Running headline: population dynamics at the range margin

Population dynamics of an expanding passerine at the distribution margin; impact of global warming

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Summary

1. Population dynamics in marginal habitats differs from dynamics at the population core. Marginal populations being demographically and genetically dependent on core habitats may have little ecological importance but are important from the evolutionary perspective. We studied adult survival, local recruitment and population growth rate ($\lambda$) in a great tit ($Parus major$) population breeding at the northern margin of its distribution from 1971 to 2007. We calculated the relative contributions of adult survival, local recruitment and immigration to $\lambda$. Population density and environmental covariables were used to explain the variation of the population parameters.

2. Highly negative and positive NAO-indices for winters (WNAO) negatively influenced $\lambda$. Both adult and juvenile birds’ survival decreased with an increase in midwinter temperature fluctuation around the freezing point.

3. The annual estimates of adult survival obtained (average $0.371\pm0.039$ SE) were lower than estimates for passerines in Europe and America on average. Low survival with large annual variation (from $0.220\pm0.047$ SE to $0.540\pm0.086$ SE) may reflect that great tits are poorly adapted to conditions at the northern margin of their distribution.

4. Temporal variation in $\lambda$ was large, (from $0.498\pm0.095$ SE to $1.856\pm0.474$ SE). The mean $\lambda$ ($1.122\pm0.124$ SE) indicates an increasing population size currently. The contribution of immigration was more important than the contributions of adult survival and local recruitment to $\lambda$.

5. The low average adult survival and local recruitment rates (average $0.06\pm0.011$ SE) with high immigration reflect the dynamics of a sink population. In the last 20 years there
has not been much change in population dynamics, adult survival and local recruitment rates are low. The long time series used in this study verified the earlier expectations of immigration to maintain the population. We have also shown that local and large-scale climate factors have influence on local population level. In the future, the changes in climate, warming, do not have only a positive effect on species at the northern margin, but increased fluctuation of temperature around the freezing point in midwinter may impair survival of resident birds.

Key-words: immigration; marginal population; Parus major; Program MARK, sink
Introduction

Populations of widely distributed species are often confronted with habitat heterogeneity. Consequently local demographic surplus may arise in good quality habitats (source), and a local demographic deficit occurs in habitats of poor quality (sink). In a source-sink dynamics system, dispersion regulates demography: peripheral populations may persist by continued immigration from the species’ range centre where reproduction is high and mortality is low (Pulliam 1988; Guo et al. 2005). Marginal populations, as compared to central populations, are more unstable and sensitive to environmental change due to their smaller population size (e.g. Grant & Antonovics 1978; Järvinen 1979), and the homogenizing effect of gene flow preventing local adaptations (e.g. Dhont et al. 1990; Blondel et al. 1993; Lenormand 2002; Kawecki 2008). Sæther et al. (2003) showed that the proportion of variability in the population fluctuations increases from centre to margin. Individuals living at their distribution border poorly respond to changes in their environment and are thus more vulnerable to unfavourable environmental conditions (Eeva, Lehikoinen & Veistola 1989).

Environmental factors strongly affect population dynamics and persistence (e.g. Sæther et al. 2000; Stenseth et al. 2002). In high latitudes there is lower availability of resources and less time for foraging due to decreasing photoperiod in winter. This imposes strong selection upon small sedentary passerines because they need more energy due to poor environmental conditions. Short term environmental conditions, during winter in particular, have been shown to affect survival of small passerines (e.g. Kluijver 1951; Lahti et al. 1998). Environmental changes over long time periods, and at a larger
geographical scale, are known to affect species distributions and interactions as well as ecological and evolutionary responses of life-history traits (Winkler et al. 2002; Parmesan 2006; Leech & Crick 2007). The North Atlantic Oscillation (NAO) is a large-scale climate phenomenon which correlates with annual variation in local climates over large areas (Hurrell 1995). The NAO accounts for changes in local weather conditions, but the main reason for the increased interest in this phenomenon during last two decades is its obvious connection to the observed and predicted climate change (e.g. Wallace, Zhang & Renwick 1995; Hurrell, Kushnir & Visbeck 2001). As a large-scale factor, NAO also reflects weather conditions outside local study areas and may therefore explain changes in immigration and population growth rates \((\lambda)\) better than local environmental variables.

Marginal habitats are important from the evolutionary perspective. Species’ ecological niche reflects traits of individuals enabling the evolution of niches. The ability of a species to adapt to marginal habitat plays a main role in the evolution of ecological niches and species ranges (Kawecki 2008). Changing environmental conditions can either constrain or accelerate the existence of a species in marginal habitats. Suitable conditions in central habitat can produce higher dispersal favouring persistence of marginal populations (Kokko & López-Sepulcre 2006). So, the environmental changes not only in local scale but also in larger scale can affect marginal populations.

Our model species, the great tit \((Parus major)\) is a widely distributed bird species faced with a variety of habitats and environmental conditions across its range (Gosler 1993). Despite the extensive knowledge on the specie's central population dynamics, information on the demography at the distribution margin is largely incomplete (e.g.
Kluyver 1951; Clobert et al. 1988; Dhont et al. 1990). Therefore, we modelled adult survival and local recruitment probabilities and $\lambda$ and their variances with two long term capture-mark-recapture data sets from a great tit population living at the northern margin of the distribution range between the years from 1971 to 2007. Further, we estimated the relative contributions of adult survival, local recruitment and immigration to $\lambda$. Since winter is the harshest season for survival of boreal passerines, we studied effects of local and global environmental variables during winter on the population dynamics. In addition to harsh climatic factors, we expected that increased competition for food and roosting places in dense winter populations affect adversely especially juvenile survival and $\lambda$. We hypothesised that as a southern newcomer, great tits in the north might benefit from global climate change when winter conditions become milder. This should be seen in the demography towards the final stage of the study.

Methods

Study species

The great tit has expanded its breeding range northwards in northern Fennoscandia during the 20th century; the first breeding records in the area date back to the 1950s (Haftorn 1957; Veistola, Lehikoinen & Iso-Iivari 1995). Previous studies suggest that the species may be maladapted to the prevailing conditions in the boreal regions, as shown by the poor breeding success compared to central populations (Orell & Ojanen 1983; Sasvári & Orell 1992; Rytkönen & Orell 2001; Rytkönen & Krams 2003). Irrespective of this, the
great tit is one of the most abundant passerines in Northern Fennoscandia (Väisänen, Lammi & Koskimies 1998).

Study area and data collection

The study was carried out in Oulu and Haukipudas, Northern Finland (ca. 65°N, 25°30’E), in an area consisting of fragmented and different aged coniferous, deciduous or mixed forests and semi-open bogs. The present population has been studied since 1969 (Orell & Ojanen 1983), when the first nest-boxes were installed. We used two data sets; from 1971 to 1984 (hereafter initial period) and from 1999 to 2007 (hereafter latter period) when the study areas remained constant. During the initial period, data were collected from an area of ca. 50 ha (Taskila, see Orell & Ojanen 1983), during the latter period, the study area was ca. 1400 ha (see Rytkönen & Orell 2001). The number of nest-boxes varied between 68 and 72 in the first and between 265 and 304 in the latter period. Annually, possible missing or broken boxes were replaced before the beginning of the breeding season. The variation in the number of nest-boxes had a negligible influence on the breeding density since a surplus of boxes was left vacant every breeding season.

Each spring, breeding great tits were captured for ringing or identified from unique combinations of numbered aluminium and coloured plastic rings. The study was based on a total of 322 (initial period) and 984 (latter period) capture histories of adult male and female great tits and on 1699 (initial period) and 3905 (latter period) capture histories of ringed fledglings. Of the ringed fledglings 57 (initial period) and 163 (latter period) were subsequently met as breeding adults in the population. Nestlings were ringed at the age of 14 days. If tag loss or deterioration was suspected the bird was recaptured and the identity
was verified by the ring number. We have no evidence that losses of colour rings would have biased the data. The great tit is known to be highly site-tenacious when established after natal dispersal (e.g. Kluyver 1951, Hildén 1979); therefore bias in survival estimates due to permanent emigration of breeders can be expected low. Despite the excess of the boxes in the area, it is possible that some birds have nested in natural holes. Thus, some unringed residents may have been misclassified as immigrants. However, especially in the initial period this bias is negligible (see Orell & Ojanen 1983).

Environmental and ecological data

We used mean winter temperatures (°C) from December to March and the number of times the daily mean temperature curve crossed 0°C during thermal winter (hereafter plus-peaks) as independent environmental covariates to explain variation in adult survival, local recruitment and $\lambda$. Thermal winter is defined to begin when daily mean temperature stays below freezing point at least for five successive days. During the initial period, the mean winter temperature averaged -8.07°C (±0.68 SE), whereas the latter period was milder with the mean of -7.28°C (±0.49 SE). The local daily precipitation and temperature data, obtained from the monthly records of the Finnish Meteorological Institute, comprises readings taken at Oulu airport, the closest (distance ca. 19 km) weather station to the study area. In addition, we also used NAO-indices for winters (hereafter WNAO) representing means from December through March. Typically, positive WNAO-values are associated with strong wind circulation in the North Atlantic causing an increase in temperatures and precipitation in northern Europe. In contrast, negative WNAO-values mean colder and dryer winters there (Hurrell 1995, Visbeck et
al. 2001). WNAO-data were obtained from ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh. WNAO-indices correlated positively ($r = 0.54$) with the amount of winter precipitation and monthly WNAO-indices with mean temperatures ($r$ varied from 0.51 to 0.62) from December to March at Oulu.

We analysed the effect of population density, i.e. the number of individuals (breeding parents and ringed fledglings), on annual population parameters. This effect was expected to occur especially in the harshest winter conditions, thus the interaction between density and environmental conditions on vital rates was explored. The effect of winter predation on great tits was considered. From the initial period, we had data on the number of roosting great tits preyed upon by the stoat (*Mustela erminea*) at nest-boxes during winter (Orell 1989). As another predation covariate we used the abundance of wintering sparrowhawks (*Accipiter nisus*) in the area, data were provided by winter bird censuses organized by the Finnish Museum of Natural History.

Modelling

Analyses were carried out with capture–recapture models for open populations (e.g. Lebreton *et al.* 1992, Pradel 1996, Nichols *et al.* 2000) implemented in program MARK (White & Burnham 1999). The models were designed to test and quantify the amount of temporal variation in the parameters of interest. In the analysis of population dynamics, annual estimates were calculated from CJS-models. The abbreviations of covariates used in modelling are `plusp` for plus-peaks, `wtemp` for mean winter temperature, `wnao` for WNAO-index, `wnao^2` for quadratic WNAO-index and `dens` for population density.
Sets of the best models are shown in Table 1. Apparent adult survival ($\Phi_{a1+}$) refers to breeding individuals that survive and stay inside the study area. In each case, the starting global model was a fully time-dependent model. The global model for adult survival was the CJS-model $\Phi_t p_t$ ($\Phi$ survival probability, $p$ recapture probability, $t$ time effect) including all observations of birds that were at least one year old.

Local recruitment ($\Phi_{a0}$) refers to fledglings that were born in the study area that survived through their first winter and bred in the area. We modelled two age classes, i.e. juveniles and adults in survival. The global model for local recruitment was time-dependent ($\Phi_{(a0,a1+)*t} p_t$) ($a0$: juvenile age class, $a1+$: adult age class).

$\lambda$ was estimated by applying Pradel’s (1996) reverse-time approach. The transition parameter estimated from a reversed encounter history is $\gamma$ (seniority parameter), which is the probability that if alive and in the population at time $i$, the individual was alive and in the population at time $i-1$. The $\lambda$ is then calculated as $\lambda_i = \Phi_i / \gamma_{i+1}$ (Nichols et al. 2000). The global model for estimating $\lambda$ was the fully time-dependent model ($\Phi_t p_t \lambda_t$). As in estimating adult survival, $\lambda$ was estimated from data sets including all observations of birds that were at least one year old. Pradel-models with covariates were fitted as advised by Franklin (2001), $\Phi$ and $p$ were completely time-dependent and constraints were applied on $\lambda$. Annual estimates of $\lambda$ (Table 2) were calculated from the best CJS-models within $0 < \Delta QAICc < 4$ (Table 1).

Model selection

Model selection was performed using the information theory approach discussed by Burnham & Anderson (2002). The parametric bootstrap approach provided in program
MARK was used to run the goodness-of-fit test (GOF) for the survival models (1000 simulations). Global models’ fitting the data are shown in Table 1.

The Akaike Information Criterion (AIC) and the corrected quasi-Akaike Information Criterion (QAICc) were used to rank the fit of each model to the data (Burnham & Anderson 2002). We considered that models with a difference in AICc of less than two units (ΔAICc < 2) were similarly supported by the data (Burnham & Anderson 2002). The overdispersion factor (c) was calculated by dividing the observed deviance of the global model by the mean expected deviance calculated from GOF simulations (Table 1). When c > 1, the models’ fit to data was ranked by QAICc and when ≤ 1, the models were ranked by AIC. Model averaging (Burnham & Anderson 2002) was used to control model selection uncertainty (several models with 0 < ΔQAICc < 4). Lastly, the biologically meaningful process variation (σ²_process: process variance) was disentangled from sampling variation using a component of variation analysis with the time-dependent model (Burnham et al. 1987; Gould & Nichols 1998). The variance components procedure of program MARK was used to estimate the means (θ̂), their process variances (σ²_process) and the 95 % confidence intervals for the relevant parameters (Table 3).

Contributions of demographic parameters to λ

Population growth can be split into components in order to estimate the relative importance of the demographic parameters. The λ is composed of adult survivors and of new individuals, either local recruits or immigrants, entering the population between i and i + 1. A multistate approach for the time-reversed data sets was used where the age of
an individual was treated as a state to estimate the relative contributions of adult survival, local recruitment and immigration to \( \lambda \) following Nichols et al. (2000).

The capture probability of the fledglings was fixed to be equal to the capture probability of the adults, because if the chicks were found, the parents were most likely captured too and vice versa. In both data sets the starting point was the model \( S_{(a0,a1+)*}p_c \Psi_{(a0,a1+)*}t \). Constant recapture probability was chosen because it was the best in both survival and Pradel-models (Table 1). The GOF-test was carried out using the program U-CARE (Choquet et al. 2005).

**Results**

**Adult survival**

In both data sets, the best model for adult survival included temporal variation in adult survival (Table 1, models 8 and 41). Based on model averaging between the best CJS-models (\( \Delta QAIc < 4 \)), the annual adult survival estimates (0.371\( \pm \)0.039 SE, initial period and 0.361\( \pm \)0.034 SE, latter period) were almost similar (Table 3). The respective temporal variances in adult survival were low and almost the same (Table 3). The average recapture probability of the adults was 0.80 in the initial period and was slightly lower, 0.72, in the latter period. Sampling variation accounted for 24.8% (initial period) and 16.5% (latter period) of the total variation (estimated as \( 1 - \hat{\sigma}_{\text{process}}^2 / \hat{\sigma}_{\text{total}}^2 \)). The annual adult survival probabilities, calculated from model averaged CJS-models, showed rather
high variation ranging from 26.2 to 54.0 % (initial period) and from 22.0 to 47.9 % (latter period; Table 2).

The model that best fit the data for adult survival included plusp and dens for the initial period and wnao and dens for the latter period (Table 1, models 1 and 34). The second best model in both periods included additive effects of wnao, dens and plusp. Other competing models ($\Delta$QAIC< 2) for the best models include the interaction with density or the effects of temperatures. The values of coefficients on the logit scales for these covariates obtained in all models within 2 AICc units from the best model (Table 4) showed that these covariates (wnao, plusp and wtemp) had a negative effect on adult survival, i.e. high values of these covariates were associated to low adult survival in both periods. The effect of density on survival was not clear: for the initial period there was a clear negative relationship (Table 4) but for the latter period the beta-parameter ($\beta$) was positive, although the 95 % confidence interval overlapped zero suggesting no effect of density on adult survival. When modelling the impact of predation pressure, the stoat-model had $\Delta$QAICc = 3.63 but the sparrowhawk-model excluded from the best models with $\Delta$QAICc > 16.

Local recruitment

The mean values of local recruitment were almost equal in the initial (0.055±0.011 SE) and the latter period (0.059±0.011 SE) (Table 3). In the initial period, the best model for local recruitment was fully constant (Table 1, model 11). In this period, there were only 57 locally born recruits and consequently little support for time dependence and weather covariates (Table 1, models 12-21). During the latter period, there were 163 locally born
recruits and time variation in annual local recruitment probability was detected (Table 1, model 44; Table 2). The amount of sampling variation was 20.8 % of the total variation. The temporal process variation in local recruitment was almost twice of that in adults (Table 3). The high variability is also seen in the annual local recruitment probabilities (latter period; Table 2), calculated from model averaged CJS-models.

Covariate models had $\Delta$QAICc $>$ 2 compared to the best model (Table 1, models 45-51). The best models included plusp-covariate with negative $\beta$-values (Table 4) reflecting poor recruitment when frequent temperature fluctuation around 0°C during winter (Fig.3).

Population growth rate ($\lambda$)

In both data sets, time variation in $\lambda$ was included in all the best CJS-models (Table 1, models 27, 28, 60 and 61). In the initial data set, sampling variation accounted for 3.1 % and in the latter data set only for 1.7 % of the total variation. Model averaged estimates of $\lambda$ increased in five years during the initial study period and declined in seven years; the mean growth rate was 1.008±0.109 SE (Table 3). During the latter period, the population size increased in five years and decreased in two years. The resulted mean $\lambda$ 1.122±0.124 SE indicates an increasing population size. In both periods, however, the 95 % confidence interval for the mean growth rate extended below unity (Table 2).

In the initial period all the best covariate-models (Table 1, models 22-25) included wnao and wnao$^2$. The $\beta$-parameters for both covariates were negative (Table 4) i.e. $\lambda$ appeared low after very cold but also after mild winters (Fig. 4). The effect of population
density on $\lambda$ was low; neither the interactions between population density and environmental factors were significant.

In the latter period the most supported covariate model (no. 55) included $wtemp$ and $dens$ as an additive effect, but several other models were within $\Delta$QAICc $< 4$ (Table 1). $\beta$-parameter for $wtemp$ in model no. 55 was negative (Table 4) indicating population decline after mild winters. $\beta$-parameter for $dens$ in model no. 55 was positive (Table 4), so population density does not seem to restrict population growth.

Demographic contributions to $\lambda$

In the initial period, the best multistate models did not include temporal variation in transition parameter ($\Psi$) (Table 1). Most likely this resulted from sparse data, i.e. low total number of recruits. Thus, temporal variation in relative contributions to $\lambda$ was not detectable. However, in the latter period, the best-fitting model included time variation in all estimated parameters except in recapture probability. A model with constant transition parameter was also within $\Delta$AIC $< 4$ (Table 1). Therefore, model averaging was used (Table 3). In the latter period, contributions of different parameters varied largely.

Contribution of adult survival varied annually from 0.257 to 0.486, local recruitment from 0.152 to 0.305 and contribution of immigrants from 0.271 to 0.600 (Table 3). On average, in the latter period, 36.1% of the great tits in the population were adults surviving from the previous year, 17.3% were local recruits and 46.6% were immigrants entered the population from outside study area. In the initial period these were in about similar proportions (Table 3).
Discussion

In particular, net immigration from core habitats can maintain permanent populations in habitats where the intrinsic population growth rate is negative and so births can never compensate for deaths (Figure 1c); such habitats are referred to as absolute sinks (Kawecki 2004).

Our results are in accordance with the hypothesis that marginal populations are sinks maintained by immigration. Variation in $\lambda$ was mostly caused by changes in immigration rate, which has slightly increased between the study periods. Consequently, $\lambda$ has increased without changes in survival or local recruitment, which were rather low throughout the study. These results reflect the great tit population at the northern margin as a sink. Variation in vital rates and $\lambda$ were best explained by weather covariates such as WNAO but in an unexpected way. The present results show that the breeding population increased in numbers and local survival was the highest when WNAO-index was close to zero (moderate winters), decreasing towards highly positive and negative indices. The observation that survival is the best over winters with average climate conditions agrees with results of Broggi et al. (2005) that the winter metabolism of northern great tits has adapted to local conditions. Contrary to our expectations great tit populations at the northern margin seem to have also other peculiarities than the governing effects of immigration in dynamics, which make them different from populations inhabiting the main distribution area in Western Europe and Britain. There even short periods of adverse weather, when food resources are covered with snow and ice, may cause severe losses to parids of broad-leaved forests (e.g. van Balen 1980). Why then do great tits suffer not only from the coldest but also from mild winters at the northern margin of the range? This topic will be discussed below in detail considering also the expected effects of climatic changes due to global warming.
Adult survival

The average annual survival estimates of breeding adults obtained from our population, 0.371 (initial period) and 0.361 (latter period), are low compared to European passerines of about the same size. Peach, Hanmer & Oatley (2001) compiled survival estimates of 50 species and in only five species’ survival was below 0.5. These values are, however, not fully comparable to ours because of methodological differences; only 12 were Jolly-Seber-estimates. Michel et al. (2006) provided CJS-estimates for 10 American titmice (Baeolophus and Poecile), ranging from 0.333 to 0.642. In most other studies of great tits the survival estimates are higher than ours ranging from 0.259 to 0.670 (Clober et al. 1988; Hörak & Lebreton 1998; Pons et al. 2003; Payevsky 2006). Similarly, other parids in the Northern Finland have higher adult survival estimates being 0.59 for the willow tit P. montanus (Lampila et al. 2006) and 0.69 for the Siberian tit P. cinctus (Orell, Lahti & Matero 1999).

In birds, the relative contribution of adult survival to $\lambda$ is usually larger than the contribution of fecundity, especially among long-lived species with small clutches (Sæther & Bakke 2000). Our results agree with that general pattern. The contribution of adult survival to $\lambda$ is greater than the contribution of local recruitment. The lowest contribution of the adults during the study ($\gamma_{a1+2005} = 0.257$) was due to both low adult survival after the previous breeding season ($\Phi_{2004} = 0.297$) and high immigration. For all intervals $\gamma_{a1+} < 0.5$, implying that adult survival was not dominantly important in comparison to local recruitment or especially to immigration, as compared to willow tits in the same study area, in where parental survival had always the greatest contribution varying from 0.475 to 0.756 (Lampila et al. 2006). In our analysis, the contribution of
adults decreased and the contributions of local recruitment and immigrants increased with increasing $\lambda$. The local recruitment contribution exceeded the importance of immigration only in the last study year.

The adult survival and local recruitment have stayed almost the same during the decades, but the amount of immigration has risen. The great tit population in Southern Finland has increased in the beginning of the 21st century (Väisänen 2006) and maybe the population growth in southern source areas generates more immigrants to north. Now, this immigration is in important role compensating the losses at the northern margin of distribution. Adult survival diminished due to increasing population density only during the initial period. In all other cases, with relation to survival or $\lambda$, the influence of higher density was weak or unclear. We expected the population density effect to be strongest considering local recruitment, but we did not find that kind of relationship. This is probably because other factors working in density-independent way override the negative effects of crowding.

Recruitment and immigration

In the north, great tits move in autumn from breeding areas to overwinter close to human settlements, (Järvinen 1980) taking advantage of food provided by man. Young individuals are more attracted than old ones. Some juveniles can undertake long migrations even hundreds of kilometres wide (e.g. Ulfstrand 1962, Bolshakov, Shapoval & Zelenova 1999). Verhulst, Perrins & Riddington (1997) reported that only 5% of the emigrant recruits from the same Wytham Wood (England) population were found breeding in the surrounding area (within 2 km) and a considerable proportion of birds
disperse further. Our result of low local recruitment, 5.5 % (initial period) and 6.0 % (latter period), is most likely explained by a dispersal exceeding the study area as suggested by Verhulst et al. (1997).

With the observed adult survival and local recruitment rates the study population would not be sustainable. Our findings confirm the earlier suggestions, based on genetic and ecological studies (Kvist et al. 1999, 2007, Rytkönen & Orell 2001), of the importance of immigration to the dynamics of the northern great tit population. The contribution of immigration to \( \lambda \) is comparable with that of adults in a single year and the most important in four study years, having the greatest proportion (0.60) in 2005. We also calculated average values for vital rates: contribution of immigration is the most important in the latter data set and equally important with adult survival in the initial one.

Migration to northern habitats probably causes adaptive problems for great tits; clutch sizes are too large, breeding success is poor in the north (Rytkönen & Orell 2001) and overwinter survival requires special behavioural or physiological adaptations. Indeed, basal metabolic rate differences between populations from Northern Finland and Southern Sweden infer local adaptations (Broggi et al. 2005). Although gene flow from the central populations may prevent local adaptations, Kvist et al. (2007) detected slight differentiation by microsatellites between the central populations and the population from Oulu. Thus, irrespective of the intensive immigration, the ecological results and among population differences at microsatellite level are not against to the suggestion of hard selection in the north against maladaptive ‘southern’ gene combinations, as suggested by the adaptation-with-gene-flow-theory (Blondel et al. 1999; Senar et al. 2006).
In comparison to willow tits studied at the same area, the contribution of immigration varies from 0.152 to 0.313 (Lampila et al. 2006), great tits have the range from 0.210 to 0.600. Proportional contributions to vital rates could be affected by capturing bias, as pointed out by Nichols et al. 2000, since some local individuals may have been considered as immigrants. However, we are confident that this potential bias does not undermine the picture described above. In reality, the amount of immigration is probably smaller than our estimates.

We also modelled recruitment parameter \( f \), because \( \lambda \) is a function of adult survival and recruitment (immigrants and local recruits). The covariates explained variation of \( f \)-models very similarly than of \( \lambda \)-models, so this strengthened the earlier observation that \( \lambda \) is mainly driven by individuals entering outside the population, because local recruitment is low.

Winter conditions

The mean winter temperature risen during the study. The decline of population size is not surprising in the cold winters when WNAO-index is very negative, but for being a southern incomer, great tits would be expected to survive better when winter conditions are less arctic. Several non-mutually exclusive explanations could account for these results. First, changes in predation may be an explanatory factor. In the initial period, the stoat-predation-model was better than time-dependent model in adult survival. \( \beta \)-parameter was negative, so the increased predation on roosting great tits in winter decreased adult survival. However, the effect of stoat predation was hidden by the stronger effects of climatic factors. The most abundant avian predator of small passerines
in winters in the north is sparrowhawk (Väisänen 2006). When winter conditions are milder, more sparrowhawks may try overwintering increasing predation pressure towards small passerines. However, the sparrowhawk-model got very low support in our analysis.

Second, paradoxically, availability of food may be a plausible explanation for increased mortality in warm winters. Dynamics of the great tit in the north is greatly affected by food supplied by man in winter (Orell 1989) that is why they tend to spend winter near human-inhabited areas. On one hand, milder temperatures may promote an earlier colonization of the rural breeding areas from wintering spots, and these early birds may fail to find enough food. Likewise, mild conditions may induce birds, which otherwise may become emigrants to remain in the study area. Such increased density may promote a higher competition at feeders, which otherwise may have less food, as sales of bird-food (personal comments from shopkeeper) and humans activity to feed is known to drop in mild winters. We studied how the number of feeding grounds in midwinter (in turn of the year) is related to mean temperature of December in Oulu surroundings in four winters from 2005 to 2008. The comparison was made to be based on the winter bird census data available from [http://www.hatikka.fi/winterbird.php](http://www.hatikka.fi/winterbird.php) and 15 census routes with the information of the number of feeding grounds along the route were selected. Due to small data, only indicative conclusions are possible, but the number of feeding trays seems to be smaller in mild winters that in colder ones. During the coldest winter (mean temperature -7.4°C) there were 102 feeding tables along the routes, but during three milder early winters (mean temperatures varied from 0°C to -1.4°C) only from 83 to 90 along the same routes.
Third, in warm and wet winters birds may be more exposed to diseases. Wet feeders with birds’ faeces are good substrates for viruses and bacteria. Infected birds may be eliminated when weather gets colder again. This is possibly at least a part of explanation for the reduced survival probability of adult and juvenile great tits in relation to increasing number of plus-peaks during thermal winter (Robb et al. 2008).

Lastly, possibly the reason is not in winter but a factor correlated to high WNAO. For example, conditions during breeding or autumn that impoverish individuals’ condition for the forthcoming winter. Maybe breeding is too exhausting for parents and they have too short time to moult or recover before winter comes. However, this breeding maladaptation hypothesis needs further testing on how survival is changing annually in relation to breeding conditions, number of fledglings per clutch and parental condition.

Climate change

According to predicted climate change, mild and NAO-positive winters are expected to be more usual in northern Europe. Global warming has been predicted to change species’ distributions: boreal species’ ranges move even further northwards and southern species expand to boreal areas (Huntley et al. 2007). According to national bird censuses, great tits have become more abundant in Finland from the 1980s’ to the beginning of the 2000s’ (Väisänen 2006). In our analyses, the observed $\lambda$ averaged unity in the initial period and indicated an increasing population in the latter period. Temporal variation in $\lambda$ was considerable during both periods. This agrees well with earlier results (Väisänen 2006), that large annual fluctuation in the population size is typical for northern great tits. Sæther et al. (2003) demonstrated that in birds, including the great tit, the proportion of
variability in the population fluctuations explained by the NAO increased with latitude.

Our results with the large variance of $\lambda$ fit very well to general pattern of marginal population dynamics (Guo et al. 2005) and the consensus that environmental unpredictability increases northwards (e.g. Järvinen 1979). As we have shown, there might be negative effects because of warmer winters on great tit population. For example in Sweden, contrary to expectations based on climate change and population increase in Finland, great tit population has decreased (BirdLife International 2004). The reduction of population size has been 20% during last 30 years, though the growth rate has turned positive during the past decade (Lindström et al. 2008). It is not clear what the reasons for decreasing are, but Sweden is situated closer to the Atlantic Ocean, and the effects of WNAO are probably stronger there.

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