Energy requirements of moult in three migratory songbird species

Franz Bairlein

Abstract

Moult is considered energetically costly. However, rather few studies address the subject in details so that a comprehensive understanding of moult costs is still lacking. This paper reports resting metabolic rates of Garden Warblers *Sylvia borin*, Blackcaps *Sylvia atricapilla* and Northern Wheatears *Oenanthe oenanthe* prior to and during moult. In all three species, metabolic rates were significantly higher in moulting birds. However, the relationships between metabolic rates and moult intensity varied between the species. While metabolic rates didn't differ between non-moulting and weak to moderate moulting birds in the Wheatears and the Blackcaps, respectively, Garden Warblers showed significantly increased metabolic rates already at weak moult. This may reflect differences in moult and migration strategies.

Key words: Blackcap, Garden Warbler, Northern Wheatear, resting metabolic rate, moult intensity

Zusammenfassung

Energetische Kosten der Mauser bei drei ziehenden Singvogelarten. – Mausern gilt als energetisch aufwändig. Allerdings haben sich nur recht wenige Arbeiten detailliert damit beschäftigt, so dass wir von einem umfassenden Verständnis der energetischen Kosten der Mauser noch weit entfernt sind. In dieser Arbeit wird über Messungen des nächtlichen Ruhestoffwechsels von Gartengrasmücken *Sylvia borin*, Mönchsgrasmücken *Sylvia atricapilla* und Steinschmätzern *Oenanthe oenanthe* vor und in Mauser berichtet. Bei allen drei Arten waren die Stoffwechselraten während der Mauser höher als bei nicht-mausernden Vögeln. Allerdings unterschieden sich die Arten in der

Art und Weise des Zusammenhangs zwischen Stoffwechselrate und Mauserintensität. Während sich die Stoffwechselraten nicht- oder schwach- bis moderat-mausernder Steinschmätzer und Mönchsgrasmücken nicht unterschieden, waren diese bei den Gartengrasmücken schon bei geringer Mauserintensität signifikant erhöht. Diese Unterschiede dürften durch die unterschiedlichen Mauser- und Zugstrategien bedingt sein.

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Introduction

Birds regularly renew their plumage, which is associated with extra energy requirements (JENNI & WINKLER 1994). These costs involve energy required for the production of feathers as well as increased thermoregulatory costs owing to the decrease of insulation during moult. In a review of energetics of avian moult KING (1980) found increased energy requirements during moult across a range of species, mostly passerines, of 9 % to 35 % above the pre-moult levels. Similar increments are reported for, e.g. Macaroni Eudytes chrysolophus and Rockhopper E. chrysocome Penguins (17 % and 12 %, respectively; BROWN 1985), Eurasian Teal Anas crecca and European Shoveler Anas clypeata (25 % and 35 %, respectively; GUOZHEN & HONGFA 1986), Long-eared Owl Asio otus (10%; WIJNANDTS 1984), European Kestrel Falco tinnunculus (29% in males and 42 % in females; DIETZ et al. 1992) or European and African Stonechats Saxicola torquata torquata, S. t. axillaris (17 % and 16 %, respectively; KLAASSEN 1995). However, much higher increases are reported as well: European Starling Sturnus vulgaris 60 % (Cyr et al. 2008), Barnacle Goose Branta leucopsis 80 % (PORTUGAL et al. 2007), Redpoll Carduelis flammea 106 % (LINDSTRÖM et al. (1993), Bluethroat Luscinia svecica 111 % (LINDSTRÖM et al. 1993). Differences in moult costs between species could be related to seasonal timing, extent, degree, duration and rate of moult (JENNI & WINKLER 1994, KLAASSEN 1995), dietary and nutritional requirements (MURPHY & KING 1984, 1992), physiological trade-offs (JENNI-EIERMANN & JENNI 1991, 1996, MERILÄ 1997, HEMBORG et al. 2001, MORENO ET AL. 2001, SANZ et al. 2004, CYR et al. 2008, MORENO-RUEDA 2010), latitude (LINDSTRÖM et al. 1993), or ambient temperature (DOLNIK & GAVRILOV 1979). Moreover, LINDSTRÖM et al. (1993) found a negative relationship between costs of moult and body mass as well as a positive one between costs of moult and mass-specific basal metabolic rate (see also KLAASSEN 1995). So far, however, too few studies exist to elaborate a conclusive understanding of the inter-specific variation of the energetic costs of moult (JENNI & WINKLER 1994).

The aim of this study is, therefore, to report results on the energetic costs of moult of three other songbird species we measured in the framework of studies on the nutritional and physiological requirements of migratory fuelling (BAIRLEIN 2002). Metabolic costs

of moult in Garden Warbler *Sylvia borin*, Blackcap *Sylvia atricapilla* and Northern Wheatear *Oenanthe oenanthe* were addressed by estimating postprandial nocturnal resting metabolic rate through measuring of oxygen consumption of birds prior to and during moult.

Material and Methods

Study species

We measured the energetic costs of moulting in Garden Warblers, Blackcaps and Northern Wheatears. The warblers were taken under license as nestlings from nests in the wild, transported to the Institute of Avian Research in Wilhelmshaven, Germany, and hand-raised. The wheatears were bred in aviaries at the Institute originating from a parental stock which was previously taken under license from the wild in Norway and hand-raised as well. At an age of approximately 60 days, all birds were kept in single cages at constant photoperiod (LD 12:12), constant room temperature (c. 20±1 °C) and constant ad libitum semi-synthetic food (BAIRLEIN 1986). Body mass was recorded five times a week in the warblers and two to three times a week in the wheatears, just after the light went on in the morning. Feather moult was recorded once a week following BERTHOLD et al. (1970). In brief, for assessing the extent of body feather moult the whole body plumage and the wing coverts were divided into 27 feather tracts, and the number of sections with moulting feathers was counted. The extent of moult was then scored into four classes: 0: no moult, 1: 1-9 sections with moulting feathers, 2: 10-18 sections with moulting feathers and 3: more than 18 sections moulting. Similarly, flight feather (primaries, secondaries, tertials) moult was scored: 0: no moult, 1: 1-6, 2: 7-12, 3: more than 12 moulting feathers. The warblers were measured during their summer moult from July to September, while the wheatears were measured from February to March during their partial winter moult. Consequently, the wheatears moulted body plumage only, while the warblers were moulting both plumage and flight feathers simultaneously. To asses the total intensity of moult in the warblers, plumage feather and flight feather scores were added for each bird, resulting in scores from 0 (no moult) to 6 (maximum moult of plumage and flight feathers). In total, we measured 7 Garden Warblers, 13 Blackcaps, and 45 wheatears. The data of the warblers were obtained as part of the PhD thesis work of LEHMANN (1999) but re-calculated here.

Measurements of RMR

Metabolic cost of moult was measured as nocturnal resting metabolic rate (RMR) at 20°C for an entire night using open circuit respirometry. Birds were put into 4 l cuvettes through which a constant flow of air of 40.0±2.0 l/h passed. The flow-speed was measured through a floating-bodies-fluxometer (DK 38 DT, Krohne, Duisburg, Germany). The air coming out of the cuvette was dried through a 3 μ molecular sieve (Merck, Darmstadt, Germany), and the CO₂-concentration after drying was measured

with an infrared CO_2 -analyser (URAS 10E, Hartmann and Braun, Frankfurt, Germany). The oxygen concentration was measured with a paramagnetic O_2 -analysator (MAGNOS 6G, Hartmann and Braun, Frankfurt, Germany). Before and after every nightly measurement, the analyzers were calibrated with two gas mixtures of known concentration (mixture 1: 20% O_2 , 2% CO_2 ; mixture 2.: 99.99% N_2). One empty cuvette, through which outside air flowed, was measured as a reference, in order to calculate the differences in O_2 concentration, i.e. the O_2 consumption. Every night the control cuvette and 5 cuvettes each with one bird were measured, alternately in a cycle of 150 seconds each, for a total duration of 12 h (a complete night). At the end of one night, every cuvette had been measured 44 times.

A DIA/DIAGO-system (Gesellschaft für Strukturanalyse, Aachen, Germany) recorded flow-speed, CO_2 and O_2 -concentration, and created a dataset for every cuvette (including the reference). The program allowed the export of all data in ASCII-form for further analysis. The oxygen consumption was calculated for every 150s-interval using the formula:

 $VO_2[l/h] = (flow*(O_{2in}-O_{2out})-VCO_2*O_{2in})/(1-O_{2in})$ where O_{2in} equals the proportion of O_2 in the air flowing into the cuvette, O_{2out} equals the proportion of O_2 in the air flowing out of the cuvette, VCO_2 equals the rate of CO_2 -production [l/h], and VO_2 the rate of O_2 -consumption [l/h]. SCHEIFFARTH & BAIRLEIN (1998) give a more precise description of the experimental setting.

The energy expenditure was derived from VO₂ by the relationship $11 O_2 = 20$ KJ. All energy data presented here are in KJ/h. Since VO₂ fluctuates during the night (SCHEIFFARTH & BAIRLEIN 1998), mostly due to initial activity of the birds, we did not include the measurements of the first hour and calculated RMR (in one night) as the average value of the lowest 20% percentile of energy expenditure for the remaining night (from the 44 measurements made over the whole night).

<u>Data analysis</u>

Variation in nocturnal resting metabolic rate (RMR) could be related to body mass, age and sex (MAGGINI & BAIRLEIN 2013). As only first year birds were used in the experiment, age was not considered in further analyses, nor was sex in the Garden Warblers as they were not sexed. For the Garden Warblers a possible relationship between metabolic rate and body mass was tested using Spearman Rank Correlation. In the blackcap and wheatear, a GLM was performed using whole-organism RMR as the response variable, and body mass and sex as fixed factors. In the warblers, the same individual birds were measured at least twice, once prior to moulting and during moult. Differences between stages were tested using t-test for paired samples or repeated-measures ANOVA, respectively. In the wheatears, two groups simultaneously differing in their extent of moult were compared. Here, we used oneway-ANOVA to test for differences in metabolic rate. Relationships between RMR and the intensity of moult were tested by repeated-measures ANOVA in the warblers, and oneway ANOVA with a posteriori LSD in the wheatears. Differences between species in the pattern of moult intensity related variation of RMR were tested using a GLM with species and moult as fixed factors. All statistical analyses were performed using IBM SPSS Statistics 20.0 (IBM Corp.). Results are considered significant with p < 0.05.



Fig. 1. Box-plots of nocturnal resting metabolic rates in *Sylvia atricapilla*, *S. borin*, and *Oenanthe oenanthe* prior to (white boxes) and during moult (grey boxes). Numbers below the boxes show sample sizes.

Abb. 1. Nächtlicher Ruhestoffwechsel von Sylvia atricapilla, S. borin, und Oenanthe oenanthe vor (weiße Box-Plots) und während der Mauser (graue Box-Plots). Die Zahlen geben die Stichprobengrößen an.

Tab. 1: Mean values (\pm s.d.) and statistics of nocturnal resting metabolic rates (RMR) in *Sylvia atricapilla*, *S. borin*, and *Oenanthe oenanthe* prior to and during moult.

Tab. 1: Mittelwerte (± Standardabweichung) und Statistik des nächtlichen Ruhestoffwechsels (RMR) von *Sylvia atricapilla, S. borin*, und *Oenanthe oenanthe* vor und während der Mauser.

Species	sample size	RMR _{no-moult}	RMR _{moult}	t-value/F-value	p-value	increment (%)
S. atricapilla	13	1.02 ± 0.10	$\begin{array}{c} 1.19 \pm 0.20 \\ 1.37 \pm 0.09 \\ 2.68 \pm 0.76 \end{array}$	2.887	0.014	17
S. borin	7	1.14 ± 0.05		5.548	0.001	20
O. oenanthe	25,20	2.27 ± 0.59		4.149	0.048	18



Fig. 2. Nocturnal resting metabolic rates in *Oenanthe oenanthe* in relation to moult intensity (for details see Methods). Letters above the boxes indicate statistical differences (with at least p<0.05), numbers below the boxes show sample sizes.

Abb. 2. Nächtlicher Ruhestoffwechsel von *Oenanthe oenanthe* in Abhängigkeit der Mauserintensität (Näheres s. Methoden). Die Buchstaben oberhalb der Kästen geben die statistischen Unterschiede an (mit mind. p<0,05), statistisch nicht verschiedene sind mit dem selben Buchstaben bezeichnet; die Zahlen darunter geben die Stichprobengröße an.





Abb. 3. Nächtlicher Ruhestoffwechsels von *Sylvia atricapilla* in Abhängigkeit der Mauserintensität (Näheres s. Methoden). Die Buchstaben oberhalb der Kästen geben die statistischen Unterschiede an (mit mind. p<0,05), die Zahlen darunter die Stichprobengrößen. Für die Mauserintensität 1 gibt es keine Messwerte.

Results

In all species, neither pre-moult nor moulting nocturnal resting metabolic rates were significantly related to body mass, nor sex in Blackcaps and Northern Wheatears, respectively. Consequently, we used whole-bird nocturnal RMR in all further analyses. In all three species nocturnal RMR during moult was significantly elevated as compared to non-moulting birds (Fig. 1, Table 1). Moreover, in all three species, RMR varied with the extent of moult but the pattern differed between species. In the wheatears, only birds in heavy body plumage moult differed from non-moulting or weak to moderate moulting birds, respectively (Fig. 2; ANOVA, F=7.646, p=0.001; LSD: 0-group vs1/2-group: non-significant; 1/2-group vs 3-group: p=0.003; 0-group vs 3-group: p=0.001).

In the warblers, RMR differed significantly over the moult scores as well (Fig. 3 and 4; repeated-measures ANOVA: *S. atricapilla*: F=15.970, n=32, p<0.001; *S. borin*: F=7.555, n=22, p=0.001). RMR didn't differ between the two warbler species (GLM, F=0.100, p=0.754) but with a significant species*moult interaction term (F=3.431, p=0.016) meaning that the pattern of RMR variation across moult scores is different in the two species. The apparent difference in RMR at high moult intensities (scores 4 and more) between Blackcaps and Garden Warblers as revealed in Figures 3 and 4, is marginally significant (t_{10} =1,921; p=0.084).



Fig. 4. Nocturnal resting metabolic rates in *Sylvia borin* in relation to moult intensity (for details see Methods). Letters above the boxes indicate statistical differences (with at least p<0.05), numbers below the boxes show sample sizes. No record at moult score 1.

Abb. 4. Nächtlicher Ruhestoffwechsel von *Sylvia borin* in Abhängigkeit der Mauserintensität (Näheres s. Methoden). Die Buchstaben oberhalb der Kästen geben die statistischen Unterschiede an (mit mind. p<0,05), die Zahlen darunter die Stichprobengrößen. Für die Mauserintensität 1 gibt es keine Messwerte.

Discussion

During a complete moult in passerines about 20-30% of total lean body mass is replaced (JENNI & WINKLER 1994). This replacement includes several physiological and metabolic adaptations, could impair thermoregulation through poor insulation, and thus requires extra energy of about 3% to 20% of the daily energy expenditure of non-moulting birds, depending on the intensity of moult (JENNI & WINKLER 1994, and references therein).

As in most other studies (see above) all three species studied revealed a significant increase in nocturnal resting metabolism during moult as compared to non-moulting. The relative increments ranged between 17 % in S. atricapilla and 20 % in S. borin (Tab. 1) which is similar to many other songbirds (KING 1980, KLAASSEN 1995) but considerably lower than reported for Bluethroat and Redpoll, respectively (LINDSTRÖM et al. 1993). However, in all three species nocturnal RMR varied with the intensity of moult as well. In the wheatears, where we measured plumage feather moult only, RMR was similar across low and moderate moult intensity and similar to non-moulting birds as well, while only birds in heavy plumage moult revealed a significantly increased metabolic rate. Thus, low to moderate plumage moult did not entail extra energetic costs, likely because these plumage moult intensities do not impair thermoregulation nor demand extra nutritional or physiological requirements, at least when measured at an ambient temperature of 20°C which is within their thermoneutral zone (MAGGINI & BAIRLEIN 2013). Also in Blackcaps at 20°C, which is within their thermoneutral zone as well (Bairlein, unpublished), birds in low moulting scores did not show a significant increase in resting metabolic rate. In Garden Warblers, however, even moderate moult entails extra basal metabolic costs though these birds were also measured within their thermoneutral zone (Bairlein, unpublished). Likely, Garden Warblers invest more energy into moult already at low intensities to speed up moult. As shown by BERTHOLD et al. (1970) rate of moult is faster and duration of moult is shorter in Garden Warblers than in Blackcaps, although feather growth itself did not differ between the two species. Increased metabolic costs at low moult intensities might compromise Garden Warblers more in scheduling their moult in relation to migration than this is the case in Blackcaps or Northern Wheatears. Usually, moult is separated in time from other energy demanding processes such as migration or breeding (e.g. HAHN et al. 1992, JENNI & WINKLER 1994, HOLMGREN & HEDENSTRÖM 1995, HEMBORG & LUNDBERG 1998, HALL & TULLBERG 2004, ECHEVERRY-GALVIS & HAU 2013). However, there was an apparent, though only marginally significant, lower metabolic rate at high moult intensities in Garden Warblers than in Blackcaps, while both species did not differ at no-moult. This may hint on that total energy expenditure for the entire moult is lower in Garden Warblers than in Blackcaps.

All in all, the obtained results support previous results of increased basal metabolic costs during moult. Nevertheless, they add to a better understanding of the energetic costs of moult, in particular, as only very few studies determined metabolic rates in

relation to moult intensity under controlled conditions. They also shed light on the likely different investments and costs of moult in species with different life histories, e.g. long- vs short-distance migrants, summer vs winter moult, or partial vs complete moult, respectively.

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