Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes

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It has been hypothesized that organisms living at different latitudes or in different environments adjust their metabolic activity to the prevailing conditions. However, do differences in energy turnover simply represent a phenotypic adaptation to the local environment, or are they genetically based? To test this, we obtained nestling stonechats (*Saxicola torquata*) from equatorial Kenya (0° N), Ireland (51.5° N), Austria (47.5° N) and Kazakhstan (51.5° N). Birds were hand-raised and kept in Andechs, Germany. We measured their resting metabolic rates (RMR) and locomotor activity at an age of *ca.* 14 months (July) and 20 months (January), when birds went through postnuptial moult (July), and neither moulted nor exhibited enlarged gonads or migratory activity (January). RMR was generally higher during moult, but differed among populations: RMR was lowest in the resident Kenyan birds, higher in mostly sedentary Irish birds, and highest in migratory Austrian and Kazakhstan birds. Thus our data demonstrate that even in birds kept from early life under common-garden conditions, the 'pace of life', as indicated by metabolic turnover, is lower in sedentary tropical than in north-temperate migratory individuals of the same species. Such intrinsically low energy expenditure in sedentary tropical birds may have important implications for slow development, delayed senescence and high longevity in many tropical organisms.

Keywords: resting metabolic rate; tropical birds; life history; pace of life; stonechat

1. INTRODUCTION

Even if organisms have similar sizes and shapes, their metabolic rates may vary manyfold (Kleiber 1961; Gillooly *et al.* 2001). For example, within a species or even a population of animals, there can still be a more than sixfold difference in resting metabolic rate (RMR) (McNab 1986; Mueller & Diamond 2001). This residual variation in RMR could allow significant insights into physiological design features and adaptations of organisms. For example, if an increase in metabolic rate reflects an increase in heart rate, and heart rate is inversely proportional to an animal's lifespan (Blaxter 1989; Prinzinger 1993), then an organism with a lower metabolic rate would have a longer lifespan. Consequently, short-lived species could have increased metabolic rates if they live in productive environments facilitating large investment in reproduction. Mueller & Diamond (2001) recently showed that this could indeed be the case as metabolic rate of *Peromyscus* mice species increases along a habitat gradient that differs 12 times in net primary productivity. However, there are many other environmental factors apart from productivity and predictability that can potentially influence the pace of life, such as predation risk

(Ghalambor & Martin 2001) and food availability (Ricklefs 1991; Martin 1995).

Here we investigate whether populations of the same species that differ strongly in life-history characteristics also show the predicted difference in metabolic rate (Ricklefs *et al.* 1996). We use a passerine bird species as our model system because birds show consistent life-history differences between different climatic zones (Martin 1995). Most temperate zone birds grow faster (Ricklefs 1976, 1980; Klaassen 1994), moult faster (Helm & Gwinner 1999), and produce more eggs per clutch than tropical birds (Klaassen 1995; Martin 1995, 1996), with only minor effects of holding conditions in aviary-kept birds (Gwinner *et al.* 1995). It has been argued that this need to 'live faster' at high latitudes exists because temperate zone birds have to cope with pronounced annual temperature fluctuations and hence have to migrate and/or prepare for unpredictable weather conditions (Calder & King 1974; Dawson *et al.* 1983; Root 1988; Klaassen & Drent 1991; Klaassen 1994; Martin 1996). However, high adult survival in tropical birds may have increased selection on somatic maintenance and precipitated a more leisurely lifestyle (Hamilton 1966; Ricklefs 1991).

We hypothesize that metabolic rate is a major hub in the network of physiological mechanisms underlying life-history traits and that it mediates major life-history trade-offs (Daan *et al.* 1996; Ricklefs *et al.* 1996; Ricklefs &

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Wikelski 2002). Indeed several studies, particularly in birds, have suggested that metabolic rates increase with latitude (Kendeigh 1944; Kendeigh & Blem 1974; Ricklefs 1976; Vleck & Vleck 1979; Weathers 1979; Bryant & Hails 1983; Hails 1983; Klaassen *et al.* 1989; Klaassen & Drent 1991; Klaassen 1995; Weathers 1997). However, latitude was not the only factor affecting metabolic rate in these studies. Weathers (1997) showed that tropical birds from sunny habitats have lower metabolic rates compared with those from forested or shady habitats. A comprehensive phylogenetically controlled study (Bennett & Harvey 1987) did not reveal a significant relation between latitude and metabolic rates, although it suggested a trend in the expected direction (higher RMRs away from the equator). One way to overcome the potential problems inherent in such general cross-species comparisons is to study one species that occurs at a variety of different latitudes (Garland & Adolph 1991, 1994). However, even such a comparison has to consider the possibility that (local) climate affects metabolic rates and heat production through acclimation processes, as documented in annual cycles of birds (Prinzinger 1993; see also Leroi *et al.* 1994; Piersma *et al.* 1995). Hence, it has to be investigated whether birds solely adapt their physiological phenotype to different environmental conditions (Garland & Adolph 1994) or whether populations living at different latitudes are genetically different in their energy metabolism (Blaxter 1989; Klaassen 1995).

To resolve this problem, we conducted a single-species common-garden experiment by raising and keeping birds from four distinct geographical locations under the same dietary, light and temperature conditions. We used the stonechat (*Saxicola torquata*) as an ideal species to investigate whether apparent phenotypic differences are based on genetically determined differences. Stonechats are small (*ca.* 15 g), open-habitat, insectivorous passerines that live at a wide range of latitudes, from northeastern Asia through Europe to southern Africa. When the birds were *ca.* 14 and 20 months old and were in the same stage of their annual cycle (moulting or wintering), we measured their total energy expenditure (EE) as well as their RMR. The results strongly suggest the existence of genetically determined differences in the 'pace of life' in birds from different latitudes and different migratory habits.

2. MATERIAL AND METHODS

We compared four populations of stonechats (figure 1): Kenyan birds (*S. t. axillaris*) are year-round residents (Dittami & Gwinner 1985; Gwinner & Scheuerlein 1999; Scheuerlein *et al.* 2001); Irish birds (*S. t. hibernans*) are partial migrants, i.e. most individuals winter in Ireland although some migrate over a distance of up to 2000 km; Austrian birds (*S. t. rubicola*) regularly migrate over short distances of 1000 to 2000 km; whereas Kazakh birds (*S. t. maura*) are long-distance migrants with winter quarters up to 5000 km away (Cramp 1988; Glutz von Blotzheim & Bauer 1988; Gwinner *et al.* 1995). Clutch size in African birds is about three, while Eurasian birds lay five to six eggs per clutch, the difference being in part genetically determined (Gwinner *et al.* 1995). The duration of post-juvenile moult is shortest in Kazakh and longest in African birds, Irish and Austrian birds again being intermediate (Helm & Gwinner 1999, 2001; B. Helm and E. Gwinner, unpublished data).

Nestlings of the four populations (figure 1) were either collected from their native habitat during the spring of 1999 and brought to Andechs, Germany, within two weeks, or were bred in Andechs in aviaries. All individuals of the African and Irish populations were collected in the field, whereas for Austrian and Kazakh birds, 16% and 50%, respectively, were collected in the field. All birds were hand-raised according to identical procedures (Gwinner *et al.* 1995). After fledging they were kept in individual cages under a constant temperature of 20–23 °C and daylength conditions simulating those experienced by Austrian birds in the wild (Gwinner & Scheuerlein 1999). Birds were housed in several rooms and randomly distributed with regard to origin. At an age of *ca.* 14 months, in July 2000, and again at an age of *ca.* 20 months, in January 2001, we measured the metabolic rate of 47 and 33 of these birds during their second-year summer and winter period, respectively. All birds moulted in summer (July); whereas in winter, birds neither moulted nor showed migratory activity and their gonads were regressed (Gwinner & Scheuerlein 1999).

(a) *Respirometry measurements*

Birds were held in individual cages throughout the experiment. Each morning, a random set of seven new birds was transported in cloth bags from their living cages to a climate-controlled chamber, where all measurements took place under simulated natural daylength conditions. Metabolic rate was measured continuously from 11.00 to 09.00 of the following day, using 36 l metabolic chambers, at 26 ± 2 °C, within the thermoneutral zone of all stonechat subspecies. To ensure all birds were indeed tested within their thermoneutral zone we conducted metabolic measurements under varying ambient temperatures. We determined the lower end of the thermoneutral zone of seven stonechats from the four populations by slowly decreasing ambient temperature in a climate controlled chamber while simultaneously measuring metabolic rate.

During metabolic measurements, birds had free access to food and water, which they used during the day, but never at night. Oxygen consumption and carbon dioxide production were recorded in a push-through respirometry system (Withers 1977) in humid ($70 \pm 5\%$) air using Sable System (Nevada, USA) equipment. External air was pumped into a temperature controlled climate chamber where it passed through a humidity controller (DG-1, Sable System). Air flow was then channelled via a needle valve through either a thermal mass flow controller (Model 840; Sierra Instruments, Amsterdam, The Netherlands) into an air multiplexer (TR-RM8; Sable Systems), or directly pushed into the multiplexer. The multiplexer directed metered air to a single chamber only, while simultaneously allowing for the flushing of air through the six remaining chambers and the baseline chamber. The flow rate of this flush air was adjusted via a bubble meter to represent the flow of the metered air within $\pm 10\%$. Flow rate was adjusted to 900 ml min^{-1} as we used fairly large metabolic chambers (36 l) to allow for the continuous measurement of EE throughout one day. The flow rate we used is a low flow rate relative to chamber volume and washout time would be more than 40 min. However, instantaneous correction, or Z-transformation, did not significantly change the outcome of the calculations. Furthermore, because we used the average of the lowest 4 min of oxygen consumption (see below) as RMR (Wikelski *et al.* 1999), our measurements are not confounded by short-term changes in metabolic activity (Martin *et al.* 2003). Upon exiting the measured chamber, metered air was dehumidified using a Peltier-Effect Condenser (PC-1; Sable Systems).

Figure 1. Distribution map (shaded areas) and sites of origin (circles) of stonechats used in this study. Arrows connect breeding grounds with approximate wintering areas. The dashed arrow for the Irish birds indicates that only some birds migrate to the Mediterranean areas whereas others spend the winter in Ireland. Kenyan birds are year-round residents. Inset: left, pair of Kazakhstan stonechats (*Saxicola torquata maura*); right, pair of central African stonechats (*S. t. axillaris*); females behind males in both pairs.

Thereafter, a subsample of that air was taken at 75 ml min^{-1} , using a subsampler mass flow meter unit (TR-SS1 and TR-FC1; Sable Systems), from within a 10 ml syringe barrel to determine fractional carbon dioxide concentration with a carbon dioxide analyser (CA-1B; Sable Systems). The remaining air then flowed through water scrubbers (drierite) into an oxygen analyser (FC-1B; Sable Systems). Ultra-low permeability Tygon tubing, with a diameter of 0.32 mm, was used in all trials. Relative humidity was continuously surveyed to the nearest 3% using an electronic humidity meter (Radio Shack, 2100, USA) both in the baseline chamber and in one measurement chamber.

We measured each chamber for 10 min, then flushed the respirometry system for 3 min to remove latent gases, and continued measurements with the next chamber. We recorded from seven birds and one empty baseline chamber, gathering a total of 12 recordings (each lasting 10 min) per bird per day. Activity recordings of birds in the metabolic chambers and/or the home cages showed that individuals were not active during the times RMR was measured (see also below). Stonechats do not eat at night (E. Gwinner, personal observation) and showed their lowest nocturnal metabolic rates in the hours before dawn (ca. 03.00–04.00), i.e. 8–10 h after their last food consumption. The apparent daily EE under laboratory conditions was calculated as the cumulative EE per bird corrected for the duration of individual measurements. Birds had no visual contact with each other during trials. After measurements, birds were weighed to the nearest 0.1 g and returned to their holding cages.

During all metabolic measurements in winter, but not in summer, we also recorded locomotor (hopping) activity of the birds using infrared light beams mounted outside the metabolic chambers. No locomotor activity was detected during the nocturnal measurements. Owing to intermittent equipment failure, our sample size for activity measurements was reduced for the Kenyan and the Irish birds as indicated in figure 2c.

(b) Data analysis

Group data are presented as means $\pm$ s.e.m. Statistical comparisons were made using general linear models (GLM) of covariance. Significant differences in group means were determined by Scheffé's *post hoc* tests. We conducted statistical calculations on whole-animal RMR and used body mass as a covariate to account for size differences among populations. However, we present mass-corrected oxygen consumption values in figure 2a.

3. RESULTS

Birds of the four populations showed significant differences in body masses: the sedentary African and partly sedentary Irish birds were heaviest, whereas the short-distance migrating Austrian and long-distance migrating Kazakhstan birds showed successively lower body masses (figure 2b; $F_{7,80} = 8.2$, $p < 0.001$; for location of population $p < 0.001$, for season $p = 0.05$).

(a) Thermoneutral zone

The average temperature inflection point at which the RMR of fasted, inactive birds (often called 'basal metabolic rate') started to increase was $22 \pm 1^\circ\text{C}$ ($n = 7$). None of the birds had an inflection point above 24°C . Thus we suggest that our metabolic measurements were conducted well within the thermoneutral zone (at 25°C) and reflect true baseline metabolic expenditures.

(b) Potentially confounding variables on resting metabolic rate: sex, sibship and rearing conditions

Next we tested whether factors other than 'location of population origin' could affect our measurements. We did

Figure 2. (a) RMR; (b) body mass; (c) activity rates (hopping per 21 h) of stonechats from four populations held in Germany under common-garden laboratory conditions (natural simulated photoperiod for Austrian birds, temperature 20–23 °C). Birds were measured during wintering condition (January 2001, shaded bars) and summer/moult condition (July 2000, open bars). Data show group means $\pm$ s.e.m. Letters below columns show statistical differences (determined by Scheffe's *post hoc* test; same letters: no significant difference; different letters: significant difference between groups, $p < 0.05$).

not detect an effect of sibship, sex or rearing conditions when all three parameters were entered as fixed factors into a GLM predicting RMR values. However, we found a strong effect of population origin and season (winter versus summer; GLM $F_{12,80} = 4.8$, $p < 0.001$; between-subjects effects for: population $p = 0.02$, season $p < 0.001$, sex $p = 0.41$, sibship $p = 0.29$, rearing conditions $p = 0.83$; all p -levels for interactions > 0.05). Thus we treated individuals as independent units for statistical analysis.

(c) *Resting metabolic rate comparisons*

To determine whether RMR reflected the overall EE of birds from different locations, we correlated (nocturnal) RMR with the EE during the light phase of the circadian cycle (excluding the dark phase), for the birds measured during the summer. We selected these times because otherwise we would have correlated RMR against a measure that includes RMR (the 24 h apparent daily EE). We are aware that our energy measure during the day still

includes diurnal RMR, but it is not yet clear in birds how maintenance costs and diurnal RMR are related (Ricklefs *et al.* 1996). In any case, the results were qualitatively similar when we used one or the other comparison. RMRs were linearly related to total daytime EE (measured during the light hours only; we used body mass as a covariate; $\text{RMR} = -21.3(\pm 18.6) + 0.56 \pm 0.04 \cdot \text{EE} + 1.66 \pm 1.3 \cdot \text{mass}$; $r^2 = 0.78$, $p < 0.001$).

We then compared RMRs among populations separately for each season to determine whether location of the population predicted the EEs of individuals. We used a GLM of covariance with population as fixed factor and body mass as covariate. Summer RMRs were significantly different among populations, whereas body mass had no significant influence ($F_{3,47} = 2.9$, $p = 0.03$; location of population $p = 0.02$, mass $p = 0.07$). During winter, RMRs also differed significantly among populations and again there was no significant effect of mass ($F_{3,33} = 2.7$, $p = 0.04$; location of population $p = 0.01$, mass $p = 0.21$). For both analyses, specific differences between the four populations as determined by *post hoc* tests are indicated by letters in figure 2a. In both seasons, African birds had the lowest RMRs, followed by Irish (winter) or Austrian birds (summer/moult), whereas Kazakhstan birds had the highest RMRs, respectively. In summer, Irish and Austrian birds had indistinguishable RMRs whereas in winter, Austrian and Kazakhstan birds had similar RMRs.

The birds' locomotor activity as quantified during the 21 h of metabolic measurements in winter differed between groups, but was not influenced by the birds' body mass (figure 2c; GLM, body mass as covariate, $F_{4,28} = 3.0$, $p = 0.03$; location of population $p = 0.04$; body mass $p = 0.47$). *Post hoc* analysis showed that the sedentary tropical birds from Kenya were least active, followed by Austrian and Irish birds. Birds from Kazakhstan showed the highest activity rates, corresponding to their high RMRs compared with the three other populations. The two temperate-zone populations (Irish and Austrian birds) did not differ from each other in their locomotor activity.

4. DISCUSSION

Our results demonstrate that metabolic rates among populations of the same species of bird differ according to latitude and/or migratory disposition. Overall, RMR was lower in resident Kenyan birds than in the predominantly resident birds from Ireland, and the RMRs of both these stationary populations were lower than those for migratory birds from Austria and Kazakhstan. In fact, long-distance migrating Kazakhstan birds had mass-specific RMRs that were about twice to four times as high as expected for a passerine bird of their size. The measurements were done during two seasons. In January, a 'quiescent' time of the year, birds of none of the subspecies moulted, had growing or enlarged gonads or exhibited nocturnal migratory restlessness. In July, when all birds moulted, they still differed in RMR as described above for January, even though absolute RMR values were higher during moult than during winter. Hence, the low RMR of the African birds compared with that of the other subspecies is compelling evidence of their intrinsically slow pace of life. It is currently unclear what factors contribute to a slow pace of life in tropical and/or sedentary birds. We consider it

unlikely that differences in the corticosterone stress response due to restraint during metabolic measurements are causally involved in RMR differences, as corticosterone secretion did not affect minimum RMR in other experiments (Buttemer *et al.* 1991; Wikelski *et al.* 1999). Nevertheless, we are investigating whether the stress response of birds with different life histories affects the metabolic response (Ricklefs & Wikelski 2002).

As it is necessary for a common-garden set-up, our birds were either collected as nestlings on their respective breeding grounds and transferred within two weeks to common-garden conditions in Germany, or they were bred in such conditions. We did not detect any effect of rearing condition and thus consider it likely that the observed differences in RMR have a strong genetic basis. Our results are in agreement with the results of Klaassen (1995) who studied annual energetics and moult rates in African and European stonechats. However, Klaassen kept birds of the two populations under different photoperiods: African stonechats under a constant equatorial and European stonechats under a changing temperate-zone photoperiod. Hence, it remained unclear from these data whether differences in RMR between the two populations were due to differences in photoperiod (Pohl 1977) or to photoperiod-independent intrinsic differences.

Latitudinal trends in RMR have already been found within other bird species (e.g. Bryant & Furness 1995). Hudson & Kimzey (1966) and Blem (1977) documented latitudinal trends in RMR in house sparrows (*Passer domesticus*) within the continental USA. However, as in Klaassen's (1995) experiment it could not be excluded that birds collected as adults at different latitudes had permanently adjusted their phenotype to the local conditions, e.g. during ontogeny (Schwabl 1993). Thus, differences in metabolic rates found in the above studies could have simply been due to phenotypic modulation rather than genetic (evolutionary) change (Kendeigh 1944; Kendeigh & Blem 1974).

Why did latitudinal trends in metabolic rates evolve? We suggest that migration does not require higher metabolic rates because it is relatively cheap energetically, compared with, for example, chick feeding or thermoregulation (Wikelski *et al.* 2003). We further suggest that year-round territoriality *per se* is not related to differences in metabolic rates. Instead, we hypothesize that temperature fluctuations in different habitats are most likely responsible for metabolic differences among populations (Root 1988). In Kazakhstan, birds can encounter below-freezing temperatures during the breeding season, whereas in the moderate climate of Ireland, temperature fluctuations are not excessive.

It is, so far, unclear whether selection acts on RMR directly, or on factors that are phenotypically related to RMR (Wikelski & Ricklefs 2001). Let us assume that natural selection acts to produce the lowest RMR under the conditions the birds are operating. Then selection may simultaneously act on other factors, such as physiological adjustments for specific environmental temperatures or the aerobic capacity for migration, that are phenotypically related to RMR. However, a narrow metabolic performance breadth in RMR may best match local environmental conditions (Huey 1991; Gilchrist 1995). Thus an RMR that is adapted to a local habitat may be directly selected

by stabilizing selection. One should keep in mind, however, that local habitats for migratory birds change seasonally, thus adjustments of RMR to local habitat could follow such seasonal trends. In any case, we hypothesize that the phenotypically adjustable trait 'metabolic rate' is related to selection processes (Schluter *et al.* 1991) generating diversification of life histories. The prediction that longevity and, hence, senescence may also be directly affected by rates of energy turnover remains an important research challenge for the future (Garland & Adolph 1991; Kirkwood 1977).

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