

Population dynamics of an expanding passerine at the distribution margin

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Individuals may be maladapted to novel environments at the species' distribution margin. We investigated population dynamics in a marginal habitat where reproduction has been proven poor. Survival, population growth rate (λ) and its components, breeding and natal dispersal were studied in great tits *Parus major* breeding at the northern margin of its distribution in northern Finland. We used long term capture–mark–recapture data sets. Study area size and population density were used to explain adult survival rates. The average annual estimates of adult survival rose from 0.371 to 0.388 between the periods of 1971–1984 and 1999–2009. The estimates are slightly lower than estimates of small passerines in Europe. Low local survival rate of fledglings (0.050–0.055) probably reflects intensified emigration from this low quality area. Temporal variation in λ was large (0.498–1.856). Despite of low adult survival and recruitment rates, the mean estimates of λ (1.008 and 1.033) indicate an overall stability in the population size. Indeed, our results suggest that the immigration has an important role in the population dynamics of northern great tits. Thus the population is demographically and genetically dependent on core habitats which may cause adaptive problems due to intensive gene flow. Given those limitations, options for evolution of local adaptations in northern distribution margins are discussed.

Species' distribution ranges change. For example, the predicted and observed global warming may shift the temperature conditions of boreal areas suitable for southern species. However, some factors, such as photoperiodism controlling breeding timing, do not change. The expanding organism has to adapt to new environment so that its range expansion is possible. 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). Species at the borders of their distribution are usually confronted with adverse conditions that cause low survival and reproduction. Thus, peripheral populations are often demographic sinks maintained by continued immigration from the species' central range where reproduction is high and mortality is comparatively low ('source-sink' dynamics; Pulliam 1988).

Range expansion over evolutionary time requires that the peripheral populations become better adapted to their habitats. However, due to high immigration rates in marginal populations, gene flow may prevent local adaptations (Dhondt et al. 1990, Lenormand 2002, Kawecki 2008). Nonetheless, if dispersal occurs at a juvenile stage, immigrants are subject to natural selection before their genes can recombine with the local gene pool.

Changing environmental conditions can either constrain or accelerate range expansions. Range expansions are favoured if environments alter to closer resemble the core areas, making it easier to adapt to the new habitats and

enhancing survival and reproduction. In addition, suitable conditions in the central habitat can increase dispersal (emigration) favouring persistence of marginal populations (Kokko and López-Sepulcre 2006). So, not only local, but also larger scale environmental changes can affect marginal populations. Clearly, however, the dynamics of marginal populations are insufficiently understood and there is a need for extensive population studies from such habitats.

In this study, we use the great tit *Parus major* as a model species. It is a widely distributed passerine bird species facing a variety of habitats and environmental conditions across its range (Gosler 1993). Its breeding range has expanded northwards in northern Fennoscandia during the 20th century; first breeding records in the area date back to the 1950s (Haftorn 1957, Veistola et al. 1995). Studies suggest that the species may be maladapted to the prevailing conditions in boreal regions, as shown by the poor breeding success when compared to central populations (Orell and Ojanen 1983, Rytönen and Orell 2001, Rytönen and Krams 2003). According to Sasvári and Orell (1992), the average clutch size in Oulu area is 9.4 with 0.8 SD and number of fledged young only 5.8 with 1.72 SD. Irrespective of this, the great tit is one of the most abundant passerines in northern Fennoscandia (Väisänen et al. 1998). Despite extensive knowledge on great tit population dynamics in core areas (Kluyver 1951, Clobert et al. 1988, Dhondt et al. 1990), information on the population demography at the distribution margin is largely incomplete.

In this study, we used long term capture–mark–recapture-data sets from a great tit population living at the northern margin of the distribution range between the years 1971–1984 and 1999–2009. During the latest decades the great tit has expanded northwards (Veistola et al. 1995) and increased in numbers especially in southern Finland (Väisänen 2006). We expected that this increase might be seen in our study periods too as increasing population size. We modelled adult survival, local recruitment probabilities and population growth rate (λ) with their variances and breeding and natal dispersal. We estimated the relative contributions of adult survival, local recruitment and immigration to λ . The main aim of the study was to increase our understanding of what determines population abundance at the northern margin of a distribution range. Is the northern great tit population maintained by continued immigration, or if observed population parameters could be explained by balanced large-scale dispersal between areas of similar demographic rates? Further insight into this question was achieved by comparing the demographic rates of northern great tit to those of representing balanced large-scale dispersal: their native boreal relative, the willow tit *Parus montanus* and southern co-specifics. Direct comparison is difficult since in the majority of studies the estimated parameters are based on return rates, which are to some extent an underestimate since recapture probabilities are not considered. In addition many of the estimates from other studies are uncertain because of short time series. However, low adult survival and the great contribution of immigration would reflect the continued immigration-system, whereas low immigration and high adult survival merely tell about balanced large-scale dispersal.

Methods

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 and Ojanen 1983), when the first nest-boxes were installed. We used two data sets; between the years 1971–1984 (hereafter initial period) and 1999–2009 (hereafter latter period) when the study areas remained constant. During the initial period, data were collected from an area of ca 0.8 km² (Taskila, Orell and Ojanen 1983), during the latter period, the study area was ca 8 km², which can be divided to four sub-areas with the sizes of 1.3 (Rusko), 3.4 (Rissasentie), 0.9 (Oinaansuo) and 2.4 km² (Vittasuo) (area description in Rytönen and Orell 2001). Rusko-area resembles Taskila-area, because some nest-boxes are located close to human settlement. The annual number of nest-boxes was approximately 70 in the first and 250 in the latter period. Every year, 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 aluminum and coloured plastic rings. The study was based

on a total of 322 (initial period) and 944 (latter period) capture histories of adult male and female great tits and on 1699 (initial period) and 4404 (latter period) capture histories of ringed fledglings. Of the ringed fledglings 57 (initial period) and 167 (latter period) were subsequently found as breeding adults in the population. Nestlings were ringed at the age of 14 d. 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 (Kluyver 1951); therefore bias in survival estimates due to permanent emigration of breeders is expected to be low. Great tits prefer nest boxes. In the same area, there are hundreds of nest holes excavated by willow tits (Lampila et al. 2006) and woodpeckers, but only few great tits nests have been found in those natural cavities.

Modelling

Analyses were carried out with capture–recapture models for open populations (Lebreton et al. 1992, Pradel 1996, Nichols et al. 2000) implemented in program MARK (White and 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 Cormack–Jolly–Seber-models (CJS-models). The covariates used in modelling are population density (*dens*) and the size (ha) of the study area (*area*).

Apparent adult survival (Φ_{a1+}) refers to breeding individuals that stay and survive inside the study area. The global model for adult survival was the CJS-model $\Phi_t p_t$ (Φ survival probability, p recapture probability, t time effect) including all observations of birds that were at least one year old. The adult survival was estimated in four sub-areas, too. The global model for adult survival in different sub-areas was the CJS-model $\Phi_g p_{g^*t}$ (g group effect).

Local recruitment (Φ_{a0}) refers to fledglings that were born in the study area, 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).

The population growth rate (λ) was estimated by applying Pradel's (1996) reverse-time approach. The transition parameter estimated from a reversed encounter history is γ (seniority parameter), which is the probability that if an individual is alive and in the population at time i , the individual was alive and in the population at time $i-1$. The population growth rate is then calculated as $\lambda_i = \Phi_i / \gamma_{i+1}$ (Nichols et al. 2000). This is so called Pradel's lambda, where the differences in capture and marking effort between the years affects the accuracy of annual estimates. The global model for estimating λ was the fully time-dependent model ($\Phi_t p_t \lambda_t$). As in estimating adult survival, λ was estimated from data sets including all observations of birds that were at least one year old. Pradel-models with covariates were fitted following Franklin (2001), Φ and p were completely time-dependent and constraints were applied on λ . Annual estimates of λ were calculated from the best CJS-models within $0 < \Delta QAIC_c < 4$.

Model selection

Model selection was performed using the information theory approach (Burnham and Anderson 2002). 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. We considered that models with a difference in AICc of less than two units ($\Delta\text{AICc} < 2$) were similarly supported by the data. The parametric bootstrap approach provided in program MARK was used to run the goodness-of-fit test (GOF) for the survival models (1000 simulations). The overdispersion factor (\hat{c}) was calculated by dividing the observed deviance of the global model by the mean expected deviance calculated from GOF simulations. When $\hat{c} > 1$, the models' fit to data was ranked by QAICc and when ≤ 1 , the models were ranked by AICc. Model averaging was used to control model selection uncertainty (several models with $0 < \Delta\text{QAICc} < 4$).

Lastly, the biologically meaningful process variation ($\sigma_{\text{process}}^2$: process variance) was disentangled from sampling variation using a component of variation analysis with the time-dependent model (Burnham et al. 1987, Gould and Nichols 1998). The variance components procedure of

program MARK was used to estimate the means ($\hat{\theta}$) and their process variances ($\sigma_{\text{process}}^2$).

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 years 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 λ 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 $S_{(a0, a1+)*t} P_c \Psi_{(a0, a1+)*t}$ (S = survival, p = recapture probability, Ψ = transition parameter). Constant recapture probability was chosen because it was the best in both survival and Pradel-models. The GOF-test was carried out using the program U-CARE (Choquet et al. 2005).

Table 1a. Model selection. np number of parameters, t time dependence, . constant effect, $a0$ juvenile, $a1+$ adult bird, $dens$ population density. In multistate models there are two fixed parameters: $S_{a0} = 0$ and $\Psi_{a0-a1+} = 0$.

1971–1984	QAICc	ΔQAICc	np	1999–2009	QAICc	ΔQAICc	np
Adult survival				Adult survival			
1 $\Phi_{dens} P_c$	518.16	0.00	3	19 $\Phi_{dens} P_t$	1531.60	0.00	11
2 $\Phi_t P_c$	522.40	4.24	14	20 $\Phi_t P_t$	1532.14	0.54	19
3 $\Phi_c P_c$	523.58	5.42	2	21 $\Phi_c P_t$	1535.94	4.34	11
4 $\Phi_t P_t$	529.75	11.59	25	22 $\Phi_t P_c$	1537.20	5.60	11
Local recruitment				Local recruitment			
5 $\Phi_{(a0, a1+)} P_c$	511.18	0.00	3	23 $\Phi_{(a0t, a1+)} P_c$	1731.02	0.00	12
6 $\Phi_{(a0dens, a1+)} P_c$	512.17	0.99	4	24 $\Phi_{(a0dens, a1+)} P_c$	1736.31	5.29	4
7 $\Phi_{(a0, a1+)+t} P_c$	523.30	12.12	15	25 $\Phi_{(a0t, a1+)} P_t$	1739.32	8.30	20
8 $\Phi_{(a0t, a1+)} P_c$	527.13	15.95	15	26 $\Phi_{(a0, a1+)} P_c$	1741.45	10.43	3
9 $\Phi_{(a0, a1+)*t} P_c$	533.72	22.54	26	27 $\Phi_{(a0, a1+)*t} P_c$	1746.41	15.39	19
10 $\Phi_{(a0, a1+)*t} P_t$	542.54	31.36	38	28 $\Phi_{(a0, a1+)*t} P_t$	1751.67	20.65	28
λ				λ			
11 $\Phi_c P_c \lambda_t$	1868.72	0.00	15	29 $\Phi_c P_t \lambda_t$	5278.10	0.00	28
12 $\Phi_t P_c \lambda_t$	1868.99	0.27	27	30 $\Phi_t P_t \lambda_t$	5282.98	4.88	20
13 $\Phi_t P_t \lambda_t$	1877.73	9.01	38	31 $\Phi_t P_c \lambda_t$	5283.79	5.69	21
14 $\Phi_c P_c \lambda_{dens}$	1910.33	41.61	4	32 $\Phi_t P_t \lambda_{dens}$	5286.29	8.19	23
Multistate models				Multistate models			
15 $S_{(a0, a1+)} P_c \Psi_{(a0, a1+)}$	AIC	ΔAIC	np	33 $S_{(a0t, a1+)} P_t \Psi_{(a0t, a1+)}$	AIC	ΔAIC	np
16 $S_{(a0t, a1+)} P_c \Psi_{(a0, a1+)}$	1104.20	0.00	3	34 $S_{(a0t, a1+)} P_c \Psi_{(a0t, a1+)}$	6044.11	0.00	29
17 $S_{(a0, a1+)} P_c \Psi_{(a0t, a1+)}$	1106.23	2.04	15	35 $S_{(a0t, a1+)} P_c \Psi_{(a0, a1+)}$	6046.68	2.57	21
18 $S_{(a0t, a1+)} P_c \Psi_{(a0t, a1+)}$	1112.72	8.52	15	36 $S_{(a0t, a1+)} P_c \Psi_{(a0, a1+)}$	6075.99	31.89	20
	1117.02	12.82	27		6076.18	32.07	12

$\hat{c} = 1.22$ for adult survival and Pradel-models, $\hat{c} = 1.30$ for the local recruitment models and $\hat{c} = 0.85$ for multistate models. Goodness-of-fit test for the global model in adult survival and Pradel-models was $p = 0.145$, local recruitment $p = 0.180$ and in multistate models $p = 0.667$.

$\hat{c} = 1.19$ for adult survival and Pradel-models, $\hat{c} = 1.09$ for the local recruitment models and $\hat{c} = 0.88$ for multistate models. Goodness-of-fit test for the global model in adult survival and Pradel-models was $p = 0.11$, local recruitment $p = 0.60$ and in multistate models $p = 0.83$.

Table 1b. β -estimates of population density covariate $dens$ (95% confidence limits).

Model	β -estimate		
1 $\Phi_{dens} P_c$	-0.004 (-0.007, -0.001)	19 $\Phi_{dens} P_t$	0.001 (0.000, 0.002)
6 $\Phi_{(a0dens, a1+)} P_c$	-0.002 (-0.006, 0.002)	24 $\Phi_{(a0dens, a1+)} P_c$	0.002 (0.0004, 0.0028)
14 $\Phi_c P_c \lambda_{dens}$	-0.001 (-0.0026, 0.00003)	32 $\Phi_t P_t \lambda_{dens}$	-0.001 (-0.001, 0.0003)

Results

Adult survival

Sets of the best models are shown in Table 1a and 2a. In both data sets, the best model for adult survival included a covariate of population density in adult survival (Table 1a, models 1 and 19). Based on β -values, during the initial period the population density effect was negative but in the latter period the effect was positive. This means that the higher population density restricted survival only during the initial period. The annual adult mean survival estimates were almost similar (Table 3; 0.371 ± 0.039 SE, initial period and 0.388 ± 0.033 SE, latter period). During the latter period, the adult survival was analysed in four sub-areas (Table 2). There were differences in survival between sub-areas; the best model included the group effect (Table 2a). However, the size of the area did not explain the survival (Table 2b); therefore we suggest that comparison between the study periods is possible. If there was extensive breeding dispersal, the larger sub-areas should have higher survival estimates. The respective temporal variances in adult survival were low and almost the same (Table 4). The average recapture probability of the adults was 0.80 in the initial period and was slightly lower, 0.73 in the latter period. Sampling variation accounted for 24.8% (initial period) and 21.4% (latter period) of the total variation (estimated as $1 - \hat{\sigma}_{process}^2 / \hat{\sigma}_{total}^2$). The annual adult survival estimates, calculated from model averaged CJS-models, showed rather high variation ranging from 0.26 to 0.54 during the initial period) and from 0.214 to 0.498 during the latter period (Table 3).

Local recruitment

The mean values of local recruitment were almost equal in the initial (0.055 ± 0.011 SE) and the latter period (0.050 ± 0.007 SE) (Table 3). In the initial period, the best model for local recruitment was fully constant (Table 1a,

Table 2a. Model selection. np number of parameters, t time dependence, \cdot constant effect, g group effect by breeding sub-area (1999–2009), $area$ size of breeding sub-area.

Model	QAICc	Δ QAICc	np
$\Phi_g p_t$	1525.49	0.01	13
$\Phi_g p_{(g+t)}$	1527.51	2.01	16
$\Phi \cdot p_{(g+t)}$	1527.93	2.43	13
$\Phi \cdot p_t$	1528.82	3.32	10
$\Phi_{(area)} p_t$	1530.81	5.31	11
$\Phi \cdot p_{(g^*t)}$	1544.57	19.08	34
$\Phi_g p_{(g^*t)}$	1547.84	22.34	38

$\hat{c} = 1.195$, Goodness-of-fit test for the global model ($\Phi_g p_{(g^*t)}$) was $p = 0.05$.

Table 2b. Mean survival estimates from the best model ($\Phi_g p_t$) in different breeding sub-areas (1999–2009).

Area	Survival	SE	Size (km ²)
1: Oinaansuo	0.364	0.029	1.0
2: Rusko	0.491	0.031	1.3
3: Vittasuo	0.427	0.029	2.4
3: Rissasentie	0.402	0.044	3.4

model 5). In this period, there were only 57 locally born recruits and consequently little support for time dependence. During the latter period, there were 163 locally born recruits and variation in annual local recruitment probability was detected (Table 1a, model 23; Table 3). 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 4). The high variability is also seen in the annual local recruitment probabilities (latter period; Table 3), calculated from model averaged CJS-models.

Population growth rate (λ)

In both data sets, time variation in λ was included in all the best models (Table 1a, models 11, 12 and 29). In the initial data set, sampling variation accounted for 3.6% and in the latter data set 14.5% of the total variation. Model averaged estimates of λ 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 four non-consecutive years and decreased in four non-consecutive years. The resulted mean λ 1.033 ± 0.093 SE indicates a stable population size. In both periods, however, the 95% confidence interval for the mean growth rate extended below unity (Table 3).

Demographic contributions to λ

In the initial period, the best multistate models did not include temporal variation in transition parameter (ψ) (Table 1a). Most likely this resulted from sparse data, i.e. low total number of recruits. Thus, temporal variation in relative contributions to λ was not detectable. However, in the latter period, the best-fitting model included time variation in all estimated parameters. A model with constant recapture probability was also within Δ AIC < 4 (Table 1a). Therefore, model averaging was used. In the latter period, contributions of different parameters varied largely. Contribution of adult survival varied annually from 0.303 to 0.734, local recruitment from 0.074 to 0.300 and contribution of immigrants from 0.161 to 0.497 (Table 3). On average, in the latter period, 44.3% of the great tits in the population were adults surviving from the previous year, 17.2% were local recruits and 38.5% were immigrants entered the population from outside the study area. In the initial period the proportions were about the same (Table 3).

Natal and breeding dispersal

The mean natal dispersal distance in the initial period was 356 m (md = 330 m, range 0–838 m) and the mean breeding dispersal distance was 201 m (md = 133 m, range = 0–1020 m). The corresponding distances in the latter period were 1138 m (md = 912 m, range = 0–4685 m) and 196 m (md = 138 m, range 0–2804 m). Both natal and breeding dispersal distances were much shorter than expected if the dispersal shifts were random within the areas: mean random shift in initial period was 860 (0–2207) m and in latter period 2884 (0–8719) m.

Table 3. Annual estimates and mean values (\pm SE) of λ , survival probabilities for adults and recruits, relative contributions of adult survival (γ_{a1+}), local recruitment (γ_{l0}) and immigration ($1 - \gamma_{a1+} - \gamma_{l0}$) to λ . Annual estimates were obtained using model averaging of CJS-models within $\Delta QAIC_c < 4$.

Year	λ	Adult survival	Year	λ	Adult survival	Local recruitment	Adult survival λ_{a1+}	Relative contributions to λ		
								Local recruitment	Recruitment λ_{l0}	Immigrants ($1 - \lambda_{a1+} - \lambda_{l0}$)
1971	—	0.286 \pm 0.062	1999	—	0.214 \pm 0.069	0.030 \pm 0.010	—	—	—	
1972	1.447 \pm 0.344	0.393 \pm 0.093	2000	0.758 \pm 0.250	0.311 \pm 0.053	0.047 \pm 0.014	—	—	—	
1973	0.583 \pm 0.133	0.281 \pm 0.064	2001	1.313 \pm 0.238	0.438 \pm 0.074	0.041 \pm 0.011	0.403 \pm 0.106	0.169 \pm 0.045	0.428 \pm 0.115	
1974	1.856 \pm 0.474	0.370 \pm 0.098	2002	1.395 \pm 0.394	0.490 \pm 0.111	0.045 \pm 0.012	0.399 \pm 0.068	0.135 \pm 0.033	0.467 \pm 0.075	
1975	0.812 \pm 0.174	0.295 \pm 0.065	2003	0.693 \pm 0.264	0.403 \pm 0.120	0.032 \pm 0.010	0.349 \pm 0.070	0.153 \pm 0.035	0.497 \pm 0.078	
1976	0.916 \pm 0.206	0.348 \pm 0.075	2004	0.866 \pm 0.321	0.258 \pm 0.075	0.076 \pm 0.026	0.519 \pm 0.108	0.159 \pm 0.049	0.321 \pm 0.118	
1977	1.274 \pm 0.267	0.540 \pm 0.086	2005	1.638 \pm 0.420	0.498 \pm 0.079	0.074 \pm 0.015	0.303 \pm 0.113	0.206 \pm 0.059	0.491 \pm 0.127	
1978	0.865 \pm 0.172	0.446 \pm 0.072	2006	1.180 \pm 0.219	0.448 \pm 0.055	0.099 \pm 0.014	0.304 \pm 0.077	0.212 \pm 0.039	0.484 \pm 0.086	
1979	1.388 \pm 0.288	0.439 \pm 0.075	2007	0.686 \pm 0.088	0.473 \pm 0.044	0.038 \pm 0.010	0.402 \pm 0.072	0.300 \pm 0.040	0.298 \pm 0.082	
1980	1.762 \pm 0.311	0.463 \pm 0.072	2008	—	—	0.048 \pm 0.016	0.734 \pm 0.058	0.105 \pm 0.028	0.161 \pm 0.064	
1981	0.536 \pm 0.086	0.262 \pm 0.044	2009	—	—	—	0.539 \pm 0.048	0.074 \pm 0.022	0.387 \pm 0.052	
1982	0.498 \pm 0.095	0.387 \pm 0.073								
Mean values										
1983	0.916 \pm 0.236	0.436 \pm 0.105	1971–1984	1.008 \pm 0.109	0.371 \pm 0.039	0.055 \pm 0.011	0.430 \pm 0.045	0.144 \pm 0.021	0.426 \pm 0.056	
1984	—	—	1999–2009	1.033 \pm 0.093	0.388 \pm 0.033	0.050 \pm 0.007	0.443 \pm 0.045	0.172 \pm 0.024	0.385 \pm 0.051	

Relative contributions of vital rates (γ) correspond to the previous year. For instance, in the year 2001, 40.3% of the population consisted of adults that survived from year 2000, 16.9% were local recruits born in the area in 2000, and 42.8% were immigrants. Annual estimates for relative contributions of vital rates were estimable only for the latter period.

Discussion

The great tit population breeding in the margins of its distribution remained stable in both study periods. Population dynamics were similar despite the different sizes of both the study areas and populations. Large between-year fluctuation in population size was not related to density suggesting a stronger influence of density-independent factors on demographic parameters. Local recruitment and adult survival were low and with relatively little variation. In contrast, immigration rates were high and with more variation, which suggests that immigration plays an important role in local population dynamics.

Survival and recruitment

Adult survival remained similar during the course of the study; 0.371 (initial period) and 0.388 (latter period). Different study area size did not explain survival. Survival probability appears rather low since it exceeded 0.5 only once in 22 yr. Reported survival estimates for great tits are lower from some eastern populations (0.26 Estonia and Russia, Hórak and Lebreton 1998, Payevsky 2006), somewhat better in central core populations of western and southern Europe (UK, Oxford 0.40–0.44, Clobert et al. 1988; the Netherlands, Hoge-Veluwe 0.43, Bauchau and van Noordwijk 1995; the Netherlands, Lauwersmeer 0.413, Tinbergen and Sanz 2004; and mostly higher in southern populations (Spain, Valencia 0.64, Greño et al. 2008) compared with our northern marginal population. We think that our estimate from Oulu reliably quantifies the situation at a distribution margin, with mortality not being inflated by increased permanent emigration of breeders from the study area (Orell 1989). The low average breeding dispersal distance also supports this suggestion. It should be mentioned that in northern Finland, other Parids preferring coniferous and mixed forests occurring within their core breeding range, have higher adult survival rates being 0.59 for the willow tit *P. montanus* (Lampila et al. 2006) and 0.69 for the Siberian tit *P. cinctus* (Orell et al. 1999).

In contrast to adult survival, our low post fledging survival estimates 5.5 and 5.0%, may be partly explainable by dispersal exceeding the study area (Orell 1985), a situation described also by Verhulst et al. (1997) from Wytham Wood. The effect of dispersal on great tit local recruitment rates is apparent when comparing isolated and mainland sites. For example, great tits born on an island population show higher philopatry (return rate 13% Vlieland) than individuals born in mainland populations (7% Hoge Veluwe; Visser and Verboven 1999, 5% Arnhem; Dingemanse et al. 2003). High apparent survival probability (13%) was reported also from orange monocultures, habitat that is also isolated from other suitable habitats (Greño et al. 2008). Local recruitment may be increased also in forest fragments compared to plots inside continuous forests (Matthysen et al. 2001). Our study area resembles the latter, i.e. continuous commercial forests without larger open habitats restraining movements of great tits. In addition to patchiness, dispersal propensities seem to be inversely related to population size and habitat quality (Doncaster et al. 1997, Matthysen et al. 2001). In our case, low breeding densities (Sasvári and Orell 1992)

Table 4. Components of temporal process variation for adult survival, local recruitment and λ with 95% confidence limits. Model averaged estimates obtained from CJS-models within $\Delta QAICc < 4$.

Parameter	Adult survival		Local recruitment		λ	
	1971–1984	1999–2009	1971–1984*	1999–2009	1971–1984	1999–2009
$\hat{\theta}$	0.371	0.388	0.055	0.050	1.008	1.033
SE ($\hat{\theta}$)	(0.313, 0.428)	(0.333, 0.443)	(0.037, 0.080)	(0.039, 0.060)	(0.801, 1.214)	(0.870, 1.196)
n	13	9	–	10	12	8
$\hat{\sigma}_{total}^2$	0.015	0.007	–	0.0003	0.138	0.062
$\hat{\sigma}_{process}^2$	0.011	0.0055	–	0.0003	0.133	0.053
CV ($\hat{\theta}$)	0.286	0.218	–	0.353	0.363	0.241

$\hat{\theta}$ weighted mean with the 95% confidence interval, SE ($\hat{\theta}$) standard error of the mean, n number of annual estimates, $\hat{\sigma}_{total}^2$ total variance, $\hat{\sigma}_{process}^2$ temporal process variance, CV ($\hat{\theta}$) coefficient of temporal process variation estimated as $\hat{\sigma}_{process}^2/\hat{\theta}$. *constant model.

and poor nesting success (Orell and Ojanen 1983, Rytkönen and Orell 2001) may accelerate emigration of local fledglings and thus contribute to the low observed local recruitment rate. Thus, high natal dispersal rates out of low-quality plots leaves a larger number of unoccupied vacancies. This facilitates immigration among habitats with sufficient spatial connectivity.

The role of density dependence was weak. A negative effect was observed only for adult survival during the initial period. In contrast, we expected the population density effect to be strongest for local recruitment. It is possible that other factors working in a density-independent way override the negative effects of crowding. Thus, population limitation through density independent factors appears more important than density-dependent regulation in the focal population.

The majority of young individuals moved very short distances resembling that reported also by Greenwood et al. (1978). However, it is difficult to obtain information on the proportion of dispersal that results to permanent emigration and therefore the extent of (natal) dispersal, making it impossible to judge the implications to apparent survival estimates. The propensity and distribution of the natal dispersal are therefore important determinants of this population parameter. Some juvenile great tits undertake long migrations extending hundreds of kilometres (Bolshakov et al. 1999). In addition, we have recorded the natal dispersal of up to 23 km in the Oulu area (Orell et al. unpubl.). The great tit population in southern Finland has increased in the beginning of the 21st century (Väisänen 2006) and it may be that the southern areas generate immigrants towards the north. This movement asymmetry could reflect variation in habitat and population specific characteristics between marginal habitat and core habitats.

Contributions to λ

With the observed adult survival and local recruitment rates the study population would not be sustainable. Thus, given the stable λ (1.033), immigration seems to have an important role in the dynamics of the present great tit population. This is supported by multi-state modelling that partitions contributions to population growth. Immigration (0.385) had roughly equal contribution with adult survival (0.443). The contribution of local recruitment exceeded that of immigration only in one year. In a willow tit population studied

at the same study area, immigration had a contribution of 0.22 (Lampila et al. 2006). 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 may be slightly smaller than our estimates. Thus, the high contribution of immigrants to the dynamics of the population is in agreement with the postulation that asymmetric migration characterises marginal populations.

Importance of immigration in this population is congruent with genetic data implying intensive gene flow to northern populations (Kvist et al. 2007). It is possible that gene flow is responsible for poor breeding success leading to too large clutch sizes for the northern areas (Rytkönen and Orell 2001, Postma and van Noordwijk 2005). Additionally, despite not been tested, overwintering requiring special behavioural and physiological adaptations, may cause lower survival for immigrants (Postma and van Noordwijk 2005), and thus low adult survival rates in general as was observed in this study. This view of local adaptations is supported by basal metabolic rate differences between northern and southern great tit populations (Broggi et al. 2005).

Relatively low adult survival and local recruitment with high contribution of immigration in λ are signs of continued immigration-system. However, the adult survival estimates reported in core habitats are not very much higher – maybe the balance large-scale dispersal exists in the north, too. In addition, the role of dispersal is not properly known. Probably the northern population system is something between these two scenarios discussed. Further research is needed.

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