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1 **Running headline: population dynamics at the range margin**

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

7

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## 1 **Summary**

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

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

14 3. The annual estimates of adult survival obtained (average  $0.371 \pm 0.039$  SE) were  
15 lower than estimates for passerines in Europe and America on average. Low survival with  
16 large annual variation (from  $0.220 \pm 0.047$  SE to  $0.540 \pm 0.086$  SE) may reflect that great  
17 tits are poorly adapted to conditions at the northern margin of their distribution.

18 4. Temporal variation in  $\lambda$  was large, (from  $0.498 \pm 0.095$  SE to  $1.856 \pm 0.474$  SE). The  
19 mean  $\lambda$  ( $1.122 \pm 0.124$  SE) indicates an increasing population size currently. The  
20 contribution of immigration was more important than the contributions of adult survival  
21 and local recruitment to  $\lambda$ .

22 5. The low average adult survival and local recruitment rates (average  $0.06 \pm 0.011$  SE)  
23 with high immigration reflect the dynamics of a sink population. In the last 20 years there

1 has not been much change in population dynamics, adult survival and local recruitment  
2 rates are low. The long time series used in this study verified the earlier expectations of  
3 immigration to maintain the population. We have also shown that local and large-scale  
4 climate factors have influence on local population level. In the future, the changes in  
5 climate, warming, do not have only a positive effect on species at the northern margin,  
6 but increased fluctuation of temperature around the freezing point in midwinter may  
7 impair survival of resident birds.

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

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## 1 **Introduction**

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

17 Environmental factors strongly affect population dynamics and persistence (e.g.  
18 Sæther *et al.* 2000; Stenseth *et al.* 2002). In high latitudes there is lower availability of  
19 resources and less time for foraging due to decreasing photoperiod in winter. This  
20 imposes strong selection upon small sedentary passerines because they need more energy  
21 due to poor environmental conditions. Short term environmental conditions, during  
22 winter in particular, have been shown to affect survival of small passerines (e.g. Kluijver  
23 1951; Lahti *et al.* 1998). Environmental changes over long time periods, and at a larger

1 geographical scale, are known to affect species distributions and interactions as well as  
2 ecological and evolutionary responses of life-history traits (Winkler *et al.* 2002;  
3 Parmesan 2006; Leech & Crick 2007). The North Atlantic Oscillation (NAO) is a large-  
4 scale climate phenomenon which correlates with annual variation in local climates over  
5 large areas (Hurrell 1995). The NAO accounts for changes in local weather conditions,  
6 but the main reason for the increased interest in this phenomenon during last two decades  
7 is its obvious connection to the observed and predicted climate change (e.g. Wallace,  
8 Zhang & Renwick 1995; Hurrell, Kushnir & Visbeck 2001). As a large-scale factor,  
9 NAO also reflects weather conditions outside local study areas and may therefore explain  
10 changes in immigration and population growth rates ( $\lambda$ ) better than local environmental  
11 variables.

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

20         Our model species, the great tit (*Parus major*) is a widely distributed bird species  
21 faced with a variety of habitats and environmental conditions across its range (Gosler  
22 1993). Despite the extensive knowledge on the specie's central population dynamics,  
23 information on the demography at the distribution margin is largely incomplete (e.g.

1 Kluyver 1951; Clobert *et al.* 1988; Dhont *et al.* 1990). Therefore, we modelled adult  
2 survival and local recruitment probabilities and  $\lambda$  and their variances with two long term  
3 capture-mark-recapture data sets from a great tit population living at the northern margin  
4 of the distribution range between the years from 1971 to 2007. Further, we estimated the  
5 relative contributions of adult survival, local recruitment and immigration to  $\lambda$ . Since  
6 winter is the harshest season for survival of boreal passerines, we studied effects of local  
7 and global environmental variables during winter on the population dynamics. In addition  
8 to harsh climatic factors, we expected that increased competition for food and roosting  
9 places in dense winter populations affect adversely especially juvenile survival and  $\lambda$ . We  
10 hypothesised that as a southern newcomer, great tits in the north might benefit from  
11 global climate change when winter conditions become milder. This should be seen in the  
12 demography towards the final stage of the study.

13

14

## 15 **Methods**

16

### 17 Study species

18 The great tit has expanded its breeding range northwards in northern Fennoscandia during  
19 the 20<sup>th</sup> century; the first breeding records in the area date back to the 1950s (Haftorn  
20 1957; Veistola, Lehtikoinen & Iso-Iivari 1995). Previous studies suggest that the species  
21 may be maladapted to the prevailing conditions in the boreal regions, as shown by the  
22 poor breeding success compared to central populations (Orell & Ojanen 1983; Sasvári &  
23 Orell 1992; Rytönen & Orell 2001; Rytönen & Krams 2003). Irrespective of this, the

1 great tit is one of the most abundant passerines in Northern Fennoscandia (Väisänen,  
2 Lammi & Koskimies 1998).

3

#### 4 Study area and data collection

5 The study was carried out in Oulu and Haukipudas, Northern Finland (ca. 65°N,  
6 25°30'E), in an area consisting of fragmented and different aged coniferous, deciduous or  
7 mixed forests and semi-open bogs. The present population has been studied since 1969  
8 (Orell & Ojanen 1983), when the first nest-boxes were installed. We used two data sets;  
9 from 1971 to 1984 (hereafter initial period) and from 1999 to 2007 (hereafter latter  
10 period) when the study areas remained constant. During the initial period, data were  
11 collected from an area of ca. 50 ha (Taskila, see Orell & Ojanen 1983), during the latter  
12 period, the study area was ca. 1400 ha (see Rytönen & Orell 2001). The number of nest-  
13 boxes varied between 68 and 72 in the first and between 265 and 304 in the latter period.  
14 Annually, possible missing or broken boxes were replaced before the beginning of the  
15 breeding season. The variation in the number of nest-boxes had a negligible influence on  
16 the breeding density since a surplus of boxes was left vacant every breeding season.

17 Each spring, breeding great tits were captured for ringing or identified from unique  
18 combinations of numbered aluminium and coloured plastic rings. The study was based on  
19 a total of 322 (initial period) and 984 (latter period) capture histories of adult male and  
20 female great tits and on 1699 (initial period) and 3905 (latter period) capture histories of  
21 ringed fledglings. Of the ringed fledglings 57 (initial period) and 163 (latter period) were  
22 subsequently met as breeding adults in the population. Nestlings were ringed at the age of  
23 14 days. If tag loss or deterioration was suspected the bird was recaptured and the identity



1 was verified by the ring number. We have no evidence that losses of colour rings would  
2 have biased the data. The great tit is known to be highly site-tenacious when established  
3 after natal dispersal (e.g. Kluyver 1951, Hildén 1979); therefore bias in survival estimates  
4 due to permanent emigration of breeders can be expected low. Despite the excess of the  
5 boxes in the area, it is possible that some birds have nested in natural holes. Thus, some  
6 unringed residents may have been misclassified as immigrants. However, especially in  
7 the initial period this bias is negligible (see Orell & Ojanen 1983).

8

9 Environmental and ecological data

10 We used mean winter temperatures ( $^{\circ}\text{C}$ ) from December to March and the number of  
11 times the daily mean temperature curve crossed  $0^{\circ}\text{C}$  during thermal winter (hereafter  
12 plus-peaks) as independent environmental covariates to explain variation in adult  
13 survival, local recruitment and  $\lambda$ . Thermal winter is defined to begin when daily mean  
14 temperature stays below freezing point at least for five successive days. During the initial  
15 period, the mean winter temperature averaged  $-8.07^{\circ}\text{C}$  ( $\pm 0.68$  SE), whereas the latter  
16 period was milder with the mean of  $-7.28^{\circ}\text{C}$  ( $\pm 0.49$  SE). The local daily precipitation and  
17 temperature data, obtained from the monthly records of the Finnish Meteorological  
18 Institute, comprises readings taken at Oulu airport, the closest (distance ca. 19 km)  
19 weather station to the study area. In addition, we also used NAO-indices for winters  
20 (hereafter WNAO) representing means from December through March. Typically,  
21 positive WNAO-values are associated with strong wind circulation in the North Atlantic  
22 causing an increase in temperatures and precipitation in northern Europe. In contrast,  
23 negative WNAO-values mean colder and dryer winters there (Hurrell 1995, Visbeck *et*

1 *al.* 2001). WNAO-data were obtained from  
2 [ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele\\_index.nh](ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/tele_index.nh). WNAO-indices correlated  
3 positively ( $r = 0.54$ ) with the amount of winter precipitation and monthly WNAO-indices  
4 with mean temperatures ( $r$  varied from 0.51 to 0.62) from December to March at Oulu.

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

14

## 15 Modelling

16 Analyses were carried out with capture–recapture models for open populations (e.g.  
17 Lebreton *et al.* 1992, Pradel 1996, Nichols *et al.* 2000) implemented in program MARK  
18 (White & Burnham 1999). The models were designed to test and quantify the amount of  
19 temporal variation in the parameters of interest. In the analysis of population dynamics,  
20 annual estimates were calculated from CJS-models. The abbreviations of covariates used  
21 in modelling are *plusp* for plus-peaks, *wtemp* for mean winter temperature, *wnao* for  
22 WNAO-index, *wnao^2* for quadratic WNAO-index and *dens* for population density.

1           Sets of the best models are shown in Table 1. Apparent adult survival ( $\Phi_{aI+}$ ) refers  
2 to breeding individuals that survive and stay inside the study area. In each case, the  
3 starting global model was a fully time-dependent model. The global model for adult  
4 survival was the CJS-model  $\Phi_t p_t$  ( $\Phi$  survival probability,  $p$  recapture probability,  $t$  time  
5 effect) including all observations of birds that were at least one year old.

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

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

20

## 21 Model selection

22 Model selection was performed using the information theory approach discussed by  
23 Burnham & Anderson (2002). The parametric bootstrap approach provided in program

1 MARK was used to run the goodness-of-fit test (GOF) for the survival models (1000  
2 simulations). Global models' fitting the data are shown in Table 1.

3 The Akaike Information Criterion (AIC) and the corrected quasi-Akaike  
4 Information Criterion (QAICc) were used to rank the fit of each model to the data  
5 (Burnham & Anderson 2002). We considered that models with a difference in AICc of  
6 less than two units ( $\Delta\text{AICc} < 2$ ) were similarly supported by the data (Burnham &  
7 Anderson 2002). The overdispersion factor ( $\hat{c}$ ) was calculated by dividing the observed  
8 deviance of the global model by the mean expected deviance calculated from GOF  
9 simulations (Table 1). When  $\hat{c} > 1$ , the models' fit to data was ranked by QAICc and  
10 when  $\leq 1$ , the models were ranked by AIC. Model averaging (Burnham & Anderson  
11 2002) was used to control model selection uncertainty (several models with  $0 < \Delta\text{QAICc}$   
12  $< 4$ ). Lastly, the biologically meaningful process variation ( $\hat{\sigma}_{process}^2$ : process variance) was  
13 disentangled from sampling variation using a component of variation analysis with the  
14 time-dependent model (Burnham *et al.* 1987; Gould & Nichols 1998). The variance  
15 components procedure of program MARK was used to estimate the means ( $\hat{\theta}$ ), their  
16 process variances ( $\hat{\sigma}_{process}^2$ ) and the 95 % confidence intervals for the relevant parameters  
17 (Table 3).

18

19 Contributions of demographic parameters to  $\lambda$

20 Population growth can be split into components in order to estimate the relative  
21 importance of the demographic parameters. The  $\lambda$  is composed of adult survivors and of  
22 new individuals, either local recruits or immigrants, entering the population between  $i$   
23 and  $i + 1$ . A multistate approach for the time-reversed data sets was used where the age of

1 an individual was treated as a state to estimate the relative contributions of adult survival,  
2 local recruitment and immigration to  $\lambda$  following Nichols *et al.* (2000).

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

9

10

## 11 **Results**

12

### 13 **Adult survival**

14 In both data sets, the best model for adult survival included temporal variation in adult  
15 survival (Table 1, models 8 and 41). Based on model averaging between the best CJS-  
16 models ( $\Delta QAICc < 4$ ), the annual adult survival estimates ( $0.371 \pm 0.039$  SE, initial period  
17 and  $0.361 \pm 0.034$  SE, latter period) were almost similar (Table 3). The respective  
18 temporal variances in adult survival were low and almost the same (Table 3). The average  
19 recapture probability of the adults was 0.80 in the initial period and was slightly lower,  
20 0.72, in the latter period. Sampling variation accounted for 24.8 % (initial period) and  
21 16.5 % (latter period) of the total variation (estimated as  $1 - \hat{\sigma}_{process}^2 / \hat{\sigma}_{total}^2$ ). The annual  
22 adult survival probabilities, calculated from model averaged CJS-models, showed rather

1 high variation ranging from 26.2 to 54.0 % (initial period) and from 22.0 to 47.9 % (latter  
2 period; Table 2).

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

17

### 18 Local recruitment

19 The mean values of local recruitment were almost equal in the initial ( $0.055 \pm 0.011$  SE)  
20 and the latter period ( $0.059 \pm 0.011$  SE) (Table 3). In the initial period, the best model for  
21 local recruitment was fully constant (Table 1, model 11). In this period, there were only  
22 57 locally born recruits and consequently little support for time dependence and weather  
23 covariates (Table 1, models 12-21). During the latter period, there were 163 locally born

1 recruits and time variation in annual local recruitment probability was detected (Table 1,  
2 model 44; Table 2). The amount of sampling variation was 20.8 % of the total variation.  
3 The temporal process variation in local recruitment was almost twice of that in adults  
4 (Table 3). The high variability is also seen in the annual local recruitment probabilities  
5 (latter period; Table 2), calculated from model averaged CJS-models.

6 Covariate models had  $\Delta QAIc_c > 2$  compared to the best model (Table 1, models  
7 45-51). The best models included *plusp*-covariate with negative  $\beta$ -values (Table 4)  
8 reflecting poor recruitment when frequent temperature fluctuation around 0°C during  
9 winter (Fig.3).

10

#### 11 Population growth rate ( $\lambda$ )

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

20 In the initial period all the best covariate-models (Table 1, models 22-25) included  
21 *wnao* and *wnao*<sup>2</sup>. The  $\beta$ -parameters for both covariates were negative (Table 4) i.e.  $\lambda$   
22 appeared low after very cold but also after mild winters (Fig. 4). The effect of population

1 density on  $\lambda$  was low; neither the interactions between population density and  
2 environmental factors were significant.

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

8

### 9 Demographic contributions to $\lambda$

10 In the initial period, the best multistate models did not include temporal variation in  
11 transition parameter ( $\Psi$ ) (Table 1). Most likely this resulted from sparse data, i.e. low  
12 total number of recruits. Thus, temporal variation in relative contributions to  $\lambda$  was not  
13 detectable. However, in the latter period, the best-fitting model included time variation in  
14 all estimated parameters except in recapture probability. A model with constant transition  
15 parameter was also within  $\Delta\text{AIC} < 4$  (Table 1). Therefore, model averaging was used  
16 (Table 3). In the latter period, contributions of different parameters varied largely.  
17 Contribution of adult survival varied annually from 0.257 to 0.486, local recruitment  
18 from 0.152 to 0.305 and contribution of immigrants from 0.271 to 0.600 (Table 3). On  
19 average, in the latter period, 36.1 % of the great tits in the population were adults  
20 surviving from the previous year, 17.3 % were local recruits and 46.6 % were immigrants  
21 entered the population from outside study area. In the initial period these were in about  
22 similar proportions (Table 3).

23



## 1 **Discussion**

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

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

26

## 1 Adult survival

2 The average annual survival estimates of breeding adults obtained from our population,  
3 0.371 (initial period) and 0.361 (latter period), are low compared to European passerines  
4 of about the same size. Peach, Hanmer & Oatley (2001) compiled survival estimates of  
5 50 species and in only five species' survival was below 0.5. These values are, however,  
6 not fully comparable to ours because of methodological differences; only 12 were Jolly-  
7 Seber-estimates. Michel *et al.* (2006) provided CJS-estimates for 10 American titmice  
8 (*Baeolophus* and *Poecile*), ranging from 0.333 to 0.642. In most other studies of great tits  
9 the survival estimates are higher than ours ranging from 0.259 to 0.670 (Clobert *et al.*  
10 1988; Hōrak & Lebreton 1998; Pons *et al.* 2003; Payevsky 2006). Similarly, other parids  
11 in the Northern Finland have higher adult survival estimates being 0.59 for the willow tit  
12 *P. montanus* (Lampila *et al.* 2006) and 0.69 for the Siberian tit *P. cinctus* (Orell, Lahti &  
13 Matero 1999).

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

1 adults decreased and the contributions of local recruitment and immigrants increased with  
2 increasing  $\lambda$ . The local recruitment contribution exceeded the importance of immigration  
3 only in the last study year.

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

15

#### 16 Recruitment and immigration

17 In the north, great tits move in autumn from breeding areas to overwinter close to human  
18 settlements, (Järvinen 1980) taking advantage of food provided by man. Young  
19 individuals are more attracted than old ones. Some juveniles can undertake long  
20 migrations even hundreds of kilometres wide (e.g. Ulfstrand 1962, Bolshakov, Shapoval  
21 & Zelenova 1999). Verhulst, Perrins & Riddington (1997) reported that only 5 % of the  
22 emigrant recruits from the same Wytham Wood (England) population were found  
23 breeding in the surrounding area (within 2 km) and a considerable proportion of birds

1 disperse further. Our result of low local recruitment, 5.5 % (initial period) and 6.0 %  
2 (latter period), is most likely explained by a dispersal exceeding the study area as  
3 suggested by Verhulst *et al.* (1997).

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

12 Migration to northern habitats probably causes adaptive problems for great tits;  
13 clutch sizes are too large, breeding success is poor in the north (Rytönen & Orell 2001)  
14 and overwinter survival requires special behavioural or physiological adaptations. Indeed,  
15 basal metabolic rate differences between populations from Northern Finland and  
16 Southern Sweden infer local adaptations (Broggi *et al.* 2005). Although gene flow from  
17 the central populations may prevent local adaptations, Kvist *et al.* (2007) detected slight  
18 differentiation by microsatellites between the central populations and the population from  
19 Oulu. Thus, irrespective of the intensive immigration, the ecological results and among  
20 population differences at microsatellite level are not against to the suggestion of hard  
21 selection in the north against maladaptive 'southern' gene combinations, as suggested by  
22 the adaptation-with-gene-flow-theory (Blondel *et al.* 1999; Senar *et al.* 2006).

1           In comparison to willow tits studied at the same area, the contribution of  
2 immigration varies from 0.152 to 0.313 (Lampila *et al.* 2006), great tits have the range  
3 from 0.210 to 0.600. Proportional contributions to vital rates could be affected by  
4 capturing bias, as pointed out by Nichols *et al.* 2000, since some local individuals may  
5 have been considered as immigrants. However, we are confident that this potential bias  
6 does not undermine the picture described above. In reality, the amount of immigration is  
7 probably smaller than our estimates.

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

13

#### 14 Winter conditions

15 The mean winter temperature risen during the study. The decline of population size is not  
16 surprising in the cold winters when WNAO-index is very negative, but for being a  
17 southern incomer, great tits would be expected to survive better when winter conditions  
18 are less arctic. Several non-mutually exclusive explanations could account for these  
19 results. First, changes in predation may be an explanatory factor. In the initial period, the  
20 stoat-predation-model was better than time-dependent model in adult survival.  $\beta$ -  
21 parameter was negative, so the increased predation on roosting great tits in winter  
22 decreased adult survival. However, the effect of stoat predation was hidden by the  
23 stronger effects of climatic factors. The most abundant avian predator of small passerines

1 in winters in the north is sparrowhawk (Väisänen 2006). When winter conditions are  
2 milder, more sparrowhawks may try overwintering increasing predation pressure towards  
3 small passerines. However, the sparrowhawk-model got very low support in our analysis.

4       Second, paradoxically, availability of food may be a plausible explanation for  
5 increased mortality in warm winters. Dynamics of the great tit in the north is greatly  
6 affected by food supplied by man in winter (Orell 1989) that is why they tend to spend  
7 winter near human-inhabited areas. On one hand, milder temperatures may promote an  
8 earlier colonization of the rural breeding areas from wintering spots, and these early birds  
9 may fail to find enough food. Likewise, mild conditions may induce birds, which  
10 otherwise may become emigrants to remain in the study area. Such increased density may  
11 promote a higher competition at feeders, which otherwise may have less food, as sales of  
12 bird-food (personal comments from shopkeeper) and humans activity to feed is known to  
13 drop in mild winters. We studied how the number of feeding grounds in midwinter (in  
14 turn of the year) is related to mean temperature of December in Oulu surroundings in four  
15 winters from 2005 to 2008. The comparison was made to be based on the winter bird  
16 census data available from <http://www.hatikka.fi/winterbird.php> and 15 census routes  
17 with the information of the number of feeding grounds along the route were selected. Due  
18 to small data, only indicative conclusions are possible, but the number of feeding trays  
19 seems to be smaller in mild winters than in colder ones. During the coldest winter (mean  
20 temperature  $-7.4^{\circ}\text{C}$ ) there were 102 feeding tables along the routes, but during three  
21 milder early winters (mean temperatures varied from  $0^{\circ}\text{C}$  to  $-1.4^{\circ}\text{C}$ ) only from 83 to 90  
22 along the same routes.

1 Third, in warm and wet winters birds may be more exposed to diseases. Wet  
2 feeders with birds' faeces are good substrates for viruses and bacteria. Infected birds may  
3 be eliminated when weather gets colder again. This is possibly at least a part of  
4 explanation for the reduced survival probability of adult and juvenile great tits in relation  
5 to increasing number of plus-peaks during thermal winter (Robb *et al.* 2008).

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

12

13 Climate change

14 According to predicted climate change, mild and NAO-positive winters are expected to  
15 be more usual in northern Europe. Global warming has been predicted to change species'  
16 distributions: boreal species' ranges move even further northwards and southern species  
17 expand to boreal areas (Huntley *et al.* 2007). According to national bird censuses, great  
18 tits have become more abundant in Finland from the 1980s' to the beginning of the  
19 2000s' (Väisänen 2006). In our analyses, the observed  $\lambda$  averaged unity in the initial  
20 period and indicated an increasing population in the latter period. Temporal variation in  $\lambda$   
21 was considerable during both periods. This agrees well with earlier results (Väisänen  
22 2006), that large annual fluctuation in the population size is typical for northern great tits.  
23 Sæther *et al.* (2003) demonstrated that in birds, including the great tit, the proportion of

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

12

13

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1 **References**

2

3 van Balen, J.H. (1980) Population fluctuations of the Great Tit and feeding conditions in  
4 winter. *Ardea*, **68**, 143-164.

5 BirdLife International (2004) *Birds in Europe: population estimates, trends and*  
6 *conservation status*. Cambridge, UK: BirdLife International.

7 Blondel, J., Dias, P.C., Maistre, M. & Perret, P. (1993) Habitat heterogeneity and life-  
8 history variation of Mediterranean Blue tits *Parus caeruleus*. *Auk*, **110**, 511-520.

9 Blondel, J., Dias, P.C., Perret, P., Maistre, M. & Lambrechts, M.M. (1999) Selection-  
10 Based Biodiversity at a Small Spatial Scale in a Low-Dispersing Insular Bird.  
11 *Science*, **285**, 1399-1402.

12 Bolshakov, C.V., Shapoval, A.P. & Zelenova, N.P. (1999) Results of bird trapping and  
13 ringing by the Biological Station “Rybachy” on the Courish Spit in 1998. *Avian*  
14 *Ecology and Behaviour*, **2**, 105-150.

15 Broggi, J., Hohtola, E., Orell, M. & Nilsson, J.-Å. (2005) Local adaptation to winter  
16 conditions in a passerine spreading north: a common-garden approach. *Evolution*,  
17 **59**, 1600-1603.

18 Burnham, K. & Anderson, D. (2002) *Model selection and multimodel inference: a*  
19 *practical information-theoretic approach*. 2<sup>nd</sup> ed. Springer, New York.

20 Burnham, K., Anderson, D.R., White, G., Brownie, C. & Pollock, K.H. (1987) Design  
21 and analysis methods for fish survival experiments based on release-recapture.  
22 *American Fisheries Society Monograph*, **5**, 1-437.

- 1 Choquet, R., Reboulet, A.-M., Lebreton, J.-D., Gimenez O., & Pradel, R. (2005) *U-CARE*  
2 *2.2 User's Manual*. CEFE, Montpellier, France.
- 3 Clobert, J., Perrins, C.M., McCleery, R.H. & Gosler, A.G. (1988) Survival rate in the  
4 great tit *Parus major* in relation to sex, age and immigration status. *Journal of*  
5 *Animal Ecology*, **57**, 287-306.
- 6 Dhont, A.A., Adriaensen, F., Matthysen, E. & Kempenaers, B. (1990) Non adaptive  
7 clutch size in tits. *Nature*, **348**, 723-725.
- 8 Eeva, T., Lehikoinen, E., & Veistola, S. (1989) Habitat preference and breeding  
9 performance in four hole-nesting passerines at the northern limit of their range.  
10 *Ornis Fennica*, **66**, 142-150.
- 11 Franklin, A.B. (2001) Exploring ecological relationships in survival and estimating rates  
12 of population change using program MARK. Pages 290-296 *In* Field, R., Warren,  
13 R.J., Okarma, H. & Sievert, P.R. editors. *Wildlife, land, and people: priorities for*  
14 *the 21st century*. Proceedings of the Second International Wildlife Management  
15 Congress. The Wildlife Society, Bethesda, Maryland.
- 16 Gosler, A. (1993) *The Great Tit*. Hamlyn, London.
- 17 Gould, W.E. & Nichols, J.D. (1998) Estimation of temporal variability of survival in  
18 animal populations. *Ecology*, **79**, 2531-2538.
- 19 Grant, M.C. & Antonovics, J. (1978) Biology of ecologically marginal populations of  
20 *Anthoxanthum odoratum*. I. phenetics and dynamics. *Evolution*, **32**, 822-838.
- 21 Guo, Q., Taper, M., Schoenberger, M. & Brandle, J. (2005) Spatial-temporal population  
22 dynamics across species range: from centre to margin. *Oikos*, **108**, 47-57.

- 1 Haftorn, S. (1957) Kjøttmeisas (*Parus m. major* L.) innvandring og nåvaerende  
2 utbredelse i Nord-Norge. *Det Kongelige Norske Videnskabers Selskab*, **30**, 14-21.
- 3 Hildén, O. (1979) A life history of a 7-year-old great tit. *Ornis Fennica*, **56**, 33-34. (In  
4 Finnish with English summary).
- 5 Hörak, P. & Lebreton, J.-D. (1998) Survival of adult great tits in relation to sex and  
6 habitat: a comparison of urban and rural populations. *Ibis*, **140**, 205-209.
- 7 Huntley, B., Green R.E., Collingham Y.C. & Willis, S. G. (2007) *A Climatic Atlas of*  
8 *European Breeding Birds*. Lynx Edicions.
- 9 Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional  
10 temperatures and precipitation. *Science*, **269**, 676-679.
- 11 Hurrell, J.W., Kushnir, Y. & Visbeck, M. (2001) The North Atlantic Oscillation. *Science*,  
12 **291**, 603-605.
- 13 Järvinen, O. (1979) Geographical gradients of stability in European land bird  
14 communities. *Oecologia*, **38**, 51-69.
- 15 Järvinen, O. (1980) *Ecological zoogeography of Northern European bird communities*.  
16 PhD thesis, University of Helsinki, Helsinki.
- 17 Kawecki, T.J. (2008) Adaptation to Marginal Habitats. *Annual Review of Ecology,*  
18 *Evolution, and Systematics*, **39**, 321-342.
- 19 Kluyver, H.N. (1951) The population ecology of the great tit, *Parus m. major* L. *Ardea*,  
20 **39**, 1-135.
- 21 Kokko, H. & López-Sepulcre, A. (2006) From Individual Dispersal to Species Ranges:  
22 Perspectives for a Changing World. *Science*, **313**, 789-791.

- 1 Kvist, L., Ruokonen, M., Lumme, J. & Orell, M. (1999) The colonization history and  
2 present-day population structure of the European great tit (*Parus major major*).  
3 *Heredity*, **82**, 495-502.
- 4 Kvist, L., Arbabi, T., Päckert, M., Orell, M. & Martens, J. (2007). Population  
5 differentiation in the marginal populations of the great tit (Paridae: *Parus major*)  
6 *Biological Journal of the Linnean Society*, **90**, 201–210.
- 7 Lampila, S., Orell, M., Belda, E. & Koivula, K. (2006) Importance of adult survival, local  
8 recruitment and immigration in a declining boreal forest passerine, the willow tit  
9 *Parus montanus*. *Oecologia*, **148**, 405-413.
- 10 Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival  
11 and testing biological hypotheses using marked animals: a unified approach with  
12 case studies. *Ecological Monographs*, **62**, 67-118.
- 13 Leech, D.I. & Crick, H.Q.P. (2007) Influence of climate change on the abundance,  
14 distribution and phenology of woodland bird species in temperate regions. *Ibis*, **149**,  
15 128-145.
- 16 Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends in Ecology*  
17 *and Evolution*, **17**, 183-189.
- 18 Lindström, Å, Green, M. Ottvall, R. & Svensson, S. (2008) *Övervakning av fåglarnas*  
19 *populationsutveckling. Årsrapport för 2007*. (Monitoring population changes of  
20 birds in Sweden. Annual report 2007). Ekologiska institutionen, Lunds universitet,  
21 Lund. [http://www.biol.lu.se/zooekologi/birdmonitoring/PDF-files/Arssrapportfor](http://www.biol.lu.se/zooekologi/birdmonitoring/PDF-files/Arssrapportfor2007kf.pdf)  
22 [2007kf.pdf](http://www.biol.lu.se/zooekologi/birdmonitoring/PDF-files/Arssrapportfor2007kf.pdf) (April 2008).

- 1 Michel, N., DeSante, D.F., Kaschube, D.R., & Nott, M.P. (2006) *The Monitoring Avian*  
2 *Productivity and Survivorship (MAPS) Program Annual Reports, 1989-2003.*  
3 NBII/MAPS Avian Demographics Query Interface.  
4 <http://www.birdpop.org/nbii/NBIIHome.asp> (December 2006).
- 5 Nichols, J.D., Hines, J.E., Lebreton, J.-D. & Pradel, R. (2000) Estimation of contributions  
6 to population growth: a reverse-time capture–recapture approach. *Ecology*, **81**,  
7 3362-3376.
- 8 Orell, M. (1989) Population fluctuations and survival of Great Tits *Parus major*  
9 dependent on food supplied by man in winter. *Ibis*, **131**, 112-127.
- 10 Orell, M., Lahti, K. & Matero, J. (1999) High survival and site fidelity in the Siberian tit  
11 *Parus cinctus*, a focal species of the taiga. *Ibis*, **141**, 460-468.
- 12 Orell, M. & Ojanen, M. (1983) Breeding success and population dynamics in a northern  
13 great tit *Parus major* population. *Annales Zoologici Fennici*, **20**, 77-98.
- 14 Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change.  
15 *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637-669.
- 16 Payevsky, V.A. (2006) Mortality Rate and Population Density Regulation in the Great  
17 Tit, *Parus major* L.: A Review. *Russian Journal of Ecology*, **37**, 180-187.
- 18 Peach, W.P., Hanmer, D.B. & Oatley, T.B. (2001) Do southern African songbirds live  
19 longer than their European counterparts? *Oikos*, **93**, 235-249.
- 20 Pons, P., Henry, P.-Y., Gargallo, G., Prodon, R. & Lebreton, J.-D. (2003) Local survival  
21 after fire in Mediterranean shrublands: combining capture-recapture data over  
22 several bird species. *Population Ecology*, **45**, 187-196.

- 1 Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and  
2 population growth rate. *Biometrics*, **52**, 703-709.
- 3 Pulliam, H.R. (1988) Sources, sinks and population regulation. *American Naturalist*, **132**,  
4 652-661.
- 5 Robb, G.N., McDonald, R.A., Chamberlain, D.E. & Bearhop, S. (2008) Food for thought:  
6 supplementary feeding as a driver of ecological change in avian populations.  
7 *Frontiers in Ecology and the Environment*, **6**, 476-484.
- 8 Rytkönen, S. & Orell, M. (2001) Great tits, *Parus major*, lay too many eggs:  
9 experimental evidence in mid-boreal habitats. *Oikos*, **93**, 439-450.
- 10 Rytkönen, S. & Krams, I. (2003) Does foraging behaviour explain the poor breeding  
11 success of great tits *Parus major* in northern Europe? *J. Avian Biol.*, **34**, 288-297.
- 12 Sæther, B.-E. & Bakke, Ø. (2000) Avian life history variation and contribution of  
13 demographic traits to the population growth rate. *Ecology*, **81**, 642-653.
- 14 Sæther, B.-E., Tufto, J. Engen, S., Jerstad, K., Røstad, O.W. & Skåtán, J.E. (2000)  
15 Population Dynamical Consequences of Climate Change for a Small Temperate  
16 Songbird. *Science*, **287**, 854-856.
- 17 Sæther, B.-E., Engen, S., Møller, A.P., Matthysen, E., Adriaensen, F., Fiedler, W.,  
18 Leivits, A., Lambrechts, M.M., Visser, M.E., Anker-Nilssen, T., Both, C., Dhondt,  
19 A.A., McCleery, R.H., McMeeking, J., Potti, J., Røstad, O.W. & Thomson, D.  
20 (2003) Climate variation and regional gradients in population dynamics of two  
21 hole-nesting passerines. *Proceedings of the Royal Society of London. Series B*,  
22 *Biological Sciences*, **270**, 2397-2404.

- 1 Senar, J.C., Borrás, A., Cabrera, J., Cabrera, T. & Björklund, M. (2006) Local  
2 differentiation in the presence of gene flow in the citril finch *Serinus citrinella*.  
3 *Biology letters*, **2**, 85-87.
- 4 Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. (2002)  
5 Ecological effects of climate fluctuations. *Science*, **297**, 1292-1296.
- 6 Ulfstrand, S. (1962) On the non-breeding ecology and migratory movements of the Great  
7 Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*) in southern Sweden. *Vår*  
8 *Fågelvärld*, Supplement 3.
- 9 Veistola, S., Lehtikoinen, E. & Iso-Iivari, L. (1995) Breeding biology of the great tit  
10 *Parus major* in a marginal population in northernmost Finland. *Ardea*, **83**, 419-420.
- 11 Verhulst, S., Perrins, C.M. & Riddington, R. (1997) Natal dispersal of great tits in a  
12 patchy environment. *Ecology*, **78**, 864-872.
- 13 Visbeck, M.H., Hurrell, J.W., Polvani, L. & Cullen, H.M. (2001) The North Atlantic  
14 Oscillation: Past, present, and future. *Proceedings of the National Academy of*  
15 *Sciences of the United States of America*, **98**, 12876-12877.
- 16 Väisänen, R.A. (2006) Maalinnuston kannanvaihtelut Etelä- ja Pohjois-Suomessa 1983-  
17 2005 (Monitoring population changes of 86 land bird species breeding in Finland in  
18 1983-2005) (in Finnish, summary in English) *Linnut vuosikirja 2005*, 83-98.
- 19 Wallace, J.M., Zhang, Y. & Renwick, J.A. (1995) Dynamic contribution to Hemispheric  
20 mean temperature trends. *Science*, **270**, 780-783.
- 21 White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from  
22 populations of marked animals. *Bird Study (Supplement)*, **46**, 120-139.

1 Winkler, D.W., Dunn, P.O. & McCulloch, C.E. (2002) Predicting the effects of climate  
2 change on avian life-history traits. *Proceedings of the National Academy of*  
3 *Sciences of the United States of America*, **99**, 13595-13599.