Reduced body mass gain in small passerines during migratory stopover under simulated heat wave conditions

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Abstract

For birds that migrate long distances, maximizing the rate of refueling at stopovers is advantageous, but ambient conditions may adversely influence this vital process. We simulated a 3-day migratory stopover for garden warblers (Sylvia borin) and compared body temperatures (Tb) and rates of refueling under conditions of a heat wave (Ta = 40 °C by day, and 15 °C at night) with those under more moderate conditions (Ta = 27 °C by day, and 15 °C at night). We measured Tb with implanted thermo-sensitive radio transmitters. Birds had significantly lower rates of body mass gain on the first day of stopover (repeated measures mixed model ANOVA, p = 0.002) affecting body mass during the entire stopover (p = 0.034) and higher maximum Tb during the day when exposed to high Ta than when exposed to moderate Ta (p = 0.002). In addition, the birds exposed to high Tb by day had significantly lower minimum Tb at night than those exposed to moderate daytime Tb (p = 0.048), even though Tb at night was the same for both groups. We interpret this lower nighttime Tb to be a means of saving energy to compensate for elevated daytime thermoregulatory requirements, while higher Tb by day may reduce protein turnover. All effects on Tb were significantly more pronounced during the first day of stopover than on days two and three, which may be linked to the rate of renewal of digestive function during stopover. Our results suggest that environmental factors, such as high Tb, constrain migratory body mass gain. Extreme high Tb and heat waves are predicted to increase due to global climate change, and thus are likely to pose increasing constraints on regaining body mass during stopover and therefore migratory performance in migratory birds.

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1. Introduction

In order to exploit favorable habitats during different seasons of the year, hundreds of bird species migrate thousands of kilometers, often flying over broad ecological barriers. Depending on the distance, birds are on the move from weeks to months, typically alternating between flight and sojourn at stopover sites where they spend time refueling. Indeed, migrants spend about 85% of their migration time at stopovers compared to 15% in active flight, and twice as much energy at stopovers than in flight (Hedenstöm and Alerstam, 1997, Wikelski et al., 2003). During spring migration, when early arrival at the breeding area is beneficial in terms of annual reproductive success (Newton, 2006; Newton, 2008), efficient rebuilding of body tissues is likely to be under selective pressure (Alerstam and Lindström, 1990; Lindström and Alerstam, 1992; Hedenstöm and Alerstam, 1997). Therefore maximizing the rate of refueling at a stopover is adaptive because it facilitates early resumption of migration.

Adaptive behavioral and physiological responses such as hyperphagia, diet selection (Baierlein 2002; McWilliams et al., 2004) and/or heterothermy (increased body temperature (Tb) at high ambient temperature (Ta) (Tieleman and Williams, 1999) and decreased Tb at low Ta (Prinzing er et al., 1991; McKechnie and Lovegrove, 2002) make it possible for birds to maximize their rate of refueling. Whereas heterothermic responses depend on the environment, food selection and rate of intake may depend on the state of the digestive tract (Karavas and Pinshow, 2000; McWilliams et al., 2004; Karavas and McWilliams 2005; McWilliams and Karavas, 2005). Passerine birds within the Afro-Palearctic migration system face the challenge of flying across a major ecological barrier, the Sahara desert. This effort has been reported to result in the catabolism of half of the digestive tract and liver mass (Hume and Biebach, 1996; Biebach, 1998; Karavas...
and Pinshow, 1998; Schwilch et al., 2002; Karasov et al., 2004; Bauchinger et al., 2005). Consequently, these birds need to rebuild their digestive tract before they can rebuild depleted fat stores. Rebuilding the digestive tract in the garden warbler (Sylvia borin), and the similar sized blackcap (Sylvia atricapilla), requires about two days, after which assimilation rate, food intake rate and body mass (m₀) gain resume normal values (Hume and Biebach, 1996; Karasov et al., 2004).

Passerine birds are capable of hypothalamic responses (Prinzinger et al., 1991; Reinersten, 1996; McKechnie and Lovegrove, 2002), and recent investigations suggest that such responses are a strategy used during migratory stopover (Wojciechowski and Pinshow, 2009). Blackcaps maintained under semi-natural conditions at a stopover site in the Negev desert had Tₐ reduced below normothermic levels, which the authors associated with low m₀ rather than with nighttime Tₐ. The authors estimated that the energy saved due to hypothemia accounts for up to 30% of the energy required to maintain normothermic Tₐ (Wojciechowski and Pinshow, 2009). In contrast, birds that are exposed to high Tₐ face increased costs for thermoregulation and maintenance of water balance (Calder and King, 1974; Tieleman and Williams, 1999). Protracted periods of high Tₐ, as commonly occurring in regions north of the Sahara desert belt during spring and autumn (Frich et al., 2002), can cause mass mortality among birds (McKechnie and Wolf, 2010). In the present study we examined how a migratory passerine species responds to high daily Tₐ during stopover after crossing the Sahara, how high Tₐ affects m₀, and how the birds' capacity to refuel is influenced by high Tₐ.

In spring 2007, we caught garden warblers in the Negev desert, kept them until they maintained constant body mass (m₀), and then deprived them of food and water for two days. Two days of food deprivation is a common manipulation used to simulate an in-flight starvation period (Gwinner et al., 1985, Gwinner et al., 1988; Bauchinger et al., 2008), and is known to cause reduced digestive tract and liver masses (Hume and Biebach 1996, Biebach 1998, Karasov and Pinshow 1998, Karasov et al., 2004). Birds were subsequently offered food and water ad libitum for three days, to simulate a 3-day stopover (days 1, 2 and 3). We allowed the birds that were exposed to Tₐ 40/15 °C to pre-fast conditions. Such an additional day was necessary for the Tₐ 27/15 °C regime. We gradually increased Tₐ to 40/15 °C, before depriving them of food and water for two days. Two of the seven birds of the stopover group were first exposed to Tₐ 27/15 °C, then to Tₐ 40/15 °C, and the remaining five birds of the stopover group were first exposed to Tₐ 40/15 °C, and then to Tₐ 27/15 °C. The birds of the constant food group saw Tₐ 40/15 °C before Tₐ 27/15 °C. The birds in the stopover group were deprived of food for the transition day and the first day of each Tₐ period. After these two days of fasting the birds were fed ad libitum for at least three days to simulate a 3-day stopover (days 1, 2 and 3). We allowed the birds that were exposed to Tₐ 40/15 °C a fourth day of stopover with ad libitum food and water, so they had sufficient time to regain m₀ to pre-fast conditions. Such an additional day was not necessary for the Tₐ 27/15 °C period.

2.2. Experimental design and Tₐ manipulation

Ambient temperature manipulation lasted 15 days and consisted of three consecutive five-day periods that each included a transition day, and then four days with a consistent day/night temperature regime. The first period had a daytime Tₐ of 27.5 °C and 15 °C at night (Tₐ 27/15 °C). The second was 40 °C by day and 15 °C at night (Tₐ 40/15 °C). The third was a repetition of the Tₐ 27/15 °C regime. We gradually increased Tₐ in the morning and decreased it in the evening to simulate natural patterns, with more pronounced changes for Tₐ 40/15 °C than for Tₐ 27/15 °C (Fig. 1). Tₐ was measured at five-minute intervals with four calibrated iButton data loggers (DS1921, Maxim Integrated Products, Sunnyvale, USA), and the temperature profile was plotted over 24 h periods (Fig. 1). Birds were exposed to Tₐ 33.75 °C by day and 15 °C at night during the transition day.

We implanted transmitters in 12 birds, but only nine birds were used in experiments; one bird lost all its tail feathers and began to molt, and transmitters failed in two others. The remaining nine birds were exposed to two successive Tₐ regimes, randomly assigned to start with Tₐ 27/15 °C or Tₐ 40/15 °C, and were either deprived of food and water for two days to simulate in-flight starvation during each of the two periods ('stopover group', n = 7), or were offered ad libitum food and water every day ('constant food group', n = 2). Two of the seven birds of the stopover group were first exposed to Tₐ 27/15 °C and then to Tₐ 40/15 °C; the remaining five birds of the stopover group were first exposed to Tₐ 40/15 °C, and then Tₐ 27/15 °C. The two birds of the constant food group saw Tₐ 40/15 °C before Tₐ 27/15 °C. The birds in the stopover group were deprived of food for the transition day and the first day of each Tₐ period. After these two days of fasting the birds were fed ad libitum for at least three days to simulate a 3-day stopover (days 1, 2 and 3). We allowed the birds that were exposed to Tₐ 40/15 °C a fourth day of stopover with ad libitum food and water, so they had sufficient time to regain m₀ to pre-fast conditions. Such an additional day was not necessary for the Tₐ 27/15 °C period.

2.3. Maintenance and measurements

Light was matched to the natural light conditions for May 17 (mean for the experiment) and held constant throughout (L:D; 14 h 45 min:9 h 15 min). Light intensity during night was 0.1–0.2 lx and ~250 lx during day as measured in the bird cages (Digital Illuminance Meter B 360, LMT Lichtmesstechnik, Berlin, Germany). Throughout the experiment, birds were fed a standard diet described by Gwinner et al. (1988) which consisted of 30% hard boiled eggs, receiver (SRX-400A W21AST with Event Log software, Newmarket, Ontario, Canada). Successive Tₐ readings for each bird and transmitter were recorded continuously, with approximately one reading per minute (range 0.33 to 2 readings per minute for each transmitter).

Fig. 1. Experimental manipulation of ambient temperature (Tₐ) plotted against time of day in heat wave experiment with garden warblers (Sylvia borin). Average data for three consecutive days are presented for Tₐ 40/15 °C (black triangles) and for Tₐ 27/15 °C (grey circles). Grey areas indicate night (lights off). Temperature was increased beginning at 06:00 h and was decreased from 18:00 h. Nighttime Tₐ is similar in both groups.
21% curd, 15% bread crumbs, 6% ground egg shells and 3% beef heart, but without the 25% commercial insect food. A single batch of this standard diet was prepared for the entire experiment and then stored frozen in daily portions. Birds were always fed twice a day to avoid the food becoming desiccated. Food and fresh water were provided two hours after lights on at 07:15 h and at 13:00 h. When food was provided in the morning, birds were weighed to ±0.1 g and cages were cleaned. Body mass change for each day was calculated as the 24 h difference between \( m_b \) measurements.

We recorded the time that we spent in the temperature chamber, and all \( T_b \) recordings during this interval, plus an additional 15 min thereafter, were removed from the data set to avoid biased \( T_b \) readings due to handling disturbance. We calculated the mean \( T_b \) for the entire day (\( T_{b, \text{day}} \)), mean \( T_b \) for the entire night (\( T_{b, \text{night}} \)), \( T_b \) \( \max \) (ten minute mean around the maximum \( T_b \) of the day) and \( T_b \) \( \min \) (ten minute mean around the minimum \( T_b \) of the night). For each of these measurements we also calculated the range, either as \( T_b \) range \( \text{day/night} \), or \( T_b \) range peaks.

We used an infrared camera (XNiteIRBoardCam; www.maxmax.com) to record nocturnal migratory restlessness (Zugunruhe) for all birds on each of the 3 nights of stopover under both \( T_a \) regimes. Two-minute intervals of video recording were analyzed for every 20-minute period throughout the night. Each two-minute interval was scored as ‘not active’ if the bird moved less than 5 times without changing the position of its legs, or if the bird moved more than five times without changing the position of its legs, or if the bird changed the position of its legs, hopped or fluttered in the cage. Each 20-min interval was counted as “with Zugunruhe” when the two-minute interval between 18–20 min was scored as active, otherwise the time step was counted as without Zugunruhe. All consecutive twenty-minute intervals were treated alike and the final quantity of Zugunruhe is presented as percentage of active 20-min intervals per total number of 20-min intervals per night.

### 2.4. Statistics

All variables were tested for normality of distribution (Kolmogorov–Smirnov Test) and for homogeneity of variance (Bartlett’s test). Body mass for the two stopover groups that differed in the sequence of \( T_a \) regimes was compared by paired sample t-tests. We used a repeated measures mixed model ANOVA to test for differences in measurements of all \( T_b \), \( m_b \) and \( m_b \) change. In the model, we accounted for the sequence of \( T_a \) regimes (either \( T_a 27/15 °C \) followed by \( T_a 40/15 °C \), or \( T_a 40/15 °C \) followed by \( T_a 27/15 °C \)) and the effect of first vs. second experimental period. We tested for differences (main effects) between treatment (constant food vs. stopover), \( T_a \) (\( T_a 40/15 °C \) vs. \( T_a 27/15 °C \)), days (days 1 to 4) and the interactions \( T_a \) × treatment, \( T_a \) × day and day × treatment. When interactions were not significant, the interaction with the highest \( p \)-value was removed and the analysis was repeated. Given that we consistently detected significant differences between treatment groups (constant food and stopover; the ‘full model’), we also tested for differences between \( T_a \) regimes, day, and their interaction (\( T_a \) × day) for only the stopover group. Main effects and interactions were tested in the analysis of the full model without further post-hoc analysis. Post hoc analysis with Bonferroni corrections for multiple testing was done for the stopover group. The original data are presented as mean ± SD, and mean ± SE for estimated marginal means in the figures.

### 3. Results

#### 3.1. Ambient temperature manipulation

Mean maximum daytime \( T_a \) for 10 min was 40.1 °C (±0.4; \( n = 5 \)) at \( T_a 40/15 °C \) and 28.3 °C (±0.2; \( n = 5 \)) at \( T_a 27/15 °C \). The mean hourly daytime maximum was 39.7 °C (±0.5; \( n = 5 \)) for \( T_a 40/15 °C \) and 27.5 °C (±0.3; \( n = 5 \)) for \( T_a 27/15 °C \). The mean daytime \( T_a \) was 31.3 °C (±0.4;
n = 5) for \( T_a \) 40/15 °C vs. 23.9 °C (± 0.5; n = 5) for \( T_a \) 27/15 °C. Nighttime \( T_b \) was constant at about 15 °C (see Fig. 1).

### 3.2. Data and distribution

All variables were normally distributed and variances met the criteria for homogeneity (for all \( T \) = 5) for \( T_a \) 40/15 °C which was not significantly different (paired sample \( T \)-test, \( t_{1,6} = 0.8, p = 0.44 \)). While \( m_b \) remained constant over time in the constant food groups for both \( T_a \) regimes, it increased in both stopover groups with the highest increase between day 1 and 2, and a higher increase in \( T_a \) 27/15 °C than \( T_a \) 40/15 °C birds (Figs. 2 and 3). Treatment groups (constant food and stopover) differed in \( m_b \) and \( m_b \) change across days as indicated by significant \( T_a \) \times day and treatment \times day interactions (Table 1). The higher mean \( m_b \) for the constant food group at the beginning of the three day period was expected, given that the constant food group was not deprived of food while the stopover group was deprived of food for two days (Fig. 2). Analyses of the stopover group alone revealed that \( m_b \) significantly changed between days and across \( T_a \) (Table 1, Fig. 3) whereas \( m_b \) change differed over the stopover days and \( T_a \) in a more complicated way; there was a significant interaction between \( T_a \) and days (Table 1, Fig. 2). Post hoc analysis revealed significant differences in \( m_b \) change between the two \( T_a \) regimes on the first day of stopover only, whereas \( m_b \) change was not significantly different between the two \( T_a \) regimes on stopover days two and three (Fig. 3). Mean \( m_b \) change over the entire stopover period (day 1 to day 4) was 4.2 ± 0.2 g for \( T_a \) 27/15 °C and 3.5 ± 0.3 g for \( T_a \) 40/15 °C which was not significantly different (paired sample \( T \)-test, \( t_{1,6} = 1.7, p = 0.136 \)). Under heat wave conditions (\( T_a \) 40/15 °C) birds showed a 26.8% gain in \( m_b \), whereas bird maintained under \( T_a \) 27/15 °C revealed a 21.9% increase in \( m_b \).

### 3.4. Body temperature measurements

The \( T_b \) range day/night of the treatment groups was significantly different between days and treatment but not between the two \( T_a \) regimes (Table 1). For the stopover group, \( T_b \) range day/night was significantly different among the three experimental days, but not between the two \( T_a \) regimes (Figs. 2 and 4). \( T_b \) range peak was different between treatment groups, \( T_a \) and days, and both these dependent variables remained significantly different between \( T_a \) and day when only the stopover group was considered (Table 1, Fig. 2). In the constant food groups the range was smaller compared to the stopover groups, and it was always smaller in both treatments at \( T_a \) 27/15 °C Compared to the corresponding treatment groups at \( T_a \) 40/15 °C (Table 1).

Mean \( T_b \) day was consistently different between the days when both the constant food and stopover group, or only the stopover group, were considered (Table 1). In contrast, \( T_b \) night differed over the stopover days and between \( T_a \) in a more complicated way when both

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**Table 1**

Summary of statistical results for repeated measures analysis and the main effects testing for differences between \( T_a \) day and treatment (treatment refers to test between constant food group and stopover group, referred to in the text as ‘full model’; six columns on the left). Included are all possible and significant interactions; and similar analysis for stopover group only (three columns at the right) testing for differences between \( T_a \) day and the interaction term \( T_a \) \^\* day. \( T_a \) refers to test between \( T_a \) 27/15 °C and \( T_a \) 40/15 °C. Day refers to test between stopover day 1, 2, and 3. For each column results are presented as F-value with degrees of freedom (DF) and p-value.

<table>
<thead>
<tr>
<th>Rm mixed model</th>
<th>Constant food group and stopover group (‘full model’)</th>
<th>Stopover group only</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment &amp; time*</td>
<td>( T_a ) &amp; ( T_a ) day &amp; ( T_a ) ^* day</td>
<td>( T_a ) &amp; ( T_a ) day &amp; ( T_a ) ^* day</td>
</tr>
<tr>
<td>( m_b ) (mean, g)</td>
<td>F on-p-value</td>
<td>F on-p-value</td>
</tr>
<tr>
<td>( m_b ) change (mean, g)</td>
<td>21.9 ± 0.003</td>
<td>57.5 ± 0.003</td>
</tr>
<tr>
<td>( T_b ) range day/night (mean, °C)</td>
<td>11.4 ± 0.017</td>
<td>38.1 ± 0.001</td>
</tr>
<tr>
<td>( T_b ) range peak (mean, °C)</td>
<td>8.5 ± 0.027</td>
<td>11.5 ± 0.002</td>
</tr>
<tr>
<td>( T_b ) max (mean, °C)</td>
<td>2.1 ± 0.018</td>
<td>0.01 ± 0.001</td>
</tr>
<tr>
<td>( T_b ) night (mean, °C)</td>
<td>2.2 ± 0.018</td>
<td>12.7 ± 0.001</td>
</tr>
<tr>
<td>( T_b ) min (mean, °C)</td>
<td>16.5 ± 0.008</td>
<td>3.4 ± 0.074</td>
</tr>
<tr>
<td>Zugunruhe (°/night)</td>
<td>9.9 ± 0.031</td>
<td>5.1 ± 0.030</td>
</tr>
</tbody>
</table>

**Bold font is used to highlight significant results for single main effects or alternatively, for significant interactions for main effects.**

* Test for Day refers to test for differences between stopover day 1, 2, 3 and 4.
the constant food and stopover group were considered, whereas there was only a difference in \( T_b \) night between days and not between \( T_b \) when only the stopover group was considered (Table 1). \( T_b \) night was lowest on the first day of stopover and increased with stopover day (Fig. 2). \( T_b \) max was significantly higher at \( T_a 40/15 \) °C compared to \( T_a 27/15 \) °C. This applied to both the constant food and stopover groups (full model), or to the stopover considered alone. For the stopover group, \( T_b \) max increased significantly after the first stopover day (Fig. 4). \( T_b \) min was consistently different between \( T_b \) a, with a significant interaction between treatment and day (full model) and with a significant difference among days in the model accounting the stopover groups only. \( T_b \) min increased with progressive stopover days (Figs. 2 and 4).

3.5. Nocturnal activity (Zugunruhe)

The amount of Zugunruhe observed during the night differed between treatment and day (\( p < 0.05 \)) and between treatment and \( T_a \) (\( p < 0.01 \); full model, Table 1; Fig. 5). In general, the amount of Zugunruhe increased significantly with stopover day (\( p < 0.001 \); both models, Table 1). Zugunruhe for the stopover group did not change with \( T_a \) (\( p = 0.071 \), Table 1).

4. Discussion

Maximum daytime \( T_b \) increased in garden warblers exposed to high daytime \( T_a 40 \) °C during a simulated stopover and minimum nighttime \( T_b \) decreased compared to when they were exposed to moderate daytime \( T_a 27 \) °C, nighttime \( T_b \) constant in both cases). These hyperthermic and hypothermic responses could not compen-
sate completely for the increased daytime thermoregulatory requirements, resulting in lower \( m_b \) change for birds exposed to higher daytime \( T_b \). Birds that encountered the high daytime \( T_b \) also had lower rates of body mass gain, but the compensatory effects associated with altered \( T_b \) may still have provided considerable savings.

\( T_b \) in small birds (~10 g) typically varies between 38.9 °C and 41.3 °C with a range of 2.5 °C (Prinzinger et al., 1991). We observed a similar range of \( T_b \) range day/night between the \( T_b \) peaks in garden warblers with mean values of 2.3 °C and 2.9 °C for birds in constant food at \( T_a 27/15 \) °C and \( T_a 40/15 \) °C, respectively. This \( T_b \) range day/night was significantly higher (1) during simulated stopover than in constant food, (2) at \( T_a 40/15 \) °C compared to \( T_a 27/15 \) °C, and (3) during the first day of stopover compared to the later days of stopover (Table 1, Figs. 2 and 3).

4.1. Ambient temperature affects body mass gain

Lower body mass increase during stopover in garden warblers exposed to high \( T_a \) likely occurred because of increased energy expenditure associated with increased costs of thermoregulation and maintenance of water balance (Calder and King, 1974; Tieleman and Williams, 1998) and changes in protein turnover (Hayashi et al., 1992; Geraert et al., 1996; Yunianto et al. 1997; Temim et al., 1999; Temim et al., 2000). Increased energy expenditure can be a consequence of
increased breathing frequency and/or the Q_{10} effect due to increased T_{b} (Calder and Schmidt-Nielsen, 1964; Calder and King, 1974; Marder and Arad, 1989). The garden warblers were clearly challenged by the 40 °C daytime T_{a} in that they had lower m_{b}, lower m_{b} gain, and higher daytime peak T_{b} compared to birds exposed to T_{a} 27/15 °C. As found in other studies, birds may increase T_{b} even when T_{a} is within their thermoneural zone to reduce energy expenditure associated with thermoregulation by reducing the T_{b} to T_{a} temperature gradient (for review see Tieleman and Williams, 1999). Garden warblers in our study were able to increase T_{b} with increasing T_{a} in part because water was provided ad libitum during the simulated stopover, so that evaporation (both respiratory and cutaneous) could dissipate heat when T_{a} was above the upper critical temperature (Calder and King, 1974; Tieleman and Williams, 1999).

Lower feeding rates during stopover in garden warblers exposed to high T_{a} may also be related to changes in digestive physiology and altered protein turnover. Nitrogen retention was significantly reduced in broilers maintained for two weeks at high constant T_{a} of 32 °C vs. T_{a} of 22 °C, an effect that was explained by reduced nutrient digestibility (Bonnet et al., 1997). Chickens maintained at higher T_{a} vs. moderate T_{a} had lower m_{b} gain and a higher food intake to m_{b} gain ratio (Dale and Fuller, 1979; Geraert et al., 1992). The range of temperatures typically used in poultry heat stress studies matches the mean T_{a} day that we used for garden warblers (31.3 °C ± 0.4, n = 5 for T_{a} 40/15 °C, 23.9 °C for T_{a} 27/15 °C). Furthermore, chickens exposed to constant high T_{a} of 32 °C vs. T_{a} of 22 °C had significantly reduced muscle turnover because of reduced protein degradation and protein synthesis, the latter being more affected by heat stress (Temim et al., 1999; Temim et al., 2000). These findings are in agreement with several other studies in young chickens during development that showed decreased protein synthesis (Geraert et al., 1996) or decreased whole-animal protein turnover under higher T_{a} compared to moderate T_{a} (Hayashi et al., 1992; Yunianto et al., 1997). The T_{b} manipulation in the present study may have had similar effects on garden warblers and may in fact be even stronger because these warblers must rebuild digestive tract and other internal organs during stopover.

Under natural conditions, the response of birds to high T_{a} is typically associated with physiological responses to economize water use (Tieleman and Williams 1998). In our experiment, birds during simulated stopover had ad libitum access to drinking water and food. Stronger effects on m_{b} and m_{b} gain and T_{b} may occur under conditions when drinking water is not available, or when access to drinking water and food is limited either by quantity or by its temporal availability. During stopover in an oasis blackcaps increased fuel deposition rates when water was supplemented compared to blackcaps that had no access to drinking water (Sapir et al., 2004). However, in the same study, lesser whitethroats (S. curruca) did not reveal such differences, indicating potential variance among species in their responses to water availability during stopover. Comparable results were obtained for blackcaps maintained under simulated stopover conditions with or without drinking water on the first day of stopover (Tsurim et al., 2008). Birds without drinking water on day 1 of a simulated stopover had lower food intake and energy intake rates, and less increase in m_{b} compared to birds that always had access to drinking water.

4.2. Nighttime compensation for increased daytime energy demands

The significantly lower nighttime T_{b} min in garden warblers during stopover under T_{a} 40/15 °C compared to T_{a} 27/15 °C suggests that birds compensate for the higher daytime energy expenditure by saving energy at night (Fig. 4). Hypothermic responses may save energy by reducing metabolic costs due to the Q_{10} effect (McKeechne and Lovegrove, 2002; Wojciechowski and Pinshow, 2009). Based on the difference between metabolic rates measured in normothermic and hypothermic blackcaps, Wojciechowski and Pinshow (2008) estimated 30% lower energy expenditure during the night for birds that reduce T_{b} below normothermic levels. Such savings of energy would be beneficial for fuel deposition of migrating birds during stopover.

The reduction in T_{b} of garden warblers during the night was not only different between the two T_{a} regimes, but also changed significantly between the stopover days (Fig. 4). The lowest nighttime T_{b} min of garden warblers occurred on the first stopover day and then increased on each of the following two nights. Birds migrating for sustained periods in the wild substantially reduce their digestive organs by up to 50% (Biebach 1998; Battley et al., 2000; Schwilch et al., 2002; Karasov et al., 2004; Bauchinger et al., 2005), a phenomenon that can be simulated by food deprivation in the laboratory (Hume and Biebach, 1996; Karasov and Pinshow, 1998; Battley et al., 2001). Small digestive tract organs upon arrival at a stopover site pose digestive limitations, i.e. reduced food intake rates, assimilation rates and body mass gain (Hume and Biebach, 1996; Karasov and Pinshow, 2000; Karasov et al., 2004; McWilliams et al. 2004, Karasov and McWilliams 2005; McWilliams and Karasov, 2005; Bauchinger et al., 2009). Rebuilding of the digestive tract in Sylvia warblers is a process that requires at least two to three days (Hume and Biebach, 1996; Karasov and Pinshow, 2000). Therefore, the initial strong effect of high daytime T_{a} on T_{b} min, and its dampening over time during stopover, may represent the physiological limitations associated with rebuilding of the digestive tract.

Increasing energy stores including rebuilding of the digestive tract, are associated with changes in migratory restlessness of birds during migration (Fusani et al., 2009, Bauchinger et al., 2008). The dampening of the effects on T_{b} min in garden warblers during stopover can be explained in part by the increase in migratory restlessness (Fig. 5, Table 2). This increase in nocturnal activity coincided with increasing m_{b} and T_{b} values that changed between the stopover days suggesting increasing fuel stores and completed rebuilding of the digestive tract. The amount of nocturnal activity was not different between the two T_{a} regimes, suggesting that the differences are caused by other factors, rather than nocturnal activity per se. However, due to the low sample size special caution is required for interpretation of non-significant results.

5. Conclusion

Birds that migrate long distances face digestive limitations upon arrival at stopover sites (McWilliams et al., 2004; Karasov and McWilliams, 2005; McWilliams and Karasov, 2005). Reduced digestive organs must be rebuilt before food intake and assimilation rates enable maximum fuel deposition rates (Gannes, 2002; Karasov and Pinshow 2000; Karasov et al., 2004; Bauchinger et al., 2009). The rate of organ renewal may determine the start of the next leg of migration and, thus, speed up the trip (Alerstam and Lindström, 1990; Lindström and Alerstam, 1992). Our results indicate that high T_{a} can impose an additional burden on migratory birds at a stopover site because body mass gain is slower if T_{a} is close to, or above, the bird’s upper critical temperature. High ambient temperature conditions experienced during migratory stopover must be considered to slow down migratory refueling affecting migration speed and subsequently delaying arrival time. Especially in spring, when early arrival at the breeding sites is generally beneficial for individual fitness (Newton, 2006; Newton, 2008) reduced migration speed due to slower refueling at stopover (Alerstam and Lindström, 1990; Lindström and Alerstam, 1992; Hedemö and Alerstam, 1997) likely reduces annual reproductive output.

Climatic extremes often occur in association with heat waves that have been arbitrarily defined as periods of more than 5 days with T_{a} more than 5 °C above the 1961–1990 normal daily T_{a} (Frith et al.,
than means (Easterling et al., 2000; Jentsch et al., 2007; Frich et al., 2010). High spring Tₚ is typical for the region north of the Sahara desert belt. The generally higher climates. The present study demonstrates the importance of investigating extrema on avian physiology and performance. Knowledge of physiological limits is a key factor for understanding the potential impacts of global change on animal performance and evolution (Travis et al., 1999).

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