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Research article

Response to high ambient temperatures in short-distance and trans-Saharan migratory species

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In consideration of current global climate change, ecophysiological research on wild birds has increased its emphasis on approaches related to thermal tolerance. Many studies have investigated how desert specialists are adapted physiologically to the hot and xeric conditions they live in. Our aim was to test whether migratory passerines from temperate areas also have physiological adaptations to cope with heat stress and whether such adaptations may be related to habitat or migration distance. Using video recording and flow-through respirometry, we measured temperatures of panting onset (T_{PANT}) of 113 individuals of 14 different species, exposed to increasing ambient temperature. Our study species differed in size, migration type (short-distance migrants vs. trans-Saharan migrants) and habitat preferences (woodland, farmland, reeds). We found that trans-Saharan migrants started panting at higher ambient temperatures (T_A) than short-distance migrants of similar size, but no difference between species from different habitats. This finding suggests that migrants facing a desert crossing may have adaptations to decrease the risk of dehydration while maintaining body temperature below the critical range. According to this, we suggest that there may be selection on traits related to the modulation of respiratory water loss in birds that cross the Sahara Desert during migration. Flexibility in these traits will be of crucial importance in a warmer future.

Keywords: Austria, autumn migration, desert crossing, heat tolerance, panting, stopover

Introduction

When endothermic organisms are exposed to ambient temperatures (T_A) close to or exceeding body temperature (T_B), maintaining homeostasis becomes a challenge. Any deviation from normothermia or normohydration caused by high T_A is defined as heat stress, which can lead to death at its worst (Bradshaw 2003). To avoid symptoms caused by heat stress, animals have evolved different behavioural strategies and



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physiological adaptations. Making use of microclimatic refugia or modifying activity patterns are common ways of behavioural thermoregulation (Bartholomew 1966, Dawson 1982, Kearney et al. 2009). The main mechanism of physiological thermoregulation in endotherms is evaporative cooling (Calder and King 1974, Dawson 1982), which is achieved through the release of endogenous heat via respiratory (RWL) and cutaneous water loss (CWL) (Williams and Tieleman 2005, McKechnie 2022). In birds, at thermoneutral T_A both paths of water loss contribute to total evaporative water loss (TEWL) in approximately equal parts, with some variation across taxa (Wolf and Walsberg 1996, Tieleman and Williams 2002).

When T_A exceeds the upper critical temperature, evaporative water loss needs to be steeply increased to satisfy the demands for evaporative cooling and maintain normothermia (Tieleman and Williams 2002, Smit et al. 2013, 2016). Most avian species use behaviourally controlled mechanisms like panting or gular fluttering to actively increase RWL (Calder and King 1974). The onset of panting (T_{PANT}) occurs at a given T_A beyond which TEWL steeply increases to enhance the efficiency of heat dissipation. During panting, RWL largely overrides CWL in terms of overall contribution to TEWL (Wolf and Walsberg 1996, Tieleman and Williams 2002). High rates of water loss through evaporative cooling can lead to dehydration (Wolf and Walsberg 1996, Albright et al. 2017), resulting in a trade-off between the maintenance of sufficient hydration and efficient heat dissipation to avoid lethal hyperthermia. Panting is also energetically costly, and metabolic rates increase concurrently with TEWL (Dawson 1982, Czenze et al. 2020).

Size plays a major role for physiological traits because of the allometric relations to various body functions (Calder and Schmidt-Nielsen 1967). While TEWL increases with body mass (M_B) (Crawford and Lasiewski 1968, Williams 1996), mass-specific TEWL is negatively correlated to M_B due to the higher surface-to-volume ratio of small birds (Bartholomew and Dawson 1953). This results in a higher vulnerability to dehydration during hot weather events in small birds compared to large birds (McKechnie and Wolf 2010, Albright et al. 2017). Given these circumstances, it would be fatal for small birds to initiate panting at relatively low T_A . Therefore, T_{PANT} generally scales negatively with body mass (Whitfield et al. 2015, Smit et al. 2016). The relatively smaller surface constrains the release of heat through CWL, thus making larger birds more dependent on heat release through the respiratory pathway (Calder and King 1974, Weathers 1981).

While desert specialists are physiologically adapted to hot climates, it seems that species of temperate regions are especially vulnerable to increasingly hot and dry weather conditions (Jiguet et al. 2006, 2010, Milne et al. 2015). Still, the T_A threshold for the physiological response to heat differs among temperate zone species (Paces et al. 2021, Cabello-Vergel et al. 2022, González-Medina et al. 2023). Migration is an important factor influencing the range of environmental conditions experienced by different species. In the

Afro-Palearctic migration system, short-distance migrants experience temperate conditions throughout the year, while trans-Saharan migrants cross the Mediterranean Sea and the Sahara Desert twice a year (Moreau 1972, Hahn et al. 2009). The idea that birds cross the Sahara in a non-stop flight to avoid this hostile environment was rejected (Bairlein 1988, Schmaljohann et al. 2007, Biebach et al. 2008). Although most species seem to speed up the desert crossing as much as possible (Adamík et al. 2016, Jiguet et al. 2019), stopovers in the desert are quite common and can be considerably long in some cases (Jenni-Eiermann et al. 2011, Maggini et al. 2015, Aispuro et al. 2023). Hence, trans-Saharan migrants spend some time in the desert, despite not being specifically adapted to arid conditions.

Additionally, the preferred microhabitat and behavioral strategies can have a great influence on the operative temperatures (i.e. the total environmental heat flow to which an organism is exposed) an animal would ultimately experience (Bakken 1992, Kearney et al. 2009). For example, a farmland bird foraging in the sun is exposed to higher operative temperatures than a woodland bird spending the day in the shade of the forest (Monge et al. 2022). Besides operative temperatures, it has been shown that monthly temperature maxima and minima can differ between these two habitats by more than 5°C, resulting in a 10°C divergence of thermal range (Suggitt et al. 2011). Therefore, habitat use may have an important impact on the evolution of thermoregulatory adaptations.

It is fundamental to understand species-specific responses to rising temperatures and increasing aridity to inform conservation under recent global climate change. Therefore, research has increased its focus on thermal tolerance in the last years (McKechnie and Wolf 2010, Noakes and McKechnie 2020, Freeman et al. 2024). In this study, we aimed to investigate whether migratory passerines from temperate areas with different migration types and habitat preferences also differ in their physiological adjustments to high T_A . We stated the hypothesis that the adaptation to different habitat types and the need to migrate across the Sahara Desert would influence the heat dissipation patterns of different species. We predicted that T_{PANT} would be lower in short-distance migrants than in similar-sized trans-Saharan migrants. We also expected woodland species to have lower T_{PANT} than species that occur in warmer or more open habitats (i.e. farmland and reed species). Because of the decreased risk of dehydration with sufficient water supply, we also expected higher T_{PANT} in farmland species compared to reed inhabitants.

Material and methods

Study site and study species

We conducted the study at the Biological Station in Illmitz, Burgenland, Austria (47°46'08"N, 16°45'58"E) between 5 August and 26 October 2021 to ensure covering the peak migration time of our study species. The site lies within the

Neusiedler See-Seewinkel National Park, situated at the transition area from the Alps in the west to the Pannonian plain in the east. The wetlands serve as an important stopover site during autumn migration and attract large numbers of birds (Dvorak et al. 2023). Standardized bird ringing is conducted at the site and birds are captured using eight mist nets, totaling 72 m. Two nets are situated in a small woodland patch (mostly *Robinia* sp. and *Sambucus nigra*), surrounded by meadows and a vineyard, four are placed along a causeway lined with trees and shrubs (the most dominant being *Rosa canina*), bordering the reed (*Phragmites australis*) belt, and two are exclusively surrounded by reeds.

We selected 14 temperate passerine species differing in size, migration type, and habitat preference (Table 1) based on the frequency of their occurrence (i.e. total number of captures) at the Biological Station Illmitz in the past three years and to cover the broadest possible range of body sizes for each migration type and habitat. We distinguished between trans-Saharan and short-distance migrants and between species living preferentially in woodlands, reeds, and farmlands. The birds were captured, measured and ringed following standard operations (Bairlein 1995). Following this, the study individuals were kept in cloth bags until the beginning of the metabolic measurement (below). Sixty-one out of 113 individuals were measured immediately (33.7 ± 11.1 min after capture), while the other 51 individuals were kept for a longer time (127.5 ± 62.4 min after capture) while waiting for an ongoing measurement to end. One barn swallow *Hirundo rustica* captured on 8 September at 20:00 h was kept overnight and measured on 9 September due to the late time of capture.

Respirometry system and experimental protocol

We used a push-mode flow-through respirometry system to measure water vapour production and metabolic rates. A stream of atmospheric air was pulled through a needle valve that was used to adjust the flow rate (with a maximum capacity of 300 L h^{-1}), before a pump pushed it into a 3 L airtight glass chamber. Depending on the size of the

bird and T_A , flow rates were manually adjusted to maintain the humidity in the chamber stable. Flow rates used were between 60 and 150 L h^{-1} . The test birds were placed inside the chamber and sat on a metal mesh platform placed above a ~1 cm thick layer of mineral oil, which collected faeces and prevented cloacal water from being included in the measurement of TEWL. To avoid poor mixing and boundary layer effects, the airstream passed through a perforated inlet into the animal chamber. The outgoing flow was measured by a custom-made gas analyser (OxBox 2, Institute of Wildlife Biology, University of Veterinary Medicine Vienna, Austria). Values for relative humidity (RH, in %) and O_2 concentration were collected every 10 seconds. The respirometry chamber was situated inside a dark box where T_A was regulated by a Peltier heating and cooling module (Sable Systems Inc.).

All birds were exposed to increasing T_A in a ramped protocol similar to those used in previous studies (Whitfield et al. 2015, Oswald et al. 2018). The test bird was acclimatized to $T_A = 30^\circ\text{C}$ for 30 min before the beginning of the measurement. A two-minute reference measurement of atmospheric air was followed by an eight-minute measurement of the air from the respirometry chamber. T_A was increased in steps of 3°C after two 10-minute rounds at each given T_A . By allowing the measurement at each T_A to last for two 10-minute rounds we ensured to have at least one round of measurements at a stable T_A , since it took our system about 8 min to reach a constant T_A after the switch. We measured individuals between 30 and 45°C but stopped the measurement earlier when noticing a clear indication of the start of panting (below). All birds measured after 30 August ($n=90$) were continuously observed using a security camera equipped with an infrared light source and live video feed. Using the live camera feed, we assigned an activity score from 1–4 (1 = sleeping/ mostly sitting still/ only single movements; 2 = less than 1/3 of time interval in motion; 3 = 1/3 to 2/3 of the time interval in motion; 4 = more than 2/3 of time interval in motion) to each bird at each measurement interval. In order to verify the T_{PANT} measures derived from the respirometry measurement (below), we also visually determined the onset of panting

Table 1. List of study species, grouped by habitat type, showing body mass (mean $\pm$ SD) and migration type. Sampling sizes (n) refer to all individuals that were used in the respirometry experiment.

Species	Body mass (g)	Habitat	Migration type
Eurasian reed warbler <i>Acrocephalus scirpaceus</i> ($n=10$)	11.6 ± 0.8	Reeds	Trans-Saharan
Savi's warbler <i>Locustella luscinioides</i> ($n=6$)	15.1 ± 1.4	Reeds	Trans-Saharan
Reed bunting <i>Emberiza schoeniclus</i> ($n=6$)	19.2 ± 2.2	Reeds	Short-distance
Great reed warbler <i>Acrocephalus arundinaceus</i> ($n=8$)	28.8 ± 1.9	Reeds	Trans-Saharan
Common chiffchaff <i>Phylloscopus collybita</i> ($n=10$)	6.7 ± 0.4	Woodland	Short-distance
Willow warbler <i>Phylloscopus trochilus</i> ($n=5$)	9.0 ± 0.9	Woodland	Trans-Saharan
Eurasian pied flycatcher <i>Ficedula hypoleuca</i> ($n=5$)	12.1 ± 0.6	Woodland	Trans-Saharan
European robin <i>Erithacus rubecula</i> ($n=10$)	16.3 ± 0.7	Woodland	Short-distance
Eurasian blackcap <i>Sylvia atricapilla</i> ($n=10$)	18.3 ± 1.1	Woodland	Short-distance
Song thrush <i>Turdus philomelos</i> ($n=10$)	69.1 ± 3.1	Woodland	Short-distance
Common whitethroat <i>Currucula communis</i> ($n=5$)	14.6 ± 1.0	Farmland	Trans-Saharan
Barn swallow <i>Hirundo rustica</i> ($n=7$)	18.1 ± 1.9	Farmland	Trans-Saharan
Red-backed shrike <i>Lanius collurio</i> ($n=10$)	28.7 ± 2.8	Farmland	Trans-Saharan
Common starling <i>Sturnus vulgaris</i> ($n=10$)	73.9 ± 6.8	Farmland	Short-distance

and denoted this as $T_{\text{PANT_OBSERVED}}$ in subsequent analysis. Depending on the occurrence of panting, tests lasted from a minimum of 76 min to a maximum of 142 min.

Data processing and statistical analysis

We transformed the measured values of RH to absolute humidity (AH, in $\text{g H}_2\text{O m}^{-3}$) using the formula $\text{AH} = C \times P_w/T$, where C is a constant of $2.16679 \text{ (gK J}^{-1}\text{)}$, P_w the partial pressure of water vapor in Pa, and T the temperature in K. We calculated P_w as P_{ws} (saturation water vapor pressure in hPa) multiplied by RH. P_{ws} was obtained using the formula $P_{ws} = A \times 10^{[m \times T/(T+T_n)]}$, where A , m and T_n are constants (respectively, 6.1164341, 7.591386, and 240.7263 for temperatures between -20 and 50°C), and T was the temperature in $^\circ\text{C}$. We then used the values of AH to calculate the rate of water vapour production ($\dot{V}\text{H}_2\text{O}$) using the equations in Lighton (2008). $\dot{V}\text{H}_2\text{O}$ was used as a proxy for TEWL. Since the AH of the incoming air varied between experiments, we used mean AH of the reference air from the beginning of the experiment until T_{PANT} as a measure of experienced humidity. We used the average M_B of the species as a proxy for body size, and individual fat score (Kaiser 1993) as a measure of potential insulating layer (and as a proxy of the bird's fuelling status at the same time). We calculated the median activity score from the beginning of the experiment to the time where T_{PANT} was reached as a measure of overall activity.

We checked for phylogenetic signal in T_{PANT} and $T_{\text{PANT_OBSERVED}}$ by creating a Newick tree with the 14 species of the study using TimeTree 5 (Kumar et al. 2022). We then used this tree to calculate Pagel's λ (Pagel 1999) and Blomberg's K (Blomberg et al. 2003). Neither T_{PANT} (Pagel's $\lambda < 0.001$; $p > 0.95$; Blomberg's $K = 0.879$; $p = 0.224$) nor $T_{\text{PANT_OBSERVED}}$ (Pagel's $\lambda = 1.977$; $p = 0.594$; Blomberg's $K = 1.092$; $p = 0.253$) showed significant phylogenetic signal, hence we did not use phylogenetic corrections in our statistical models. We determined T_{PANT} as the T_A at which EWL sharply started increasing. To do this, we first fitted linear regression models describing $\dot{V}\text{H}_2\text{O}$ as a function of T_A for each individual. Following this, we performed a broken-stick analysis using the *segmented* function provided by the 'segmented' package in R (Muggeo 2009) to obtain T_A breakpoints, similarly to previous studies (Milne et al. 2015, Oswald et al. 2018, Paces et al. 2021). Breakpoints in the regressions of $\dot{V}\text{H}_2\text{O}$ with T_A were then assessed for every individual showing a significant two-sided regression pattern. Trials that failed to show a clear breakpoint or did not increase obviously in $\dot{V}\text{H}_2\text{O}$ at any given temperature were excluded from the analysis (11 out of 113). In 80 of 113 birds we also determined T_{PANT} visually ($T_{\text{PANT_OBSERVED}}$) by assessing the beginning of panting from the live video feeds from the infrared cameras.

To test the impact of all the independent variables (average species' M_B , fat score, migration type, habitat, AH and activity) on the response variables (T_{PANT} and $T_{\text{PANT_OBSERVED}}$), we fitted linear models in R ver. 4.3.2 (www.r-project.org).

Before doing so, we checked for possible outliers in our data by plotting dotcharts of each variable, and computed correlation coefficients, as well as variance inflation factors (VIF) of all possible combinations of explanatory variables to test for multicollinearity. Since M_B is correlated to basal metabolic rate, we did not add metabolic rate correlates such as $\dot{V}\text{O}_2$ to the models in further analyses. We did not observe multicollinearity among the other explanatory variables ($\text{VIF} < 2$).

For both T_{PANT} and $T_{\text{PANT_OBSERVED}}$, we first created a full model including all explanatory variables and the interaction of migration type with M_B as well as the interaction of habitat with M_B . We tested whether a linear mixed-effects model (LMM) including species as a random factor would improve the result, but the AIC of such models was slightly higher than without the random effect. However, the results of the final models were comparable. Therefore, we simply show the results of the linear models here. Using a backwards stepwise model selection algorithm based on AIC, we dropped non-significant variables and/or interactions to find the best-fit models for each dependent variable. We performed model checks using methods in the 'DHARMA' package in R (Hartig 2022) and did not detect major violations of the model assumptions after creating standard diagnostical plots of residual distribution. We also checked for phylogenetic signal in the model residuals and found no significant signal in both final models for T_{PANT} (Pagel's $\lambda < 0.001$; $p > 0.95$; Blomberg's $K = 0.839$; $p = 0.967$) and $T_{\text{PANT_OBSERVED}}$ (Pagel's $\lambda = 1.435$; $p = 0.319$; Blomberg's $K = 1.024$; $p = 0.208$).

Results

Temperature of panting onset

The final model describing T_{PANT} contained the explanatory variables migration type and activity (Table 2). Short-distance migrants showed significantly lower T_{PANT} than trans-Saharan migrants ($\beta = -1.76 \pm 0.56$, $p < 0.001$; Fig. 1A). T_{PANT} was lower in birds that had higher activity scores ($\beta = -0.49 \pm 0.23$, $p = 0.035$).

The final model describing $T_{\text{PANT_OBSERVED}}$ contained the same variables, but also M_B , AH, and the interaction term between M_B and migration type (Table 2). M_B showed a small but significant negative effect on $T_{\text{PANT_OBSERVED}}$ ($\beta = -0.12 \pm 0.56$, $p = 0.042$). Trans-Saharan species were observed to start panting at significantly higher T_A than short-distance migrants ($\beta = -2.96 \pm 1.21$, $p = 0.017$; Fig. 1C). $T_{\text{PANT_OBSERVED}}$ was lower in birds that had higher activity scores ($\beta = -0.73 \pm 0.31$, $p = 0.021$). The interaction between M_B and migration type was retained in the final model but had no significant effect (Table 2). Despite habitat dropping out of the final model, reed inhabitants showed a tendency to start panting at higher T_A than farmland and woodland species (Fig. 1D).

Individual curves representing $\dot{V}\text{O}_2$ and $\dot{V}\text{H}_2\text{O}$ in relation to T_A in all study species are shown in the Supporting information.

Table 2. Results of the final linear regression models describing each T_{PANT} (the value of T_A where a sharp increase in EWL was observed) and $T_{PANT_OBSERVED}$ (the value of T_A where we could visually assess the beginning of panting). The T_{PANT} model had a residual SD of 1.990 on 76 degrees of freedom. Adj. $R^2=0.168$, $F_{2,76}=8.894$, $p < 0.001$. The $T_{PANT_OBSERVED}$ model had a residual SD of 2.191 on 64 degrees of freedom. Adj. $R^2=0.281$, $F_{5,64}=6.397$, $p < 0.001$. Statistically significant ($p < 0.05$) results are highlighted in bold. For migration type, trans-Saharan migrants represent the intercept to which short-distance migrants are compared. For habitat, reeds represent the intercept value to which the other two habitats are compared. Cells were left empty when the variable was not included in the final model.

		Estimate	SD	t value	p-value
Intercept	T_{PANT}	38.110	0.578	65.995	< 0.001
	$T_{PANT_OBSERVED}$	38.303	1.798	21.298	< 0.001
Average body mass of the species (M_B)	T_{PANT}				
	$T_{PANT_OBSERVED}$	-0.115	0.056	-2.076	0.042
Migration type (short-distance migrants)	T_{PANT}	-1.755	0.455	-3.854	< 0.001
	$T_{PANT_OBSERVED}$	-2.955	1.210	-2.442	0.017
Activity	T_{PANT}	-0.493	0.230	-2.147	0.035
	$T_{PANT_OBSERVED}$	-0.733	0.310	-2.367	0.021
Absolute humidity (AH)	T_{PANT}				
	$T_{PANT_OBSERVED}$	0.223	0.142	1.575	0.120
$M_B \times$ Migration type (short-distance)	T_{PANT}				
	$T_{PANT_OBSERVED}$	0.080	0.057	1.404	0.165

Discussion

Our study gave support to the prediction that the crossing of the Sahara Desert on migration is associated with thermoregulatory parameters suggesting increased heat tolerance. Contrary to our expectation, the species' habitat specialization did not correlate as strongly with these parameters. These results suggest that trans-Saharan migrants are prepared to cope with the aridity and high T_A to which they will be exposed during the oncoming desert crossing. Trans-Saharan migrant species had higher T_{PANT} , allowing them to increase

the range of T_A in which they can thermoregulate without incurring the costs of evaporative water loss associated with panting. Since at the time of sampling all our test birds were juveniles that never crossed the desert before, it is possible that higher T_{PANT} is an innate adaptation of these species. This suggests that temperate species migrating between their breeding grounds and the Afrotropics twice a year may have evolved a response to the harsh conditions they face during their journey by buffering the need for RWL.

It is not apparent from our data whether the higher T_{PANT} itself is the main avenue to reduce RWL, or just the

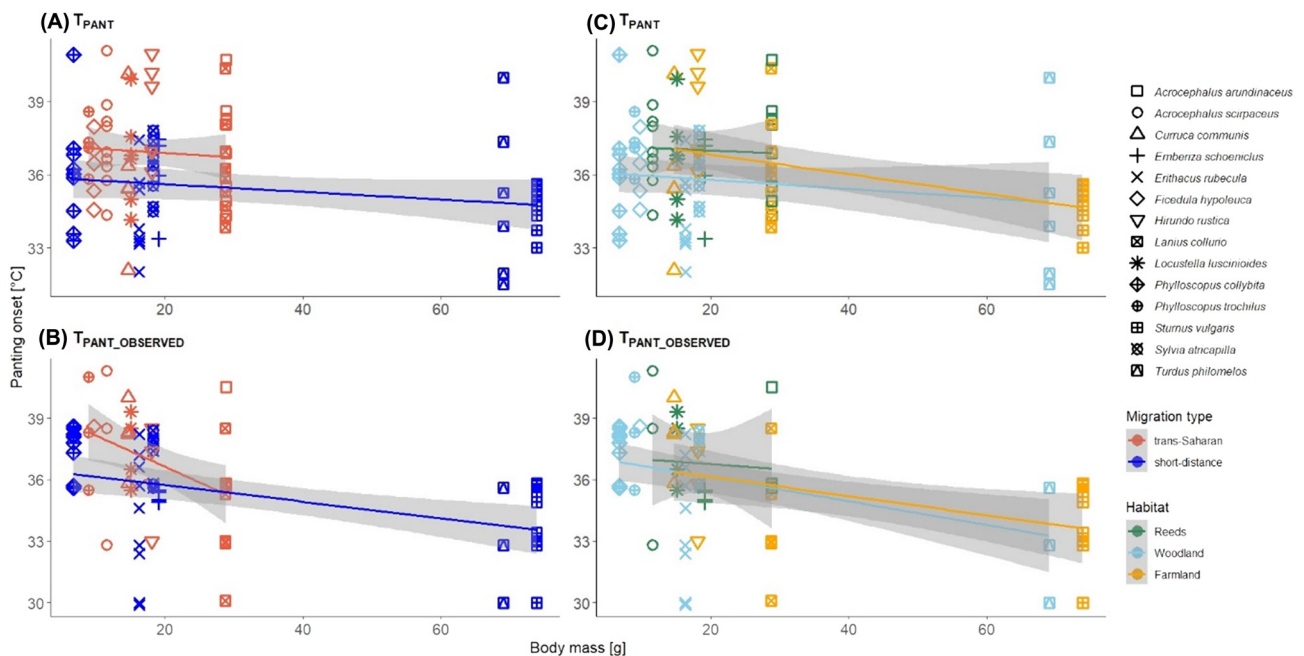


Figure 1. T_{PANT} (the value of T_A where a sharp increase in EWL was observed) and $T_{PANT_OBSERVED}$ (the value of T_A where we could visually assess the beginning of panting) of migratory passerines ($n = 102$), measured at the Biological Station Illmitz from August to October 2021. In (A) and (B) T_{PANT} and $T_{PANT_OBSERVED}$ values each are shown as a function of M_B (average values per species) for trans-Saharan and short-distance migrants, and the same values are represented differentiating birds by habitat in (C) and (D). Each symbol represents a different species.

consequence of other mechanisms. Schmidt-Nielsen et al. (1970) for example mentioned that morphological features in the nasal passages of desert birds could reduce RWL as a result of counter-current heat exchange, but to date no experimental evidence has provided support to the hypothesis (Williams and Tieleman 2005). Facultative hyperthermia, i.e., allowing T_B to rise above the normal range to store excess heat and therefore reduce water loss could be another mechanism resulting in higher T_{PANT} (Tieleman and Williams 1999, Nilsson et al. 2016, Smit et al. 2016, Gerson et al. 2019), as well as the reduction of metabolic rate. This could be achieved by decreased breathing frequencies and endogenous heat production, which would cause lower RWL and delay the necessity of panting (Williams and Tieleman 2000, Smit et al. 2016, Wojciechowski et al. 2021). Our data does not support this scenario since the measured rate of oxygen consumption ($\dot{V}O_2$) was comparable between both migratory strategies, after controlling for size (Supporting information). We also did not find evidence for a reduction of CWL (Supporting information) as described in desert specialists (Lee and Schmidt-Nielsen 1971). We did not measure CWL and RWL separately, but since both contribute approximately equally to TEWL at thermoneutral T_A (Wolf and Walsberg 1996, Tieleman and Williams 2002), we would have expected to find lower $\dot{V}H_2O$ before T_{PANT} in trans-Saharan migrants than in short-distance migrants.

Contrary to our expectation, habitat did not affect T_{PANT} and $T_{PANT_OBSERVED}$. One potential drawback of our study might have been the lack of a reed species comparable in size to the common starling (*Sturnus vulgaris*, habitat: farmland, $M_B \approx 73.9$ g) and song thrush (*Turdus philomelos*, habitat: woodland, $M_B \approx 69.1$ g) in our sample. Therefore, our conclusion might only be valid in the size range where all habitats were represented. In addition, our sample during migration may have contained a mix of individuals with different acclimation to temperature and humidity, depending on their (unknown) origin. However, our data suggest that temperate avian species do not adapt their physiological response to heat to the (micro)habitats they use. Despite considerable differences in the physical environment between fine-scaled habitat types (Suggitt et al. 2011), constraints imposed by the habitat on thermoregulation may not be strong enough to be reflected in the physiological traits of their inhabitants. Nevertheless, heterogeneous landscapes consisting of various habitat types blending into each other are favourable for behavioural thermoregulation strategies (Basson et al. 2017, Logan et al. 2019). Here, an evasion into more beneficial microhabitats when exposed to extreme hot weather events can be accomplished easily. Focusing on behavioural adjustments to compensate for physiological restrictions is often described and considered to be just as effective when animals are exposed to warm conditions (Bartholomew 1966, Adolph 1990, Kearney et al. 2009, Cunningham et al. 2015). Charles Bogert, who studied behavioural thermoregulation in North American lizards even concluded that behavioural flexibility could buffer the negative effects of exposure of an

organism to harsh environmental conditions to the extent that it would diminish selection pressure (Bogert 1949). In light of climate change, the later termed 'Bogert effect' may ultimately have fatal consequences, as species that solely rely on behavioural strategies are likely to benefit from it in the short term but will be limited to adapt physiologically in the long term (Buckley et al. 2015).

While most studies on migration physiology traditionally focused on energetics, aspects related to environmental constraints still remain rather understudied. By comparing multiple species of different size, migration type and habitat specialization, we found first insights on how ecological aspects may influence thermoregulatory features of temperate species when exposed to high temperatures. While trans-Saharan migrants seem to have, at least to some extent, a physiological predisposition to cope with the high temperatures they will encounter, short-distance migrants are more likely to rely on behavioural thermoregulation. This could be viewed as support for the southern ancestry hypothesis (Safriel 1995, Rappole and Jones 2002) whereby European-African migrants originated from tropical ancestors. Hence, one would assume that long-distance migrating birds, are less vulnerable to global warming because of their physiological prerequisites. Still, European-Afrotropic migrant species are regularly confronted with challenging conditions and have been documented to decline to a greater extent than non-migrants and short-distance migrants for decades (Vickery et al. 2023). Ongoing desertification in Northern Africa (Nicholson et al. 2018) and increasingly frequent heat waves (Coumou and Robinson 2013) further exacerbate the challenges of migration across the Sahara, thus leading to higher mortality rates, especially in small birds (McKechnie and Wolf 2010, Albright et al. 2017). Our findings show that trans-Saharan migrants increase their water savings through a reduction of RWL. This may have occurred as a response to selection for animals surviving in hot and dry environments, even if only for a relatively short period of their yearly cycle. Flexibility in the adjustment of the mechanisms of heat dissipation could be the key to a successful crossing of the desert in a warming scenario and deserves detailed investigation in the future.

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Author contributions

Julian Hasenbichler: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Flora Bittermann:** Investigation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Gilbert Hafner:** Investigation (supporting); Project administration (supporting); Resources (equal); Writing – review and editing (supporting). **Thomas Zechmeister:** Project administration (supporting); Resources (equal); Writing – review and editing (supporting). **Ivan Maggini:** Conceptualization (lead); Methodology (equal); Project administration (equal); Supervision (lead); Validation (supporting); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the PHAIDRA Repository: <https://phaidra.vetmeduni.ac.at/o:3289> (Hasenbichler et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Adamík, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., Laaksonen, T., Liechti, F., Procházka, P., Salewski, V. and Hahn, S. 2016. Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. – *Sci. Rep.* 6: 21560.
- Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. – *Ecology* 71: 315–327.
- Aispuro, A. A., Canoine, V., Illa, M., Fusani, L. and Maggini, I. 2023. Stopover territoriality in songbirds crossing the Sahara: aggression and energetics during migration. – *Behav. Ecol. Sociobiol.* 77: 57.
- Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E. and Wolf, B. O. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. – *Proc. Natl Acad. Sci. USA* 114: 2283–2288.
- Bairlein, F. 1988. How do migratory songbirds cross the Sahara? – *Trends Ecol. Evol.* 3: 191–194.
- Bairlein, F. 1995. European-African songbird migration network. Manual of field methods, rev. edn, vol. 32. – https://ifv-vogelwar.te.de/fileadmin/resources/Beringerzentrale/esf_manual.pdf.
- Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. – *Am. Zool.* 32: 194–216.
- Bartholomew, G. A. 1966. The role of behavior in the temperature regulation of the masked booby. – *Condor* 68: 523–535.
- Bartholomew, G. A. and Dawson, W. R. 1953. Respiratory water loss in some birds of southwestern United States. – *Physiol. Zool.* 26: 162–166.
- Basson, C. H., Levy, O., Angilletta Jr, M. J. and Clusella-Trullas, S. 2017. Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. – *Funct. Ecol.* 31: 856–865.
- Biebach, H., Friedrich, W., Heine, G., Jenni, L., Jenni-Eiermann, S. and Schmidl, D. 2008. The daily pattern of autumn bird migration in the northern Sahara. – *Ibis* 133: 414–422.
- Blomberg, S. P., Garland Jr, T. and Ives, A. R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. – *Evolution* 57: 717–745.
- Bogert, C. M. 1949. Thermoregulation in reptiles, a factor in evolution. – *Evolution* 3: 195–211.
- Bradshaw, D. 2003. Vertebrate ecophysiology: an introduction to its principles and applications. – Cambridge Univ. Press.
- Buckley, L. B., Ehrenberger, J. C. and Angilletta, M. J. 2015. Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. – *Funct. Ecol.* 29: 1038–1047.
- Cabello-Vergel, J., González-Medina, E., Parejo, M., Abad-Gómez, J. M., Playà-Montmany, N., Patón, D., Sánchez-Guzmán, J. M., Masero, J. A., Gutiérrez, J. S. and Villegas, A. 2022. Heat tolerance limits of Mediterranean songbirds and their current and future vulnerabilities to temperature extremes. – *J. Exp. Biol.* 225: jeb244848.
- Calder, W. A. and Schmidt-Nielsen, K. 1967. Temperature regulation and evaporation in the pigeon and the roadrunner. – *Am. J. Physiol.* 213: 883–889.
- Calder, W. A. and King, J. R. 1974. Thermal and caloric relations of birds. – In: Farner, D. S. and King, J. R. (eds), *Avian biology*. – Academic Press, pp. 259–413.
- Coumou, D. and Robinson, A. 2013. Historic and future increase in the global land area affected by monthly heat extremes. – *Environ. Res. Lett.* 8: 034018.
- Crawford, E. C. and Lasiewski, R. C. 1968. Oxygen consumption and respiratory evaporation of the Emu and Rhea. – *Condor* 70: 333–339.
- Cunningham, S. J., Martin, R. O. and Hockey, P. A. 2015. Can behaviour buffer the impacts of climate change on an arid-zone bird? – *Ostrich* 86: 119–126.
- Czenze, Z. J., Kemp, R., Jaarsveld, B., Freeman, M. T., Smit, B., Wolf, B. O. and McKechnie, A. E. 2020. Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species. – *Funct. Ecol.* 34: 1589–1600.
- Dawson, W. R. 1982. Evaporative losses of water by birds. – *Comp. Biochem. Physiol. A* 71: 495–509.
- Dvorak, M., Grüll, A., Ranner, A., Laber, J., Berg, H.-M., Pellinger, A., Hadarics, T. and Kohler, B. 2023. Die Vogelwelt des Neusiedler See-Gebietes. – Verlag des Naturhistorischen Museums Wien.
- Freeman, M. T., Coulson, B., Short, J. C., Ngcamphalala, C. A., Makola, M. O. and McKechnie, A. E. 2024. Evolution of avian heat tolerance: the role of atmospheric humidity. – *Ecology* 105: e4279.

- Gerson, A. R., McKechnie, A. E., Smit, B., Whitfield, M. C., Smith, E. K., Talbot, W. A., McWhorter, T. J. and Wolf, B. O. 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. – *Funct. Ecol.* 33: 597–607.
- González-Medina, E., Playà-Montmany, N., Cabello-Vergel, J., Parejo, M., Abad-Gómez, J. M., Sánchez-Guzmán, J. M., Villegas, A., Gutiérrez, J. S. and Masero, J. A. 2023. Mediterranean songbirds show pronounced seasonal variation in thermoregulatory traits. – *Comp. Biochem. Physiol. A* 280: 111408.
- Hahn, S., Bauer, S. and Liechti, F. 2009. The natural link between Europe and Africa – 2.1 billion birds on migration. – *Oikos* 118: 624–626.
- Hartig, F. 2022. Dharm: residual diagnostics for hierarchical (multi-level/mixed) regression models. – <https://CRAN.R-project.org/package=DHARMA>.
- Hasenbichler, J., Bittermann, F., Hafner, G., Zechmeister, T. and Maggini, I. 2025. Data from: Response to high ambient temperatures in short-distance and trans-Saharan migratory species. – PHAIDRA Repository, <https://phaidra.vetmeduni.ac.at/o:3289>.
- Jenni-Eiermann, S., Almasi, B., Maggini, I., Salewski, V., Bruderer, B., Liechti, F. and Jenni, L. 2011. Numbers, foraging and refuelling of passerine migrants at a stopover site in the western Sahara: diverse strategies to cross a desert. – *J. Ornithol.* 152: 113–128.
- Jiguet, F., Julliard, R., Thomas, C. D., Dehorter, O., Newson, S. E. and Couvet, D. 2006. Thermal range predicts bird population resilience to extreme high temperatures. – *Ecol. Lett.* 9: 1321–1330.
- Jiguet, F., Devictor, V., Ottvall, R., Van Turnhout, C., Van der Jeugd, H. and Lindström, Å. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. – *Proc. R. Soc. B* 277: 3601–3608.
- Jiguet, F. et al. 2019. Desert crossing strategies of migrant songbirds vary between and within species. – *Sci. Rep.* 9: 20248.
- Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. – *J. Field Ornithol.* 64: 246–255.
- Kearney, M., Shine, R. and Porter, W. P. 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. – *Proc. Natl Acad. Sci. USA* 106: 3835–3840.
- Kumar, S., Suleski, M., Craig, J. M., Kasprowicz, A. E., Sanderford, M., Li, M., Stecher, G. and Hedges, S. B. 2022. TimeTree 5: an expanded resource for species divergence times. – *Mol. Biol. Evol.* 39: msac174.
- Lee, P. and Schmidt-Nielsen, K. 1971. Respiratory and cutaneous evaporation in the zebra finch: effect on water balance. – *Am. J. Physiol.* 220: 1598–1605.
- Lighton, J. R. B. 2008. Measuring metabolic rates: a manual for scientists. – Oxford Univ. Press.
- Logan, M. L., van Berkel, J. and Clusella-Trullas, S. 2019. The Bogert effect and environmental heterogeneity. – *Oecologia* 191: 817–827.
- Maggini, I., Hama, F., Robson, D., Rguibi Idrissi, H., Bairlein, F. and Gargallo, G. 2015. Foraging behavior of three species of songbirds during stopover in southeastern Morocco during spring migration. – *J. Field Ornithol.* 86: 266–276.
- McKechnie, A. E. 2022. Regulation of body temperature: patterns and processes. – In: Scanes, C. G. and Dridi, S. (eds), *Sturkie's avian physiology*, 7th edn. – Academic Press, pp. 1231–1264.
- McKechnie, A. E. and Wolf, B. O. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. – *Biol. Lett.* 6: 253–256.
- Milne, R., Cunningham, S. J., Lee, A. T. K. and Smit, B. 2015. The role of thermal physiology in recent declines of birds in a biodiversity hotspot. – *Conserv. Physiol.* 3: cov048.
- Monge, O., Schulze, C. H., Dullinger, S., Fusani, L. and Maggini, I. 2022. Unshaded coffee imposes a heavier load on thermoregulation than shaded coffee for birds in a tropical mountainous region. – *Global Ecol. Conserv.* 36: e02117.
- Moreau, R. E. 1972. The Palaearctic-African bird migration systems. – Academic Press.
- Muggeo, V. M. 2009. Segmented: an R package to fit regression models with broken-line relationships. – *R News* 8: 20–25.
- Nicholson, S. E., Funk, C. and Fink, A. H. 2018. Rainfall over the African continent from the 19th through the 21st century. – *Global Planet Change* 165: 114–127.
- Nilsson, J.-Å., Molokwu, M. N. and Olsson, O. 2016. Body temperature regulation in hot environments. – *PLoS One* 11: e0161481.
- Noakes, M. J. and McKechnie, A. E. 2020. Phenotypic flexibility of metabolic rate and evaporative water loss does not vary across a climatic gradient in an Afrotropical passerine bird. – *J. Exp. Biol.* 223: jeb220137.
- Oswald, K. N., Lee, A. T. K. and Smit, B. 2018. Seasonal physiological responses to heat in an alpine range-restricted bird: the Cape rockjumper (*Chaetops frenatus*). – *J. Ornithol.* 159: 1063–1072.
- Paces, B., Waringer, B. M., Domer, A., Burns, D., Zvik, Y., Wojciechowski, M. S., Shochat, E., Sapir, N. and Maggini, I. 2021. Evaporative water loss and stopover behavior in three passerine bird species during autumn migration. – *Front. Ecol. Evol.* 9: 704676.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. – *Nature* 401: 877–884.
- Rappole, J. H. and Jones, P. 2002. Evolution of old and new world migration systems. – *Ardea* 90: 525–537.
- Safriel, U. N. 1995. The evolution of palearctic migration – the case for southern ancestry. – *Isr. J. Ecol. Evol.* 41: 417–431.
- Schmaljohann, H., Liechti, F. and Bruderer, B. 2007. Songbird migration across the Sahara: the non-stop hypothesis rejected! – *Proc. R. Soc. B* 274: 735–739.
- Schmidt-Nielsen, K., Hainsworth, F. R. and Murrish, D. E. 1970. Counter-current heat exchange in the respiratory passages: effect on water and heat balance. – *Respir. Physiol.* 9: 263–276.
- Smit, B., Harding, C. T., Hockey, P. and McKechnie, A. E. 2013. Adaptive thermoregulation during summer in two populations of an arid-zone passerine. – *Ecology* 94: 1142–1154.
- Smit, B., Zietsman, G., Martin, R. O., Cunningham, S. J., McKechnie, A. E. and Hockey, P. A. R. 2016. Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. – *Clim. Change Resp.* 3: 9.
- Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B. and Thomas, C. D. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. – *Oikos* 120: 1–8.
- Tieleman, B. I. and Williams, J. B. 1999. The role of hyperthermia in the water economy of desert birds. – *Physiol. Biochem. Zool.* 72: 87–100.
- Tieleman, B. I. and Williams, J. B. 2002. Cutaneous and respiratory water loss in larks from arid and mesic environments. – *Physiol. Biochem. Zool.* 75: 590–599.

- Vickery, J. A., Mallord, J. W., Adams, W. M., Beresford, A. E., Both, C., Cresswell, W., Diop, N., Ewing, S. R., Gregory, R. D., Morrison, C. A., Sanderson, F. J., Thorup, K., Van Wijk, R. E. and Hewson, C. M. 2023. The conservation of Afro-Palaearctic migrants: what we are learning and what we need to know? – *Ibis* 165: 717–738.
- Weathers, W. W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. – *Physiol. Zool.* 54: 345–361.
- Whitfield, M. C., Smit, B., McKechnie, A. E. and Wolf, B. O. 2015. Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. – *J. Exp. Biol.* 218: 1705–1714.
- Williams, J. B. 1996. A phylogenetic perspective of evaporative water loss in birds. – *Auk* 113: 457–472.
- Williams, J. B. and Tieleman, B. I. 2000. Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. – *J. Exp. Biol.* 203: 3153–3159.
- Williams, J. B. and Tieleman, B. I. 2005. Physiological adaptation in desert birds. – *BioScience* 55: 416–425.
- Wojciechowski, M. S., Kowalczyńska, A., Colominas-Ciuró, R. and Jefimow, M. 2021. Phenotypic flexibility in heat production and heat loss in response to thermal and hydric acclimation in the zebra finch, a small arid-zone passerine. – *J. Comp. Physiol. B* 191: 225–239.
- Wolf, B. O. and Walsberg, G. E. 1996. Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. – *J. Exp. Biol.* 199: 451–457.