Repeatability and individual correlates of basal metabolic rate and total evaporative water loss in birds: A case study in European stonechats

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ARTICLE INFO

ABSTRACT

Basal metabolic rate (BMR) and total evaporative water loss (TEWL) are thought to have evolved in conjunction with life history traits and are often assumed to be characteristic features of an animal. Physiological traits can show large intraindividual variation at short and long timescales, yet natural selection can only act on a trait if it is a characteristic feature of an individual. The repeatability of a trait, a measure of the portion of variance that is caused by differences among individuals, indicates if it is a characteristic feature of an individual. We measured repeatability of BMR and TEWL of 18 captive European stonechats (Saxicola torquata rubicola) within the winter season. Repeatability was 0.56 for BMR and 0.60 for mass-specific BMR. Age and body mass had a significant effect on variation in BMR. Also after accounting for this variation, BMR remained repeatable. TEWL and mass-specific TEWL showed nonsignificant repeatabilities of 0.11 and 0.12, respectively. We conclude that BMR is a characteristic feature of an individual in our population of European stonechats, whereas TEWL is not. We discuss our results in the context of a review of currently available estimates of repeatability of BMR and TEWL for birds.

1. Introduction

Levels of energy expenditure and water loss in birds vary with environment (Klaassen, 1995; Wikelski et al., 2003; Tieleman et al., 2003a), season (Weathers and Sullivan, 1993; Webster and Weathers, 2000) and workload (Wiersma et al., 2005). These physiological traits are thought to have evolved in conjunction with life history or fitness characteristics such as clutch size and survival, that are known to be heritable (Gibbs, 1988; Godfray et al., 1991). Several studies suggest that the variation in energy expenditure and water loss among species and populations has a genetic basis as well (Klaassen, 1995; Williams, 1996; Wikelski et al., 2003; Tieleman et al., 2003a). However, knowledge of the basis for physiological variation among individuals within populations of wild birds is scant, despite an increasing interest in relating individual physiological characteristics to performance and fitness (Burness et al., 2001; Verhulst et al., 2006). Physiological traits can show large phenotypic flexibility within individuals at short (days or weeks) and long (months or years) timescales (Piersma et al., 1996; McKechnie et al., 2007). Yet, selection of traits can only have evolutionary consequences if the traits are characteristic features of an individual that, in addition, display interindividual variation within the population.

A common measure for the extent to which a trait is a characteristic feature of an individual is repeatability. It expresses which proportion of the overall phenotypic variation, the sum of inter- and intraindividual variation, is caused by interindividual variation (Lessells and Boag, 1987). Interindividual phenotypic variation can be partitioned into environmental variation, arising from external circumstances that affect the animal permanently, and genetic variation (Falconer and McKay, 1996). Therefore repeatability normally sets an upper limit to heritability (Boake, 1989; Falconer and Mackay, 1996; Dohm, 2002). Inter- and intraindividual variation may vary between populations, because of environmental and/or genetic differences. Hence repeatability and heritability are population measures.

Basal metabolic rate (BMR) and total evaporative water loss (TEWL) are widely used as measures of energy expenditure and water loss in inter- or intraspecific studies of birds in different environments or at different times of the year. BMR is defined as the minimum energy expenditure of a postabsorptive animal measured during the rest phase and at thermoneutral temperatures (King, 1974). It is related to overall daily energy expenditure in the field (Nagy, 1987; Daan et al., 1990), activity (Deerenberg et al., 1998; Nudds and Bryant, 2001), food availability and diet (Mueller and Diamond, 2001; McNab, 2003), and is at least partly explained by organ sizes and body composition (Daan et al., 1990; Piersma et al., 1996; Tieleman et al., 2003b). Comparative studies of water balance use total evaporative water loss (TEWL), the sum of cutaneous and respiratory water loss, as

yardstick (Dawson, 1982; Williams, 1996; Tieleman et al., 2003a). The water balance may be subject to similar selective pressures as energy expenditure, especially in birds experiencing high ambient temperatures or scarcity of drinking water, e.g. in deserts or during migration.

Studies of repeatability of BMR (Bech et al., 1999; Horak et al., 2002; Tieleman et al., 2003b; Rønning et al., 2005; Vézina and Williams, 2005) and especially TEWL (Tieleman et al., 2003b) in birds are scarce. A recent meta-analysis of repeatability of metabolism included 6 estimates for avian BMR (Nespolo and Franco, 2007). The study concluded that repeatability of metabolism could be generalized across taxa and no further studies were needed, but failed to consider conflicting data among bird studies. Nespolo and Franco (2007) did not include two species reported by Tieleman et al. (2003b) that showed no repeatability in BMR, nor a study by Vézina and Williams (2005). Furthermore, repeatability is a population measure and presence and magnitude can differ among populations. Compiling all available estimates of repeatability for BMR of birds, we found that values ranged from 0.00 to 0.87 and 22% of the repeatabilities were non-significant. Compiling all available estimates of repeatability for TEWL of birds, we found that values ranged from 0.00 to 0.73 and 60% of the repeatabilities were non-significant. (Table 1). This variation in repeatability among species and populations indicates that there are considerable differences in the extent to which BMR and TEWL are characteristic features of an individual, and hence for the possibility of natural selection to act on these traits.

We studied repeatability and individual variation of BMR and TEWL in captive European stonechats (*Saxicola torquata rubicola*) during the winter season. Because repeatability depends on inter-individual variation as well as intraindividual variation, we explored factors that potentially influence these components: age, sex, hatching location and body mass of birds. We focused on variation in BMR and TEWL within a single season to determine whether these traits are characteristic features of a given individual at a given time of the year. This knowledge is crucial when interpreting the possible evolutionary mechanisms underlying physiological differences among environments and seasons.

2. Materials and methods

2.1. Birds

Stonechats (*Saxicola torquata rubicola, Muscicapidae*), small passerines with a wide geographic distribution (latitudinal range 71° N to 35° S) (Urquhart, 2002), are ideal organisms to study evolutionary questions related to seasonality and environment (Gwinner and Scheuerlein, 1999; Helm and Gwinner, 1999). We measured BMR and TEWL of 18 stonechats from a central European population. Twelve individuals were first ($n=6$), second ($n = 2$) or third ($n = 4$) generation birds bred at the Max Planck Institute for Ornithology, Andechs, Germany, and six were taken as nestlings from the field, moved to the institute and hand-raised (Gwinner et al., 1987). Their ages were 1 ($n = 7$), 2 ($n = 6$), 3 ($n = 1$), 4 ($n = 3$), and 5 ($n = 1$) years. Individuals were kept in separate cages, in rooms with controlled temperature (20–22 °C) and under wintering day length (40° N 11° E), and had access to ad libitum food.

Free living European stonechats normally migrate in March and October and spend the winter in the Mediterranean. We measured our captive individuals two ($n = 14$) or three ($n = 4$) times during the winter period, between 7 December 2005 and 13 February 2006. Average time between measurements equaled 24.7 days (range 12–41 days). Winter is a quiescent period for stonechats (Helm et al., 2005): none of the birds were molting, migrating, or breeding. Stonechats are nocturnal migrants, and show nighttime activity during the migratory periods even when kept in captivity. To verify that we really measured birds in the quiescent period we recorded nighttime activity with a passive infrared sensor.

2.2. Laboratory setup and measurements

At least one hour before we started the experiments we removed water and food, to let birds empty their digestive tract. We moved birds into 13.5 l metal metabolic chambers with Plexiglas lids that could be closed air-tight, sitting inside a climatic chamber with a constant temperature of 35 °C±0.5 °C, within the thermoneutral zone of European stonechats (Tieleman, 2007). In the metabolic chambers a mesh wire platform was placed over a layer of paraffin oil, thus excluding water evaporating from feces from the measurements.

We used standard flow-through respirometry methods to measure O_2-consumption and H_2O-production of stonechats (Gessaman, 1987). Compressed air from a tank was pumped through the system, causing a positive pressure in the metabolic chambers. Air passed through silica gel-soda lime-silica gel filters to remove water and CO_2 and subsequently through calibrated mass-flow controllers (model 5850E, Brooks, Hatfield, PA, USA) set at 500 mL/min. Before experiments started we led a stream of air that by-passed the metabolic chambers through a dewpoint hygrometer (model M4-DP, General Eastern, Fairfield, CT, USA), to measure dewpoint of the dry incoming air. Subsequently the air was led through the metabolic chambers.

The outgoing air passed through the dewpoint hygrometer to measure its water content. Subsequently CO_2 and H_2O were removed using silica gel–ascarite–silica gel filters and the O_2-content of the air was measured with an oxygen analyzer (Oxzilla, Sable Systems, Las Vegas, NV, USA). A reference stream of dry air without CO_2, which by-passed the metabolic chambers, was immediately led to the oxygen analyzer. We recorded atmospheric pressure, air temperature inside

Table 1
Literature overview of repeatability (r) and interindividual coefficients of variation (CV) of whole-organism, mass-adjusted (mcBMR) and mass-specific (msBMR) values of BMR and whole organism and mass-specific TEWL (msTEWL) of birds

		n	R	P	Measure	CV	Reference
BMR	Stonechat	18	0.56	0.002	BMR	7.7	This study
	Stonechat	18	0.60	<0.001	msBMR	8.4	This study
	Zebra finch	18–20	0.41–0.52	<0.001	mcBMR	4.5–6.3	Rønning et al., 2005
	Zebra finch	19–37	0.29–0.63	<0.001	mcBMR	6.6–13.5	Vézina and Williams, 2005
	Kittiwake	8–19	0.35–0.52	0.01–0.03	mcBMR	11.4–14.4	Bech et al., 1999
	Greenfinch	28	0.65–0.87	<0.01	msBMR		Horak et al., 2002
	Skylark	14	−0.17	0.79	BMR	18.2*	Tieleman et al., 2003b
	Woodlark	14	0.17	0.29	BMR	23.0*	Tieleman et al., 2003b
	Spike-heeled lark	20	0.66	0.001	BMR	16.7*	Tieleman et al., 2003b
	Dunn's lark	16	0.48	0.03	BMR	9.0*	Tieleman et al., 2003b
	Hoopoe lark	14	0.57	0.02	BMR	8.0*	Tieleman et al., 2003b
TEWL	Stonechats	18	0.11	0.53	TEWL	9.6	This study
	Stonechats	18	0.12	0.51	msTEWL	10.8	This study
	Skylark	14	0.73	<0.001	TEWL	26.8*	Tieleman et al., 2003b
	Woodlark	14	0.22	0.09	TEWL	28.0*	Tieleman et al., 2003b
	Spike-heeld lark	10	−0.04	0.56	TEWL	19.1*	Tieleman et al., 2003b
	Dunn's lark	16	0.50	0.03	TEWL	33.9*	Tieleman et al., 2003b
	Hoopoe lark	14	−0.10	0.64	TEWL	19.7*	Tieleman et al., 2003b

*Coefficients of variation are based on mass-adjusted values of BMR and TEWL. Mass-adjusted values were calculated as the residual of the regression of BMR on body mass. Two values for repeatability represent multiple measurements for repeatability. Some studies distinguish between sex, others report repeatability measurements on short and long time scales. All measurements were done on non-breeding individuals except Bech et al. (1999).

each metabolic chamber, temperature of the hygrometer, dewpoint, and difference in O_2-content between sample and reference air streams with a data logger (model CR23X, Campbell Scientific, Logan, UT, USA).

All BMR and TEWL measurements were done during night. We only used measurements obtained at least three hours after birds were put in the metabolic chambers, and only when O_2-consumption and dewpoint had been stable for at least ten minutes. To calculate BMR from O_2-consumption we used Eq. (2) from Hill (1972) using a conversion factor of 20.1 kJ/mL O_2 (Schmidt-Nielsen, 1997). TEWL was calculated following Tieleman et al. (2002). We weighed birds immediately before and after the metabolic measurements and used the average of these two measurements for further analysis.

2.3. Statistical analysis and repeatability calculation

We performed multilevel random effects analyses in MLwiN 2.02, with 2 levels: level 2 was individual and level 1 was measurement. We also included fixed effects to consider effects of age, sex, hatching location (wild or captive) and body mass. Because we had no a priori expectation to find a linear relation between age and BMR or TEWL, we treated age in years as discrete variable. We first calculated the repeatability based on a model without fixed effects. We then calculated the repeatability based on a model that included all fixed effects. Backward elimination of non-significant fixed effects ($P > 0.05$) was used as model selection criterion. We used the likelihood-ratio test and χ^2-statistic to evaluate statistical significance.

Stonechats varied in body mass between individuals, but also between measurements on the same individual. Understanding the effects of body mass on variation in BMR and TEWL among and within individuals requires also partitioning the variation in body mass itself into inter- and intraindividual components. Hence, we first explored the inter- and intraindividual variation in body mass and calculated the repeatability of body mass per se. We then investigated how inter- and intraindividual variation in body mass affected BMR and TEWL differently by partitioning body mass in average body mass of individuals (M[av]) and deviation from average body mass of individuals on the day of measurement (M[dev]) (Van de Pol and Verhulst, 2006). Because natural selection may also act on mass-specific BMR and TEWL (Speakman, 2005; Tieleman et al., 2006), we also calculated mass-specific values by dividing BMR and TEWL by body mass.

Repeatability was calculated with the equation repeatability = (interindividual variance)/(intraindividual variance + interindividual variance) (Lessells and Boag, 1987). We obtained the inter- and intraindividual variances from the multilevel models. Standard errors were calculated following Becker (1984). To be able to compare variation in BMR with variation in TEWL, and with variation reported in the literature we calculated interindividual and intraindividual coefficients of variation (CV) as CV = (standard deviation)/mean. Interindividual CV was obtained by first calculating average values per individual and then calculating standard deviation and mean of these individual averages. Intraindividual CV was obtained by calculating the average of individual CV's, which were obtained by taking standard deviations and means per individual. We compared the interindividual CV's of BMR and TEWL following Zar (1996) and the intraindividual CV's with a Wilcoxon test (SPSS 14). We repeated all statistical calculations using log-transformed values for BMR, TEWL and body mass. Because this did not improve the fit of the regression line through BMR and body mass ($r^2 = 0.16$ vs. $r^2 = 0.18$) and TEWL and body mass ($r^2 = 0.07$ vs. $r^2 = 0.05$), we do not report the results.

3. Results

3.1. Body mass

Repeatability of body mass of stonechats was 0.23 ± 0.21, and not significant ($\chi^2_1 = 1.136$, $P = 0.29$). The CV's at the inter- and intraindivi-

dual level equaled 7.9 and 6.4, respectively. This indicates that both inter- and intraindividual variation in body mass need to be considered when evaluating variation in BMR and TEWL.

3.2. Basal metabolic rate

Whole-organism BMR had a significant repeatability of 0.56, indicating that intraindividual variation was relatively small compared with interindividual variation (Table 1; Fig. 1A). Inter- and intraindividual CV's were 7.7 and 4.8, respectively.

We explored factors that potentially influenced variation in BMR at the interindividual (age, sex, hatching location, M[av]) and intraindividual (M[dev]) level, and taking into account the significant factors recalculated the repeatability of whole-organism BMR. Of the factors potentially contributing to interindividual variation in whole-organism BMR, age and M[av] had a significant effect (Fig. 2) while sex and hatching location did not have a significant effect (Fig. 3; Table 2A). At the intraindividual level, M[dev] had a significant effect on variation in BMR (Fig. 3; Table 2A). In the final model, with age, M[av] and M[dev], repeatability of BMR was 0.47 ± 0.17 ($\chi^2_1 = 6.057$, $P = 0.013$).

Mass-specific BMR (i.e. BMR divided by body mass) had a significant repeatability of 0.60 (Table 1). Interindividual variation was significantly affected by age ($\chi^2_4 = 12.696$, $P = 0.013$) but not by sex ($\chi^2_1 = 0.304$, $P = 0.58$) and hatching location ($\chi^2_1 = 0.784$, $P = 0.38$). When the factor age was included in the model mass-specific BMR had a repeatability of 0.33 ± 0.19 ($\chi^2_1 = 2.676$, $P = 0.11$).
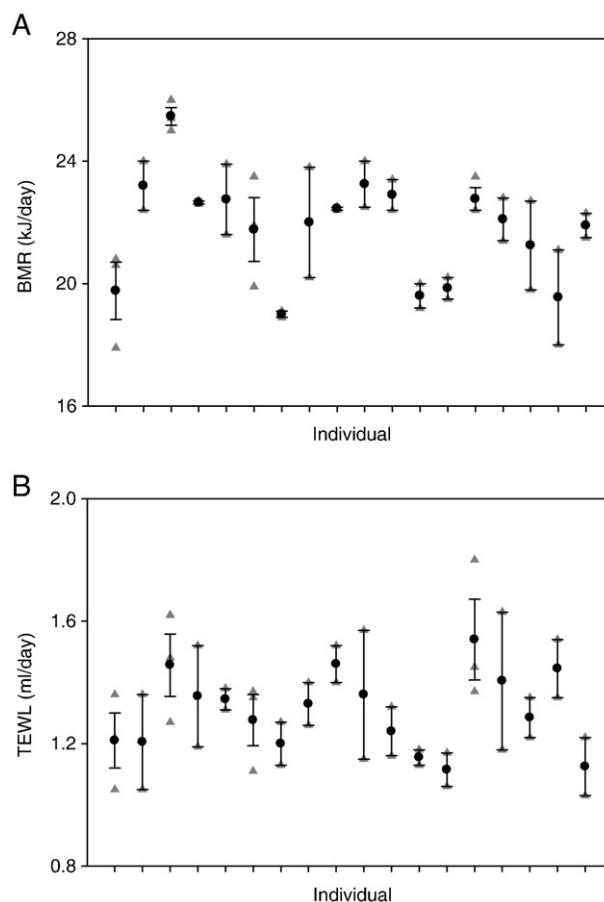
Fig. 1. Variation in measurements of (A.) whole-organism BMR and (B.) whole-organism TEWL per individual. Symbols with error bars represent means ± S.E.M. Grey symbols depict separate measurements on the same individual. Individuals are listed in random order.
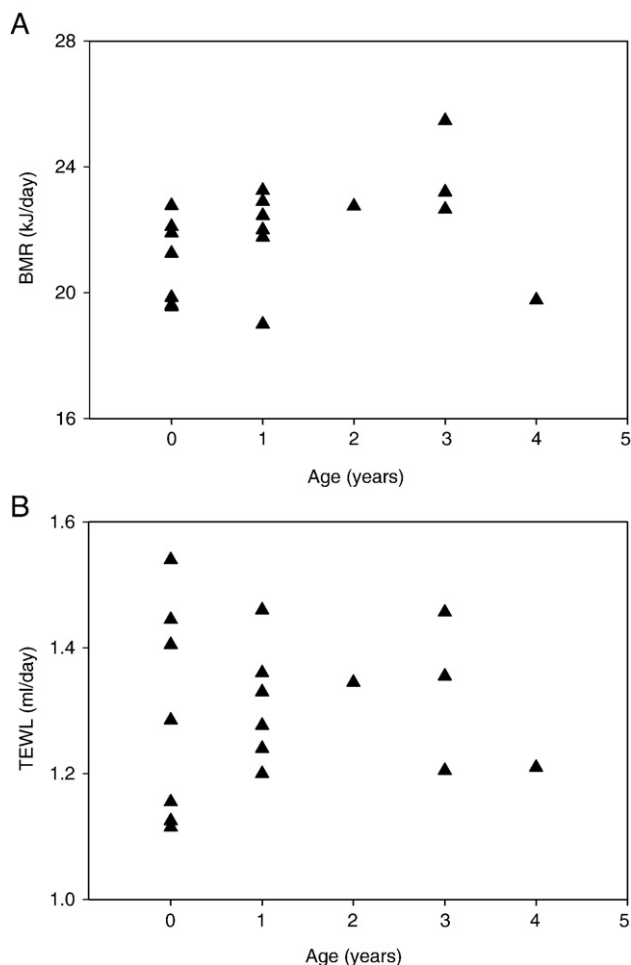
Fig. 2. (A) BMR and (B) TEWL in relation to age. Triangles represent average BMR and average TEWL of individuals.

3.3. Total evaporative water loss

Repeatability of whole-organism TEWL was 0.11±0. 21, indicating that intraindividual variation is relatively large compared with interindividual variation (Table 1; Fig. 1B). Inter- and intraindividual CV's were 9.6 and 11.3 respectively.

None of the factors age, sex, hatching location and body mass, which could affect interindividual variation in TEWL, and hence repeatability, had a significant effect on the model (Table 2B; Fig. 3). M[dev], which could influence intraindividual variation and therefore repeatability, also had no significant effect on the model (Table 2B; Fig. 3).

We divided TEWL by body mass to calculate mass-specific TEWL. Age, sex and hatching location remained nonsignificant factors (age: $\chi^2_4 = 5.510$, $P = 0.24$, sex: $\chi^2_1 = 0.460, P = 0.50$, hatching location: $\chi^2_1 = 2.310$, $P = 0.13$), and repeatability of mass-specific TEWL was 0.12±0. 21 (Table 1).

3.4. Difference in repeatability between BMR and TEWL

To explore why repeatability estimates for BMR differed from those for TEWL, we compared the interindividual and intraindividual variance components between BMR and TEWL. The interindividual CV of BMR did not differ significantly from the interindividual CV of TEWL (CV of BMR=7.7, CV of TEWL=9.6, $Z=0.662$, $P = 0.53$). However, the intraindividual CV of BMR was significantly lower than the intraindividual CV of TEWL (CV of BMR=4.8, CV of TEWL=11.3, $Z=-3.027$, $P = 0.002$). Hence, the low repeatability for TEWL was attributable to a relatively high

intraindividual variation and not to a relatively low interindividual variation, compared with BMR.

4. Discussion

In stonechats, BMR was a repeatable trait and a characteristic feature of an individual that correlated with body mass and age, but not with hatching location and sex. In contrast, TEWL was poorly repeatable, and did not covary with body mass, age, hatching location or sex. Body mass itself was poorly repeatable in this stonechat population as well, indicating that it varied more within than among individuals. In the following section, we will compare our results with findings from other studies, reflect on possible underlying mechanisms, and discuss repercussions for the evolutionary potential of these physiological traits.

Our estimates of repeatability for BMR in stonechats fall within the range previously reported for birds, and result in a total of 8 out of 10 populations in which BMR is repeatable (Table 1). The interindividual coefficient of variation (CV) in stonechat BMR was intermediary when compared with other bird populations. Surprisingly, the two populations for which the repeatability of BMR was non-significant also had the highest interindividual CV. This means that in these two populations not only the variation among individuals but also the variation within individuals was large. Repeatability of TEWL was also within the range of reported values, resulting in 2 out of 6 avian populations in which TEWL is repeatable. In stonechats, intraindividual CV of TEWL exceeded that of BMR. High intraindividual variation of TEWL was responsible for low estimates of repeatability. Repeatability is calculated as a ratio to intra-individual variation (see above). Hence, if intraindividual variation of a measure is generally high, the power for detecting individual consistency is low, unless interindividual variation is very high as in some species of larks shown in Table 1. In stonechats, the interindividual CV of TEWL was the lowest reported so far, and the study has consequently low power for concluding that TEWL is inconsistent within individuals. Body mass showed low and non-significant repeatability. In captive European stonechats, with access to ad libitum food, body mass is a highly dynamic trait (personal observation), and our individuals increased and decreased considerably in weight during the time of the experiment.

The interindividual variation in BMR was to a considerable part explained by age, whereas TEWL was not significantly affected by this factor (Fig. 2). Older stonechats had a higher BMR. This result is in
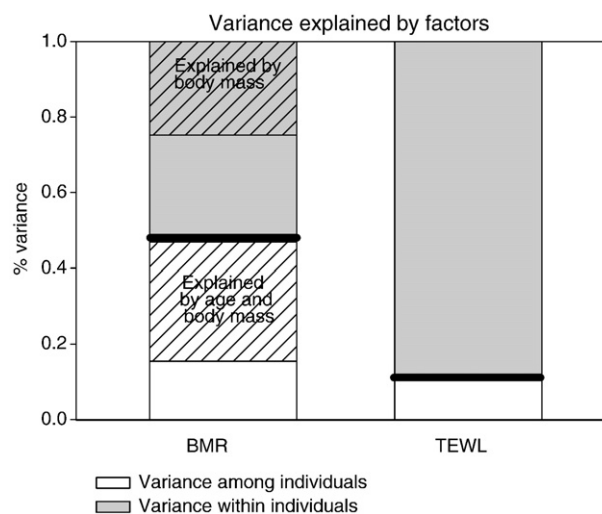

Fig. 3. Partitioned variances of BMR and TEWL and the factors that significantly explained part of the variances. White is the variance among individuals, grey is the variance within individuals. 39% of the within-individual variance and 14% of the among-individual variance was explained by body mass, and 50% of the among-individual variance of BMR was explained by age.

Table 2
Values of χ^2, degrees of freedom (*df*) and *P*-values for factors which possibly explained variation in (A) BMR and (B) TEWL

Variable	χ^2	df	P
A			
Average body mass	4.557	1	0.03
Deviation from average body mass	14.105	1	<0.001
Hatching location	0.803	1	0.37
Age	12.764	4	0.01
Sex	0.300	1	0.58
B			
Average body mass	0.512	1	0.47
Deviation from average body mass	0.073	1	0.79
Hatching location	0.878	1	0.35
Age	4.094	4	0.39
Sex	2.342	1	0.17

χ^2-Values are based on a model including all significant factors.

contrast with the only three other studies that investigated the association between age and BMR in birds, two of which found no association between BMR and age (Blackmer et al., 2005; Moe et al., 2007) and one found a decrease with age (Broggi et al., 2007). In mammals, the direction of the association between age and metabolism also varies among studies (Harper, 1998; Even et al., 2001; Speakman et al., 2002; Speakman et al., 2004). Associations between age and metabolism in these studies are attributed to factors such as age-related changes in body composition, to a change in activity or to selective early death of individuals with different metabolic rates, but are incompletely understood. It is possible that in our population age-related selective death occurs in birds with low metabolic rate.

Body mass did not correlate with TEWL at the inter- or intraindividual level in our stonechat population; yet, it did correlate with BMR. The variation in body mass and BMR within individuals may be attributable to changes in body composition, and especially in the size of organs with relatively high levels of metabolism, such as kidney and liver (Kersten and Piersma 1987; Daan et al., 1990; Piersma et al., 1996). However, without biochemical studies, we cannot exclude (additional) changes at the tissue level, such as mitochondrial density and function, to explain variation in BMR.

For natural selection to act on a trait it has to be variable among individuals, be a characteristic feature of an individual, and have a genetic background (Falconer and Mackay, 1996). At least the first two of these criteria are met for BMR in most avian populations studied, including the stonechats of this study, and for TEWL in a third of the avian populations studied, excluding the stonechats (Table 1). The next step in understanding the potential for selection in these physiological traits in birds is studying heritability, which so far has been done in mammals (Hayes et al., 1998; Johnson and Speakman, 2000; Nespolo et al., 2003; Ksiazek et al., 2004) and only one bird species (Rønning et al., 2007). Assuming that the mammalian results of a genetic basis for BMR can be extrapolated to birds in general (see also Rønning et al., 2005), we can conclude that an evolutionary interpretation of the mechanisms underlying variation in BMR, for example among seasons and populations, is appropriate. TEWL is as yet a less studied trait in birds and more repeatability studies in different populations and over different time spans will be useful to gain better evolutionary understanding of this trait.

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