Metabolic rate and evaporative water loss in the silky starling (*Sturnus sericeus*)

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Abstract: To better understand the physiological characteristics of the silky starling (*Sturnus sericeus*), its body temperature (T_b), basal metabolic rate (*BMR*), evaporative water loss (*EWL*) and thermal conductance (*C*) elicited by different ambient temperatures (T_a) (5−30 °C) were determined in the present study. Our results showed that they have a high T_b (41.6±0.1 °C), a wide thermal neutral zone (*TNZ*) (20−27.5 °C) and a relatively low *BMR* within the *TNZ* (3.37±0.17 mL O_2/g·h). The *EWL* was nearly stable below the *TNZ* (0.91±0.07 mg H_2O/g·h) but increased remarkably within and above the *TNZ*. The *C* was constant below the *TNZ*, with a minimum value of 0.14±0.01 mL O_2/g·h·°C. These findings indicate that the *BMR*, T_b and *EWL* of the silky starling were all affected by T_a, especially when T_a was below 20 °C and the *EWL* plays an important role in thermal regulation.

Keywords: Silky starling (*Sturnus sericeus)*; Basal metabolic rate; Body temperature; Evaporative water loss

Endotherms rely primarily on energy metabolism to maintain a constant body temperature. For birds, keeping an optimal energy balance is a key survival strategy, and is primarily achieved by adjusting morphology, physiology and behavior in response to the energy requirements of the environment (Bozinovic, 1992; Weathers, 1997; Lovegrove, 2003). The energy metabolism of birds is affected by many environmental and physiological factors, including body mass, food quality/quantity, especially temperature, which significantly affects the metabolic heat production and thermoregulation (McNab, 2009).

The basal metabolic rate (*BMR*) is the minimum rate of heat production needed to maintain normal physiological mechanisms, and is the minimum energy required by basic metabolic functions necessary to keep animals awake (McKechnie & Wolf, 2004). *BMR* is an important parameter in both inter-specific and intra-specific comparisons of energy metabolism, reflecting both energy consumption levels in individuals or species and adaptations of a species to their environments (Burton & Weathers, 2003; McKechnie et al, 2006).

Thermoregulation is conducted by balancing heat production and heat dissipation. The evaporative water loss (*EWL*) is the main way animals dissipate heat and includes both cutaneous (*CWL*) and respiratory water loss (*RWL*) (Dawson, 1982; Tieleman & Williams, 2002). *EWL* differs in different temperatures and habitat conditions, e.g. the *EWL* of desert animals is lower than that of those living in wet areas (Williams, 1996; Tieleman & Williams, 1999; Tieleman et al, 2003a; Tieleman et al, 2002; Williams et al, 2012). *EWL* has an important role in maintaining thermal balance, especially for animals living in hot and dry environments. Consequently, the ability to reduce *EWL* has an important adaptive significance (Tieleman et al, 1999; Tieleman & Williams, 2002;

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Tieleman et al, 2003b). So far, the research on *EWL* has been mainly focusing on the desert rodents (Tieleman & Williams, 1999; Tieleman et al, 2003b; Bozinovic & Gallardo, 2006; Zhu et al, 2008b), especially the relationship of their *EWL* and the ambient temperature (T_a) (MaCmillen et al, 1977; Donald, 1992; Williams & Tieleman, 2000; Zhu et al, 2008a). However, the publications on the EWL in birds are little (Xia et al, 2013).

The silky starling (*Sturnus sericeus*; Passeriformes, Sturnidae) is a summer resident of vast areas of southern and southeastern China that migrates to North Vietnam and the Philippines in winter (MacKinnon & Phillipps, 2000). Their preferred habitats are broadleaf and coniferous-broadleaf mixed forests, but they can also be found in orchards and farmland. The silky starling primarily feeds on insects, fruits and seeds. Studies have found that the silky starling has a high body temperature (T_b), a high thermal conductance (*C*), as well as a low *BMR* with a relatively wide thermal neutral zone (*TNZ*) (Zhang et al, 2006).

To investigate the mechanisms of small birds adapting to a broad range of temperature, in this study, the effects of T_a on the metabolic rate, body temperature and *EWL* of the silky starling have been evaluated. We hypothesized that the warm-adapted bird species, e.g. the silky starling, will reduce their energy expenditure by decreasing *BMR* but increasing *C* in response to warm ambient temperatures. Furthermore, because of their mesic habitats, their *EWL* will be higher than the metabolic water production (*MWP*).

MATERIALS AND METHODS

Animals

Ten silky starlings were captured in Wenzhou city (N27°29′, E120°51′), Zhejiang Province, China, during June of 2008 and were then transported to the laboratory and singly caged in enclosures (50 cm×30 cm×20 cm, length×width×height) under natural photoperiod and temperature of 28 °C. Their mean body mass at capture was 69.01±0.42 g (61.0−77.4 g). Food and water were supplied *ad libitum*. After three weeks acclimation, subjects were exposed to different T_a ranging from 5 °C to 30 °C.

Metabolic rates

The *BMR* of silky starlings was expressed as oxygen consumption per hour per gram of body mass (mL O_2/·g·h).and it was measured by using an open–circuit respirometry system (AEI technologies S–3A/I, USA). The volume of the metabolic chamber was 3.6 L and the water in it was absorbed by silica gel. The experimental temperatures were set at 5, 10, 15, 20, 22.5, 25, 27.5 and 30 °C, respectively. The chamber temperature was controlled within ±0.5 °C by a SHP-250 artificial climate box. Dry CO_2–free air was pumped through the chamber at 300 mL/min using a flow control system (AEI technologies R–1, USA) calibrated with a general purpose thermal mass flow-meter (TSI 4100 Series, USA) (Xia et al, 2013). All measurements were conducted between 2000h and 2400h. Animals were under fasting 4 h before being put into the metabolic chamber. Metabolic measurements commenced after birds had acclimatized to the chamber for 1 h. To calculate *BMR*, 10 continuous stable minimum recordings were taken over a 1 h period. Body mass and temperature were measured before and after each *BMR* measurement session.

Evaporative water loss (*EWL*)

A ‘U’ tube containing silica gel was placed behind the respiratory chamber and weighed to the nearest 0.1 mg. Any water lost by birds in the experimental chamber would be absorbed by the silica gel and thus could be measured by reweighing the tube at the end of each 30 min experimental period. A 30 min session without bird served as the control. Differences between treatments and control were taken as measurements of EWL.

Thermal conductance (*C*)

The thermal conductance (*C*) (mL O_2/g·h·°C) was calculated according to Aschoff (1981):

$$C=MR\ /\ (T_b-T_a) \tag{1}$$

where, *MR* is the metabolic rate (mL O_2/g·h), T_b is the body temperature (°C) and T_a is the ambient temperature (°C).

The dry thermal conductance (C_{dry}) was calculated according to Williams (1999):

$$C_{dry}=(BMR-EWL)/(T_b-T_a) \tag{2}$$

where, oxygen consumption was converted to energy expenditure using 20.09 J/mL O_2 consumed (Schmidt–Nielsen, 1997), the *EWL* converted to energy expenditure using 2.43 J/mg H_2O consumed (Burton & Weathers, 2003).

Metabolic water production/evaporative water loss (*MWP/EWL*)

EWL and *MWP* could be used to evaluate the efficiency of water regulation. *MWP* was estimated from oxygen consumption values, assuming that in average, 1 mL of O_2 yields 0.62 mg of metabolic water (Williams, 1999).

Data Analysis

Data were analyzed via the SPSS statistical package for Windows18.0. The effects of T_a on *BMR*, *C* and *EWL* were determined by ANOVA and linear regression analysis. Graphs were generated via Origin 8.0. All results are expressed as mean±*SE,* with $P<0.05$ being considered statistically significant.

RESULTS

Body mass and body temperature (T_b)

Body mass and T_b were stable over the range of experimental T_a, and no significant fluctuation in T_b at T_a was detected ($P>0.05$). Mean values of body mass and T_b were 69.01±0.42 g and 41.63±0.08 °C, respectively.

Basal metabolic rate (*BMR*)

BMR and T_a were significantly correlated at T_a below 20 °C or above 27.5 °C, which could be described by the following equations, respectively (Figure 1):

$$BMR\ (\text{mL } O_2/\text{g·h})=5.75(\pm 0.29)–0.12(\pm 0.02)T_a \quad (R^2=0.963, P<0.001, n=40) \tag{3}$$

$$BMR\ (\text{mL } O_2/\text{g/h})=–1.64(\pm 0.25)+0.19(\pm 0.09)T_a \quad (R^2=0.159, P<0.05, n=20) \tag{4}$$

BMR was remained stable at 20 °C$<T_a<$27.5 °C, but was significantly lower at T_a=15 °C or T_a=30 °C, which suggests that the thermal neutral zone (*TNZ*) of silky starlings was ranged from 20 °C (lower critical temperature) to 27.5 °C (upper critical temperature). The mean value of BMR within the TNZ was 3.36±0.09 mL O_2/g·h.

Thermal conductance (*C*)

Below the *TNZ*, *C* was not significantly correlated with T_a ($P>0.05$), averaging at 0.15±0.01 mL O_2/g·h·°C (Figure 2). Within and above the *TNZ*, *C* increased significantly with T_a in a linear fashion as described by the following equation:

$$C\ (\text{mL } O_2/\text{g·h·°C})=–0.19(\pm 0.03)+0.02(\pm 0.00)T_a \quad (R^2= 0.846, P<0.001, n=50) \tag{5}$$

Evaporative water loss *(EWL)*

EWL was stable below the *TNZ* (0.91±0.07 mg H_2O/g·h, $P>0.05$), but, increased significantly within and above the *TNZ* (Figure 3), which could be described by the following equation:

$$EWL\ (\text{mg } H_2O/\text{g·h})=–3.38\ (\pm 0.33)+0.26\ (\pm 0.01)\ T_a \quad (R^2= 0.961, P<0.001, n=50) \tag{6}$$

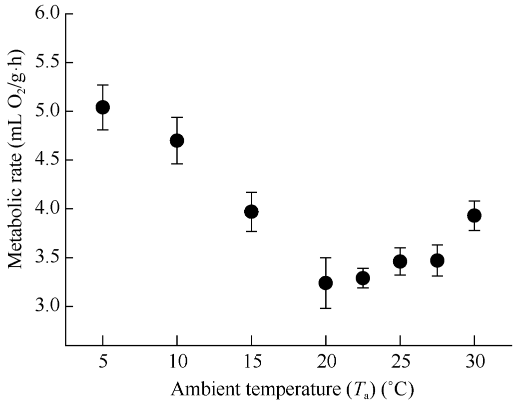

Figure 1 Metabolic rate of the silky starling as a function of ambient temperature (T_a) (n=10)

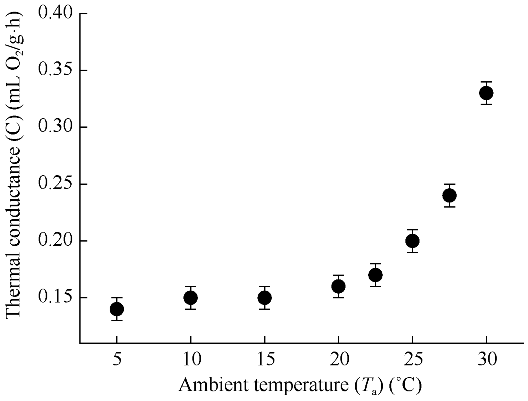

Figure 2 Thermal conductance (*C*) of the silky starling as a function of ambient temperature (T_a) (n=10)

C_{dry} increased with T_a (Figure 4). At 20 °C$<T_a<$ 30 °C, their relationship could be described by the following equation:

$$C_{dry}\ (\text{mL } O_2/\text{g·/h·°C})=–0.24\ (\pm 0.05)+0.02\ (\pm 0.00)\ T_a \quad (R^2=0.923, P<0.001, n=40) \tag{7}$$

The ratio of *EWL/BMR* was positively correlated with T_a (Figure 5) as described by the following equation:

$$EWL/BMR\ (\%)=(\text{mg } H_2O/\text{mL } O_2)=–0.73\ (\pm 0.18)+0.07\ (\pm 0.01)\ T_a\ (R^2=0.970, P<0.001, n=50) \tag{8}$$

The ratio of *MWP/EWL* was negatively correlated with T_a (Figure 6). Above the *TNZ*, their relationship could be described by the following equation:

$$MWP/EWL(\%)=2.01(\pm 0.16)–0.05(\pm 0.01)T_a \quad (R^2= 0.966, P<0.001, n=50) \tag{9}$$

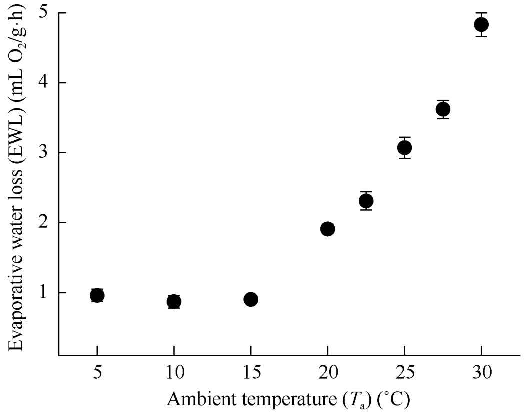

Figure 3 Evaporative water loss (*EWL*) of the silky starling as a function of ambient temperature (T_a) (n=10)

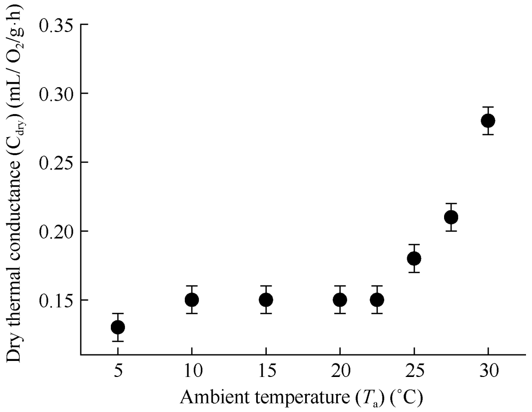

Figure 4 Dry thermal conductance (C_{dry}) of the silky starling as a function of ambient temperature (T_a) (n=10)

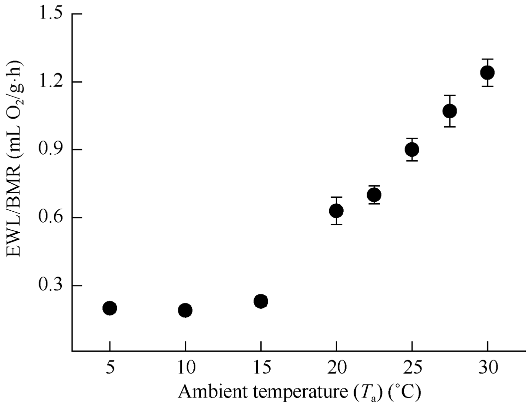

Figure 5 *EWL/BMR* of the silky starling as a function of ambient temperature (T_a) (n=10)

The percentage of evaporative heat loss to total heat production (*EHL/HP*) was increased with T_a (Figure 7). Above the *TNZ*, their relationship could be described by the following equation:

$$EHL/HP\ (\%)=-9.01\ (\pm 2.07)-0.80\ (\pm 0.08)\ T_a \quad (R^2=0.974,\ P< 0.01,\ n=50) \qquad (10)$$

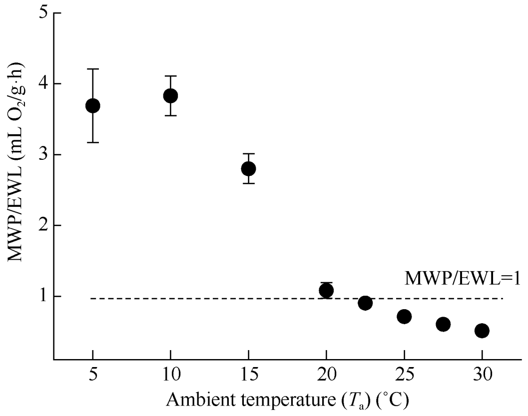

Figure 6 *MWP/EWL* of the silky starling as a function of ambient temperature (T_a) (n=10)

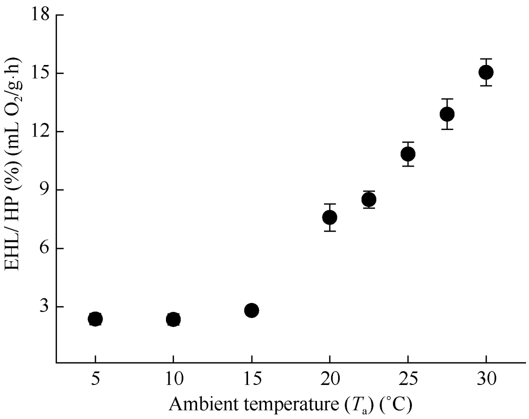

Figure 7 *EHL/HP* of the silky starling as a function of ambient temperature (T_a) (n=10)

DISCUSSION

Given the potential conditions posed by global warming or climate change, exploring the physiological characteristics of birds' adaptation to the changeable environments may be of previously unconsidered significance. In this study, we found that the silky starlings had a reduced *EWL* at T_a>20 °C, which was beneficial for them to acclimate to the seasonally hot weather.

Body temperature

Birds primarily maintain a constant body temperature by altering their heat production and heat dissipation mechanisms (McNab, 1983; Silva, 2006). The body temperature of birds is generally higher than that of mammals because most birds have higher physiological maintenance costs (McNab, 2009). Similarly, small birds' body temperatures are slightly higher than those of large birds for the same reason (McNab, 2009). Although birds are homeotherms, their T_b can vary in response to changes in their environment, physiology and behavior, including diurnal rhythm and seasonal changes (Liu et al, 2005; Zheng et al, 2008), e.g. the iridescent hummingbird (*Calypte anna*) (Donald, 1992) and Chinese bulbul (*Pycnonotus sinensis*) (Zhou et al, 2010) are often experience hypothermia in cold weather. Birds reduce their body temperature by reducing metabolic heat production. Low body temperature can decrease energy consumption at night and in winter (McKechnie & Lovegrove, 2002). Our results show that silky starlings maintain their thermostasis by increasing metabolic heat production and lowering thermal conductance at T_a fell below the *TNZ*, however, increasing metabolic heat production at T_a within and above the *TNZ*. At high T_a, to shed excess heat, silky starlings increase their evaporative water loss by increasing thermal conductance and slightly increasing T_b. This phenomenon has great adaptive significance because during hot summer, the bigger the difference is between T_b and T_a, the better the excess heat could be dissipated.

Basal metabolic rate and thermal conductance

BMR provides the energy required to maintain the basic activities of life (Dawson, 2003), and it has become a main criterion for assessing both inter- and intra-specific differences in energy metabolism. The BMR of birds, especially in passerine, is higher than that of mammals (Lasiewski & Dawson, 1967; Aschoff and Pohl, 1970; Kendeigh et al, 1977; McNab, 2009). Birds adapt to the environment by changing their BMR (Liu et al, 2005; McNab, 2009). Climate is one of the most important factors determining energy consumption. Therefore, BMR directly reflects the cold tolerance of animals exposed to low temperatures. Birds living in temperate climates, such as the red-billed leiothrix (*Leiothrix lutea*), yellow-browed bunting (*Emberiz achrysophrys*), waxwing (*Bombycilla garrulous*) and black-faced buntings (*Emberiza spodocephala*), are more cold tolerant than tropical birds and have higher BMR because in cold conditions, more energy are required to maintain metabolic process and body temperature (Liu et al, 2005; Li et al, 2005; Wiersma et al, 2007).

In this study, we found that at T_a below the *TNZ*, the *BMR* of the silky starling increased to produce more heat to maintain basic life activities, a constant T_b and a balanced energy budget. Within the *TNZ*, T_b and *BMR* were relatively stable. Above the *TNZ, BMR* slightly increased, presumably to maintain homeostasis. So, we hypothesize that the low *BMR* is an adaptation to the hot and humid environment.

Animal thermal conductance mainly depends on the ratio of their surface area to volume and is also affected by T_a. Small birds have a relatively large surface area and poor thermal insulation resulting in relatively high thermal conductance (Aschoff, 1981; Bartholomew et al, 1983; Schmidt-Nielsen, 1997). To maintain thermostasis, thermal conductance minimizes at low temperature to retain body heat, and increases at high temperature to dissipate excess heat. The thermal conductance of silky starlings and Chinese bulbuls is 100% and 126% of the value predicted from body size, respectively (Zhang et al, 2006; Lin et al, 2010). Similarly, in summer, the thermal conductance of the waxwing and black-faced bunting is 153% and 157% of the value predicted from body size, respectively (Li et al, 2005). The difference between actual and predicted thermal conductance indicates that in hot conditions, the capacity of birds to dissipate heat enhances. In this study, we found that the thermal conductance of silky starlings increased with the increasing of T_a above the TNZ, suggesting that silky starlings maintain a constant T_b by shedding excess heat. Below the *TNZ*, thermal conductance minimized at 0.149±0.028 mL O_2/g·h·°C (126% of the value predicted from their body size), suggesting that high thermal conductance plays an important role in the adaptations of silky starlings to different climates.

Thermal neutral zone

An animal's *TNZ* is the range of environmental temperatures within which temperature regulation can be achieved simply by controlling heat loss, without either metabolic thermogenesis or evaporative cooling. Within the *TNZ*, metabolic rate therefore is unaffected by ambient temperature (Schmidt, 1997). The *TNZ* is itself, however, affected by environmental conditions. In cold and dry climates, such as the arctic, a wide *TNZ* and a low critical temperature in small birds are important to reduce energy consumption and water evaporation, , e.g. the *TNZ*s of the common redpoll (*Carpodacus roseus*), brambling (*Fringilla montifringilla*), pallas's rosy finch (*Acanthis flammea*), waxwing and black-faced bunting are 25−28 °C, 25−30 °C, 22.5−27.5 °C, 18−27 °C and 20−26 °C respectively (Liu et al, 2004; Li et al, 2005). Conversely, birds that live in hot and humid habitats tend to have a high thermal conductance, narrow *TNZ* and higher critical temperature, e.g., the *TNZ*s of the red-billed leiothrix (*Leiothrix lutea*) and Dunn's Lark (*Eremalauda dunni*) are 30.0–32.5 °C and 31.5–43.6 °C, respectively (Liu et al, 2005; Tieleman et al, 2002). In this study, a relatively broad TNZ in the silky starling was found (20–27.5 °C), which is beneficial for them to acclimate to a wide range of temperatures and to decrease energy expenditure in cold weather.

Evaporative water loss

An animal's metabolism includes both substance and energy metabolism, and water metabolism plays an important role between these (Bozinovic & Gallardo, 2006). Birds excrete excess water through pulmonary, respiratory and skin surface evaporative water loss. EWL is affected by T_a and humidity, e.g. in four different lark species, Tieleman & Williams (2002) found that their EWLs were low at low T_a, but increased rapidly at $T_a >$ 35 °C; in 12 different lark species, Tieleman et al (2003a) found that their *EWL*s were negatively correlated with the aridity gradient of habitats. Our results showed that because body temperature regulation was not necessary in the balanced heat budget below the *TNZ* (*MWP/EWL*=1, T_a=20 °C), EWL was irrelevant with T_a. Above the *TNZ* ($T_a > 20$℃), birds need more water to maintain the balance of water loss in hot season, so the *EWL* increased but *MWP/EWL* decreased with T_a. *EHL/HP* increased with T_a at 20 °C$<T_a<$30 °C, and maximized (15.05%) at T_a=30 °C. We presume that this was due to the increased heat production and therefore unbalanced heat budget in high temperature (above the *TNZ*). In our study, silky starlings dissipated excess heat and maintained a stable T_b by increasing their thermal conductance and *EWL*, suggesting that *EWL* plays an important role in the thermoregulation of small birds in hot climates.

In conclusion, our results indicate that silky starlings have a low *BMR*, a high body temperature, a high thermal conductance, a high *EWL*, as well as a relatively wide *TNZ*, and among which, *EWL* plays an important role in the metabolism and body temperature regulation. We presume that these physiological characteristics in birds are outputs of multiple-mechanism adaptations.

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