

Basal metabolic rate and energetic cost of thermoregulation among migratory and resident blue tits

Anna L. K. Nilsson, Jan-Åke Nilsson and Thomas Alerstam

A. Nilsson (anna.nilsson@bio.uio.no), Centre for Ecological and Evolutionary Synthesis, Dept of Biology, Univ. of Oslo, PO Box 1066, Blindern, NO-0316 Oslo, Norway. – J.-Å. Nilsson and T. Alerstam, Dept of Animal Ecology, Lund Univ., Ecology Building, SE-22362 Lund, Sweden.

Metabolic rates may be informative of adaptations to migration or wintering at high latitudes and may therefore be particularly interesting in partial migrants requiring adaptations to both migration and residency. To study the extent of physiological adaptations in migratory and resident blue tits *Cyanistes caeruleus* during the period of autumn migration in southern Sweden, we measured basal metabolic rate (BMR) and cost of thermoregulation at 0°C (CTR0). In contrast to other migrants en route, migratory blue tits had lower BMR than residents. As migratory blue tits travel extraordinarily slowly on autumn migration and residents suffer from harsher climate and severe competition, residents may need dynamic adjustments that involve larger metabolic costs than migrants. Resident males had lower CTR0 than migrants and resident females. Resident males are socially dominant, which suggests that they have priority of access to food sources during summer and early autumn. They also spend more time on moult, which would give them the time and energy needed for molting into a plumage of higher insulation quality than is possible for migrants and resident females.

The basal metabolic rate (BMR) is defined as the rate of energy expenditure of a post-absorptive animal at rest in a thermoneutral setting when it is not involved in growth or reproduction (McNab 1997) and it has been proposed to increase when there is a need for enhanced aerobic capacity (Bennett and Ruben 1979, Nilsson 2002, Sears et al. 2009). Therefore, inhabiting environments differing in metabolic requirements or adopting different strategies may explain some of the variation in BMR within and between individuals (Broggi et al. 2004, McKechnie 2008).

In temperate, seasonal environments, the non-breeding season is often characterized by a deterioration of environmental conditions, e.g. shorter days, lower temperatures and lack of renewable food sources. One way to deal with this seasonality is to migrate from the breeding grounds to wintering grounds in more benign environments. This movement involves high energy expenditures during flight and high demands on food intake and fuelling prior to flights. Long-endurance flights requiring a high aerobic capacity (Swanson 2011) and physiological changes in organs necessary for the completion of long flights and for efficient foraging during stopovers (Jenni and Jeni-Eiermann 1992, Hume and Biebach 1996, Piersma and Lindström 1997) may both call for an increase in BMR (Piersma et al. 1995, Lindström et al. 1999, Lindström and Rosén 2002).

In contrast to escaping seasonal variation by migrating, many birds remain and winter on their northern breeding grounds. One of the major metabolic adjustments to wintering at high latitudes involves the process of winter acclimatization, which

is considered to be an important adaptation for survival at high latitudes during the non-breeding season (Cooper and Swanson 1994, Cooper 2002, Broggi et al. 2004, Swanson 2011). Winter acclimatization involves an increased BMR leading to enhanced shivering capacity and endurance, resulting in an increased thermogenic capacity and cold resistance (Swanson 1991, Liknes et al. 2002). Adaptations for wintering in cold climates and reduced cost of thermoregulation may include improved thermogenic efficiency of winter acclimatized individuals, improved insulation capacity of the plumage (Middleton 1986, Swanson 1991, Cooper 2002) and facultative hypothermia, i.e. reduced body temperature at night (Grubb and Pravosudov 1994, Nord et al. 2009).

Thus, metabolic adjustments of BMR and the cost of thermoregulation are important indicators of adaptations to migration or wintering at high latitudes. Accordingly, metabolic measurements would be especially informative in partial migrants (populations of animals comprising of both migrants and residents: Chapman et al. 2011), enabling us to compare individuals from the same population that will either migrate or remain on the breeding grounds during the winter. This will also indicate how flexible the physiological adaptations are in a system where individuals might switch migratory strategy between years (Nilsson et al. 2008). Thus, the aim of the study was to compare BMR and the cost of thermoregulation of migratory and resident blue tits *Cyanistes caeruleus*, a common partial migrant in Scandinavia, in order to compare the metabolic adjustments between the two strategies. Metabolic adjustments to autumn

migration should be well developed during the study period whereas adjustments to winter conditions might not yet be fully developed at this time. In line with previous estimates of BMR in obligate migrants, we predict an overall higher BMR in migrant than in resident blue tits. As a consequence of potential physiological and structural adjustments to wintering in cold climates, we also predict the cost of thermoregulation to be lower for residents.

Material and methods

The blue tit *Cyanistes caeruleus* is a partial migrant, with juveniles and females predominating among migrants (Heldbjerg and Karlsson 1997). A varying number of blue tits are observed to pass Falsterbo on autumn migration, numbers decreasing with an increase in beech mast crop and increasing with an increased breeding population density (Nilsson et al. 2006). Blue tits differ from many obligate migrants by proceeding slowly on migration, moving only moderate distances from breeding to wintering grounds (Nilsson et al. 2008).

We measured BMR of juvenile blue tits during 2001–2003 and metabolic rate in conditions below the thermoneutral zone during 2002–2003. We used juveniles only, because both migrants and residents contain large numbers of this age group. In total, 54 migrating and 61 resident blue tits were captured and measured in the study. Birds were mistnetted and their age and sex determined according to Svensson (1992). The category migratory juvenile blue tits were caught at the migratory passage site of Falsterbo (55°23'N, 12°49'E), southwestern Sweden, between 21 September and 23 October each year. At the trapping site at Falsterbo, there were two pairs of local blue tits but they were ringed before the migrants start to arrive (Nilsson et al. 2010). The category resident juvenile blue tits were captured at an inland site close to Lake Krankesjön (55°42'N, 13°28'E) in southern Scania between 19 September and 28 October. Among the 61 residents captured at the inland site, 25 were individuals with a known capture history in the population. Some of the unringed blue tits at this site may be migrating blue tits captured as they passed the area from more northern breeding areas. Based on recapture rates of ringed and unringed individuals prior to and during the migratory period in this population (Nilsson et al. unpubl.), the contribution of potential migrants to the category residents is estimated to be 30%, i.e. 10.8 individuals in our sample. Consequently, we compared the metabolic rates between the group of birds which had been ringed as nestlings or shortly after fledging during the preceding breeding season in the same area, thus birds of a known non-migratory origin, with the group of previously unringed birds captured at the inland site. Neither BMR nor the metabolic cost of thermoregulation at 0°C differed between these two groups of birds ($p > 0.66$ in both cases) and we therefore pooled the data. During the period of capturing blue tits, environmental conditions start to deteriorate at the breeding grounds. Temperatures decrease and in four out of the ten preceding years (1994–2003), minimum temperatures in October were below 0°C for at least one day.

Birds were transported by car to Lund for measurements of energy consumption over night in a respirometer. During

transport and before and between measurements, birds had access to water and ad lib mealworms *Tenebrio* sp. During the first night in captivity, BMR was measured and during the second night the metabolic rate at 0°C. We define the cost of thermoregulation at 0°C (CTR0) as the difference between the energy expenditure at 0°C and BMR. In 2001 when only BMR was measured, birds were kept for one night only. Birds were released in the morning following the last night of measurements at the site of capture. The study was performed under licenses from the Swedish Ethical Committee for Animal Experiments.

The metabolic rate of the blue tits was measured in an open-circuit respirometer. It consisted of dryers (silica gel), pumps, flow controls, and oxygen analyzers, and had four channels enabling us to measure four birds simultaneously (for more details on the respirometer set-up see Nilsson and Råberg 2001). During the evening, each bird was placed separately in airtight respirometer chambers (1.6 l) inside the darkness of a climate cabinet (Hereaus). Air was passed through the respirometer chambers with a flow of 10 l h⁻¹ into the oxygen analyzers and the oxygen levels were compared with reference air taken from outside, the difference being a measure of the bird's oxygen consumption (ml O₂ min⁻¹). Oxygen consumption was recorded on a data logger every minute during the measurement sessions. BMR was measured at 25°C, i.e. within the thermoneutral zone (Gavrilov and Dolnik 1985) whereas the energy consumption in a cold environment was measured at 0°C, mimicking late autumn night temperatures in the area of residency. BMR and metabolic rate at 0°C were measured as the lowest single value of running 10 min averages during the night. Since the average measurement bout was 11 h, this ensured that the value for BMR was taken when the birds were in a post-absorptive state, i.e. at least three h after a meal (Klaassen and Biebach 1994). VO₂ was calculated according to the equation in Klaassen et al. (1997). Oxygen consumption was then converted to metabolic rate by assuming an energetic equivalence of 19.8 kJ per 1 litre O₂.

To describe the winter climate on the inland site and a site approximately 80 km to the southwest of this site, the wintering grounds for the resident and migrating blue tits (Nilsson et al. 2008), respectively, we used the average temperature for the period 1961–1990 for the inland study site (www.smhi.se/klimatdata/meteorologi/temperature) and an area close to Copenhagen, Denmark (www.dmi.dk/dmi/index/danmark/klimanormaler.htm). Average temperatures were for the two sites, respectively, January: -1.0 and +0.1°C, February: -1.0 and -0.1°C and December: +0.8 and +1.8°C. Thus, the site with resident blue tits were on average 1°C colder during the winter months compared with the site where most of the migrants spent the winter.

Statistical analyses

Our aim was to explain the variation in BMR and CTR0 (the dependent variables) by the following factors (independent variables): year, sex, migratory status (migrant or resident) entered as fixed factors and date, mass (after the night in the respirometer) and tarsus length (for the years 2002–2003) entered as covariates. The full model also included all the

interactions between migratory status and the other independent variables. A general linear model (GLM) was used to test if the independent variables could explain a significant part ($p < 0.05$) of the variation in the dependent variable. The full model was reduced by a backward stepwise procedure, starting with the interactions, until only significant factors remained. All averages are presented as means \pm SE. All statistical analyses were performed in SPSS 16.0.

Results

We found no size difference, as measured by tarsus length, between resident (19.3 ± 0.078 mm) and migrant (19.3 ± 0.069 mm) blue tits (t -test: $t_{81} = 0.52$, $p = 0.6$). The migrants were, however, slightly, but significantly heavier (10.9 ± 0.106 g) than the residents (10.6 ± 0.089 g) after the first night of metabolic measurements (t -test: $t_{113} = 2.11$, $p = 0.037$).

Basal metabolic rate

We found the commonly observed positive relationship between BMR and mass (Fig 1). However, a significant part of the variation in BMR could also be explained by year and migratory status (GLM; Year: $F_{2,110} = 19.0$, $p < 0.001$; Mass: $F_{1,110} = 54.8$, $p < 0.001$; Migratory status: $F_{1,110} = 8.43$, $p < 0.004$). This means that, after accounting for the effects of year and mass, residual BMR was significantly ($p < 0.004$) lower for migrants (-0.42 ± 0.18 kJ h⁻¹) than residents (0.37 ± 0.23 kJ h⁻¹). Date, sex, tarsus length and all interactions with migratory status had no significant effect and were removed from the final model.

Cost of thermoregulation

The variation in CTR0 could be explained by year and sex, while the effects of migratory status and the interaction between migratory status and sex were not quite significant (GLM; Year: $F_{1,73} = 13.3$, $p = 0.001$; Sex: $F_{1,73} = 7.94$, $p = 0.006$; Migratory status: $F_{1,73} = 3.28$, $p = 0.074$; Migratory status \times Sex: $F_{1,73} = 3.05$, $p = 0.085$). Males had on average lower CTR0 (14.8 ± 0.5 kJ h⁻¹) than females (15.7 ± 0.3 kJ h⁻¹). Mass, potentially important for thermal conductance and thereby CTR0, did not explain any significant part of the variation in CTR0 ($F_{1,72} = 0.016$, $p = 0.90$). To further investigate the interaction between migratory status and sex, we tested the model for each sex separately. Among females only year could explain any significant variation in CTR0 (GLM; Year: $F_{1,48} = 9.61$, $p = 0.003$). However, among males both year and migratory status had an effect on CTR0 (GLM; Year: $F_{1,25} = 4.48$, $p = 0.044$; Migratory status: $F_{1,25} = 5.06$, $p = 0.034$; Fig 2).

Discussion

Basal metabolic rate

We predicted BMR of migrants to be higher than BMR of residents in the partially migrating blue tit, but found the opposite pattern, indicating that these migrants do not

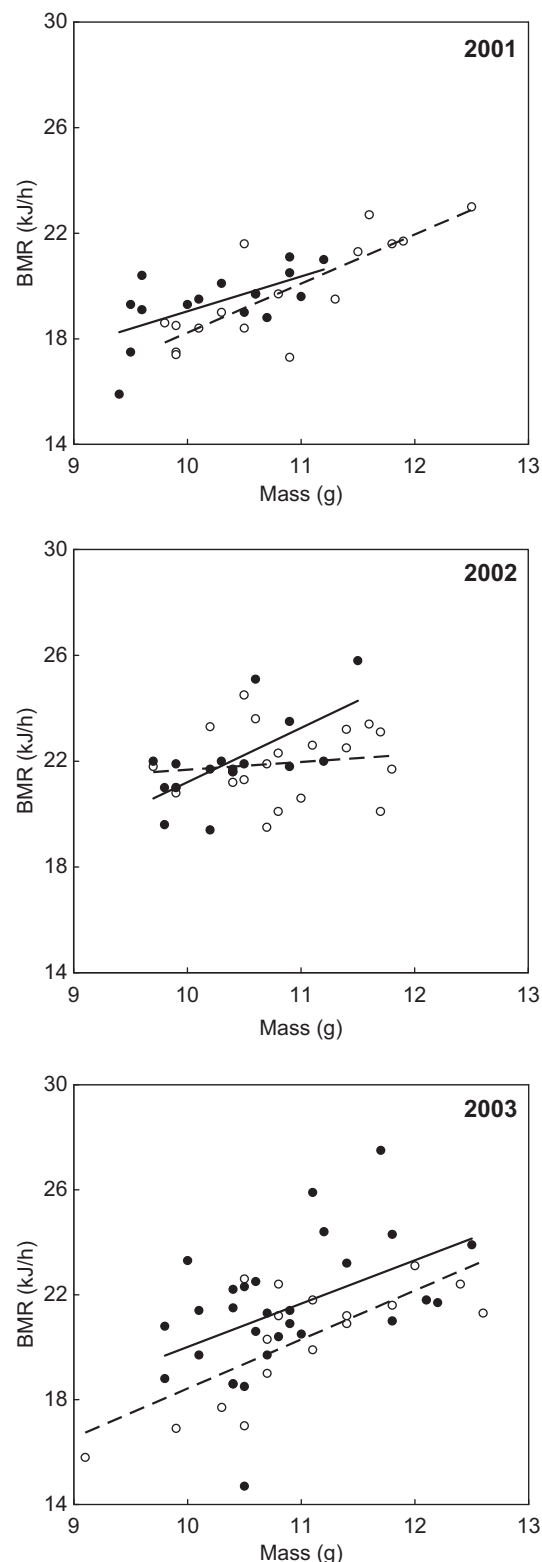


Figure 1. The relation between BMR (kJ h⁻¹) and mass (g) for the years 2001–2003 among resident and migrating blue tits. Closed circles and solid line refer to resident and open circles and broken line refer to migrating blue tits.

adopt specific physiological adaptations for migration as has been reported for obligate migrants (McKechnie 2008, Swanson 2011). Furthermore, in a population of partially migrating great tits in Russia, individuals returning from

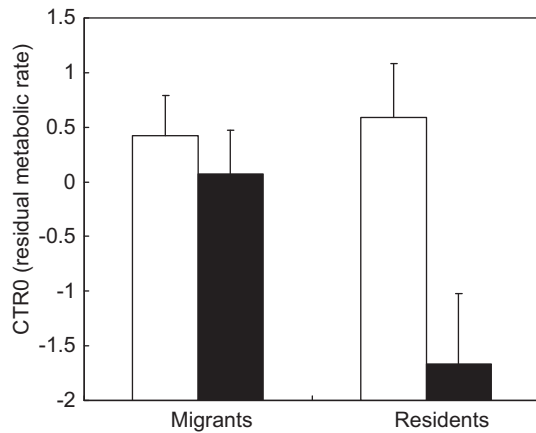


Figure 2. The mean (\pm SE) difference between metabolic rate at 0°C and at thermoneutrality, i.e. CTR0, corrected for year (residual metabolic rate) of migratory and resident blue tits. Open bars represent females and closed bars males. Sample size is for female migrants: $n = 22$; male migrants: $n = 12$; female residents: $n = 28$ and for male residents: $n = 16$.

spring migration had higher BMR than residents (Kerimov and Ivankina 1999). As spring migration usually is more time constrained than autumn migration (Fransson 1995, Kokko 1999), great tits returning to their breeding areas might migrate faster than our blue tits on autumn migration and thereby enhancing their flight and fueling speed with a consequent increase in BMR. Furthermore, measurements of the BMR of returning great tits were taken in April, at a time when BMR of residents had already declined from their wintering values (Kerimov and Ivankina 1999). If spring migration is more time constrained than autumn migration, the absence of increased metabolic rate in blue tits during autumn migration is also concurrent with studies on long-distance migratory passerines in the New World (Swanson 1995, Swanson and Dean 1999). Swanson and Dean (1999) compared the metabolic rate in four neotrophic migrants during spring, summer and autumn and found only spring values to be elevated. Pre-migratory red knots *Calidris canutus*, among other wader species, have been shown to have higher BMR than birds that have reached their wintering grounds (Piersma et al. 1996, Lindström 1997). Especially, the fueling periods in between flight bouts, seem to be associated with increased BMR (Lindström et al. 1999). However, waders and other obligate migrants migrate fast whereas blue tits are among the species with the slowest recorded migration speed (Hildén and Saurola 1982, Nilsson et al. 2008). Thus, as blue tits are very slowly proceeding on their short (median distance 82 km; Nilsson et al. 2008) migratory journey, it might not be necessary to adopt specific physiological adaptations for migration. As they are migrating during day-time, they might forage extensively en route, thereby precluding the need for metabolic adaptations for fast fueling. The difference in mass between migrants and residents were small but significant, indicating that migrants might have stored some fuel for their migratory journey. Alternatively, birds faced by unpredictable food availability are heavier than birds in a predictable setting (Witter et al. 1995). Juvenile migrants like the ones in our study are first-time migrants and the food availability en route is most likely unpredictable, while residents remain in a known area.

Migrating blue tits did not only seem to lack metabolic adjustments in line with that of obligate migrants, they actually had lower BMR than residents. Two, non-mutually exclusive explanations may account for this result. 1) Resident blue tits, remaining on breeding grounds at high latitudes, are on average expected to face harsher winter conditions than migrants. Both between and within species, there is a general latitudinal trend in BMR, where birds spending the winter in northerly areas spend more energy and have higher BMR than birds spending the winter further south (Weathers 1979, Root et al. 1991, Broggi et al. 2004). Metabolic adjustments are considered to be a major component of winter acclimatization (Swanson 2011) explaining this latitudinal variation in BMR. Part of this acclimatization process is initiated in anticipation of harsh winter conditions as BMR increases during autumn to peak at mid-winter irrespective of temperatures (Broggi et al. 2007). It is, however, questionable if the 1°C difference in average winter temperatures between the wintering sites of resident and migrating blue tits is enough to explain the difference in BMR. 2) Alternatively, the high BMR in residents might not primarily be an adaptation to the winter but a consequence of adopting the resident strategy during autumn. This might include increased energy demands for maintaining high social status and territoriality on the breeding grounds (Dhondt 1981). Competition for positions in winter flocks could potentially be more energy demanding, resulting in higher BMR, than the environmental conditions migrants are expected to face during migration. In line with this, territorial great tits were found to have higher BMR than transient ones (Kerimov and Ivankina 1999). Furthermore, residents might be socially dominant over migrants (Smith and Nilsson 1987) and dominant birds have been suggested to have higher BMR than subdominants (Hogstad 1987).

Cost of thermoregulation

We found no overall significant difference in CTR0 between migratory and resident blue tits although residents tended to have lower CTR0 than migrants. Adaptations to wintering conditions, such as improved acclimatization among residents, could thus not unambiguously be detected during autumn. However, the single category with the smallest cost for thermoregulation turned out to be resident males (Fig. 2). This category is also the one containing the most dominant individuals (Smith and Nilsson 1987, Korsten et al. 2007). It is not obvious that the timing or onset of winter acclimatization during autumn should be dominance-dependent. However, dominance based differences in the timing and extent of the partial moult of juveniles after fledging, including the body plumage that is important for insulation (Ginn and Melville 1983), might be important for the conductance of the plumage. Females are subdominant to males (Perrins 1979) and migrants in general are on average hatched later during the breeding season compared to residents (Smith and Nilsson 1987), consequently starting to moult later than earlier born juveniles (Dhondt 1973). Thus, subdominance in resident females and late moult in migrants could potentially lead to a lower plumage quality (cf. Nilsson and Svensson 1996) among these groups of juveniles compared to resident males. Plumage quality affects

the energy expenditure in winter, with a high quality plumage reducing the energetic costs of thermoregulation (Middleton 1986, Swanson 1991, Nilsson and Svensson 1996, Cooper 2002).

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