LOCAL ADAPTATION TO WINTER CONDITIONS IN A PASSERINE SPREADING NORTH:
A COMMON-GARDEN APPROACH

JULI BROGGI,1,2 ESA HOHTOLA,1,3 MARKKU ORELL,1,4 AND JAN-ÅKE NILSSON5,6
1Department of Biology, University of Oulu, P.O. Box 3000, Fin-90014 Oulu, Finland
2E-mail: juli.broggi@oulu.fi
3E-mail: esa.hohtola@oulu.fi
4E-mail: markku.orell@oulu.fi
5Department of Ecology, Animal Ecology, University of Lund, S-223 62 Lund, Sweden
6E-mail: jan-ake.nilsson@zooekol.lu.se

Abstract.—Sedentary passerine birds living in temperate and boreal regions need a high metabolic capacity for thermogenesis to survive winter conditions. As a consequence of the increased thermogenic capacity, basal energetic demands rise at a time when resources and time to acquire them decrease. In a previous study, great tits (Parus major) from two localities in Fennoscandia with contrasting winter conditions differed in their metabolic response to ambient temperature. To investigate the physiological basis underlying interpopulation differences we performed a common-garden experiment to test whether these differences were genetically based. We found basal metabolic rate to be higher in birds originating from transferred eggs from the southern population compared to the ones from the northern population, contrary to the relationship among birds living in their region of origin. Despite previous evidence suggesting that gene flow prevents local adaptation at the northern range limits of a species expanding northward, we found that great tits differ in their reaction norm to winter conditions according to the population of origin.

Key words.—Basal metabolism, basal metabolic rate, divergence-with-gene-flow model, genotype-by-environment interaction, Parus major, reaction norm, winter acclimatization.

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Winter survival is a key episode in the life history of sedentary passerine birds living in temperate and boreal regions. During this period, energy requirements increase at the same time as resources and time to acquire them decrease. Thus, selection pressure on heat production capacity is probably strong on small birds wintering in temperate regions. Heat in birds is produced by shivering, primarily in the flight muscles. In situations where an increased sustained work rate is needed, this increased energy expenditure is in most cases (e.g. cold endurance [Liknes et al. 2002; Swanson 2005; Broggi et al. 2004; but see Dawson et al. 1983], migratory disposition [Lindström 1997], and breeding [Nilsson 2002]) accompanied by a rise in the resting metabolic rate (MR). The mechanism behind this relation includes the need for an enlarged alimentary tract and other organs for processing more food, which is a physiological adaptation having a high cost in terms of resting MR (Alexander 1999). Because the increased metabolic machinery required for an enhanced heat production capacity probably results in higher maintenance costs (Swanson 1993), we predict that the winter increase in resting MR is an important component of the strategy employed to withstand winter conditions.

Recent evidence suggests that intraspecific variation in resting MR has a strong genetic component (Wikelski et al. 2003; Ksiazek et al. 2004). Nevertheless, resting MR is a plastic character that not only varies among populations, but also at an individual level (Bech et al. 1999; Hörak et al. 2002; Labocha et al. 2004). Thus, variation among individuals may be determined by several factors at the same time. These can be genetic, developmental, or environmental and may also be due to strategic decisions (Dawson et al. 1983; Burness et al. 1998; Swanson and Olmstead 1999; Nilsson 2002; Wikelski et al. 2003).

Species distributions are restricted and change with time and environmental conditions, even in the absence of geographic barriers that physically limit further expansion (Hoffmann and Blows 1994). For example, physiological constraints due to abiotic factors such as temperature are known to be important in delimiting such ranges (Root 1988; Hoffmann and Blows 1994; Parsons 1998). However, some species with wide distribution ranges may experience very different winter conditions. In some cases local adaptations may arise, but phenotypic plasticity is usually assumed to account for most of the adjustments to prevailing local conditions (Ricklefs and Wikelski 2002). Since physiological and behavioral traits are decisive in adapting to new habitats, such traits are likely to be important targets of selection. Thus, identifying the mechanisms underlying physiological and behavioral changes would help our understanding of the reasons for successful colonization events or extinctions (Ricklefs and Wikelski 2002).

The great tit (Parus major L.) is a newcomer in northern Europe, and several lines of evidence suggest that many aspects of its breeding behavior are governed by ‘‘southern rules,’’ and may thus be maladapted to the boreal regions (Koskimies 1989; Rytkönen and Orell 2001). This situation could be maintained by gene flow from southern populations, which would prevent local adaptations to prevailing conditions ( Kvist et al. 1999). Whether this argument applies to winter survival strategies is unknown.

In a previous study, we showed that great tits from Oulu in Finland (northern population) and Lund in Sweden (southern population) differ in their metabolic response to ambient
temperature: birds from the northern population had an overall higher MR for all temperatures tested (Broggi et al. 2004). To investigate the basis underlying interpopulation differences in basal MR, we performed a common-garden experiment to find out whether the differences observed between populations are genetically determined.

MATERIALS AND METHODS

Study Animals and Experimental Set-Up

Thirty great tit eggs from Lund (55°40′N, 13°25′E) were removed from different nests (two eggs per nest) soon after laying and stored at +4°C and then brought to Oulu by plane. Another 30 eggs were gathered from nests in the study area in Oulu (65°N, 25°30′E). Details on the study areas are given elsewhere (Broggi et al. 2004).

Two days after foster mothers in Oulu started to incubate, we replaced the original clutches with foster eggs. Thus, foster mothers incubated homogeneous clutches from either the northern or the southern population. Because great tits lay eggs earlier in Lund than in Oulu, eggs from Lund were fostered to nests where females started incubating early so the storage time in the refrigerator would be similar between the two groups. Consequently, eggs from Lund hatched on average five days earlier than eggs from Oulu. Hatching success and body mass or wing length as measured at six weeks of age did not differ between groups (P > 0.15). After one week, larvae of the fly Calliphora spp. and mealworms Tenebrio molitor were supplied to the parents beside the nests.

Just before fledging, nestboxes with the chicks were moved inside aviaries together with one of the parents. Parents continued to feed the chicks during the first weeks after fledging, and after a few weeks chicks were able to feed for themselves. Fly larvae and mealworms were provided ad libitum as well as fresh water with dissolved commercial vitamin-complex. Ant pupae Formica rufa s.l. and moth caterpillars Orthosia gothica, O. incerta, and Cerastis rubricosa were collected and grown during the summer months and provided once a week. In late summer a food mixture (tuna fish, baked cereals, beans, eggs, carrots, and apples) was included in the diet, together with sunflower seeds, peanuts, and pork fat. The live protein supply was then slowly reduced according to their consumption. Outdoor aviaries were circular cages made of metallic mesh net with a diameter of 4 m and a height of 3 m. Freshly cut spruce, pine, and birch branches were provided regularly and placed inside each aviary.

At six weeks of age, fledglings were individually ringed and measured (mass, wing, and tarsus length) and reallocated to the aviaries, each individual sharing a cage with no more than six other birds from the same origin and separated from their foster parents. Roosting nestboxes and feeders were also installed according to the number of birds per cage. Because some birds escaped from the aviaries, sample size was reduced from the initial 14 individuals from the northern population, 12 from the southern population, and four parents in midsummer to the final 12 northern population birds, eight southern population birds, and four parents at late autumn. Some birds escaped from the aviaries, sample size was reduced from the initial 14 individuals from the northern population, 12 from the southern population, and four parents in midsummer to the final 12 northern population birds, eight southern population birds, and four parents at late autumn. All birds had their basal MR measured within a period of two weeks from late October to early November 2003. The median day length during the period of measurements was 1 h 30 min shorter in Oulu than in Lund: a corresponding day length in Lund was attained 23 days later.

Metabolic Measurements

Basal MR is defined as the average minimum oxygen consumption under postabsorptive digestive conditions during the resting phase of the daily cycle of nongrowing, nonreproductive animals at thermoneutrality (McNab 1997). Thus, basal MR was measured during the night in an open-circuit respirometer. After dusk each bird was placed in an individual, sealed metabolic chamber (1.6 L) in a dark climate cabinet at a constant temperature of 25°C throughout the night (Broggi et al. 2004). The thermoneutral zone for winter aclimatized great tits has previously been shown to range from +15°C to +30°C (J. Broggi, unpubl. data), in line with studies on other small species from different latitudes (Dawson and Carey 1976; Reinertsen and Haftorn 1986). The respirometer consisted of a four-channel set and one oxygen analyzer (S-3A Ametek, AEI Technologies, Naperville, IL) that received air samples through a valve system. Outdoor air was pumped through the metabolic chambers at a rate of 300 ml/min (flow controllers: FMA-A2407, Omega Engineering, Stamford, CT) and then directed to the analyzer. CO₂ and water were removed before and after the chambers by means of silica gel and soda lime scrubbers. The valve system switched in periods of 12 min between channels and outdoor air. Analyzer readings were recorded every minute on a computer, and minimum night averages were determined over three-hour periods between 2300 and 0400 h for every bird. The closest outdoor-air reading was used as reference to control for any possible analyzer drift. Appropriate equations to calculate oxygen consumption were used (Hill 1972). All procedures were conducted in agreement with the local ethical committee.

RESULTS

Foster juveniles originating from the southern and northern populations did not differ with respect to mass, wing, or tarsus length (t-test: P > 0.13 in all cases). However, basal MR differed markedly between these two groups of juveniles (Fig. 1). Location of origin was the only factor significantly related to basal MR (F₁,₁₈ = 15.0; P = 0.001) in a multiple regression equation that included cage, mass at the end of basal MR measurements, tarsus length, and sex. Including the adult foster parents in the analysis also resulted in significantly higher basal MR for juveniles from the southern population compared to the other two categories (Tukey post-hoc test: P = 0.003 in both cases), whereas juveniles from the northern population and foster parents from the northern population did not differ in basal MR (Tukey post-hoc test: P = 0.56; see Fig. 1).

During the same period (autumn 2003), additional great tits were captured in the same study areas in Lund and Oulu. The basal MR of these birds was similar to that found in wild birds measured in the winter–spring of 2001 (Broggi et al. 2004), and thus we could compare their basal MR with that of the foster birds. The basal MR of foster juveniles from the northern population did not differ significantly from basal MR of wild birds (Fig. 2; t₂₇ = 0.89, P = 0.38). However,
foster juveniles from the southern population had a significantly higher basal MR than birds staying in the south population (Fig. 2; $t_{18} = 8.76, P = 0.001$). The results were consistent even when we restricted the wild-caught sample to include only juveniles (t-tests; northern population: $t_{18} = 1.48; P = 0.16$; southern population: $t_{56} = 10.6; P < 0.001$).

**Discussion**

The different metabolic responses to the same conditions of individuals originating from different populations strongly implies a genetic basis for adaptations to varying winter conditions, manifested as differences in basal MR. However, the influence of maternal effects (i.e., differences in yolk composition) cannot be completely ruled out with the present experimental design (Schwabl 1993). Contrary to previous findings suggesting that gene flow from southern populations prevents local adaptations to arise in northern Fennoscandia (Kvist et al. 1999), it appears that great tits are adapted to metabolically react to the local environment. In agreement with the divergence-with-gene-flow model, local adaptations may arise when selective forces are strong enough to override the effect of gene flow (Smith et al. 1997; Blondel et al. 1999).

The differences observed in this common-garden experiment were in the opposite direction to the ones found in a previous study (Broggi et al. 2004), as foster birds from the southern population had a significantly higher basal MR than foster birds from the northern population. Although we did not raise birds from the northern population in Lund, and the actual amount of change in MR was thus not quantified, our results suggest that the reaction norms of the two locally adapted genotypes have different slopes, resulting in a genotype-by-environment interaction. This is in line with adjustments of basal MR in birds to hot environments. Differences in basal MR between populations from different regions could be explained by genetically based differences in the response to the same environmental gradient (Tieleman et al. 2003). Thus, basal MR appears to be a plastic character, because foster birds from the southern population strongly react to changes in the environment. The proximate mechanism triggering such differential response to the environment is open for speculation, with the most likely candidates including cues that vary on a latitudinal basis; for example, temperature (Swanson and Olmstead 1999), photoperiod (Wickelski et al. 2003), or a combination of both. However, increasing the energy budget more than necessary is a risky strategy, especially when food supplies and the time available for foraging are decreasing.

There are several possible mutually nonexclusive explanations for the difference between foster birds from the two populations in their local adaptations to the prevailing environment. Such mechanisms include poorer insulation or lower digestive efficiency in birds from the southern as compared to the northern population, both cases resulting in the need to process more food for the same cold endurance. Finally, birds from the two populations may be investing equally in cold endurance but birds from the northern population may downregulate other functions that would otherwise have resulted in a basal MR at the same level as birds from the southern population. Assuming that a high thermogenic capacity increases basal metabolism (however, for other relationships between energy expenditure and basal MR, see Deerenberg et al. 1998; Nudds and Bryant 2001), the benefits may have to be traded off against costs of an increased overall metabolism (Hammond and Diamond 1997). Functions that could be compromised in order to reduce overall basal MR may include, for example, disease resistance or DNA repair mechanisms. Selection against increased maintenance costs may be especially high at northern latitudes, because such high costs would increase starvation risk in an environment with low food availability (Broggi et al. 2004). Furthermore, very high metabolic rates may incur long-term costs due to excessive oxidative stress (Nilsson 2002; Wiersma et al. 2004) or other physiological costs of a high rate of living.
(Daan et al. 1996). Reduced levels of disease resistance and DNA repair mechanisms as well as increased levels of oxidative stress predict shorter life spans of birds inhabiting harsh winter environments as compared to those living in more benign regions. Thus, the fact that Oulu is close to the northern border of the species distribution underlines the possibility that metabolic constraints may be determining such distribution limits in agreement with Root (1988). However, artificially supplied food may provide some species with the opportunity to expand their energy budget and colonize new areas that otherwise would remain unsuitable.

This study suggests that great tits from different latitudes have different reaction norms for metabolic adjustments to winter conditions. Future research needs to address the extent to which these differences are adaptive and how they arise, thus furthering our understanding of how different populations may react to new environmental conditions including changing climates due to global warming.

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LITERATURE CITED


