low level of inbreeding is inevitable because the individuals tend to share common ancestors. The inbreeding coefficient F_{IS} measures the fractional reduction in heterozygosity of an inbred subpopulation relative to a random-mating subpopulation with the same allele frequencies and the value of F_{IS} is the reduction in heterozygosity among the inbred organisms (Hartl & Clark 1997). The inbreeding coefficient is calculated as:

$$F_{IS} = \frac{H_S - H_I}{H_S},$$

where H_S is the mean expected heterozygosity within a particular random-mating subpopulation and H_I is the mean observed heterozygosity per individual within subpopulation (Hartl & Clark 1997).

2.3.1 The extra-pair paternity (EPP) in the willow tit

The extra-pair young (EPY) were identified from broods born in 2002 and 2003 (II). Paternity was tested from those nestlings of which both parents were sampled (117 pairs, 793 nestlings). The social male was included as the candidate father and the chick was considered to be an EPY if the social male was excluded as the biological father.

We calculated correlations between the parent heterozygosity (for male and female separately) and percentage of EPY within brood (%EPY). We used the homozygosity by loci (HL) as a measure of genetic diversity. HL is defined as:

$$HL = \frac{\sum E_h}{\sum E_h + \sum E_j},$$

where E_h and E_j are the expected heterozygosities of the loci that an individual bears in homozygosis (h) and in heterozygosis (j), respectively (Aparicio *et al.* 2006). A positive correlation between female HL and %EPY could be expected if a female with high homozygosity tried to increase offspring heterozygosity by engaging in EPCs. A positive correlation between the male HL and %EPY would indicate that females paired to a homozygous male seek EPCs. We also calculated correlation between the heterozygosity by locus, as difference in size of the two alleles in a locus, to see if any particular locus had strong correlation with the %EPY. A negative correlation between the heterozygosity in a certain locus and %EPY might indicate that a particular locus is linked to a trait which is more advantageous in a heterozygote state. A Bonferroni correction was applied when multiple testing was done. We fitted a logistic linear regression with the occurrence of EPY in the brood as the binary response variable HL of each parent, year and the estimated age of each parent as response variables.

Age, body size (wing length in millimetres and body mass in grams), heterozygosity (HL), and pairwise relationship coefficients (Queller & Goodnight 1989, Lynch & Ritland 1999) of the parents of mixed paternity broods and monogamous broods were compared to see if the female paired to an inferior male (young, small, or homozygous) is more likely to search for extra-pair copulations (EPC). The pairwise relationship coefficient following Queller and Goodnight (1989) is calculated for individuals x (with alleles a and b) and y (with alleles c and d):

$$r_{xy} = \frac{0.5\left(S_{ac} + S_{ad} + S_{bc} + S_{bd}\right) - p_a - p_b}{1 + S_{ab} - p_a - p_b},$$

where p_a and p_b are the frequencies of alleles a and b in the population. S is the indicator variable for sharing the pairs of alleles. If the reference individual is homozygous, $S_{ab} = 1$, while if heterozygous, $S_{ab} = 0$. In total, there are six S's corresponding to the six ways of choosing two objects without replacement from a pool of four objects. The reciprocal estimates of r_{xy} and r_{yx} can be arithmetically averaged to refine the pairwise estimates for the individuals x and y (Lynch & Ritland 1999). The other estimator used here is the Lynch and Ritland (1999) estimator:

$$r_{xy} = \frac{p_a\left(S_{bc} + S_{bd}\right) + p_b\left(S_{ac} + S_{ad}\right) - 4p_a p_b}{\left(1 + S_{ab}\right)\left(p_a + p_b\right) - 4p_a p_b}.$$

We compared the body size (wing length and mass) and genetic diversity between the EPY, within-pair young (WPY), and offspring of monogamous parents (MOY). Because the data structure for tests of differences between EPY, WPY and MOY are highly unbalanced, the comparisons were conducted with linear mixed models using the restricted maximum likelihood (REML) approach. The heterozygosity-fitness correlations were examined with the capture-recapture methods for open populations and program MARK (White & Burnham 1999) where the local recruitment probability in relation to heterozygosity was studied using the HL as a covariate.

2.3.2 Flying squirrel population differentiation

To determine if the habitat loss and isolation have deteriorated the genetic variability of the flying squirrel populations the amount of genetic variation was estimated (IV). Allelic richness (R), alleles per locus, observed heterozygosity (H_O), and expected heterozygosity (H_E) were estimated for each of the populations. Furthermore, the populations were tested for the signature of a bottleneck using three different mutation models: the infinite allele model (IAM), the stepwise mutation model (SMM) and the two-phase model (TPM, Cornuet & Luikart 1996, Piry *et al.* 1999, Garza & Williamson 2001). The effective population sizes were calculated for each population (N_e, Peel *et al.* 2004).

Population differentiation was estimated in several different ways. The methods included the calculation of pairwise F_{ST} (Weir & Cockerham 1984) and R_{ST} (Michalakis & Excoffier 1996) values for each population pair, AMOVA with three different groupings of the populations, calculation the log likelihood of different clusters (K) and finally, the assignment tests (Pritchard *et al.* 2000). The correlation between the genetic and geographic distances was tested with the Mantel test (Slatkin 1993).

3   Results and discussion

3.1   Survival and recruitment in the willow tit

Willow tit adult survival during the study ranged from 0.50 in 2000–2001 to 0.66 in 1997–1998. The average during 1991–2002 was 0.59 (± 0.02; SE), which is relatively high for a small bird. Survival estimates for other species, such as the black-capped chickadee *Parus atricapillus* (0.37–0.51) or Carolina chickadee *P. carolinensis* (0.48– 0.53, Michel *et al.* 2006), are lower than for the willow tit, except for the estimates from the Siberian tit *P. cinctus* ($\bar{x}$ = 0.69, Orell *et al.* 1999b). Temporal variance in adult survival was low during the study (CV = 0.07). To get a more complete picture I analysed the data accumulated since 2002 until 2007 not included in paper I. Exceptionally poor adult survival (0.46 ± 0.04) was found in period 2001–2002. Thus, there were two successive winters with poor survival in 2001–2002, leading to the smallest observed population size of 129 adults (Fig. 3). However, the subsequent survival from 2002 to 2006 has stayed above the long-term average (0.60–0.65).
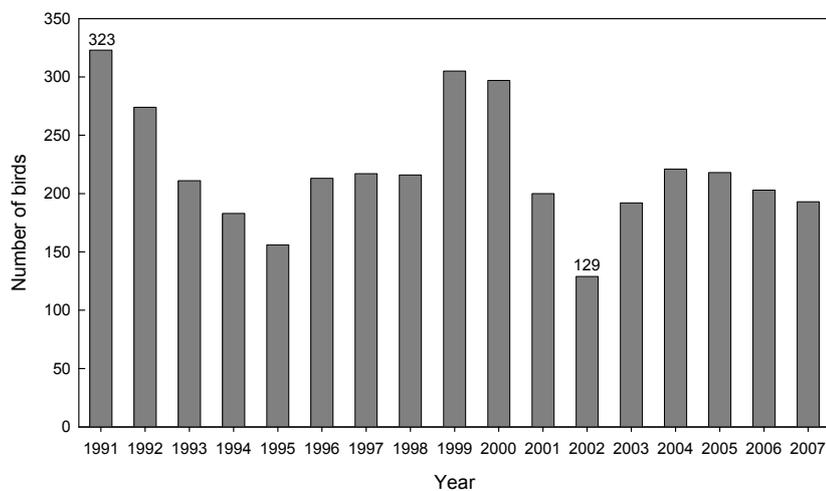

Fig. 3. The willow tit population size 1991–2007.

The local recruitment rate of the willow tit was on average 0.06 (± 0.01; SE) with high temporal variation (CV = 0.61). The years of poor adult survival were bad for the recruits as well. Only 2% of the birds born in the area in 2000 recruited to the population in 2001 whereas 13% of the birds born in 1997 recruited to the population the following year. Indeed, adult survival and local recruitment were positively correlated (r = 0.70, p = 0.03).

3.1.1 Willow tit heterozygosity and fitness

There was a weak but not significant association between homozygosity and local recruitment (IV). The models with homozygosity by loci as a covariate were included within ΔAICc < 2 from the best model. The best model was the starting model with two age classes (a2) in survival (Φ) and recapture (P) probabilities and no covariates: $[\Phi_{(a2-t/c)} P_{(a2-t/c)}]$. The first-year survival and recapture rate were modelled as time dependent (t) and adult survival and recapture rate were kept constant (c) to avoid overly complex models. The top model with HL indicated a non-significant but negative effect of homozygosity on local recruitment (β_{HL} = −1.04, 95% CI: −2.93–0.86), meaning that birds with high HL could be less likely to recruit to the population. However, data from more years are needed to see if this association can be confirmed, because the number of local recruits each year is fairly low. In fact, local recruitment may not be the best trait to use when studying heterozygosity-fitness correlations in the willow tit because on average only 6% of the juveniles recruit to their natal population (I) and the temporal variation in recruitment rate is high. Confounding factors such as weather and food availability are likely to overpower the effect of heterozygosity on recruitment probability. Nevertheless, even weak heterozygosity-fitness correlations do affect the populations in the evolutionary time scale because small differences in individual fitness determine the passage of genes to the following generations and affect the genetic composition of future populations. Heterozygous birds can be expected to be more long-lived than the more homozygous individuals. However, no difference in heterozygosity between birds of different ages was found, except that high homozygosity values were found only in the nestlings, not adult birds. This could indicate that birds with very high HL tend to perish at a very young age.

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3.2 Survival and recruitment in the flying squirrel

Adult survival probability appears to be lower and more variable in the flying squirrel than in the willow tit although the variability in flying squirrel survival could not be fully explored due to sparse data that favours constant models (III). In Mustasaari the average adult survival of the flying squirrel was lower (0.43 ± 0.07, SE) than in Byrkö (0.53 ± 0.04). In Eugmo I found evidence of decreasing adult survival during the study. The first estimate (1994–1995) of adult survival was 0.62 (± 0.07) and the last estimate (2003–2004) only 0.34 (± 0.07). There is more than one possible explanation for the difference in adult survival between Mustasaari and Byrkö, but it may reflect the viability of populations in different landscapes. The habitat quality in the study areas has not been formally assessed, but the habitats in Mustasaari may be of poorer quality than in Byrkö, resulting in 1) higher emigration or 2) reduced over-winter survival. It can also be speculated that 3) the predation pressure may differ between areas. The individuals in Mustasaari may be more susceptible to predation than individuals in other populations because the average patch size is smaller in Mustasaari (4.9 hectares in 2004) than in Byrkö (5.7 ha) or Eugmo (8.1 ha). For example, the eagle owl (*Bubo bubo*) is known to occasionally breed in the area and is suspected to be behind the population crash in 1996. Adult survival estimates for flying squirrels are rare in the literature. Our estimates are quite low compared to ones presented for the northern flying squirrel *Glaucomys sabrinus* in British Columbia, Canada (0.85, Ransome & Sullivan 2004), Douglas squirrel *Tamiasciurus douglasii* (0.85, Ransome & Sullivan 2004), and the fox squirrel *Sciurus niger* (0.66–0.73, Conner 2001), but similar to the estimates of northern flying squirrel survival in the eastern Washington Cascade Range, USA (0.45–0.59, Lehmkuhl *et al.* 2006). However, the last estimate may be biased because it includes juveniles. The estimates for the northern flying squirrel reveal that the differences between populations within species may be quite large.

We were able to estimate the average local recruitment probability for the flying squirrel in Mustasaari and Byrkö populations. Despite the apparent difference in adult survival the estimates of local recruitment were fairly similar for both areas. In Mustasaari the male recruitment probability was higher 0.30 (± 0.06) than the probability of female recruitment 0.23 (± 0.05). The sex difference in estimates is expected, because female flying squirrels have a tendency to disperse further than males during natal dispersal (Hanski *et al.* 2001b). Therefore, the difference in estimates in Mustasaari is probably not due to

actual differences in survival (although it can not be ruled out). However, in Byrkö the sex difference was not found and the estimate for both sexes was 0.27 (± 0.04). The reason for this difference between estimates in Mustasaari and Byrkö is unknown, but it may be due to high sampling variance associated to sparse data or perhaps different dispersal patterns related to differences in landscape connectivity in these populations. These estimates are similar to ones for the northern flying squirrel (0.28–0.35) in different habitats in Washington Cascade Range (Lehmkuhl *et al.* 2006). On the other hand, these numbers are not directly comparable, because Lehmkuhl *et al.* (2006) estimated *f*, which is the rate of addition from births and immigration, rather than recruitment probability of the locally born animals (Φ_{a0}). The latter is lower because it does not include immigrants.

3.3   Population growth (λ) in the willow tit

The willow tit population growth rate has been close to one (0.99, CV = 0.20) during 1991– 2002, indicating no change in average population size (Fig. 3). However, there has been substantial variation in the growth rate over the years, ranging from notable increase in 1997–1998 (1.31 ± 0.10, SE) to clear decline in 2000–2001 (0.71 ± 0.07). Despite the average $\lambda \approx 1$, population projections imply some concern about the willow tit population viability (I). For example, the probability that the average growth rate is 0.9 (i.e. 10% decline) is 0.62 (0.59–0.65; 95% CI) in 10 years, 0.72 (0.69–0.75) in 20 years and 0.85 (0.83–0.87) in 50 years. The lowest values of λ were associated with the years of low adult survival.

3.3.1 *Relative contributions of survival, recruitment and immigration to λ*

The relative contributions ("retrospective elasticities") of the vital rates to the λ varied substantially between years. On average, the contribution of adult survival to λ was high (64%) compared to that of local recruitment (14%) and immigration (22%). This is a common characteristic in long-lived species with small clutches (Sæther & Bakke 2000). The high temporal variance highlights the fact that average values do not necessarily describe the population dynamics very well (Nichols *et al.* 2000). It is worth noting here that low *contribution* of, for example, adult survival to λ in any given year is not necessarily due to low adult survival

probability, but due to high immigration and/or recruitment rates that have had high impact on λ. For the willow tit the main conservation concern is the adult survival that has the highest contribution to the population growth rate. Thus, even a small decline in adult survival probability will have a substantial impact on λ. In addition, immigration and juvenile survival with high temporal variation are probably hard to manage although local recruitment should respond positively to factors increasing adult survival because the two are correlated. Natural selection buffers variation in vital rates that have large impact on fitness (Pfister 1998). Adult survival has a high contribution to λ but because of its low variance it contributes little to the variation in λ. The local recruitment and immigration are variable and induce most of the variation observed in the growth rate.

3.4 The growth rate and source-sink status of the flying squirrel populations

In all of the flying squirrel populations studied, the uncertainty in the estimates of population growth was quite large (III). Nevertheless, the estimated average λ was consistently below unity in all populations. The results indicate decline in areas that are considered as the stronghold for the flying squirrel populations in Finland. The flying squirrel density is high in the western part of the country (3.2 females/km^2 forest area) and decreases towards the east. The average female density in the whole distribution area of Finland is 0.9/km^2 (Hanski 2006). Temporal variation in λ was detected in Mustasaari, but not in other populations. This does not indicate that there was no year-dependent variation in the population growth rate, only that this variation was relatively small in the sense of bias-variance trade off (Burnham & Anderson 2002). The estimates for Eugmo are the most precise ones and also the most worrisome. The observed decline in adult survival is reflected in the population growth rate, which declined from 1.08 (± 0.06, SE) to 0.78 (± 0.08) in just 10 years. The models suggest that the population decline in Eugmo is related to habitat loss ($\beta_{habitat} = 0.001$, 95% CI: 0.0003–0.003).

We used the estimated mean adult survival, local recruitment and birth rate for each population to examine the range of values for (unknown) adult and juvenile emigration probabilities that determine source-sink status of the three populations. The population is a source, if:

$$\Phi^M_{a1+} + 1.15\Phi^M_{a0} \succ 0.316$$
$$\Phi^E_{a1+} + 1.14\Phi^E_{a0} \succ 0.319$$
$$\Phi^B_{a1+} + 1.14\Phi^B_{a0} \succ 0.163$$

for Mustasaari, Eugmo and Byrkö, respectively (see Fig. 4 in paper III). For Byrkö the emigration probability of adults and juveniles was estimated from the mark-recapture data. Although the the emigration probabilities from Byrkö to Eugmo are probably underestimated, these flying squirrel populations are most likely sinks barely maintained by immigration.

3.5 Genetic variation in the flying squirrel

A total of 37 alleles were observed across six microsatellite loci, ranging from three in PvolE6 to 11 in Pvol41. The average number of alleles was lowest in Eugmo (3.0) and highest in Vaasa (5.5). The mean expected heterozygosity was 0.517 (0.147, SD). Heterozygosity, allelic diversity and alleles / locus were low in Eugmo compared to other populations. The fixation index F_{IS} in Eugmo was positive, but not significantly. Overall, the heterozygosities observed here were low compared to the results of Selonen *et al.* (2005). They found $H_O = 0.53–0.75$ and $H_E = 0.56–0.77$. They also found the lowest values in Luoto (which is the area of Byrkö and Eugmo combined).

The effective population size (N_e) was estimated with NeEstimator (Peel *et al.* 2004). N_e in Vaasa was 40.2 (linkage disequilibrium method; 95% CI: 27.3–65.5) or 46.9 (heterozygote excess method, CI not available), in Byrkö 22.7 (LD, 13.1–50.3, 95% CI) or 18.6 (HE), and in Eugmo 167.6 (LD, 95% CI: 21.9–infinity). Because the Eugmo estimate had very little confidence we combined the adjacent populations to get an overall estimate for the peninsula. For Byrkö and Eugmo combined the estimate of effective population size was 23.9 (LD, 95% CI: 15.8–38.9). The low confidence of the N_e estimates is probably due to small amount of loci and individuals.

During a bottleneck event rare alleles are lost quickly whereas heterozygosity decreases more slowly (Maruyama & Fuerst 1985, Wang 2005). However, even low levels of immigration quickly regain the genetic variation after the population decline (Keller *et al.* 2001, Busch *et al.* 2007). No compelling evidence for a bottleneck in any of the flying squirrel populations was found. This result suggests that a detectable amount of genetic variation has not been lost in these

populations, and that the genetic diversity could be preserved if sufficient dispersal between the populations is maintained. A bottleneck is hard to demonstrate because of the assumption of a completely isolated population and this analysis may have been affected by the small number of loci (Spong & Hellborg 2002).

3.5.1 Flying squirrel population differentiation

The flying squirrel populations have diverged because of drift or founder effects. Analysis of molecular variance (AMOVA) showed that the differentiation was mainly within and among populations. The populations were grouped in three different ways. First, all populations were in the same group (Vaasa, Pietarsaari, Eugmo, Byrkö). Second, Vaasa was separated from the other three populations (Vaasa // Pietarsaari, Eugmo, Byrkö). Third, Byrkö and Eugmo were treated as one group, Vaasa as one group and Pietarsaari as one (Vaasa // Pietarsaari // Eugmo, Byrkö). Depending on the grouping, 9–23% of the variation was observed among populations and about 15% among groups. The variation between populations was significant, but variation among groups was not.

The global F_{ST} was 0.23. The pairwise F_{ST} was significant for all population pairs, even for Byrkö and Eugmo that are adjacent on the same peninsula (0.11). Also Selonen et al. (2005) found significant differentiation between flying squirrel populations in Finland, except for Anjalankoski, where two adjacent populations were studied ($F_{ST} = 0.002$). They also showed an isolation-by-distance pattern which was not found to be significant in this study, probably because of our smaller sample. The correlation between the genetic and geographic distances was however, quite high (Mantel test: $p = 0.08$, $r = 0.92$).

Of all the individuals sampled in Byrkö 88% were assigned into their sampling population. Similarly, 80% of individuals sampled in Pietarsaari, and 96% sampled in Vaasa were assigned into their sampling population. In Eugmo, 35% of the flying squirrels sampled there were assigned into the sampling population. The assignment test is sensitive to the mutation model used, number of individuals in the sample, number of loci, and degree of differentiation among populations (Cornuet *et al.* 1999). In the whole data, six individuals were assigned as first-generation migrants in the sampling population. The estimated number of migrants between Byrkö and Eugmo was 2–8 depending on the method used and < 1.5 between other population pairs. The minimum observed number of dispersers from the capture-recapture data is four juveniles dispersing

from Byrkö to Eugmo in 10 years and none to the opposite direction, which corresponds to 0.4 individuals per year and less than one per generation. Although some individuals are inevitably missed with capture-recapture methods, it is notable that no emigrants from Eugmo were found to recruit in the thoroughly studied (and fairly small) Byrkö area in ten years. This could be due to higher productivity of Byrkö compared to Eugmo. However, it may be that in the large Eugmo area more individuals remain unmarked and are not recognised as emigrants from Eugmo when entering Byrkö and the number of observed migrants is likely to be an underestimate of migration due to incomplete monitoring of the Eugmo population. Nevertheless, the number of effective migrants must be somewhere between the estimates from mark-recapture data and microsatellite data. The estimates based on DNA suggest that migration is sufficient to compensate for bottleneck effects, i. e. more than one migrant per generation (Wang 2004). However, the populations have differentiated, indicating that the number of migrants is smaller than required for compensation.

3.5.2 Habitat availability for the flying squirrels

The flying squirrel populations in the west coast of Finland inhabit small remains of old growth forests, scattered in landscape dominated by forestry, agriculture and urban areas. The study areas have lost 30% of the habitat suitable for the flying squirrel during the past decade, followed by considerable decrease in average patch size (24–36%, own observations). These flying squirrel populations may currently be at or below the extinction threshold. In Mustasaari and Eugmo the amount of suitable habitat is only 10% of the total landscape area and in Byrkö the estimate is 21%. Correspondingly, Byrkö is the most viable population if judged from adult survival or realized population growth rate.

In Northern Finland the occupancy of the flying squirrel was predicted by habitat quality characteristics and physical connectivity (Reunanen *et al.* 2002). The occupied patches tended to be larger and contain more deciduous rich forests than the unoccupied ones and they tended to have higher number of connections to the neighbouring patches (Reunanen *et al.* 2002). An example of the importance of landscape level threshold in habitat availability was provided by Pakkala *et al.* (2002). They studied the abundance of the three-toed woodpecker *Picoides tridactulys* in landscapes with differing metapopulation capacity. Metapopulation capacity quantifies both the effects of total habitat area and degree of fragmentation to the viability of a metapopulation (Hanski 2005). The

three-toed woodpecker is associated with mature forests with dead trees and is listed near threatened in the IUCN category (Rassi *et al.* 2001). Pakkala *et al.* (2002) concluded that the woodpeckers were mainly found in good quality habitat patches and that parts of the studied population may currently inhabit regions where the availability of good quality habitats is under the landscape level threshold required by the three-toed woodpecker.

3.6 The changing landscape

Abundance of forest species is related to habitat availability. There may be a threshold in habitat availability under which the population viability decreases. Low colonisation ability and narrow tolerance for different environmental conditions largely explains the decline of most forest species (Hanski 2005). Andrén (1994) suggested that the fragmentation effects may become severe when the amount of suitable habitat falls below 20%. Hanski (2005) suggested, a bit more cautiously, that the population density is likely to decline at 10–30% and that the extinction probability may sharply increase below 10%.

The amount of good quality breeding habitat is undoubtedly the most important factor to the species' persistence. However, the view must be taken beyond considering only good-quality breeding habitat and hostile matrix that the animals can not use. Animal movement and population size could be most economically enhanced by preserving and creating "dispersal habitat" in the matrix (Wiegand *et al.* 2005). Dispersal habitat is suitable for movement but not breeding, i.e. low quality habitat. Increasing dispersal habitat to the otherwise hostile matrix decreases dispersal mortality and enhances movement between patches (Wiegand *et al.* 2005). Provided that the breeding habitats are preserved this could be a reasonable approach for the flying squirrel, because the juvenile dispersers use low quality habitats for roosting during dispersal (Selonen & Hanski 2004).

3.6.1 Forestry and fragmentation

Forestry has been shown to negatively affect both southern *Glaucomys volans* and northern *G. sabrinus* flying squirrel (Taulman *et al.* 1998, Carey 2000), birds (Lampila *et al.* 2005) and forest-dwelling small mammals, for example the grey-sided vole (Ecke *et al.* 2006). The high values of F_{ST} and low migration estimates suggest that dispersal of the flying squirrel may be compromised in these

populations. The heterozygosity and allelic diversity of Prince of Wales flying squirrels *Glaucomys sabrinus griseifrons* inhabiting islands are lower than heterozygosity of mainland populations in Alaska (Bidlack & Cook 2002). It seems that Eugmo is practically an island compared to other studied populations. It is possible that the population is already suffering from the effects of reduced genetic variation. Demographic data presented in paper III show that these populations are in decline and in Eugmo both adult survival and λ have declined notably during the past 10 years.

Väisänen *et al.* (1998) suggested that forestry practices have reduced the amount of suitable willow tit breeding and wintering territories and decreased the carrying capacity of the habitats in general. Woodland area positively influences the breeding success of great and blue tits in the highly fragmented landscapes of Great Britain (Hinsley *et al.* 1999). In our study population, birds occupying territories with clear cut areas have to enlarge their winter territory size to compensate for the habitat loss after clear cuts (Siffczyk *et al.* 2003). There are costs related to large territories e. g. in the form of increased time used in defending the territory against other willow tit flocks, or because more time has to be spent moving between the foraging areas. The main factor that affects the willow tit winter survival is probably reduced food availability. Winter feeding experiments have increased survival in several bird species and the willow tit is no exception (see Lahti *et al.* 1998 and references herein).

3.6.2 Dispersal in fragmented landscapes

Local recruitment rate is highly variable in the willow tit and less so in the flying squirrel. For the endangered flying squirrel, comparisons of the vital rates between different populations in different landscapes would be useful. At present it is unknown if the estimates presented here represent the vital rates of a viable population, or if they are from a population that suffers from habitat loss and fragmentation. The results from Eugmo suggest that the latter may be the case at least in adult survival. In the flying squirrel more than one-quarter of animals recruit in their natal population whereas the rate is only 6% for the willow tit. Thus, the role of natal dispersal is greater in the willow tit, but it cannot be ignored in the case of the flying squirrel either. Furthermore, because of its poor dispersal ability the flying squirrel movements are more likely disturbed by man-made barriers. Forecasting the effects of habitat loss and fragmentation to local recruitment is not straightforward. If the winter mortality of juveniles increases,

or if their willingness to disperse increases as the natal habitat deteriorates, the recruitment rate decreases. On the other hand, if dispersal is riskier because of increased isolation of the patches, more juveniles may end up stuck in their natal area, increasing the local recruitment rate and inbreeding.

Fragmentation has been shown to affect movement among patches in gray-tailed voles *Microtus canicaudus* (Wolff *et al.* 1997) and apparent lack of dispersal has been identified as a major issue in the Delmarva fox squirrel *Sciurus niger cinereus* conservation (Hilderbrand *et al.* 2007). The factors that determine the persistence of subpopulations in the landscape are mainly patch size and probability of migrants arriving to the patch ("connectivity", Hanski 2005). The flying squirrel may be affected not only by habitat loss per se, but also by the isolation of habitat patches. It is able to use low quality habitats for dispersal but it does avoid crossing open areas (Selonen & Hanski 2004). Natal dispersal distances are large (up to almost 9 km) in flying squirrel compared to its size (Hanski *et al.* 2001b). However, fragmentation has been shown to affect pairing success and nest predation in birds, which are very mobile compared to small mammals (Lampila *et al.* 2005). In less mobile taxa the fragmentation effects are probably even more pronounced.

3.7 Extra-pair paternity and female mate choice in the willow tit

Out of 793 sampled chicks 53 (6.7%) were classified as EPY. The percentage of EPY was higher in 2002 (8.1%) than 2003 (5.5%). In 2002 altogether 14 nests and in 2003 11 nests were classified as mixed-paternity nests (25 broods, 21.4%). In three broods all the chicks were sired by other than the social father.

3.7.1 Differences between offspring

The EPY appeared to be less homozygous (HL_{EPY} = 0.17 ± 0.03, SE) than monogamous offspring (HL_{MOY} = 0.23 ± 0.01), but the difference was not significant (REML: $F_{1,115}$ = 3.76, p = 0.06). The EPY and MOY were similar in body mass (EPY = 11.10 g ± 0.15, MOY = 10.96 ± 0.08; F = 0.74, p = 0.39) and wing length (EPY = 41.39 mm ± 0.86, MOY = 40.61 ± 0.36; $F_{1,115}$ = 1.13, p = 0.29).

There was a significant difference in genetic quality between maternal half-siblings in mixed paternity broods ($F_{1,21}$ = 5.54, p = 0.03). HL was lower in EPY (0.174 ± 0.026) compared to the WPY (0.253 ± 0.022). There were no differences

in body mass (EPY = 11.10 g ± 0.15, WPY = 11.23 ± 0.17; $F_{1,21}$ = 0.34, p = 0.56) or wing length (EPY = 41.39 mm ± 0.86, WPY = 41.22 ± 0.84; $F_{1,21}$ = 1.70, p = 0.19) between the maternal half-siblings.

These results indicate that females do gain indirect benefits from the EPP in form of increased genetic quality of their offspring, but fertility insurance may partly explain why they seek EPCs because pairing with infertile male is very costly to the female. We have no data on willow tit fertility and this information is missing for most bird species. However, estimates of infertility for the great and the blue tit are 1–2% (Krokene *et al.* 1998). Evidence for the fertility insurance has been found in the red bishop *Euplectes orix* where the extrapair offspring were less immunocompetent than the within-pair offspring (Edler & Friedl 2008).

3.7.2 Male quality and paternity

The pairwise relationship coefficients were not higher in pairs with mixed paternity than in the monogamous pairs (t-test: p > 0.1 for both coefficients). The HL was similar between monogamous and EPC-engaging females and between males that lost paternity and those that did not (t-test: all p > 0.1). There was no correlation between the parent HL and percentage of EPY (%EPY) within the brood when examining the average from all loci (male: r = 0.132, p = 0.224; female r = −0.007, p = 0.950). When we examined the locus by locus correlations between heterozygosity and %EPY (8 loci), we found one significant negative correlation in one locus in the females (PmaTGAn33, r = −0.178, p < 0.05). In the male parents, one negative (Pat2-43, r = −0.193, p < 0.05) and one positive correlation was found (Pocc6, r = 0.218, p < 0.05). Despite of the significance of these correlations, they are weak and could have emerged by chance alone out of altogether 16 correlations. In fact none of the correlations remain significant after a Bonferroni correction.

The level of EPP is positively related to genetic similarity of pairs in several species (Tarvin *et al.* 2005, Freeman-Gallant *et al.* 2006, Eimes *et al.* 2005), but this relationship has not always been found (Edly-Wright *et al.* 2007). In order to choose a more heterozygous male, the females have to be able to assess their partner's genetic quality. The willow tit is a sexually monomorphic species and the males do not have any distinct plumage characters indicative of their quality, at least not visible to human eye. However, differences may still exist between males. Plumage colour variation has been shown to be related to a male's social rank, and consequently to female preference, in the black-capped chickadees

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(Mennill *et al.* 2003). The females may also use male song as means of assessing the quality of a potential partner. The willow tit song is simple, but appears to be an honest signal of male nest defence behaviour, nestling feeding effort, and winter survival (Welling *et al.* 1997). Male quality is related to male age and older males spend more time singing than yearling males (Welling *et al.* 1997). Singing ability is positively related to fitness in e. g. song sparrow *Melospiza media* (Reid *et al.* 2005) and subdesert mesite *Monias benschi* (Seddon *et al.* 2004). In many monogamous passerines male age is important in securing paternity at their own nest and gaining EPCs (Bouwman *et al.* 2007, Schmoll *et al.* 2007, Lubjuhn *et al.* 2007).

3.7.3 Temporal variance in EPP

EPP was more common in 2002 when the population density was extremely low (2.7 pairs per km^2). Between 2002 and 2003 a lot of first-year birds entered the population, increasing the density to 4.0 pairs per km^2. These results contradict to the expectation that high population density is positively correlated to the rate of EPP because in dense populations individuals have more opportunities to engage in EPCs (Møller & Ninni 1998). Lack of good quality partners in 2002 may have restricted female mate choice more than in 2003, resulting in more need for compensating for the mate quality and consequently higher EPP. In 2002 there were no differences between the average ages of breeders relative to their monogamy (EPC ♀ = 2.5 years ± 0.47, monog. ♀ = 2.9 yr. ± 0.26, social ♂ = 2.6 yr. ± 0.44, monog. ♂ = 2.8 yr. ± 0.24; Wilcoxon: all p > 0.1). However, in 2003 the EPC engaging females were older than monogamous females (EPC ♀ = 3.3 years ± 0.69, monog. ♀ = 1.9 yr ± 0.18; p = 0.04 with Bonferroni correction). There was no difference between the cuckolded and not cuckolded males (social ♂ = 2.4 yr. ± 0.73, monog. ♂ = 2.0 yr. ± 0.19; p = 0.97). In 2003, females paired up with young males may have engaged more in EPCs than females paired up with older males. The within-pair age difference (female – male age) between the mixed-paternity pairs (difference = 0.91, e. g. male is on average younger) and monogamous pairs (diff. = −0.06) was not statistically significant (Wilcoxon: p = 0.24).

Adult survival is related to the rate of EPP. Short-lived species with low probability of surviving to the next breeding season are expected to tolerate higher rates of EPP than ones with high survival probability (Griffith *et al.* 2002). In the willow tit average adult survival is high for its body size (around 60%).

Thus, according to this theory EPP in the willow tit is expected to be fairly low. Temporal variance in survival could affect the rate of EPP if birds foretell their future survival by the previous winter. Two years is not enough to formally study this, but the rate of EPP was higher in 2002 after exceptionally low adult survival (46%) and lower after a good winter 2002–2003 when adult survival probability was 0.66. However, the effects of density and survival cannot be distinguished with these data.

4　Conclusions and future directions

In this work I used individual-based capture-recapture data and genetic markers to achieve understanding of the demographic and genetic processes operating in small and declining populations of two different species.

The adult survival in the willow tit was found to be high and the most influential vital rate to the population growth rate. Local recruitment and immigration have high variation, inducing variation in the population growth rate. The conservation concern for the willow tit is the adult survival because of its high contribution to the population growth rate, but because local recruitment and adult survival are positively correlated, recruitment would respond positively to any conservation measure increasing adult survival. Immigration rate is difficult to manage, except by ensuring the overall possibilities of breeding and survival of the species in the boreal forests by preserving the species' habitats. This will benefit several other more demanding (and declined) species, such as the capercaillie *Tetrao urogallus*, the Siberian jay *Perisoreus infaustus*, and the flying squirrel. The results concerning the flying squirrel are worrying because all population growth estimates indicate population decline and the adult survival is decreasing in Eugmo, most likely due to habitat loss that jeopardises the adult survival and fragmentation that limits dispersal. The genetic analyses strengthen the view of populations doing poorly, because the heterozygosities in all the populations and particularly in Eugmo were rather low and the high F_{ST} values indicate low dispersal.

The willow tit is not expected to face problems in the genetic variability in the near future because it is highly mobile compared to the flying squirrel. However, genetic diversity is more generally related to various aspects of fitness. The heterozygosity – fitness correlations found in this study were weak, but future work on this topic would be interesting. At least the willow tit females do try to ensure high heterozygosity for their offspring by extra-pair copulations or divorce if a better male than the current partner is available. Heterozygous extrapair young are genetically "well equipped" to the future challenges and are expected to have high fitness.

Following work should investigate the spatial variation in individual performance and the dispersal processes in these populations. The questions about the variation in EPP rate and heterozygosity – fitness correlations among years remain mainly unanswered. The heterozygosity – fitness correlations could be

studied by analysing several more years of data, more loci and possibly by experiments.

For the flying squirrel it is vital to study the performance of individuals in the remaining small forest patches to determine the size and quality of the patches that can support flying squirrels and the ones that apparently can not. Present estimates of survival and genetic diversity can be used to reconstructing a meaningful PVA and projections for these populations.

One major future challenge in population ecology that has not been discussed in this work is the climate change and the various ways it may affect animal populations. Interactions between habitat loss and climate change may be severe. In their paper Thomas *et al.* (2004) estimated that on the basis of their mid-range climate-warming scenarios for 2050, 15–37% of species in the sample regions and taxa will be committed to extinction. Despite the criticism towards the climate envelope models they are considered to provide useful first approximation to the impact of climate change (Pearson & Dawson 2003). The winters in Finland are predicted to become warmer and rainier which may have unexpected consequences on wintering animals that are adapted to cold and dry conditions. Starvation because of high energy consumption during extremely cold conditions may become rarer, enhancing winter survival. On the other hand, effects of warm and moist weather on food availability, disease epidemics, or predator community are difficult to predict.

References

Andreassen HP, Hertzberg K & Ims RA (1998) Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. Ecology 79: 1223–1235.

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

Anonymous (1992) Council Directive 92/43/EEC. Official Journal of the European Communities.

Aparicio JM, Ortego J & Cordero PJ (2006) What should we weigh to estimate heterozygosity, alleles or loci? Molecular Ecology 15: 4659–4665.

Baillie JEM, Hilton-Taylor C & Stuart SN (eds) (2004) 2004 IUCN Red List of Threatened Species. A Global Species Assessment. Gland, Switzerland and Cambridge, UK. IUCN.

Beissinger SR & McCullough DR (eds) (2002) Population Viability Analysis. Chicago, The University of Chicago Press.

Bensch S, Andrén H, Hansson B, Pedersen HC, Sand H, Sejberg D, Wabakken P, Åkesson M & Liberg O (2006) Selection for Heterozygosity Gives Hope to a Wild Population of Inbred Wolves. PLoS ONE 1: e72. doi:10.1371/journal.pone.0000072.

Bidlack AL & Cook JA (2002) A nuclear perspective on endemism in northern flying squirrels (*Glaucomys sabrinus*) of the Alexander Archipelago, Alaska. Conservation Genetics 3: 247–259.

Bouwman KM, van Dijk, R. E., Wijmenga JJ & Komdeur J (2007) Older male reed buntings are more successful at gaining extrapair fertilizations. Animal Behaviour 73: 15–27.

Brodin A, Lahti K, Lens L & Suhonen J (1996) A northern population of Willow Tits *Parus montanus* did not store more food than southern ones. Ornis Fennica 73: 114–118.

Brouwer L, Komdeur J & Richardson DS (2007) Heterozygosity-fitness correlations in a bottlenecked island species: a case study on the Seychelles warbler. Molecular Ecology 16: 3134–3144.

Burnham KP, Anderson DR, White GC, Brownie C & Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. Bethesda, USA, American Fisheries Society.

Burnham KP & Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-theoretic Approach (2nd edition). New York, Springer-Verlag.

Busch JD, Waser PM & Dewoody JA (2007) Recent demographic bottlenecks are not accompanied by a genetic signature in banner-tailed kangaroo rats (*Dipodomys spectabilis*). Molecular Ecology 16: 2450–2462.

Carey AB (2000) Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. In: Goldingay RL & Scheibe JS (eds) Biology of gliding mammals. Fürth, Germany, Filander Verlag: 45–66.

Caswell H (2001) Matrix population models: construction, analysis, and interpretation. Sunderland, Massachusetts, Sinauer Associates.

Choquet R, Reboulet A-, Lebreton J-D, Gimenez O & Pradel R (2005) U-CARE 2.2 User's Manual (Utilities-CApture-REcapture). ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR.

Coltman DW, Pilkington JG, Smith JA & Pemberton JM (1999) Parasite-mediated selection against inbred Soay sheep in a free-living, island population. Evolution 53: 1259–1267.

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

Cornuet JM & Luikart G (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics 144: 2001–2014.

Cornuet J, Piry S, Luikart G, Estoup A & Solignac M (1999) New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153: 1989–2000.

Cramp S & Perrins CM (eds) (1993) The Birds of the Western Palearctic, Vol. 7. Oxford, Oxford University Press.

Crnokrak P & Roff DA (1999) Inbreeding depression in the wild. Heredity 83: 260–270.

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

Edler R & Friedl TWP (2008) Within-pair young are more immunocompetent than extrapair young in mixed-paternity broods of the red bishop. Animal Behaviour 75: 391–401.

Edly-Wright C, Schwagmeyer PL, Parker PG & Mock DW (2007) Genetic similarity of mates, offspring health and extrapair fertilization in house sparrows. Animal Behaviour 73: 367–378.

Eimes JA, Parker PG, Brown JL & Brown ER (2005) Extrapair fertilization and genetic similarity of social mates in the Mexican jay. Behavioral Ecology 16: 456–460.

Ekman J (1979) Coherence, composition and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *P. cristatus*. Ornis Scandinavica 10: 56–68.

Excoffier L, Laval G & Schneider S (2005) Arlequin version 3.0: an integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1: 47–50.

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61: 603–610.

Frankham R (1996) Relationship of genetic variation to population size in wildlife. Conservation Biology 10: 1500–1508.

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

Frankham R, Ballou JD & Briscoe DA (2002) Introduction to Conservation Genetics. Cambridge University Press, Cambridge.

Freeman-Gallant CR, Wheelwright NT, Meiklejohn KE & Sollecito SV (2006) Genetic similarity, extrapair paternity, and offspring quality in Savannah sparrows (*Passerculus sandwichensis*). Behavioral Ecology 17: 952.

Garza CJ & Williamson GE (2001) Detection of reduction in population size using data from microsatellite loci. Molecular Ecology 10(2): 305–318.

Gould WR & Nichols JD (1998) Estimation of temporal variability of survival in animal populations. Ecology 79: 2531–2538.

Griffith SC, Owens IP & Thuman KA (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. Molecular Ecology 11: 2195–2212.

Hanski I (2002) Metapopulations of animals in highly fragmented landscapes and population viability analysis. In: Beissinger SR & McCullough DR (eds) Population viability analysis. Chicago, The University Of Chicago Press: 86–108.

Hanski I (2005) The Shrinking World: Ecological Consequences of Habitat Loss. Oldendorf/Luhe, Germany, International Ecology Institute.

Hanski IK (1998) Home ranges and habitat use in the declining flying squirrel *Pteromys volans* in managed forests. Wildl Biol 4: 33–46.

Hanski IK (2006) Liito-oravan *Pteromys volans* Suomen kannan koon arviointi. Loppuraportti. Helsinki, Suomi, Luonnontieteellinen Keskusmuseo, Helsingin Yliopisto.

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

Hanski IK, Henttonen H, Liukko U, Meriluoto M & Mäkelä A (2001a) Biology and conservation of the Siberian flying squirrel (*Pteromys volans*) in Finland (In Finnish with English summary). The Finnish Environment 459. Helsinki, Finnish Ministry of Environment.

Hanski IK, Mönkkönen M, Reunanen P & Stevens P (2001b) The ecology of the flying squirrel (*Pteromys volans*) in Finland. In: Goldingay R & Scheibe J (eds) Biology of Gliding Mammals. Fürth, Germany, Filander Verlag.

Hartl DL & Clark AG (1997) Principles of population genetics. 3rd edition. Canada, Sinauer Associates Inc.

Hilderbrand RH, Gardner RH, Ratnaswamy MJ & Keller CE (2007) Evaluating population persistence of Delmarva fox squirrels and potential impacts of climate change. Biological Conservation 137: 70–77.

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

Hinsley SA, Rothery P & Bellamy PE (1999) Influence of woodland area on breeding success in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. Journal of Avian Biology 30: 271–281.

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

Ims RA, Rolstad J & Wegge P (1993) Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for capercaillie grouse *Tetrao urogallus* in boreal forest? Biological Conservation 63: 261–268.

IUCN (2007a) European Mammal Assessment. http://ec.europa.eu/environment/nature/conservation/ species/ema/. Cited on 25 August 2008.

IUCN (2007b) 2007 IUCN Red List of Threatened Species. www.iucnredlist.org. IUCN, Gland, Switzerland and Cambridge, UK.

Jensen H, Bremset EM, Ringsby TH, Sæther B-E (2007) Multilocus heterozygosity and inbreeding depression in an insular house sparrow metapopulation. Molecular Ecology 16: 4066–4078.

Keller LF, Jeffery KJ, Arcese P, Beaumont MA, Hochachka WM, Smith JNM & Bruford MW (2001) Immigration and the ephemerality of a natural population bottleneck: evidence from molecular markers. Proceedings of the Royal Society of London Series B, Biological Sciences 268: 1387–1394.

Koivula K & Orell M (1988) Social rank and winter survival in the willow tit *Parus montanus*. Ornis Fennica 65: 114–120.

Kouki J & Väänänen A (2000) Impoverishment of resident old-growth forest bird assemblages along an isolation gradient of protected areas in eastern Finland. Ornis Fennica 77: 145–154.

Krokene C, Rigstad K, Dale M & Lifjeld JT (1998) The function of extrapair paternity in blue tits and great tits: good genes or fertility insurance? Behavioral Ecology. 9: 649–656.

Lahti K, Orell M, Rytkoenen S & Koivula K (1998) Time and food dependence in willow tit winter survival. Ecology 79: 2904–2916.

Lampila P, Mönkkönen M & Desrochers A (2005) Demographic Responses by Birds to Forest Fragmentation. Conservation Biology 19: 1537–1546.

Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142: 911–927.

Lande R (2002) Incorporating Stochasticity in Population Viability Analysis. In: Beissinger SR & McCullougch DR (eds) Population Viability Analysis. University Of Chicago Press, Chicago: 18–40.

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

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

Lehikoinen E & Turun lintutieteellinen yhdistys (2003) Varsinais-Suomen linnut (Birds of Southwest Finland). Turku, Turun lintutieteellinen yhdistys.

Lehmkuhl JF, Kistler KD, Begley JS & Boulanger J (2006) Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16: 584–600.

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Lillandt BG, Bensch S & von Schantz T (2001) Parentage determination in kin-structured populations: microsatellite analyses in the Siberian jay *Perisoreus infaustus* during a 25-year population study. Avian Science 1: 3–14.

Lubjuhn T, Gerken T, Brun J & Schmoll T (2007) Yearling male great tits, *Parus major*, suffer more strongly from cuckoldry than older males. Zoology 110: 387–397.

Lynch M & Ritland K (1999) Estimation of pairwise relatedness with molecular markers. Genetics 152: 1753–1766.

Mäkelä A (1996) Liito-oravan (*Pteromys volans* L.) ravintokohteet eri vuodenaikoina ulosteanalyysin perusteella. In: Report on the status of Flying Squirrel (*Pteromys volans*) in Finland 1996. WWF Finland Expert Group for Flying Squirrel: 60–62.

Maruyama T & Fuerst PA (1985) Population bottlenecks and nonequilibrium models in population genetics. II. Number of alleles in a small population that was formed by a recent bottleneck. Genetics 111: 675–689.

Mennill DJ, Doucet SM, Montgomerie R & Ratcliffe LM (2003) Achromatic color variation in black-capped chickadees, *Poecile atricapill*a: black and white signals of sex and rank. Behavioural Ecology and Sociobiology 53: 350–357.

Michalakis Y & Excoffier L (1996) A generic estimation of population subdivision using distances between alleles with special interest to microsatellite loci. Genetics 142: 1061–1064.

Michel N, DeSante DF, Kaschube DR & Nott MP (2006) The Monitoring Avian Productivity and Survivorship (MAPS) Program annual reports 1989–2003. http://www.birdpop.org/nbii/NBIIHome.asp (December 2006).

Møller AP & Ninni P (1998) Sperm competition and sexual selection: a meta-analysis of paternity studies of birds. Behavioural Ecology and Sociobiology 43: 345–358.

Morris WF & Doak DF (2002) Quantitative conservation biology. Theory and practice of population viability analysis. Sunderland, USA, Sinauer Associates Inc.

Nichols JD, Hines JE, Lebreton J-D & Pradel R (2000) Estimation of contributions to population growth: A reverse-time capture-recapture approach. Ecology 81: 3362–3376.

Nichols JD & Hines JE (2002) Approaches for the direct estimation of λ, and demographic contributions to λ, using capture-recapture data. Journal of Applied Statistics 29: 539–568.

Orell M & Ojanen M (1983) Breeding biology and population dynamics of the willow tit *Parus montanus*. Annales Zoologici Fennici 20: 99–114.

Orell M & Koivula K (1988) Cost of reproduction: Parental survival and production of recruits in the willow tit *Parus montanus*. Oecologia 77: 423–432.

Orell M, Koivula K, Rytkönen S & Lahti K (1994) To breed or not to breed: causes and implications of non-breeding habit in the willow tit *Parus montanus*. Oecologia 100: 339–346.

Orell M, Rytkönen S, Koivula K, Ronkainen M & Rahiala M (1996) Brood size manipulations within the natural range did not reveal intragenerational cost of reproduction in the Willow Tit *Parus montanus*. Ibis 138: 630–637.

Orell M, Lahti K, Koivula K, Rytkönen S & Welling P (1999a) Immigration and gene flow in a northern willow tit (*Parus montanus*) population. Journal of Evolutionary Biology 12: 283–295.

Orell M, Lahti K & Matero J (1999b) High survival rate and site fidelity in the Siberian Tit *Parus cinctus*, a focal species of the taiga. Ibis 141: 460–468.

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

Overall ADJ, Byrne KA, Pilkington JG & Pemberton JM (2005) Heterozygosity, inbreeding and neonatal traits in Soay sheep on St Kilda. Molecular Ecology 14: 3383–3393.

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

Pearson RG & Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography 12: 361–371.

PECBMS (2007) State of Europe's common birds 2007. CSO/RSPB, Prague, Czech Republic.

Peel D, Ovenden JR & Peel SL (2004) NeEstimator: software for estimating effective population size. Queensland Government, Department of Primary Industries and Fisheries.

Pfister C (1998) Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proceedings of the National Acadademy of Sciences 95: 213–218.

Pimm SL & Brooks TM (2000) The sixth extinction: how large, where, and when? In: Raven. PH & Wiliams T (eds) Nature and human society. The quest for a sustainable world: Proceedings of the 1997 forum on biodiversity. National Academy Press: 46–62.

Pimm S, Raven P, Peterson A, Sekercioglu CH & Ehrlich PR (2006) From the Cover: Human impacts on the rates of recent, present, and future bird extinctions. Proceedings of the National Academy of Sciences 103: 10941.

Piry S, Luikart G & Cornuet JM (1999) BOTTLENECK: a computer program for detecting reductions in the effective population size using allele frecuency data. Journal of Heredity 90: 502–503.

Pradel R (1996) Utilization of Capture-Mark-Recapture for the Study of Recruitment and Population Growth Rate. Biometrics 52: 703–709.

Pritchard JK, Stephens M & Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155: 959.

Pulliam HR (1988) Sources, Sinks, and Population Regulation. American Naturalist 132: 652–661.

Queller DC & Goodnight KF (1989) Estimating relatedness using genetic markers. Evolution 43: 258–275.

Randall DA, Pollinger JP, Wayne RK, Tallents LA, Johnson PJ & Macdonald DW (2007) Inbreeding is reduced by female-biased dispersal and mating behavior in Ethiopian wolves. Behavioral Ecology 18: 579–589.

Ransome DB & Sullivan TP (2004) Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. Journal of Mammalogy 85: 206–215.

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

Reed DH & Frankham R (2003) Correlation between fitness and genetic diversity. Conservation Biology 17: 230–237.

Reed DH, Nicholas AC & Stratton GE (2007) Genetic quality of individuals impacts population dynamics. Animal Conservation 10: 275–283.

Reid JM, Arcese P, Cassidy A, Hiebert SM, Smith, J. N. M., Stoddard PK, Marr AB & Keller LF (2005) Fitness Correlates of Song Repertoire Size in Free-Living Song Sparrows (*Melospiza melodia*). American Naturalist. 165: 299–310.

Reid JM, Arcese P, Keller LF, Elliott KH, Sampson L & Hasselquist D (2007) Inbreeding effects on immune response in free-living song sparrows (*Melospiza melodia*). Proceedings of the Royal Society of London Series B, Biological Sciences 274: 697–706.

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

Reunanen P, Nikula A, Mönkkönen M, Hurme E & Nivala V (2002) Predicting occupancy for the Siberian flying squirrel in old-growth forest patches. Ecological Applications 12: 1188–1198.

Rotella JJ & Hines JE (2005) Effects of tag loss on direct estimates of population growth rate. Ecology 86: 821–827.

Runge JP, Runge MC & Nichols JD (2006) The Role of Local Populations within a Landscape Context: Defining and Classifying Sources and Sinks. The American Naturalist 167: 925–938.

Sæther B-E, Engen S, Islam A, McCleery R & Perrins C (1998) Environmental stochasticity and extinction risk in a population of a small songbird, the Great Tit. The American Naturalist 151: 441–450.

Saether BE, Ringsby TH & Roskaft E (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. Oikos 77: 217–226.

Sæther BE & Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653.

Sanbrook J & Russell DW (2001) Molecular Cloning -A Laboratory Manual 3rd: Cold Spring Harbor Laboratory Press, New York.

Schmiegelow, F. K. A. & Mönkkönen M (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12: 375–389.

Schmoll T, Mund V, Dietrich-Bischoff V, Winkel W & Lubjuhn T (2007) Male age predicts extrapair and total fertilization success in the socially monogamous coal tit. Behavioral Ecology 18: 1073–1081.

Seddon N, Amos W, Mulder RA & Tobias JA (2004) Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird. Proceedings of the Royal Society of London Series B, Biological Sciences 271: 1823–1829.

Selonen V, Hanski IK & Stevens PC (2001) Space use of the Siberian flying squirrel *Pteromys volans* in fragmented forest landscapes. Ecography 24(5): 588–600.

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

Selonen V, Painter JN & Hanski IK (2005) Microsatellite variation in the Siberian flying squirrel in Finland. Annales Zoologici Fennici 42: 505–511.

Shaffer M, Watchman LH, Snape III, W J & Latchis IK (2002) Population viability analysis and conservation policy. In: Beissinger SR & McCullough DR (eds) Population Viability Analysis. Chicago, University Of Chicago Press: 123–146.

Shaffer ML (1981) Minimum Population Sizes for Species Conservation. BioScience 31: 131–134.

Siffczyk C, Brotons L, Kangas K & Orell M (2003) Home range size of willow tits: a response to winter habitat loss. Oecologia 136: 635–642.

Slatkin M (1993) Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47: 264–279.

Spielman D, Brook BW, Briscoe DA & Frankham R (2004) Does Inbreeding and Loss of Genetic Diversity Decrease Disease Resistance? Conservation Genetics 5: 439–448.

Spong G & Hellborg L (2002) A Near-extinction Event in Lynx: Do Microsatellite Data Tell the Tale? Conservation Ecology 6: 15 [online] URL: http://www.consecol.org/vol6/iss1/art15/.

Tarvin KA, Webster MS, Tuttle EM & Pruett-Jones S (2005) Genetic similarity of social mates predicts the level of extrapair paternity in splendid fairy-wrens. Animal Behaviour 70: 945–955.

Taulman JF, Smith KG & Thill RE (1998) Demographic and behavioral responses of southern flying squirrels to experimental logging in Arkansas. Ecological Applications 8: 1144–1155.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus, BFN, de Siqueira, MF, Grainger A & Hannah L (2004) Extinction risk from climate change. Nature 427: 145–148.

Väisänen RA (2005) Monitoring population changes of 84 land bird species breeding in Finland in 1983–2004. In: Linnut-vuosikirja 2004: 105–119.

Väisänen RA, Lammi E & Koskimies P (1998) Distribution, numbers and population changes of Finnish breeding birds. Helsinki, Finland, Otava.

Wang J (2004) Application of the One-Migrant-per-Generation Rule to Conservation and Management. Conservation Biology 18: 332–343.

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Wang J (2005) Estimation of effective population sizes from data on genetic markers. Philosophical transactions of the Royal Society of London Series B, Biological Sciences 360: 1395–1409.

Watkinson AR & Sutherland WJ (1995) Sources, sinks and pseudo-sinks. Journal of Animal Ecology 64: 126–130.

Weir BS & Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38: 1358–1370.

Welling PP, Rytkönen SO, Koivula KT & Orell MI (1997) Song Rate Correlates With Paternal Care and Survival in Willow Tits: Advertisement of Male Quality? Behaviour 134: 891–904.

White GC & Burnham KP (1999) Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement): 120–138.

White GC, Franklin AB & Shenk TM (2002) Estimating parameters of PVA models from data on marked animals. In: Beissinger SR & McCullough DR (eds) Population viability analysis. Chicago & London, The University of Chicago Press: 169–190.

Whiteman NK, Matson KD, Bollmer JL & Parker PG (2006) Disease ecology in the Galápagos Hawk (*Buteo galapagoensis*): host genetic diversity, parasite load and natural antibodies. Proceedings of the Royal Society of London Series B, Biological Sciences 273: 797–804.

Wiegand T, Revilla E & Moloney KA (2005) Contributed Papers: Effects of Habitat Loss and Fragmentation on Population Dynamics. Conservation Biology 19: 108–121.

Williams BK, Nichols JD & Conroy MJ (2002) Analysis and Management of Animal Populations. USA, Academic Press.

Wilson DD & Reeder DM (eds) (1993) Mammal species of the world. Washington DC, Smithsonian Institute Press.

Wistbacka R, Köykkäri S, Jakobsson R & Nyman B (1996) Flygekorrens förekomst och biotopval i Jakobstad och Larsmo 1989–1993. In: WWF Finland Expert Group for Flying Squirrel 1996. Report on the status of Flying Squirrel (*Pteromys volans*) in Finland: 26–34.

Wolff JO, Schauber EM & Edge WD (1997) Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conservation Biology 11: 945–956.

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