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Abstract

European-African long-distance migratory birds cross the Sahara Desert twice a year. Generally, they fly during the night and stop over during the day. Once landed, they have to decide whether to refuel or to rest. In general, xerophilic bird species breeding and / or overwintering in arid habitats cross the desert with rather low fat stores and actively forage during stopover, while mesophilic species often carry enough fat reserves to cross the desert without refuelling en route. However, the underlying physiological adaptations causing this difference remain unclear. In this study, I measured cutaneous water loss (CWL) and temperature of panting onset of three closely related trans-Saharan migratory songbird species to test the hypothesis that species which actively refuel in the desert have a lower surface-specific CWL and a higher temperature of panting onset. These adaptations would allow them to sustain higher levels of activity in a desert environment and to extend the daily time window for foraging while keeping a low risk of dehydration. As expected, the mesophilic Blackcaps had a significantly higher surface-specific CWL and a lower temperature of panting onset than the xerophilic Lesser Whitethroats and Willow Warblers. This result corresponds to prior studies which showed that Willow Warblers actively refuel en route and carry relatively low fuel loads despite being a mesophilic species. This study demonstrated for the first time that surface-specific CWL and the temperature of panting onset coincide with the observed refuelling strategies in three trans-Saharan migratory songbird species. Thus, physiological constraints for maintaining a healthy water balance may be of major importance in the evolution of species-specific refuelling strategies in extremely arid climate conditions. This knowledge will provide valuable insights into the species' response to climate change and contribute to the urgent need for research about distribution patterns, habitat use and feeding ecology of declining trans-Saharan migratory bird species at their staging sites.

Keywords: water balance, cutaneous water loss, temperature of panting onset, refuelling strategies, arid habitat adaptations, Sahara, warblers

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1. Introduction

Every year around 2.1 billion European-African migratory passerine and near-passerine birds cross the Sahara during their autumn migration to reach their wintering grounds further south in Africa (Hahn et al. 2009). Hence, they face a large ecological barrier with extremely arid climate conditions. Radar observations have shown that most songbirds do not overfly the Sahara in one non-stop flight, neither in spring nor in autumn, but rather fly at night and stop over during the day (Schmaljohann et al. 2007). On average, the ground speed of migrating songbirds crossing the Sahara is 50 km/h (Schmaljohann et al. 2007), which confirms an estimation of the crossing duration of 40 to 60 h, since the desert is between 2200 km and 2500 km wide (review: Bairlein 1988). Thus, migratory passerines are forced to spend at least a few days in areas where food and water are scarce and extremely high temperatures may occur, since they are not able to cross the desert within a single non-stop flight. The observed migration pattern of nocturnal flight and stopover during the day, as well as the observed ground speed were the same in passerines crossing the Negev desert in Israel, just north of the Sahara-Arabian desert belt (Bruderer 1994). In addition, the same study provides reason to assume that the migration strategy does not change between the desert regions in eastern Egypt (belonging to the Sahara-Arabian desert belt) and the Negev desert (Bruderer 1994).

Once landed, the birds have to decide whether to simply rest or to use the time for foraging (Biebach et al. 1986, Bairlein 1988, Lavee et al. 1991, Bairlein 1992, Jenni-Eiermann et al. 2011). This decision is dictated principally by the amount of stored fat, which is the primary energy source for long-distance flight of migratory birds (Jenni & Jenni-Eiermann 1998, McWilliams et al. 2004). Birds that carry enough fat stores to continue their migration will not forage during their desert stopover (Bairlein 1988). Accumulating large fat deposits prior to the Sahara crossing might be beneficial, since stopover sites that enable foraging are scarce in the Sahara (Moreau 1972). On the other hand, flying with little stored fat increases manoeuvrability and decreases the energetic cost of transport (Pennycuick 2008). Hence, if a bird accumulates large fat deposits prior to the Sahara crossing, flying may be more difficult, but the animal will probably not be forced to find one of the scattered oases that offer refuelling opportunities. In this case, a shaded location anywhere in the desert will serve as a suitable opportunity to spend the diurnal stopover, while keeping the risk of dehydration low (Biebach et al. 1986, Bairlein 1988, Schmaljohann et al. 2007, Jenni-Eiermann et al. 2011).

Observational studies showed that the refuelling strategies used and the resulting body condition observed at desert stopover sites indeed vary from species to species (Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013, Maggini et al. 2015). These differences appear to be linked to adaptations to arid habitats: while species that can be considered rather xerophilic in their breeding habitat (e.g. many Mediterranean species) and spend the winter in the Sahel rely on refuelling in the desert, mesophilic species from central and northern Europe that winter in African subtropical forests rather gain their fat reserves prior to the desert crossing and use desert sites only for short-term resting (Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013, Maggini et al. 2015). However, while most investigated xerophilic species seem to follow this refuelling strategy pattern, the observed refuelling strategies are more diverse in mesophilic species (Jenni-Eiermann et al. 2011, Hama et al. 2013). Interestingly, studies in Israel during autumn migration showed that the foraging behaviour and fat accumulation of migratory Blackcaps (Sylviidae: *Sylvia atricapilla*, a mesophilic species) at a desert stopover site is influenced by water availability while this is not the case in Lesser Whitethroats (Sylviidae: *Sylvia curruca*, a xerophilic species) (Shirihai et al. 2001, Sapir et al. 2004, Tsurim et al. 2008). In addition, Lesser Whitethroats are able to achieve the same fuel deposition in a wide range of habitats, while this appears to be restricted to a rather specific habitat type offering ideal feeding conditions, such as high amounts of lipid- and fat-rich fruits, in Blackcaps (Sapir et al. 2004). These findings suggest that adaptations to arid environmental conditions may facilitate en route refuelling in Lesser Whitethroats, which is in line with the observed refuelling strategies of other xerophilic bird species (Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013, Maggini et al. 2015). While the underlying physiological mechanisms or adaptations causing this pattern are currently not known, the studies by Sapir et al. (2004) and Tsurim et al. (2008) point out that the availability of water and maintenance of birds' water balance can have a crucial influence on refuelling strategies of migratory songbirds. Total evaporative water loss (TEWL) is the main source of water loss to the environment in small passerines and can be five times greater than their urinary faecal water loss (Bartholomew 1972, Dawson 1982, Williams & Tieleman 2000). It is the only physiological cooling mechanism in birds and is the sum of the bird's respiratory water loss (RWL) and its cutaneous water loss (CWL) (Dawson & Whittow 2000, review: Williams & Tieleman 2005). CWL accounts for approximately 50 % of TEWL in a small desert passerine (Wolf & Walsberg 1996), 50 % to 70 % of TEWL in four different lark species (Tieleman & Williams 2002) and on average

65 % of TEWL in 12 temperate-zone passerine species when measured in their thermoneutral zone (Ro & Williams 2010). However, when exposed to high temperatures, passerines increase both their CWL and RWL, but the latter to a much stronger extent, often via active panting, so that RWL is the main avenue of water loss when the bird is exposed to heat stress (Wolf & Walsberg 1996, Tieleman & Williams 2002). For instance, in the Verdin (Remizidae: *Auriparus flaviceps*), CWL increases by 122 % from 30 °C to 50 °C but only accounts for 14 % of TEWL at 50°C because RWL increases by 3052 % in this temperature range (Wolf & Walsberg 1996). In four different lark species CWL accounts for 25 % of TEWL at 40°C and only rises by 45 % to 72 % between 25°C and 40°C in two of those species, while in the others there is no significant increase of CWL (Tieleman & Williams 2002). However, RWL rises significantly in this temperature range in all species, on average by 666.5 % (Tieleman & Williams 2002). Birds experiencing such high rates of TEWL may have difficulties to maintain body temperatures below critical values while keeping their body adequately hydrated (Webster 1991). Thus, it is an obvious challenge, especially for diurnal birds in desert environments, to reduce TEWL while remaining within their normothermic range. Interestingly, it could be shown that birds from deserts have a lower TEWL than species from mesic areas (Williams 1996). More precisely, the lipid composition of the stratum corneum of the skin of different lark species inhabiting either arid or mesic habitats differs and influences their CWL such that the desert species have a 29 % lower surface-specific CWL than their relatives from mesic habitats in their thermoneutral zone (Tieleman & Williams 2002, Haugen et al. 2003, a, b). Similarly, different populations of House Sparrows (Passeridae: *Passer domesticus*) living either in a desert environment or in a mesic habitat differ in the composition of the stratum corneum as well as in their surface-specific CWL (Muñoz-García & Williams 2005). This pattern was also found in 20 different bird species covering a gradient from desert to mesic species (Champagne et al. 2012). A reduction of RWL in desert birds was discussed, but no experimental evidence could yet be found (Williams & Tieleman 2005). However, it was found that species which do not drink, but rely on food as their water source, start panting at a higher temperature than drinking bird species in the Kalahari Desert (Smit et al. 2016). The ambient air temperature at which RWL starts to increase sharply as a mechanism to avoid hyperthermia (hereafter: temperature of panting onset) sets the time boundaries in which a bird can stay active during the day in a desert environment without having to cope with the massive water loss implied in cooling the organism via RWL (Smit et al. 2016). Interestingly, the non-drinking species

use wing-drooping as an alternative heat dissipation behaviour to a greater extent than drinking species, and use it to delay the onset of panting, probably as a result of selective pressure to reduce water loss from evaporative cooling in an arid environment (Smit et al. 2016).

Based on these findings, I hypothesize that trans-Saharan migratory songbird species differ in their stopover strategies because they have different physiological adaptations to save water in arid climate conditions. These adaptations may result from the aridity of their breeding or overwintering grounds. In particular, I predict that bird species which actively refuel en route have a lower surface-specific CWL and a higher temperature of panting onset than species which rely on pre-departure fattening for their desert crossing. Both adaptations could ultimately enable the respective bird species to be more active in arid climate conditions without experiencing critically high rates of evaporative water loss. To my knowledge, neither surface specific CWL nor the temperature of panting onset has so far been measured in long-distance migrants. If this hypothesis is true, species which breed and winter in arid habitats (xerophilic species) would have a lower surface-specific CWL and a higher temperature of panting onset, which enables them to rely on en route refuelling in desert habitats to a greater extent than species inhabiting mesic breeding and wintering grounds (mesophilic species). Therefore, lower surface-specific CWL and a higher temperature of panting onset in xerophilic bird species could provide a physiological explanation for the different refuelling strategy patterns observed in previous studies (Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013, Maggini et al. 2015).

In this study, I measured and compared surface-specific CWL of migratory Blackcaps (a mesophilic species) and Lesser Whitethroats (a xerophilic species) staging during their autumn migration at a stopover site in the Negev desert, Israel. This closely related species pair was chosen because Sapir et al. (2004) and Tsurim et al. (2008) showed that water availability influences fat accumulation and feeding behaviour of Blackcaps at a desert stopover site while this was not the case in Lesser Whitethroats. In addition, the Willow Warbler (*Sylviidae: Phylloscopus trochilus*) was also included in this study. Despite being a rather mesophilic species, Willow Warblers were observed to actively forage at a desert stopover site in spring (Maggini et al. 2015) and spend more time foraging at desert stopover sites during spring migration than the likewise mesophilic Blackcaps (Jenni-Eiermann et al. 2011). Hama et al. (2013) reported that Willow Warblers carry relatively

low fuel loads compared to other mesophilic species, such as Blackcaps, during autumn migration at a desert oasis. Thus, according to my hypothesis, I predicted that Blackcaps would have a higher surface-specific CWL than Lesser Whitethroats and Willow Warblers.

An additional aim of this study was to determine whether an area offering the opportunity to drink water is a more attractive stopover site for individuals with relatively high surface-specific CWL. I predicted that surface-specific CWL values within all three species would be higher when water was provided to the migrants at artificial drinking sites.

Finally, I recorded the temperature of panting onset and compared this measurement among the same three species. Smit et al. (2016) showed for 30 bird species from the Kalahari Desert that the temperature at which 50 % of the observed individuals of one bird species started panting is negatively correlated with body size and the individuals' activity in hot conditions. In addition, it is higher in species that do not drink but mostly rely on food as their water source. Thus, they concluded that the evaporative cooling demands and the trade-off between activity and water loss are more pronounced in larger birds, due to their smaller surface area / volume-ratio (Weathers 1981, Smit et al. 2016). In my study, I measured temperatures of panting onset in a respirometry setup, where the individual birds were immobilised to a high degree and thus their activity most likely did not influence the measurements. Blackcaps are the largest of the three study species and rely on drinking water for refuelling to a higher extent than Lesser Whitethroats (Sapir et al. 2004). Willow Warblers forage more actively in extremely arid climate conditions than Blackcaps (Jenni-Eiermann et al. 2011) and rely – in contrast to Blackcaps – largely on en route refuelling during desert crossing (Hama et al. 2013). Therefore, I predicted that Blackcaps would have a lower temperature of panting onset than Lesser Whitethroats and Willow Warblers.

2. Materials and Methods

2.1. Study period and Study sites

Data was collected in September 2017 (6.9.2017 - 26.9.2017) and September 2018 (4.9.2018 - 27.9.2018) at suitable stopover sites for migratory songbirds in the Negev desert, Israel. This country is situated within the eastern Mediterranean flyway, where large numbers of migratory birds on their way from / to their breeding grounds in Europe and Asia to / from their wintering grounds in Africa concentrate every autumn and spring (Curry-Lindahl 1981, review: Frumkin et al. 1995).

In September 2017, I conducted the fieldwork around Lake Yeruham (site A: 30.988568°N, 34.897029°E, site B: 30.983554°N, 34.900815°E), which covers an area of about 1.5 km² and is situated in the northern part of the Negev desert. Site A was close to the shore of the lake and the vegetation around the mistnets was dominated by *Phragmites australis*, *Tamarix aphylla* and *Tamarix nilotica* as well as *Xanthium strumarium*. Site B was around 600 m to the south-east of the lake, at man-made stone terraces where the most common plant species were *Acacia raddiana*, *Atriplex halimus*, *Morus sp.* and *Phragmites australis*. In addition, I caught some of the study birds at Midreshet Ben Gurion (30.857913°N, 34.781929°E), Sde Boker, located around 18 km south-west of Lake Yeruham. At this site, the nets were set up in an experimental pistachio plantation (1.7 ha) situated at the edge of the settlement, and the vegetation was dominated by *Acacia saligna*, *Atriplex halimus*, *Pistacia atlantica* and *Pistacia lentiscus*. In September 2018, I collected all data at Midreshet Ben Gurion, Sde Boker. At all three sites, I found suitable and permanent drinking places for birds within 500 m of the nets (site A: Lake Yeruham, sites B & C: freshwater reservoirs), and small puddles of water were likely available much closer to the sites throughout the whole study period due to frequent leakages of water pipes and agricultural activities in the sampling areas.

2.2. Study species

In this study, I investigated Blackcaps, Lesser Whitethroats and Willow Warblers. These three species differ in body mass and wing length (Shirihai & Svensson 2018, own data in Tab. 1). While Blackcaps and Willow Warblers are mesophilic bird species (Baker 2010, Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013), Lesser Whitethroats are rather xerophilic at least in their wintering grounds, where they prefer savannas with

scattered trees or thornbush savanna (Snow & Perrins 1998, Shirihi et al. 2001, Sapir et al. 2004). In contrast, Blackcaps and Willow Warblers winter mainly in forested areas, although they are both highly adaptable (Snow & Perrins 1998, Shirihi et al. 2001, Sapir et al. 2004, Baker 2010). Even though both species are mesophilic, they have different refuelling strategies: while migratory Blackcaps rely mainly on pre-departure fattening rather than refuelling in desert oases for their spring as well as autumn migration, Willow Warblers spend more time foraging en route and carry relatively low fuel loads (Jenni-Eiermann et al. 2011, Hama et al. 2013, Maggini et al. 2015). The refuelling strategy of Lesser Whitethroats on the other hand is not thoroughly studied and has - to my knowledge - not yet been directly compared with Blackcaps and Willow Warblers.

Table 1: Mean body mass and wing length (mean \pm 1 standard deviation) of the songbird species measured in this study.

Species	body mass (g)	wing length (mm)
Blackcap (<i>S. atricapilla</i> , n = 205)	17.9 \pm 2.5	76.7 \pm 2.0
Lesser Whitethroat (<i>S. curruca</i> , n = 118)	12.7 \pm 1.7	67.0 \pm 2.1
Willow Warbler (<i>P. trochilus</i> , n = 134)	9.0 \pm 1.1	67.2 \pm 3.2

2.3. Bird capture

During the study I trapped birds using mistnets of 16 mm mesh size (length: 12 or 18 m, height: 2.5 m). In 2017, capture started when the mistnets were opened at 5:30 am, and lasted until at least five birds of the study species had been caught. Then the nets were closed and trapping stopped. Two to ten mistnets were deployed simultaneously, depending on the number of local helpers available. I played song recordings of Lesser Whitethroats and Willow Warblers via speakers positioned below the nets to attract the target species and facilitate their capture. I did not use vocalisations of Blackcaps because the trapping success of this species was already sufficient without tape luring. I marked all caught birds with metal rings, identified them to species level and determined their sex and age (Svensson 1992, Winkler & Jenni 2007, Demongin 2016, Svensson et al. 2009). Next, I estimated visual fat scores on a scale from 0 (no fat visible) to 8 (fat covering the entire ventral side of the bird) following Kaiser (1993), and the development of the flight muscle on a scale from 0 (muscle concave around the sternum) to 3 (muscle bulging, sternum no longer visible) (Bairlein et al. 1995). Then, I measured wing length (precision \pm 0.5 mm, method: maximum chord, Svensson 1992), tarsus length, skull length and skull width, using a calliper (precision: \pm 0.1 mm). Finally, I weighed the birds using a portable scale (precision: \pm 0.1 g). After these measurements, I held the birds in cotton bags, brought them to a small laboratory and measured them in a respirometry

setup (see below). They were kept in the shade throughout the whole procedure. The choice of the mistnetting site for each individual day was dictated by the availability of local ornithologists and the trapping success of the two rarer target species (Lesser Whitethroat and Willow Warbler) in the previous days.

In 2018, captures started at 5:30 and lasted until the air temperature exceeded 30 °C in the shade. Usually, captures were stopped between 11:00 am and 1:00 pm. I used 19 mistnets but no tape luring, because the study birds were captured within a local constant effort ringing project, which should not be disturbed. All caught birds were measured in the same way as 2017, but visual fat scores were estimated after the measurement of surface-specific CWL to avoid any unnatural moistening of the birds' skin. In addition, the time at which each bird was extracted from the mistnet was recorded. All focal birds were held in cotton bags and kept in the shade between extraction from the net and measurement of surface-specific CWL (see below). They were released immediately after the measurement. In both seasons, all individuals that did not belong to the focal species were ringed and released after the standard measurement procedures.

2.4. Field CWL measurements

I measured surface-specific CWL of the study species during the field season of 2018. During the whole procedure, I wore laboratory latex gloves to avoid any moistening of the bird's skin by human sweat. First, I extracted the bird from the bird bag and recorded time, air temperature and air moisture at the beginning of the measurement using a mobile digital thermo- and hygrometer (NeKan EU). Then I measured the bird's body temperature by pressing a K-Type thermocouple against its bare skin at the right wing joint, while opening the wing by hand. The measurement was read by a digital thermometer (Signstek Dual Channel). As soon as I had positioned the sensor correctly, I folded the wing and pressed it slightly against the electrode in its natural position. I noted the temperature as soon as the measurement was stable for some seconds. After that, I exposed the unfeathered parts of the bird's skin under its left wing by striking apart the feathers which cover this part of the body. I conducted this procedure with the fingers and not by blowing on the feathers to avoid any unnatural moistening of the bird's skin prior to the measurement. Once I exposed a flat, naked skin area of at least 50 mm², I started the measurement procedure. I took five surface-specific CWL measurements, using a factory calibrated VapoMeter™ (Delfin Technologies, Ltd., Kuopio, Finland, du Plessis et al. 2013, hereafter: Vapometer), following the instructions provided by the device on its screen and

the user manual. I waited one minute before taking the first measurement. This was necessary because the first measurement was consistently higher than the following measurements when starting immediately (pers. observation). My data suggested that the bird's skin is relatively moist right after exposure and it takes some time until repeatable and reliable measurements can be taken using the Vapometer. To take a measurement, I used the small adapter for the Vapometer, which covers 16 mm² of skin (Muñoz-Garcia & Williams 2007, Muñoz-Garcia et al. 2012). After the start of the device and a calibration phase, I pressed it gently against the exposed skin patch of the bird. One measurement took about 20 to 30 s. After a subsequent ventilation phase, I was able to obtain the next measurement. The measurement unit was g H₂O/(m² skin*h). After five measurements, I estimated the visual fat scores of the bird (Kaiser 1993) and then released the bird. I conducted the whole process, from the bird's extraction from the bird bag until its release, in the shade. It took between 7 to 10 minutes per bird. If I pressed the device too tightly against the bird's body, the measurement was extremely high and was subsequently repeated. I did the same when the bird moved a lot during the procedure and I could therefore not guarantee constant skin contact of the adapter. I used the Vapometer only on optically healthy, rather flat parts of the skin without wounds, scars or any other aberrant appearances. Every bird could be identified individually by its unique metal ring number and was only measured once in the course of this study.

2.5. Water manipulation

In 2018, during the collection of the field CWL data, water availability was manipulated at the mistnetting site. On 4.9.2018, five puddles of water were created using waterproof plastic sheets and fresh tap water. They were placed in the shadow of large bushes with a distance of 6 to 12 m to the closest mist net, with the exception of one puddle which was dug directly below a net. They had a diameter of 70 to 100 cm and a water depth of 3 to 5 cm was kept constant for five consecutive days. A large stone and some twigs in every puddle were provided to offer comfortable drinking places for small migratory songbirds. In addition, the plastic sheets were covered with soil before the puddles were filled to achieve a more natural setting. After the first period with filled puddles, they were kept dry for five days and then the procedure was repeated in this alternating manner until the end of the field season. The water regime change was always conducted at 10 pm. In total, water was provided on 13 sampling days, while the puddles were dry on 11 days.

One additional artificial waterbody was already present at the site before the start of the study, which was about 150 cm long and 70 cm wide, was built of concrete and had vertical walls. This reservoir was most likely not a suitable drinking place for any birds and none were ever observed to use it for drinking or bathing. However, in order to manipulate the water availability for birds at the site as consistently as possible, it was covered with wire mesh (0.5 cm mesh size) when the experimental ponds were dry and uncovered when water was provided at the experimental puddles.

2.6. Respirometry

To measure the temperature of panting onset, as well as RWL and CWL, I used a flow-through respirometry setup in 2017. The bird was held in a respirometry chamber divided

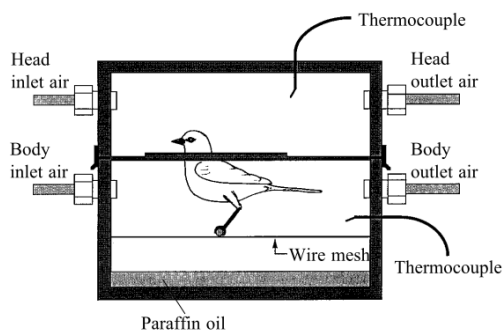


Figure 1: Two-compartment metabolic chamber to separately measure respiratory water loss and cutaneous water loss of a bird. Image from Wolf & Walsberg (1996).

into two sections, its head protruding through a latex membrane forming the barrier between the two sections (Fig. 1, Wolf & Walsberg 1996). This allowed separate measurements of CWL (the bottom part of the chamber) and RWL (the upper part of the chamber). When using this method, cutaneous evaporation from the head is recorded together with respiratory evaporation. This imprecision can be corrected mathematically by

subtracting the estimated cutaneous evaporation from the head's surface (Wolf & Walsberg 1996). For this reason, I recorded skull length and width. The upper section of the chamber was 14 cm high and the bottom section had a height of 18 cm. Both chambers were 25 cm wide and 25 cm long. The respirometry chamber was completely made out of Plexiglas. In the bottom part of the chamber, the bird could perch on an iron mesh. Below the mesh, a layer of 1 cm paraffin oil caught the bird's droppings to prevent the droppings' water loss from influencing the measurements. Air was pulled through the chamber with two separate flows, one for the upper and one for the bottom part of the chamber. Before entering the chamber, the airflows passed through a column of Drierite™ to dry. The air was then pumped into a custom-made analyser (OxBox 2, Institute of Wildlife Biology, University of Veterinary Medicine Vienna, Austria) for measurement of O₂ consumption, while a subset of air from both airflows ran through water vapour analysers (Q-S 161, Qubit Systems, Kingston, Canada) before being merged with the rest of the flow that entered the OxBox. After the O₂ measurement, the

air was expelled into the environment. Tygon R-3603 vacuum tubing (8 mm diameter) was used throughout the whole system.

I performed the measurements using a sliding heating protocol. To achieve this, I placed the respirometry chamber with the bird inside a cooler / heater box (35 l MobiCool G35). I started the measurement at ambient temperature every day and set the flow rate through the chamber to 200 l/h to enable a quick washout of the humidity accumulated in the chamber during the positioning of the bird. Preliminary tests without a bird showed that > 95 % of the humidity was washed out within 15 minutes. After the washout period, I decreased the flow to 40 l/h and the heating was started. Thus, the temperature progressively increased during the procedure. I continued the measurement for no less than five minutes after noticing a sharp increase in water vapour production in the upper chamber, which was a clear indication of the onset of panting. A custom-made temperature logger inside the respirometry chamber recorded ambient temperature every minute (precision: ± 0.1 °C). On average, one measurement took one hour. At the end, I provided the bird with some water and subsequently released it, while the respirometry chamber as well as the cooler / heater box were cooling down. Then I sampled the next bird in the same way, but I switched the cooler / heater box to maximum cooling during the 15-minute washout period to again reach a starting temperature within the thermoneutral zone for the next bird. This was necessary because the box would not cool down quickly enough by itself during the time between two measurements. This protocol was the same for all sampling days in the field season of 2017.

In addition, I conducted a dry run without a bird at least once per day to establish a daily baseline measurement of the remaining moisture in the system after washout, against which I could assess the measurements recorded in the setup containing a bird. Drierite™ does not remove 100 % of the moisture in the incoming flow, therefore it is not correct to assume that the incoming air is completely dry. During the dry runs, I performed the measurement procedure and all manual operations with the box in the same way as if there had been a bird inside. On the last day of the field season in 2017, I conducted ten of these dry runs consecutively, to be able to estimate how the baseline changes from one measurement to the next.

2.7. Data analysis: Field CWL measurement and Water manipulation

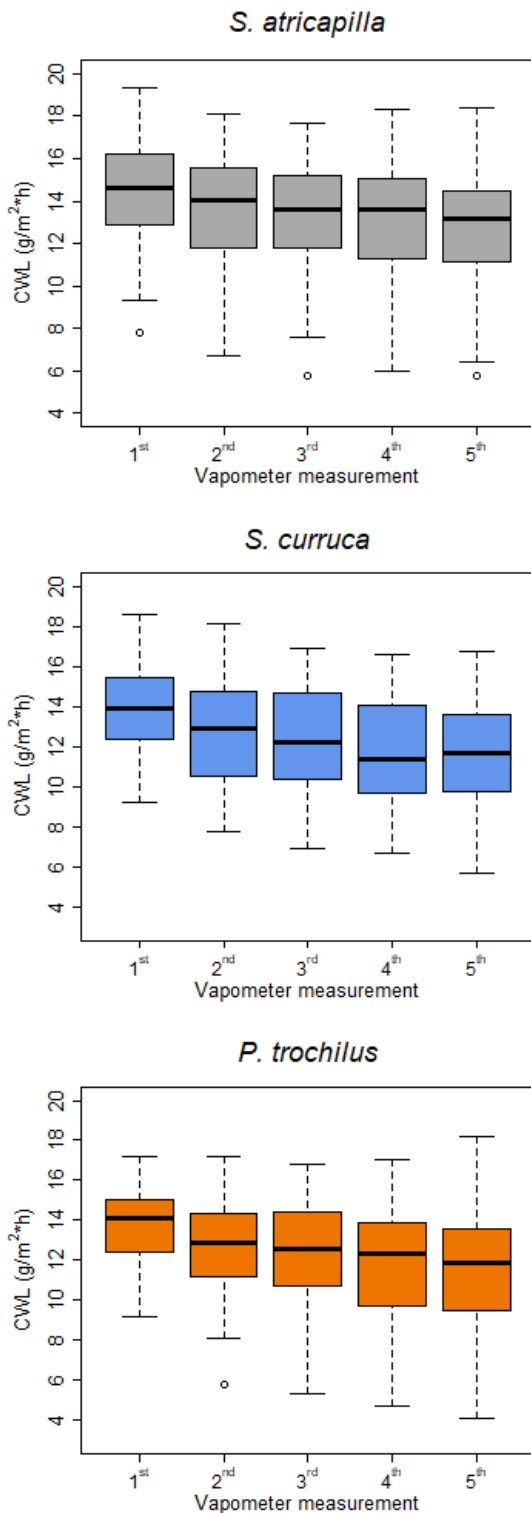


Figure 2: Comparisons of the absolute Vapometer measurement values in five consecutive measurements. The average of the 3rd, 4th and 5th measurement was chosen as response variable in this study. Blackcap (*S. atricapilla*): n = 144, Lesser Whitethroat (*S. curruca*): n = 73, Willow Warbler (*P. trochilus*): n = 101

I conducted the whole data analysis with the software R 3.5.1 (R Core Team 2018). In addition to base R, I used the packages “multcomp”, “segmented”, “car” and “mgcv” (Hothorn et al. 2008, Muggeo 2008, Fox & Weisberg 2011, Wood 2017). To assess differences in surface-specific CWL between the focal species, I used the average of the three lowest Vapometer measurements as response variable, because the measured values decreased gradually from the first to the fifth measurement, reaching a plateau between the third and fifth (Fig. 2). I had to account for the changing environmental conditions during every sampling day in the analysis, because the measurements changed notably and consistently between the moist, cold mornings and the hot, dry hours around noon. It is known that ambient temperature as well as air moisture influence CWL of passerines (Wolf & Walsberg 1996, Tieleman & Williams 2002, Gerson et al. 2014, Champagne et al. 2016). Unfortunately, I was not able to manipulate those two variables independently from each other in this study and thus they are highly correlated. I used ambient air moisture as predictor variable rather than temperature, because temperature does not influence CWL in the observed way and extent (Wolf & Walsberg 1996, Tieleman & Williams 2002, Champagne et al. 2016). The cited studies reported constant levels of CWL below 30 °C for six different passerine species, and a slight increase in CWL between 30 °C and 35 °C in some species, while in others this rise occurs

between 35 °C and 40 °C (Wolf & Walsberg 1996, Tieleman & Williams 2002, Champagne et al. 2016). All measurements I obtained were at 35 °C or less and I recorded only 8.6 % of those (31 of 362) at ambient temperatures higher than 30 °C. In addition, I did not find an increase in surface-specific CWL values between 30 °C and 35 °C, but I did between 20 °C and 28 °C. Consequently, I am confident that changes in ambient air moisture rather than ambient temperature caused the observed pattern according to the cited literature. I compared surface-specific CWL between the species with a linear regression model. I used surface-specific CWL values as response variable and air moisture (in a quadratic polynomial term), species, and the two-way interaction of those two terms as explanatory variables. I calculated a 4th-root transformation of the variable air moisture beforehand to improve the non-tendency assumption in the model's residuals. After examining the results, I recalculated the same model without the non-significant interaction term to run a post-hoc multiple comparison of moisture-corrected, species- and surface-specific CWL means using Tukey contrasts. For this analysis, I used the function "glht" from the "multcomp" package (Hothorn et al. 2008). I checked both models for violations of the underlying assumptions using the diagnostic plots described in Crawley (2013). In addition, I calculated the local maxima of the three species-specific relationships between surface-specific CWL and air moisture, to determine under which ambient air moisture conditions CWL reaches its maximum. I obtained these values using the "predict" function in base R (R Core Team 2018). I used the residuals of the model with the interaction term as response variable in three additional linear regression models, to determine if residual surface-specific CWL (hereafter: residual CWL) was significantly influenced by any of the following variables: water in the puddles (no / yes), date, ambient air temperature, waiting time in the bag (CWL measurement time - extraction time from the net), body temperature, size-corrected body mass, age and sex (only testable in Blackcaps, because Willow Warblers and Lesser Whitethroats do not show obvious features for sex identification in the field). I calculated size-corrected body mass using the formula: $[(\text{body mass} / \text{wing length}) * (\text{mean wing length of the species})]$. I eliminated non-significant predictor variables one by one, beginning with the variable with the highest *p*-value. In the end, I only retained the variables in the model with a significant effect on residual CWL and I checked the diagnostic plots for major violations of the model assumptions (Crawley 2013). Finally, I calculated the correlation between visual fat score estimation and size corrected-body mass for every species (Pearson's *r*).

I examined all combinations of predictor variables used in the described models for strong multicollinearity using scatterplot matrices and correlation coefficients (Pearson's r). All calculated $|r|$ - values were below 0.7, which is considered to be a suitable indicator value above which multicollinearity severely distorts model estimations (review: Dormann et al. 2013).

2.8. Data analysis: Respirometry

The water vapour analysers I used in the respirometry setup provided relative humidity values in % (RH). To get the absolute CWL (g/h) and RWL (g/h) of the measured birds, I transformed RH into absolute humidity (AH) using the formula $AH (g/m^3) = C * P_w / T$, where C is a constant of 2.16679 gK/J, P_w the vapour pressure in Pa, and T the temperature in K. I calculated P_w as P_{ws} (saturation vapour pressure in hPa) * RH. P_{ws} was obtained using the formula $P_{ws} = A * 10^{[m * T / (T + T_n)]}$, where A , m and T_n are constants (respectively 6.1164341, 7.591386, and 240.7263 for temperatures between -20 °C and $+50$ °C), and T was the temperature in °C. I took these formulas from Wagner & Pruß (2002). I calculated CWL and RWL by multiplying AH from the bottom and the upper chamber by the flow rate and adjusting the units. I used the average values during a period of 500 seconds where the measurement was constant. Baseline air humidity was subtracted from these values to obtain CWL and RWL values. To obtain baseline air humidity I took values measured during the daily dry runs (see above). Since Drierite™ was not consistent in providing a constant baseline humidity, I modelled these values to predict baselines at any given time when the experiments were conducted. To do this, I used a generalized additive modelling approach (GAM) with air humidity of the dry run as a response variable, and date and time of day as explanatory variables. I then took the predicted values from this model at any date and time of the experiments with birds to be subtracted from the measured values for CWL and RWL. However, these calculations yielded highly doubtful outcomes in several cases, such as negative absolute RWL and CWL values. The reasons for this outcome are not clear, but it is possible that the variation in water retention by the Drierite™-columns was much larger and unpredictable, so that the GAM-predicted values were not as close to reality as expected. Other possible factors were the use of a Plexiglas chamber and of Tygon tubing that can deliver imprecise humidity measurements (Lighton 2008). Thus, due to the unreliability of the measurements, I did not conduct any of the planned further analyses of CWL, RWL and O₂ consumption based on this dataset and consequently these data will not be mentioned

further in this study. However, I included the analysis of the temperature of panting onset here, because the estimation of this temperature is not affected by the described difficulties of baseline estimation.

I analysed species-specific differences in the temperature of panting onset using the software R 3.5.1 (R Core Team 2018). I synchronized the ambient temperature measurements recorded by the thermologger with the RWL measurements taken by the water vapour analysers to obtain one value of RWL and its according temperature every minute. Then, I excluded the first 25 minutes (15 minutes washout + 10 minutes equilibrium establishment) of the measurement. Finally, I determined the breakpoint in the curve between the 26th minute of the measurement procedure and its end using the “segmented” function provided by the “segmented” package (McKechnie & Wolf 2009, Whitfield et al. 2015). I used the calculated breakpoint as the temperature of panting onset for every individual. Sometimes the linear increase in RWL after the onset of panting became exponential towards the end of the measurements: I removed such points prior to the calculation of the segmented regression due to their high leverage on the estimate. Birds failing to show a clear breakpoint were not included in the analysis (12 out of 88). This was often the case when the cooling provided by the cooler / heater box during the washout phase was not sufficient to lower the temperature in the respirometry chamber below the temperature of panting onset of the next bird. I compared the temperatures of panting onset between species using a one-way ANOVA, because the normality assumption was met, as was the homogeneity of variances between the samples (Levene’s Test from medians: $F_{2,73} = 0.473$, $p = 0.625$). I used a Tukey HSD post-hoc test to examine species-specific differences at a 95 % confidence level and relied on adjusted p -values taking the multiple comparisons into account for interpretation.

3. Results

3.1. Field CWL measurements and Water manipulation

In the course of this study, I obtained 362 surface-specific CWL measurements from the three study species (Blackcap: $n = 165$, Lesser Whitethroat: $n = 89$, Willow Warbler: $n = 108$).

Surface-specific CWL was influenced by ambient air moisture in all three species and differed significantly between the species (linear model: Fig. 3, Tab. 2), but the relationship between ambient air moisture and surface-specific CWL was similar in all species, since the interaction between the predictor variables species and air moisture was not significant (Tab. 2). In general, surface-specific CWL increased with decreasing air moisture, reached a maximum at medium moisture conditions and decreased again when the air became drier (Fig. 3, Tab. 3). Blackcaps had a higher surface-specific CWL than Lesser Whitethroats (Tukey contrasts: adj. $p = 0.002$) and Willow Warblers (Tukey Contrasts: adj. $p = 0.009$), which did not differ in their respective surface-specific CWL (Tukey contrasts: adj. $p = 0.823$).

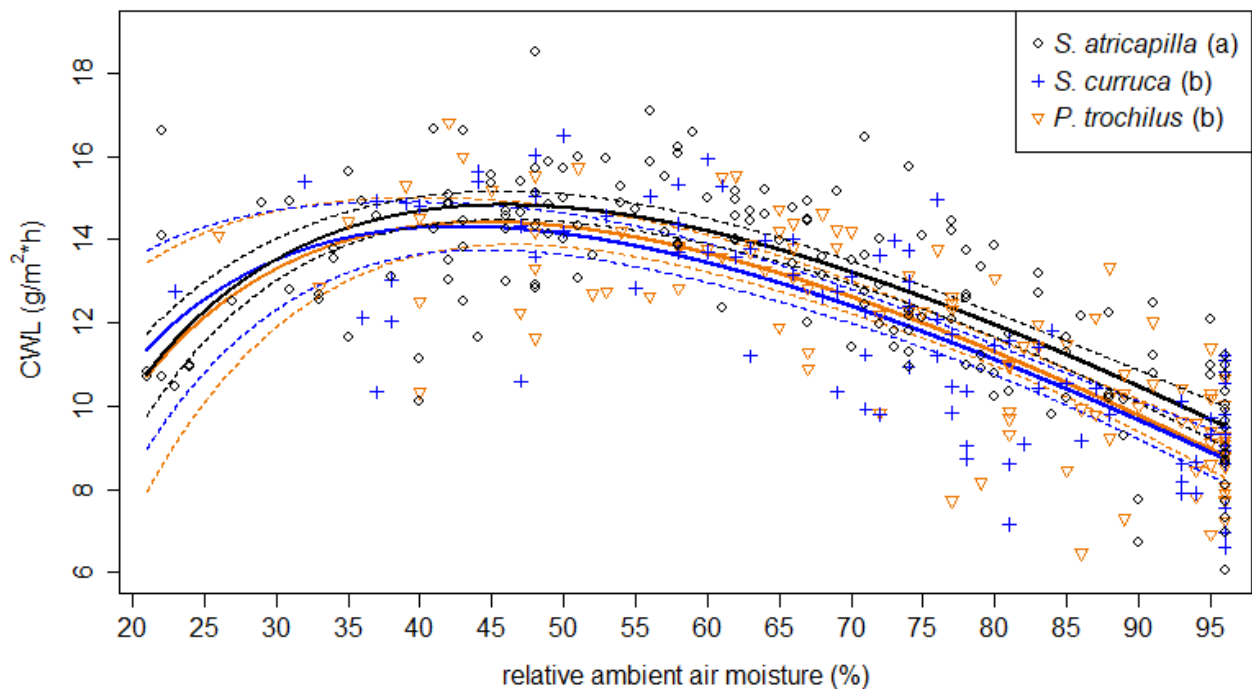


Figure 3: Relationship between relative ambient air moisture and surface-specific cutaneous water loss (CWL) in three trans-Saharan migratory songbird species. Species marked with the same letters (a, b) are not significantly different (Tab. 2, Tab. 3). Dashed lines represent 95 % confidence intervals for the solid species-specific regression lines. Blackcap (*S. atricapilla*, black, circles): $n = 165$, Lesser Whitethroat (*S. curruca*, blue, crosses): $n = 89$, Willow Warbler (*P. trochilus*, orange, triangles): $n = 108$.

Table 2: Outcome of a linear model with surface-specific cutaneous water loss (CWL) as response variable. Air moisture was used as linear and quadratic term. The interaction term is included to show that there is no species-specific difference in the relationship between ambient air moisture and surface-specific CWL. See a visualisation of the model in Fig. 3. (df = degrees of freedom).

Explanatory variable	df	Sum of squares	F	p
poly(air moisture, 2)	2	1413.05	311.413	< 0.001
Species	2	17.09	7.531	< 0.001
poly(air moisture, 2) x species	4	3.38	0.372	0.828
Residual standard error = 1.506 on 353 df, adj. $R^2 = 0.6362$, $F_{8,353} = 79.92$, $p = < 0.001$				

Table 3: Calculated species-specific maxima of surface-specific cutaneous water loss (CWL). The air moisture at which the maxima were achieved are summarized together with their lower and upper 95 % confidence level in brackets (Fig. 3). (max. = maximum).

Species	max. CWL (g/m²*h)	Air moisture (%)
Blackcap (<i>S. atricapilla</i> , n = 165)	14.8 (14.4, 15.2)	45.8 (36.8, 55.7)
Lesser Whitethroat (<i>S. curruca</i> , n = 89)	14.3 (13.7, 14.9)	42.8 (25.0, 55.2)
Willow Warbler (<i>P. trochilus</i> , n = 108)	14.4 (13.8, 15.0)	44.6 (27.0, 56.3)

In addition, body temperature, body mass and water in the puddles (no / yes) influenced the species-specific residual CWL (three linear models: Tab. 4). While body mass and water in the puddles negatively affected residual CWL, the relationship between body temperature and residual CWL was positive (Tab. 4). Residual CWL of Blackcaps was significantly influenced by body temperature and body mass, while in Lesser Whitethroats it was affected by body temperature and water in the puddles (Tab. 4). In Willow Warblers, water in the puddles as well as body mass affected residual CWL (Tab. 4).

Date, ambient air temperature, waiting time in the bag, age and sex (only tested in Blackcaps) did not significantly influence residual CWL.

Size-corrected body mass was highly correlated with visual fat score estimation in all three study species (Blackcap (n = 165): $r = 0.778$, $p = < 0.001$, Lesser Whitethroat (n = 89): $r = 0.75$, $p = < 0.001$, Willow Warbler (n = 108): $r = 0.628$, $p = < 0.001$).

Table 4: Results of three linear models (one per species) examining variables that influence the species-specific residual cutaneous water loss (see model in Fig. 3 and Tab. 2). Non-significant predictors were eliminated in a stepwise way. (corr. coeff. = estimated correlation coefficient, df = degrees of freedom, f = female, m = male, u = sex not available).

Species: Blackcap (<i>S. atricapilla</i> , n = 162, f = 82, m = 75, u = 4)					
Explanatory variable	df	Sum of squares	F	p	corr. coeff.
body temperature	1	16.91	9.339	0.003	0.243
size-corrected body mass	1	19.97	11.028	0.001	-0.154
Residual standard error = 1.346 on 159 df adj. R^2 = 0.1024, $F_{2,159}$ = 10.18, p = < 0.001					
Species: Lesser Whitethroat (<i>S. curruca</i> , n = 89)					
Explanatory variable	df	Sum of squares	F	p	corr. Coeff
body temperature	1	16.475	8.603	0.004	0.303
water (no / yes)	1	19.93	10.407	0.002	-0.85
Residual standard error = 1.384 on 86 df adj. R^2 = 0.162, $F_{2,86}$ = 9.505, p = < 0.001					
Species: Willow Warbler (<i>P. trochilus</i> , n = 108)					
Explanatory variable	df	Sum of squares	F	p	corr. Coeff
size-corrected body mass	1	8.286	4.243	0.042	-0.266
water (no / yes)	1	28.743	14.717	< 0.001	-1.217
Residual standard error = 1.398 on 105 df adj. R^2 = 0.137, $F_{2,105}$ = 9.48, p = < 0.001					

3.2. Respirometry: Temperature of Panting onset

In the course of this study, I estimated the temperature of panting onset of 76 birds (Blackcap: $n = 30$, Lesser Whitethroat: $n = 25$, Willow Warbler: $n = 21$).

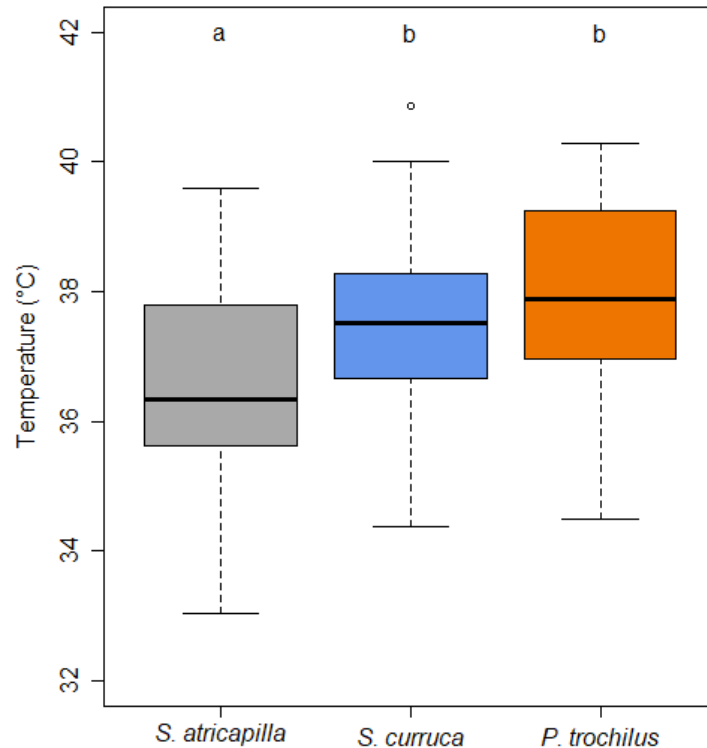


Figure 4: Temperature of panting onset in the three study species. Species marked with the same letters (a, b) were not significantly different. Blackcap (*S. atricapilla*, grey): $n = 30$, Lesser Whitethroat (*S. curruca*, blue): $n = 25$, Willow Warbler (*P. trochilus*, orange): $n = 21$.

The temperature of panting onset differed significantly between the three study species (one-way ANOVA: $F_{2,73} = 5.137$, $p = 0.008$, Fig. 4). Blackcaps started panting at a lower temperature (mean ± 1 standard deviation: $36.5 \text{ }^{\circ}\text{C} \pm 1.6 \text{ }^{\circ}\text{C}$) than Lesser Whitethroats (mean ± 1 standard deviation: $37.6 \text{ }^{\circ}\text{C} \pm 1.5 \text{ }^{\circ}\text{C}$, Tukey HSD post-hoc Test: adj. $p = 0.048$) and Willow Warblers (mean ± 1 standard deviation: $37.9 \text{ }^{\circ}\text{C} \pm 1.8 \text{ }^{\circ}\text{C}$, Tukey HSD post-hoc Test: adj. $p = 0.02$). Lesser Whitethroats and Willow Warblers did not differ in their temperature of panting onset (Tukey HSD post-hoc Test: adj. $p = 0.804$).

4. Discussion

4.1. Field CWL measurements

In this study, I found differences in surface-specific CWL between different trans-Saharan migratory songbird species. The absolute measured values (estimated maxima: Blackcap 35.5 mg H₂O/cm²*d, Lesser Whitethroat 34.3 mg H₂O/cm²*d, Willow Warbler 34.6 mg H₂O/cm²*d) were within the range of surface-specific CWL rates of 12 temperate zone passerine bird species (21.8 mg H₂O/cm²*d to 35.8 mg H₂O/cm²*d) measured in dry conditions below 16 % relative ambient air moisture (Ro & Williams 2010). As expected, Blackcaps (a mesophilic species) had a higher surface-specific CWL than Lesser Whitethroats (a xerophilic species) and Willow Warblers (a mesophilic species). However, these differences (mean difference between 21 % and 96 % relative ambient air moisture: 3.3 % and 3.2 % respectively) were smaller than the 29 % difference in CWL measured in desert lark species when compared to closely related mesic species (Tieleman & Williams 2002) or the 25.6 % difference in CWL between House Sparrows from a desert habitat and individuals from a mesic habitat (Muñoz-Garcia & Williams 2005). The different magnitude of the recorded difference in this study probably represents the smaller aridity gradient in the habitats used by the studied species. In addition, it is possible that the difference would be larger during spring migration than during autumn migration, as Blackcaps overwinter in more mesic habitats than Lesser Whitethroats (Snow & Perrins 1998, Shirihai et al. 2001, Sapir et al. 2004). Nevertheless, this finding may provide a physiological explanation for the observation that water availability influences fat accumulation and feeding behaviour of staging Blackcaps, while this is not the case in Lesser Whitethroats (Sapir et al. 2004). In addition, it gives reason to assume that bird species with a lower surface-specific CWL can rely on refuelling in arid habitats during their migration to a higher extent than species with a higher surface-specific CWL. Thus, the reported link between the observed stopover strategy of migratory songbird species and their habitat use outside of migration (Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013, Maggini et al. 2015), can at least partly be explained by overall lower rates of water loss as a result of a physiological adaptation to arid climate conditions. Even though the difference in surface-specific CWL between the likewise mesophilic Blackcaps and Willow Warblers does not fit the described mesophilic / xerophilic species pattern, it is still important to note that it coincides with the available studies about their stopover strategies: Blackcaps had a higher surface-specific CWL,

carry higher fuel loads and forage less actively en route than Willow Warblers, which had a lower surface-specific CWL, carry less fat and forage more actively in desert oases (Jenni-Eiermann et al. 2011, Hama et al. 2013, Maggini et al. 2015).

In this study, my main focus was on the comparison of surface-specific CWL between species, because the used respirometry setup did not produce reliable measurements (see: Materials and Methods). In further projects, it would be interesting to compare CWL, RWL and thus TEWL between species to test whether the differences in surface-specific CWL reported here are also reflected in overall differences of the species' TEWL.

4.2. Water manipulation

I recorded a significant negative relationship between water supplementation and surface-specific CWL values in Lesser Whitethroats and Willow Warblers, but not in Blackcaps. Thus, contrary to my expectation, I found species-specific differences in the response to water availability and individuals with lower CWL were captured when water was available. On the one hand, this indicates that the filled puddles generally did not attract birds with a higher surface-specific CWL, which would have been the case if the small-scale water manipulation in this study had been sufficient to be perceived by the migrants in the night or early morning, when they have to decide where to land (review: Chernetsov 2006). On the other hand, higher surface-specific CWL measurements in Lesser Whitethroats and Willow Warblers during periods without water supplementation could result from a higher activity of individuals with a relatively high surface-specific CWL searching for water or water-rich food. Apart from the manipulated puddles, leakages of water pipes in the area occurred regularly and provided suitable alternative drinking sites. But, as they occurred randomly in the surrounding area and were normally not present for a long time (due to regular repair), they may have induced higher activity in individuals with relatively high surface-specific CWL searching for a place to drink. Consequently, as more active birds are more likely to get caught in mistnets, birds with high surface-specific CWL were captured less numerously when the puddles were filled and the birds did not have to leave the site nor move around to find a drinking opportunity. However, I did not find a negative effect of water in the puddles on the surface-specific CWL measurements in Blackcaps. Since Blackcaps do not forage as actively en route as Willow Warblers (Jenni-Eiermann et al. 2011), were less active at the study site during the study period than the other two focal species (B. Waringer pers. communication), had a lower temperature of panting onset and higher surface-specific CWL than the other two species,

it is possible that their general stopover strategy is to stay in the shade and save water by remaining inactive. Thus, the species-specific negative relationship between available water in the puddles and surface-specific CWL reported in this study may indicate that a species' refuelling strategy for the Sahara crossing coincides with its disposition to actively look for drinking water in desert environments.

4.3. Respirometry: Temperature of Panting onset

The results of this study confirmed the prediction that Blackcaps have a lower temperature of panting onset than Willow Warblers and Lesser Whitethroats. The mean values I measured in the three species (Blackcap: 36.5 °C, Lesser Whitethroat: 37.6 °C, Willow Warbler: 37.9 °C) are in the range of temperatures (31.3 °C - 46 °C, mean: 39.3 °C) at which 50 % of the individuals from 33 different Kalahari Desert bird species are known to begin panting (Smit et al. 2016). This result indicates that Blackcaps can only use a shorter window of time for daily activity in desert environments without having to pant, which would imply high rates of RWL (Smit et al. 2016). Consequently, this observation may represent an additional explanation why Blackcaps forage less actively en route and carry higher fuel loads than Willow Warblers (Jenni-Eiermann et al. 2011, Hama et al. 2013). Although the temperature of panting onset did not differ significantly between Lesser Whitethroats and Willow Warblers, the species' mean was higher in the smaller Willow Warbler. This is in line with a study by Smit et al. (2016), who reported that larger bird species start panting at lower temperatures than smaller ones. However, different adaptations to optimize heat loss in arid conditions, such as the ability to cope with high body temperatures during facultative hyperthermia (Smit et al. 2016), the dependence on wing-drooping as alternative heat dissipation behaviour (Smit et al. 2016) or the reduction of the metabolic rate (Williams & Tieleman 2005) may also influence the temperature of panting onset of different species.

4.4. Variables influencing field CWL measurements

The observed relationship between ambient air moisture and CWL demonstrates that CWL is dependent on the gradient of water vapor pressure between the animal and the environment. This confirms the results of former studies (Lasiewski et al. 1966, Webster & King 1987, Powers 1992). However, in this study, I found a quadratic relationship between air moisture and CWL that was not observed in the cited literature. Based on the current scientific knowledge, I assume that the barrier function of the bird's stratum

corneum defines the maximum surface-specific CWL level recorded. The stratum corneum is the outermost layer of a bird's integument and consists of flat, dead cells (corneocytes), which are embedded in a lipid matrix (Bouwstra 1997). This matrix forms the primary barrier for water vapor diffusion from the animal's body to the environment (Menon et al. 1992, Simonetti et al. 1995, Meuwissen et al. 1998). Its lipid composition and arrangement appears to be crucial to determine the rate of surface-specific CWL (e.g. Haugen et al. 2003, a, b, Muñoz-Garcia & Williams 2005, Champagne et al. 2012). However, it remains unclear why there was an unexpected decrease in surface-specific CWL in very dry conditions compared with medium air moisture levels, at which the maximum surface-specific CWL levels were recorded. Only small numbers of birds were caught at very low ambient air moisture levels (which corresponded to higher air temperatures) and probably these birds, which were still active in such challenging environmental conditions, were individuals with a very low surface-specific CWL. This scenario seems to be likely, because of the large intraspecific variation in surface-specific CWL values throughout the sampled species as well as air moisture conditions. Alternatively, birds captured at low air moisture may have experienced dehydration, which also leads to low CWL-rates (Arad et al. 1987, Maloney & Dawson 1998). Thus, the reduction of surface-specific CWL at low ambient air moisture levels could be due to a sampling effect. Consequently, the ambient air moisture levels of the species' surface-specific CWL maxima reported in this work should be interpreted as the upper ambient air moisture boundary of the highest surface-specific CWL rates in the investigated species, and not as true maxima. This is also the reason why I used the focal species' estimated maxima of surface-specific CWL at the beginning of the discussion section for comparison reasons and not any lower values recorded at drier conditions. In order to overcome these shortcomings in future studies, it would be beneficial to measure every individual bird several times at the same temperature but at different moisture levels in a climate chamber, where water is provided to the bird ad libitum. This approach would, on the one hand, solve the problem of the highly correlated environmental variables temperature and air moisture present in this study, and on the other hand enable CWL measurements of almost certainly not dehydrated birds at low ambient air moisture levels.

Finally, I found a significant influence of body temperature (in Blackcaps and Lesser Whitethroats) as well as size-corrected body mass (in Blackcaps and Willow Warblers) on residual CWL. Birds increase their body temperature in hot environments up to 5 °C to reduce their evaporative water loss, which allows them to forage even during the

warmest times of the day (Tieleman & Williams 1999, Smit et al. 2013, Nilsson et al. 2016). It is possible, though, that the increase in body temperature does not compensate completely for the increase in CWL, resulting in the pattern observed in two out of the three species studied. Since size-corrected body mass was highly correlated with the visual fat score estimation and I found a negative effect of size-corrected body mass on surface-specific CWL, I conclude that birds with larger fat stores have a lower surface-specific CWL than leaner birds. However, to my knowledge, a reduction in surface-specific CWL due to large amounts of stored fat has not been described in the scientific literature. Fat is mainly accumulated in sub-cutaneous adipose depots and not in the stratum corneum (review: Guglielmo 2018). Therefore, I assume that this pattern rather demonstrates that fat birds are only active if they have a low individual surface-specific CWL, while lighter birds are forced to move for foraging irrespectively of their surface-specific CWL. Thus, in general, lean birds try to refuel at the stopover site, but fat ones stay in the shade and avoid evaporative water loss, except when their surface-specific CWL is low or when they are dehydrated and thus must look for drinking water. More precisely, this pattern was highly significant in Blackcaps, which fits the observation that Blackcaps cannot efficiently refuel in a wide variety of desert habitats (Sapir et al. 2004), had the highest surface-specific CWL of the three study species, had the lowest temperature of panting onset of all study species and do not actively forage en route in general, but rather rely on large amounts of stored fat accumulated prior to desert crossing (Jenni-Eiermann et al. 2011, Hama et al. 2013). I assume that this behavioural adaptation is also present in the likewise mesophilic Willow Warblers and the more xerophilic Lesser Whitethroats, although I could not find a statistically significant effect of size-corrected body mass on residual CWL in the latter species. However, I would expect a much smaller effect in these species, because they would not experience comparatively high evaporative water losses during activity in arid climate conditions due to their lower surface-specific CWL and their higher temperature of panting onset (this study). Consequently, this could provide an explanation, together with the smaller sample size, why I did not find this pattern in Lesser Whitethroats and only found a marginally significant effect of size-corrected body mass in Willow Warblers.

4.5. Variables without an effect on field CWL measurements

Catching date had no significant influence on surface-specific CWL, which indicates that there is no reason to assume that individuals with lower / higher surface-specific CWL

differ in their timing of migration, at least in the range of my study period and in the three study species. In addition, as already described (see: Materials and Methods), the effect of temperature on surface-specific CWL throughout the studied temperature range should be negligible compared to ambient air moisture. This assumption seems to be supported by the fact that I could not find a significant influence of ambient air temperature on residual CWL. Moreover, I included the waiting time in the bag in the analysis to check if the moisture of the bird's skin changes while it is kept in the cotton bird bags. Apparently, the air exchange through the bag's tissue is sufficient to eliminate this possible influence. Finally, neither age nor sex (in Blackcaps) influenced the residual CWL, which provides reason to assume that there are no pronounced age- or sex-related differences in the study species' composition of the stratum corneum reflecting an assumed absence of age- or sex-specific differences in the habitat use of these widely distributed and highly adaptable bird species (Shirihai et al. 2001, Baker 2010).

5. Conclusion

The results of this study suggest that a species' surface-specific CWL and its temperature of panting onset are two important physiological parameters that might play a crucial role in the evolution of different desert-crossing strategies in small trans-Saharan migratory songbirds. While some species rely on en route refuelling to cross the Sahara, others gain the necessary amounts of fat prior to the desert crossing (Jenni-Eiermann et al. 2011, Arizaga et al. 2013, Hama et al. 2013). Both strategies are successful and enable billions of birds to cross this large ecological barrier twice a year (Hahn et al. 2009). However, many European-African migratory bird species are declining and especially trans-Saharan migrants do so to a greater extent than resident or short-distance migrants (review: Vickery et al. 2013). In the non-breeding areas, anthropogenic habitat degradation and changing climate conditions are most likely interacting driving factors of the observed declines (Vickery et al. 2013). Climate change leads to more arid climate conditions for the whole African continent (Nicholson et al. 2018), potentially imposing constraints to birds using both refuelling strategies while crossing the desert. While species which rely on pre-departure fattening might be confronted with the energetic challenge of carrying even higher fat loads in order to be able to cross an enlarged desert barrier, species which refuel en route might have even more difficulties to find suitable oases for efficient fat accumulation.

While research on the mentioned driving factors of the species' declines is required, there are also still many gaps in our knowledge about migratory bird species' distribution patterns, habitat use and foraging ecology at staging sites (Vickery et al. 2013). This study is a contribution to the research necessary to close these knowledge gaps by identifying potential physiological underpinnings that constrain the birds' behaviour during a challenging phase of their migration. However, many open questions on the physiological mechanisms involved in the evolution of different refuelling strategies and their species-specific consequences for the entire migration process remain to be addressed, in order to develop and implement efficient conservation measures.

6. References

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7. Appendix: Zusammenfassung

Zugvögel, die in Europa brüten, aber südlich der Sahara überwintern, müssen zwei Mal im Jahr diese große ökologische Barriere überqueren. Dabei fliegen sie in der Regel nachts, während sie tagsüber am Boden bleiben. Sind die Vögel gelandet, können sie entweder Nahrung suchen oder rasten. Im Allgemeinen entscheiden sich xerophile Vogelarten, die in trockenen Gebieten brüten oder überwintern, für Ersteres, während mesophile Arten ihre Fettreserven oft schon vor der Wüstenüberquerung ausreichend aufgestockt haben, sodass sie in diesen Situationen nicht aktiv auf Futtersuche gehen. Es ist bislang unbekannt, welche physiologischen Anpassungen dieses Verhaltensmuster hervorrufen. Im Rahmen dieser Studie habe ich den Wasserverlust über die Haut (WH) dreier nahverwandter trans-Sahara ziehende Singvogelarten gemessen und die Umgebungstemperatur, bei der die Tiere beginnen zu hecheln (UH). Ziel war es, zu untersuchen, ob Vogelarten, die in der Wüste aktiv auf Nahrungssuche gehen, einen niedrigeren oberflächenspezifischen WH haben und eine höhere UH. Diese beiden Anpassungen würden den Vögeln erlauben, in Wüstenbedingungen länger aktiv zu sein ohne ein übermäßiges Dehydrierungsrisiko einzugehen. Wie erwartet, hatten die mesophilen Mönchsgrasmücken einen signifikant höheren oberflächenspezifischen WH und eine niedrigere UH als die xerophilen Klappergrasmücken und die ebenfalls mesophilen Fitisse. Dieses Ergebnis stimmt mit jenen von früheren Arbeiten überein, die herausgefunden haben, dass Fitisse in der Wüste aktiv auf Nahrungssuche gehen und mit relativ geringen Fettreserven die Sahara überqueren, obwohl es sich um eine mesophile Vogelart handelt. Diese Studie hat daher zum ersten Mal gezeigt, dass der oberflächenspezifische WH und die UH einer Vogelart mit ihrem Verhalten während der Zwischenlandungen in der Wüste übereinstimmen. Dies legt den Schluss nahe, dass physiologische Limitierungen bei der Aufrechterhaltung eines ausreichenden Hydrationszustandes eine wichtige Rolle in der Evolution der artspezifischen Strategien des Nahrungserwerbs in ariden Gebieten gespielt haben. Die Kenntnis solcher limitierender Faktoren kann zu einem besseren Verständnis der artspezifischen Reaktionen auf den Klimawandel führen und leistet einen Beitrag zu der dringend benötigten Forschung über die Verteilungsmuster, die Habitatwahl und die Nahrungsökologie der abnehmenden trans-Sahara ziehenden Vogelarten bei ihren Rastplätzen.