Thermoregulation in African Green-Pigeons (*Treron calvus*) and a re-analysis of insular effects on basal metabolic rate and heterothermy in columbid birds

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ABSTRACT

Columbid birds represent a useful model taxon for examining adaptation in metabolic and thermal traits, including the effects of insularity. To test predictions concerning the role of insularity and low predation risk as factors selecting for the use of torpor, and the evolution of low basal metabolic rate in island species, we examined thermoregulation under laboratory and semi-natural conditions in a mainland species, the African Green-Pigeon (*Treron calvus*). Under laboratory conditions, rest-phase body temperature (T_b) was significantly and positively correlated with air temperature (T_a) between 0 °C and 35 °C, and the relationship between

resting metabolic rate (RMR) and T_a differed from typical endothermic patterns. The minimum RMR, which we interpret as basal metabolic rate (BMR), was 0.825 ± 0.090 W. Green-pigeons responded to food restriction by significantly decreasing rest-phase T_b, but the reductions were small (at most ~ 5 °C below normothermic values), with a minimum T_b of 33.1 °C recorded in a food-deprived bird. We found no evidence of the large reductions in T_b and metabolic rate and the lethargic state characteristic of torpor. The absence of torpor in *T. calvus* lends support to the idea that species restricted to islands that are free of predators are more likely to use torpor than mainland species that face the risk of predation during the rest-phase. We also analysed interspecific variation in columbid BMR in a phylogenetically-informed framework, and verified the conclusions of an earlier study that found that BMR is significantly lower in island species compared to those that occur on mainlands.

INTRODUCTION

The evolution of avian metabolic and thermal traits is thought to be influenced by a number of environmental factors. At a global scale, basal metabolic rates (BMR, i.e., minimum maintenance energy demands during normothermy) vary with environmental temperature, both in terms of interspecific variation (Jetz et al., 2008; Weathers, 1979; White et al., 2007), and the magnitude and direction of seasonal adjustments within individuals (Smit and McKechnie, 2010a). Species in the tropics tend to have lower BMR and maximum resting and active metabolic rates than their temperate-zone counterparts (Wiersma et al., 2007), although the link

between latitude and daily energy expenditure is less clear (Anderson and Jetz, 2005; Tieleman et al., 2006). In addition, species inhabiting desert environments have significantly lower BMR (by ~20 %) and daily energy expenditure (by ~50 %) compared to their mesic counterparts (Tieleman and Williams, 2000; Tieleman et al., 2003), presumably reflecting the scarcity and unpredictability of food resources in arid habitats. A second broad suite of avian physiological traits which has been predicted to be correlated with metabolic variables such as BMR (McKechnie and Lovegrove, 2006) is the avian capacity to reduce rest-phase energy demands through facultative reductions in metabolic rate and body temperature (T_b; collectively referred to as heterothermy). Reviews of avian hetereothermy have not so far revealed any clear links between interspecific variation and climatic variables (Brigham et al., 2012; McKechnie and Lovegrove, 2002; Prinzinger et al., 1991; Schleucher, 2004). Instead, the occurrence of heterothermy seems to be more closely linked to phylogeny and broad categories of food resources, with the limited available data suggesting that heterothermy is most pronounced in phylogenetically older taxa that feed on spatially and temporally unpredictable diets such as nectar, aerial insects, or fruit (McKechnie and Lovegrove, 2002; McKechnie and Mzilikazi, 2011; Schleucher, 2004).

Compared to environmental variables such as aridity and temperature, the influence of insularity (i.e., distribution restricted to islands) on the evolution of avian metabolic and thermal traits has received relatively little attention. McNab (2009) reported no significant effect of insularity per se on avian BMR, but noted that his analysis was likely confounded by the frequent evolution of flightlessness in island birds, and the close link thought to exist between flightlessness and low BMR (McNab, 1994). A mechanistic link between flightlessness and low avian BMR has been suggested to involve the smaller pectoral muscle mass of flightless *vs*

volant species (McNab, 1994), although this argument is difficult to reconcile with the observation that the major internal organs, and not flight muscles, seem to be the major determinants of BMR (Daan et al., 1990; Piersma, 2002).

One avian taxon that is in many ways ideal for addressing the role of factors such as insularity on the evolution of metabolic and thermal traits is the Columbiformes, the order containing pigeons, doves and allies. Globally, approximately 300 extant species of columbids (all volant) occur in habitats ranging from hyperarid deserts to tropical rainforests, and the taxon has undergone spectacular evolutionary radiations, most notably in southeast Asia and Oceania (Baptista et al., 1997; Gibbs et al., 2001; Pereira et al., 2007). An analysis of interspecific variation in BMR among 16 columbid species revealed significantly lower values on islands compared to mainlands (McNab, 2000). However, the latter analysis did not evaluate phylogenetic signal (Pagel, 1999) in body mass (M_b) or BMR data, nor in any way account for the potential problem of non-independence of physiological data resulting from hierarchical patterns of descent from common ancestors (Felsenstein, 1985).

The evolution of low metabolic rates (in particular, low BMR) may be expected to be functionally linked to the evolution of the capacity for pronounced heterothermy, since both these traits reduce overall energy requirements and are thus likely to be subject to selection in environments where energy demands regularly exceed supply (McKechnie and Lovegrove, 2006). The energetic benefits of heterothermy are fairly well understood (Geiser, 1993, 2004; Heldmaier and Ruf, 1992), but far less is known about the physiological and ecological costs. Consequently, it remains unclear why many birds that *a priori* would seem good candidates to use pronounced torpor and/or hibernation on account of their M_b and phylogenetic position, including barbets (Piciformes: Lybiidae) and small owls (Strigidae), apparently do not do so

(McKechnie and Smit, 2010; Smit and McKechnie, 2010b). Similarly, the absence of pronounced torpor in passerines [with the possible exception of swallows (Hirundiniidae; Prinzinger and Siedle, 1988) and sunbirds (Nectariniidae; Downs and Brown, 2002)] is difficult to explain, given that most species are small and some are year-round residents in temperate regions with long, severe winters (McKechnie and Lovegrove, 2003; Reinertsen, 1983; Reinertsen and Haftorn, 1986).

Schleucher (2001) examined heterothermy in three columbids, and found that two small granivorous species, the African Namaqua Dove (*Oena capensis*) and Australasian Diamond Dove (*Geopelia cuneata*), exhibited shallow rest-phase hypothermia similar to that previously documented in several other columbid species (Jensen and Bech, 1992b; Laurila and Hohtola, 2005; MacMillen and Trost, 1967; Phillips and Berger, 1991; Rashotte et al., 1988; Rashotte et al., 1991; Walker et al., 1983). In all these species, the depth of heterothermy increased with a continuation of fasting, but none reduced their T_b by more than 10 °C below normothermic levels. However, Schleucher (2001) found that a third species, the Cloven-feathered Dove (*Drepanoptila holosericea*), did indeed use torpor. Both captive-bred individuals she studied entered a non-responsive lethargic state at air temperatures (T_a) < 15 °C, and drastically reduced their rest-phase T_b to a minimum of 24.8 °C and metabolic rate to 33 % of normothermic values (Schleucher, 2001). Schleucher's findings prompted McKechnie and Lovegrove (2006) to suggest that the presence of torpor in *D. holosericea* but apparent absence thereof in *O. capensis* and *G. cuneata* may have evolved through selection associated with predation risk and the consequences of continental *vs* insular distributions for variation in energy supply. Whereas *O. capensis* and *G. cuneata* are granivores that occur on continents and are presumably buffered from large fluctuations in energy availability by being able to avoid areas with scarce food, *D.*

holosericea is a strictly frugivorous species restricted to the oceanic islands of New Caledonia, an area of just ~ 19,000 km^2. Moreover, New Caledonia has no native mammalian or reptilian predators that could pose a nocturnal threat to *D. holosericea* (Bauer and Vindum, 1990; Rouys and Theuerkauf, 2003), unlike the situation for *O. capensis* and *G. cuneata* (Skinner and Chimimba, 2005; Strahan, 1991).

To further examine interspecific variation in the metabolic and thermal physiology of columbid birds, we investigated patterns of thermoregulation in a frugivorous species that occurs on mainland Africa, namely the African Green-Pigeon (*Treron calvus*). Our goals were twofold. First, we tested the prediction that *T. calvus* would use shallow heterothermy but not daily torpor comparable to that of *D. holosericea*. The genus *Treron* is in the same subfamily (Treroninae) as *Drepanoptila* and is also almost entirely frugivorous (Baptista et al., 1997; Dean, 2005). However, whereas during the recent evolutionary history of *D. holosericea* it would presumably have been safe to enter a lethargic state due to the absence of predators, there are several mammalian species in the Afrotropics that are likely to prey on roosting *T. calvus* (Skinner and Chimimba, 2005). Second, we measured BMR in *T. calvus*, and combined this datum with previously published values for other columbid species to test the prediction that the BMR of columbids with insular distributions is lower than that of mainland species (McNab, 2000). Although McNab's analysis supported this prediction, the lack of phylogenetically-informed approaches in his study means that these findings need to be verified using appropriate statistical techniques.

MATERIALS AND METHODS

Study site and species

African Green-Pigeons (*Treron calvus*) are diurnal birds widespread across southern and east Africa (Dean, 2005). Wild green-pigeons were captured with mist nets on the University of Pretoria (UP) Hatfield campus (25°45' S, 28°14' E), and were housed in individual cages (~ 1.5 m^3) within outdoor aviaries on the UP experimental farm (25°45' S, 28°15' E). The green-pigeons were provided with water *ad libitum*, and a mixture of chopped fruits (pear, apple, banana and papaya) and soft-bill pellets (Avi-Products, Linkhills, KZN, South Africa). A daily ration of 70 g of food (well-fed treatment) was associated with the maintenance of approximately constant M_b, with a mean ± SD of 218.2 ± 15.1 g (n = 12) for well-fed birds. To test the thermoregulatory responses of *T. calvus* to restricted feeding, we used a two-day food restriction protocol, where the green-pigeons received 20 g of food on the first day and no food on the second day. Body mass was measured using a model ALC-810.2 scale (ACCULAB Sartorius Group, Arvada, Colorado, USA).

Laboratory measurements of metabolic rate and body temperature

Metabolic rates, evaporative water loss (EWL) rates, T_b and T_a within metabolic chambers were measured in the Zoology Building, University of Pretoria, using the experimental setup described by Cory Toussaint and McKechnie (2012), with modifications as listed below. Green-pigeons were placed individually inside 9-L plastic containers. A layer of mineral oil (~1 cm) on the bottom of each chamber prevented the evaporation of faeces and urine, with plastic mesh used to elevate the birds approximately 10 cm above the oil layer. The metabolic chambers were placed in a darkened, soundproof, temperature-controlled cabinet (Model KMF 720, Binder, Tuttlingen, Germany).

Signals from temperature-sensitive passive integrated transponder (PIT) tags (Destron Fearing, South St Paul, Minnesota, USA), injected subcutaneously between the scapulae of each pigeon after calibration, were detected using an antenna (Racket Antenna, Biomark, Boise, Idaho, USA) positioned on top of each metabolic chamber and connected to a PIT tag reader (Model FS2001F-ISO, Biomark, Boise, Idaho, USA). A thermistor probe (Sable Systems, Las Vegas, Nevada, USA) was secured into the lid of each metabolic chamber to monitor T_a.

For most metabolic rate and EWL measurements we used the same setup of atmospheric air dried with silica gel columns in series as Cory Toussaint and McKechnie (2012). However, for a small subset of measurements an adsorption dryer (Ecodry K-MT 3, Parker Zander, Charlotte, North Carolina, USA) was used to scrub water vapour and carbon dioxide from incurrent air provided by a compressor. Flow rates of approximately 2500 mL min^{-1} through the chambers were maintained during measurements, so that oxygen depletion between incurrent and excurrent air was less than 0.5 %. Maximum water vapour partial pressure in the chamber was 1.17 kPa, but was maintained below 0.7 kPa (equivalent to dewpoint $\approx$ -6.5 °C) for the vast majority of runs. The 99 % equilibrium time (Lasiewski et al., 1966) for this setup was approximately 16.5 min. The flow rate for each channel was regulated using a mass flow controller (Model FMA5520, Omega Engineering, Bridgeport, New Jersey, USA) regularly calibrated against a soap bubble flow meter (Baker and Pouchot, 1983). The water vapour, carbon dioxide and oxygen analysers were the same as those used by Cory Toussaint and McKechnie (2012), with the only difference in calibration procedures from the latter study being that we spanned the water vapour analyser using the oxygen dilution method of Lighton (2008). Water vapour pressure and fractional [O_2] and [CO_2] were recorded every 5 s. Two green-pigeons were measured simultaneously, with each cycle lasting for one hour: baseline air for 8.3

min, followed by air from the chambers in sequence for 23.3 min each, and finally baseline air for the last 5 min. This cycle was repeated all night and birds spent 13 – 15 h in the chambers.

Laboratory experimental protocol

To investigate relationships between resting metabolic rate (RMR), evaporative water loss (EWL) and T_b in *T. calvus*, we initially measured RMR and T_b over T_as ranging from 0 – 35 °C in 5 °C increments in random order. All birds were maintained on the well-fed treatment during these measurements, and the sample size at each of the different T_as varied from six to ten. Some of these initial runs involved green-pigeons maintained at a constant T_a over the entire rest-phase period, whereas others involved a change in T_a approximately halfway through the rest-phase, with a minimum of 6 h spent at each T_a.

We then measured RMR and T_b in the green-pigeons under well-fed and restricted feeding regimes at three T_a values: 5.5 ± 0.5 °C, 15.7 ± 0.3 °C, and 25.4 ± 0.3 °C respectively (hereafter, 5 °C, 15 °C and 25 °C, respectively). For runs at 25 °C and 15 °C the temperature cabinet was programmed to remain at a single temperature all night, but for runs at 5 °C it was programmed to gradually decrease from 20 °C to 5 °C between 18:00 and 21:00, remain at 5 °C for eight hours until 05:00, and then gradually increase to 20 °C at 07:00. Measurements at each T_a were first done using well-fed green-pigeons, and then repeated 3 – 15 days later after the same birds had been food-restricted (n = 10). During well-fed measurements, food was removed at approximately 15:00 in the afternoon prior to an experimental run, about 150 min before the birds were placed in the chambers. This allowed for the assumption that metabolic measurements are representative of post-absorptive metabolism, as the mean digesta retention time for a 220-g bird is estimated to be 93.6 min (Karasov, 1990).

Rates of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were calculated as per Cory Toussaint and McKechnie (2012), and converted to metabolic rate (Watts) using the thermal equivalence data in Table 4.2 in Withers (1992). For each metabolic rate datum, the mean T_b value was calculated for a corresponding 30-min interval that included the time at which $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were measured. We calculated total thermal conductance (C_{total}; mW °C^{-1} cm^{-2}) as

$$C_{total} = \frac{RMR}{(T_b - T_a)A_b}$$

and dry heat transfer coefficient (C) as

$$C = \frac{RMR - EHL}{(T_b - T_a)A_b}$$

where EHL is evaporative heat loss (W) and A_b is surface area in cm^2, predicted using the equation provided by Walsberg and King (1978). Occasional intermittent PIT tag reception resulted in incomplete T_b data records for some birds, and consequently sample sizes for T_b, C_{total} and C were sometimes smaller than those for RMR and EWL.

Measurements of body and air temperature in outdoor aviaries

Subsequent to the laboratory component of this study, Thermochron iButtons (model 1922L, Maxim Dallas Semiconductors, Sunnyvale, California, USA) were surgically implanted into the abdominal cavities of the green-pigeons (n = 9; same individuals as those used for laboratory measurements) by a veterinarian. The iButtons were coated with surgical wax prior to implantation, and were programmed to record T_b (resolution = 0.0625 °C) every 10 min. Before implantation the iButtons were calibrated against a mercury thermometer in a temperature-controlled circulating water bath (Model F34-ME, Julabo, Seelbach, Germany), over a

temperature range of 20 – 45 °C. The T_a at the aviary was recorded every 10 min for the duration of the study period by a weather station (Vantage Pro2, Davis Instruments, Haywood, California, USA) calibrated against a mercury thermometer.

Body temperature data collected within eight days of surgery were discarded, resulting in a T_b dataset for each pigeon over a 20-day period. Each individual was subjected to a restricted feeding protocol once during this period. We recorded the M_b of the green-pigeons every three days when they were well-fed, and daily during restricted feeding. The iButtons were surgically removed at the end of the study, and a 14-day recovery period was allowed before releasing the birds.

The amplitudes of circadian T_b cycles (R_T) were calculated for each bird, by determining the difference between the respective means of the five highest and five lowest T_b values recorded each day. The daily heterothermy index (HI) was also calculated for each pigeon, thus quantifying the temporal variation of T_b from the optimal T_b (considered to be the modal T_b; T_{mod}) on a daily basis (Boyles et al., 2011). The HI was calculated as

$$HI = \sqrt{\frac{\Sigma(T_{b-mod} - T_{b-i})^2}{n-1}}$$

where T_{b-mod} is the modal active-phase T_b of an individual, T_{b-i} is the T_b at time i, and n is the number of times T_b is sampled per 24-h period (Boyles et al, 2011).

Data analyses

Values are presented as mean ± SD. To compare thermoregulation between well-fed and food-restricted treatments, we analysed relationships between response variables (RMR, T_b, R_T and HI) and predictor variables (T_a, feeding regime and % M_b loss) with generalised linear mixed

models (GLMM) in R 2.13.1 (R Development Core Team, 2011) using *nlme* (Pinheiro et al., 2009). *Post hoc* tests of multiple comparisons of means were also conducted (Tukey Contrasts for mixed-effects models) where appropriate, using *multcomp* (Hothorn et al., 2008) and *mvtnorm* (Genz et al., 2011). There were no interactions between predictor variables that had a significant effect on the response values, and thus interaction effects were excluded.

We also included a comparative analysis of BMR in columbids (see Electronic Supplementary Material) to verify McNab's (2000) conclusions regarding the lower BMR of island species compared to their mainland counterparts. We used the M_b and BMR data from Table 1 in McNab (2000), and converted the rates of oxygen consumption in the latter source to Watts using a conversion of 20.083 J mL O_2^{-1}. We added data for *Drepanoptila holosericea* (Schleucher, 2002) and *Oena capensis* (Schleucher, 2001). We used the BMR and M_b values for *Ptilinopus melanospilus* reported by Schleucher (2002) in preference to those reported by McNab (2000), since the former author examined seven birds whereas the latter examined only one. For the same reason, we used data for *Streptopelia senegalensis* from McKechnie et al. (2007; n = 30) instead of those reported by Kendeigh et al. (1977), in which no sample sizes were provided. In the case of *Ducula pinon*, McNab (2000) and Schleucher (2002) reported very similar BMR values each based on two birds, and we averaged the BMR and M_b values from these two studies. For all analyses we used log_{10}-transformed M_b and BMR data. We used island vs mainland categorisations as per McNab (2000), but did not distinguish between small and intermediate islands. Additional species added to the analysis were categorised using the same criteria as McNab (2000). We did not include climatic variables such as temperature, primary productivity or mean annual precipitation in the analysis, since the data for many species are from captive-bred birds in zoos (McNab, 2000).

To test for phylogenetic signal and conduct phylogenetically-independent analyses, we sampled 100 phylogenies for the 30 species in our data set from www.birdtree.org (Jetz et al., 2012) and used the majority rules consensus tree identified using the program Mesquite (Maddison and Maddison, 2011) for our analyses. We used the MatLab program PHYSIG_LL.m to test for phylogenetic signals in M_b and BMR using randomisation tests for mean-squared error and by calculating the K-statistic (Blomberg et al., 2003). Both M_b ($K = 0.704$, P $= 0.001$) and BMR ($K = 0.673$, P $= 0.001$) exhibited significant phylogenetic signal, and so we tested for a difference between mainland and island species using both ordinary least squares (OLS) and phylogenetically informed least squares (PGLS) regressions using the MatLab program REGRESSIONv2.m (Lavin et al., 2008). Log-transformed M_b was included as a continuous predictor variable, and distribution (island vs mainland) as a categorical predictor variable.

RESULTS

Relationships between metabolic rate, body temperature and air temperature
Interactions between metabolic heat production, evaporative heat loss and T_b in African Green-pigeons did not match the classic model of endothermic homeothermy. Over the range of T_a we investigated (~0 – 35 °C), mean T_b varied between approximately 37 °C and 39 °C, and was significantly positively correlated with T_a (Pearson Product Moment $r = 0.508$, P $= 0.002$; Fig. 1). Patterns of RMR were similarly variable; no obvious thermoneutral zone (TNZ) was evident, and both T_b, RMR and EWL were lower at $T_a \approx 0$ °C than $T_a \approx 5$ °C (Fig. 1,2). Visual inspection of the RMR, EWL and conductance data suggested inflection points for all these variables around $T_a \approx 15$ °C; to more rigorously evaluate this possibility we fitted two-segment linear

("broken-stick") regression models to the data. In all cases these models provided significant fits, and identified inflection points between $T_a \approx 15$ and 20 °C (RMR, EWL) or between $T_a \approx 20$ and 25 °C (C_{total} and C; Fig. 1,2). The minimum mean RMR (0.825 ± 0.090 W) was measured at $T_a \approx 33$ °C, and we consider this the basal metabolic rate (BMR) for *T. calvus*.

Heterothermy under laboratory conditions

The RMR increased significantly as T_a decreased (GLMM, $F_{1,46} = 7.396$, $p = 0.009$; Fig. 3a). In contrast, T_b decreased significantly as T_a decreased (GLMM, $F_{1,37} = 13.316$, $p < 0.001$; Fig. 3b). These patterns in T_b variation occurred regardless of whether birds were food-restricted or well-fed (Fig. 3).

After restricted feeding, green-pigeons had a significantly lower M_b compared to well-fed birds (GLMM, $F_{1,57} = 67.016$, $p < 0.001$), but showed no evidence of torpor. The mean minimum T_b during food restriction was 35.4 ± 1.1 °C (n = 9), with a single lowest value of 33.2 °C. Green-pigeons lost 4.0 ± 1.9 % of their initial M_b from the morning of the onset of restricted feeding, until the following afternoon just prior to the experimental run. Despite showing the same trends in RMR and T_b with T_a as well-fed birds, food-restricted birds had significantly lower RMR by 20.8 ± 10.3 % (GLMM, $F_{1,46} = 9.526$, $p = 0.003$; Fig. 3a) and T_b by 1.2 ± 0.8 °C (GLMM, $F_{1,37} = 30.059$, $p < 0.001$; Fig. 3b). The green-pigeons' T_b decreased significantly with increasing % M_b loss (GLMM, $F_{1,14} = 8.908$, $p = 0.010$); but % M_b loss had no significant effect on RMR (GLMM, $F_{1,16} = 0.700$, $p = 0.415$). One of the food-restricted green-pigeons died during measurements at $T_a = 5$ °C. The T_b of this bird slowly but steadily declined from 39.5 °C on entering the chamber at 17:20, with no indication of the defense of a T_b setpoint.

Heterothermy in outdoor aviaries

Under semi-natural conditions in outdoor aviaries the T_b of *T. calvus* showed a typical avian

circadian cycle (Fig. 4). The R_T of well-fed green-pigeons was 4.7 ± 1.1 °C, and significantly

increased with decreasing mean daily T_a (GLMM, $F_{1,168} = 26.849$, $p < 0.001$; Fig. 5a) and

minimum daily T_a (GLMM, $F_{1,168} = 19.960$, $p < 0.001$) regardless of whether birds were food-

restricted or well-fed.

A transient increase in T_b was often observed during the active-phase, generally at similar

times in different birds (Fig. 4). These increases did not occur at the same time every day, but

were more common in the late morning. They do not appear to be directly related to the daily

peak in T_a and generally occurred over a brief period of approximately 30 – 40 min, with T_b

rapidly increasing about 2 – 3 °C above normothermic active-phase values and then decreasing

again (Fig. 4b). A period of colder weather occurred from 5 – 7 September, during which the

maximum daily T_a was never above 17.8 ˚C (Fig. 4). In the days following (but not during) this

colder period, some birds decreased their rest-phase T_b (Fig. 4).

There was no evidence of torpor, but a number of individuals significantly decreased their

rest-phase T_b during nights subsequent to restricted feeding (GLMM, $F_{2,24} = 26.219$, $p < 0.001$;

Fig. 4d,f). The mean minimum T_b was 35.2 ± 1.3 °C (n = 9), with a single lowest value of 33.1

°C. *Post hoc* analyses showed that individuals had significantly lower rest-phase T_b after each

consecutive day of restricted feeding (Tukey, $p < 0.001$; Fig. 4d,f). The R_T significantly

increased with a continuation of restricted feeding (GLMM, $F_{2,24} = 46.058$, $p < 0.001$; Fig. 5b)

and a reduction in M_b (GLMM, $F_{1,7} = 23.331$, $p = 0.002$), indicating the use of shallow rest-

phase hypothermia. *Post hoc* analyses also indicated that green-pigeons significantly and

progressively increased their R_T on each consecutive day of restricted feeding, and R_T was 1.3

±0.5 °C higher compared to well-fed birds on the second day of restricted feeding (Tukey, p <0.001; Fig. 5b). In contrast to R_T, daily HI values did not vary significantly with mean T_a (GLMM, $F_{1,168} = 0.177$, $p = 0.675$; Fig. 4c), minimum T_a (GLMM, $F_{1,168} = 0.052$, $p = 0.819$), restricted feeding (GLMM, $F_{2,24} = 0.355$, $p = 0.705$; Fig. 5d), or M_b loss (GLMM, $F_{1,7} = 0.130$, $p = 0.729$).

Columbid basal metabolic rate – effect of island vs mainland distributions

A PGLS regression model with Pagel's λ-transformation provided the best fit to the BMR data (Table 1). In this model, and in all other models fitted, the BMR of island species was significantly lower than that of mainland species (Table 2, Figure 6). The predicted BMR for a 200-g species is approximately 12 % lower for islands than mainlands, and the corresponding difference for a 500-g species is approximately 19 %.

DISCUSSION

Patterns of normothermic rest-phase thermoregulation in African Green-pigeons differed in several respects from the classical endothermic thermogenic defense of a well-defined T_b set-point (Dawson and Whittow, 2000; Scholander et al., 1950). In addition to the comparatively variable T_b, the relationship between RMR and T_a was not characterised by a clear TNZ in which RMR is independent of T_a. Instead, an inflection point was evident in the RMR-T_a relationship, above which RMR continued to gradually decrease with increasing T_a. Similarly, EWL began increasing at $T_a \approx 18$ °C, a far lower value than expected for a bird this size (McKechnie and Wolf, 2010). Collectively, the relationships between RMR, EWL, conductance and T_b in *T. calvus* suggest an atypical pattern of avian thermoregulation (Scholander et al., 1950). Although

Weathers (1981) noted that avian T_b is often comparatively labile on account of birds' typically small size and low thermal inertia, a comparison of T_b variation in *T. calvus* to that of a typical small passerine illustrates our point. Normothermic T_b in the 22-g red-headed finch (*Amadina erythrocephala*) varied by $\sim 1°C$ over $T_a = 0 - 35°C$ (Figure 1A in McKechnie & Lovegrove 2003). In contrast, the corresponding range of normothermic T_b in *T. calvus* is approximately twice as wide (Figure 1), despite this species being $\sim$ 10-fold larger. Moreover, T_b in *A. erythrocephala* was not significantly correlated with T_a.

A cursory comparison of our RMR and T_b data reveals an apparent discrepancy in that values during the well-fed measurements (Fig. 3) at $T_a = 5 °C$ were substantially lower than the corresponding values observed earlier when the overall patterns of thermoregulation were investigated (Fig. 1). We cannot identify any obvious reason for this discrepancy, but we do not believe that it changes our conclusions. If the T_b and RMR data for well-fed birds at $T_a = 5 °C$ presented in Fig. 1 are replaced with those plotted in Fig. 3, the correlation between T_b and T_a is strengthened, not weakened.

Although all the columbids investigated by McNab (2000) showed patterns of T_b and RMR that approximately matched typical endothermic homeothermy, Schleucher's (2002) data for three species, namely *Ptilinopus melanospilus*, *Drepanoptila holosericea* and *Ducula pinon* reveal variation in rest-phase T_b quantitatively similar to that we have documented in *T. calvus*, with significant positive correlations between T_b and T_a in the three former species. Regression models fitted to RMR *vs* T_a for these species did not intercept the x-axes at $T_a = T_b$, a central prediction of classic endothermic homeothermy (Scholander et al., 1950). Moreover, C_{total} (designated C_{wet} by the latter author) in *P. melanospilus* and *D. holosericea* began to increase at T_a values around 20 °C (see Fig. 1 of Schleucher, 2002), similar to the pattern in *T. calvus*.

Collectively, these observations suggest that thermoregulation in the subfamily Treroninae may differ in several respects from typical avian patterns.

Our results support the prediction that *T. calvus* uses shallow rest-phase hypothermia but not daily torpor, and at no time did wild-caught green-pigeons show the lethargic state characteristic of daily torpor as observed in *D. holosericea* (Schleucher, 2001). Instead, green-pigeons responded to restricted feeding by using shallow rest-phase hypothermia, a response observed in several other columbids (Jensen and Bech, 1992a; Laurila and Hohtola, 2005; MacMillen and Trost, 1967; Phillips and Berger, 1991; Schleucher, 2001). The reduction in RMR of ~ 21 % observed under laboratory conditions is similar to those observed by Schleucher (2001) in *O. capensis* and *G. cuneata* after 24-hr fasting periods, although these species showed more pronounced hypothermia than *T. calvus* (Schleucher, 2001). The fractionally greater heterothermic responses in these species compared to *T. calvus* could reflect their substantially lower M_b (both ~ 35 g).

In the outdoor aviaries, *T. calvus* increased the depth of rest-phase hypothermia with a continuation of fasting and loss of M_b, as R_T was significantly and progressively increased over the two consecutive days of restricted feeding. An increase in R_T with fasting also occurred in *Columba livia* and *S. roseogrisea*, although these species elevated R_T by substantially higher values (Laurila and Hohtola, 2005; Walker et al., 1983). However, this was under more extreme conditions than in our study, with lower T_a and/or longer periods of fasting (Laurila and Hohtola, 2005; Walker et al., 1983). Although our restricted feeding protocol was less intense than in some other thermoregulatory studies on columbids (Jensen and Bech, 1992a; MacMillen and Trost, 1967; Walker et al., 1983), the fact that one of our food-restricted birds died during a

laboratory experimental run suggests that these green-pigeons were energy-stressed and close to their thermoregulatory limits.

In contrast to R_T, daily HI values did not change significantly with T_a, restricted feeding or M_b loss in *T. calvus*. The R_T value only considers the difference between the daily extremes of T_b, and it could be argued that HI provides a better representation of heterothermic responses as it integrates the depth and duration of decreases in T_b by an individual (Boyles et al., 2011). The lack of significant increases in HI during restricted feeding may be a result of the transient increases in day-time T which would have been incorporated in the calculation of HI values and may have influenced the results obtained when comparing this metric across different T_a and feeding regimes.

Captive birds and mammals are generally less likely to use torpor and/or hibernation compared to free-ranging populations (Geiser et al., 2000), and recordings of T_b in free-ranging *T. calvus* individuals would be necessary to completely rule out the possibility of this species using torpor. However, we are satisfied that our comparison of *T. calvus* and *D. holosericea* is valid, because a) the two individuals of the latter species examined by Schleucher (2001) were captive-bred birds held in a zoo, whereas we examined wild-caught birds and b) the torpor bouts reported by Schleucher (2001) occurred under conditions of *ad libitum* feeding at $T_a < 15$ °C. In the present study, we exposed green-pigeons to $T_a \approx 5$ °C combined with restricted feeding, and thus consider it very unlikely that the absence of daily torpor is merely an artifact of our study involving birds temporarily held in captivity.

The lack of torpor in *T. calvus* provides support, albeit very preliminary, for the hypothesis that nocturnal predation risk and a continental distribution select against the use of torpor in columbids, whereas pronounced heterothermy is more likely to evolve in island species

not threatened by nocturnal predators. *D. holosericea* is confined to the islands of New Caledonia, and likely experiences periodic fruit shortages due to variable rainfall caused by the El Niño Southern Oscillation phenomenon (ENSO; McKechnie and Lovegrove, 2006; Philander, 1983; Stone et al., 1996). Furthermore, it would presumably have been safe for these doves to enter a non-responsive lethargic state at night due to the absence of native nocturnal, arboreal predators on this island (Bauer and Vindum, 1990; Rouys and Theuerkauf, 2003), although rats (*Rattus* spp.) and feral cats (*Felis catus*) have been introduced in recent millennia (Rouys and Theuerkauf, 2003). In contrast, *T. calvus* occurs in southern and east Africa, and although it also experiences variable rainfall on account of ENSO (Nicholson and Kim, 1997; Stone et al., 1996), it can potentially evade food shortages via nomadic movements. Moreover, the use of torpor and the associated lethargic state would impose a substantial predation risk on roosting *T. calvus*, due to the presence of nocturnal, arboreal predators (Nowak and Paradiso, 1999; Skinner and Chimimba, 2005).

Another factor potentially involved in the variation between *D. holosericea* and *T. calvus* in their use of torpor concerns their gut morphology. Gibb and Penny (2010) placed *Drepanoptilia* within *Ptilinopus* (fruit-doves), which have thin-walled gizzards and short, wide intestines, and digest fruit pulp but defaecate seeds intact (Gibbs et al., 2001; Goodwin, 1983; Lambert, 1989). In contrast, *Treron* spp. grind and digest small seeds on account of their muscular, grit-containing gizzards and long, narrow intestines (Cowles and Goodwin, 1959; Goodwin, 1983; Lambert, 1989). This difference raises the possibility that the overall digestive efficiency of *Treron* is higher than that of fruit-doves, potentially reducing selection for energy conservation via torpor. However, the degree to which seeds contribute to the energy balance of *Treron* green-pigeons remains unclear. Moreover, at a broader scale the avian taxa in which the

capacity for torpor is most pronounced feed on diverse diets ranging from dilute nectar (e.g., hummingbirds) to aerial insects (e.g., caprimulgids) and fruit (e.g., mousebirds). The latter observation suggests that the temporal and spatial predictability of food resources may be more important than their nutritional properties in driving the evolution of torpor. Nevertheless, the potential importance of variation in gut morphology among columbids in terms of energy balance and factors selecting for energy conservation deserves further investigation.

The near-global distribution of columbids, combined with their rapid evolutionary radiation on islands (Gibbs et al., 2001; Pereira et al., 2007) and the fact that the occurrence of torpor has been confirmed in one species (Schleucher, 2001), makes them a potentially useful model for testing hypotheses regarding the ecological determinants of avian heterothermy. Moreover, the influential recent phylogenetic study of Hackett et al. (2008) placed the Columbidae in the same phylogenetically ancient clade that includes the caprimulgids (nightjars and allies), Apodidae (swifts) and Trochilidae (hummingbirds), all groups well known for pronounced heterothermy, suggesting that the physiological capacity for torpor may be greater in this group than currently thought.

Our analysis of interspecific variation in columbid BMR supports the idea that species that occur on islands have evolved lower BMR than their mainland counterparts, verifying the conclusion reached by McNab (2000). This analysis has several limitations. First, the sample sizes for several species are small (in some cases n = 1; see McNab 2000). Few studies have examined the influence of data based on small sample sizes in comparative analyses, but Jetz et al. (2008) found that this did not affect the patterns in their interspecific analysis of avian BMR in any meaningful way. Second, our analysis implicitly assumes that BMR is a fixed, species-specific parameter. In reality, avian BMR is a variable trait constantly adjusted in response to

environmental conditions (reviewed by McKechnie 2008), including in tropical and subtropical species (Maldonado et al., 2009; Smit and McKechnie, 2010a; van de Ven et al., 2013). Finally, as already mentioned we could not account for fine-scale variation in climatic conditions across the ranges of the species included in the analysis because many of the data were obtained from captive-bred birds, whereas others were from wild-caught individuals.

Most investigations of island adaptations in birds have focused on morphology (Blondel et al., 1999; Clegg et al., 2002; Grant, 1968; Wright and Steadman, 2012) or immune function (Matson, 2006), but the lower BMR of island columbids suggests that avian maintenance metabolic rates are also subject to selection associated with insularity. Lovegrove (2000) predicted that low BMR should evolve in island mammals on account of unpredictable ENSO-driven patterns of rainfall on many islands, combined with the inability of most mammals to migrate away from islands during periods of food shortage. These arguments may be expected to apply equally to birds that are sedentary and which do not leave islands through nomadic movements or migration during periods of food shortage, and we suggest that the comparatively low BMR of island species reflects sources of selection similar to those proposed by Lovegrove (2000) for insular mammals.

In summary, our results reveal that an Afrotropical frugivorous columbid shows patterns of thermoregulation that differ in several respects from typical endothermic patterns, uses shallow heterothermy under conditions of low T_a and restricted feeding, but apparently does not have the capacity for daily torpor. The marked contrast between heterothermy in *T. calvus* and *D. holosericea* supports the notion that predation risk and insular *vs* continental distributions are two key determinants of torpor in birds. Furthermore, the lower BMR of columbid birds on islands compared to mainland species supports the idea that insularity is associated with more

pronounced selection for energy conservation. Taken together, these patterns raise the possibility of an insular metabolic syndrome in columbids involving both reduced maintenance metabolic costs and the capacity for torpor, although we predict the latter is correlated with degree of predation risk and is more pronounced in species on predator-free islands. The Columbidae, in particular those species restricted to islands, potentially represent a useful model system for elucidating the selective forces acting on both metabolic rates and heterothermic responses in birds.

ACKNOWLEDGEMENTS

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Table 1. Regression models fitted to $\log_{10}M_b$ (body mass; g) and $\log_{10}BMR$ (basal metabolic rate; W) data for 30 species of columbids (see Electronic Supplementary Material) using ordinary least squares (OLS) or phylogenetically informed approaches. "Distrib." is a categorical variable indicating whether species are distributed on mainlands or islands. For phylogenetically informed models, we applied various branch length transformations available in the MatLab program REGRESSIONv2.m, namely phylogenetic generalised least squares (PGLS; Brownian motion, i.e., no transformation), Ornstein–Uhlenbeck (Reg OU), Grafen's ρ (Reg ρ), and Pagel's λ (Reg λ; Lavin et al., 2008). The model with the lowest Akaike Information Criterion (AIC) and corrected AIC (AICc) values, indicating best fit, is indicated in bold. Akaike weights (w_i) are also provided.

Model	Intercept	SE	Slope	SE	Distrib.	SE	Ln max. likelihood	Transform parameter	R^{2*}	AIC	AICc	w_i
OLS	-1.618	0.114	0.662	0.043	0.079	0.038	32.069	----	0.903	-56.139	-54.539	0.030
PGLS	-1.555	0.139	0.626	0.052	0.077	0.029	28.344	----	0.849	-48.688	-47.088	< 0.001
Reg OU	-1.612	0.112	0.661	0.045	0.070	0.033	33.224	$d = 0.262$	0.890	-56.448	-53.948	0.035
Reg ρ	-1.642	0.104	0.671	0.041	0.076	0.031	35.337	$\rho = 0.227$	0.909	-60.674	-58.174	0.291
Reg λ	**-1.651**	**0.101**	**0.673**	**0.040**	**0.080**	**0.030**	**36.130**	**$\lambda = 0.483$**	**0.915**	**-62.260**	**-59.760**	**0.643**

*Not comparable between conventional and phylogenetically informed regressions (Lavin et al. 2008).

Table 2. F-ratios and probabilities for various regression models (see Table 1 legend for explanations) comparing basal metabolic rate (BMR) between columbids occurring on islands and mainlands. The best-fit model is indicated in bold (see Table 1).

Model	Distribution	
	$F_{1,27}$	P
OLS	4.318	0.047
PGLS	6.876	0.014
Reg OU	4.594	0.041
Reg ρ	6.013	0.021
Reg λ	**7.138**	**0.013**

Figure legends

Figure 1. Relationships between body temperature (T_b, top panel) and resting metabolic rate (RMR; bottom panel) and air temperature (T_a) in African Green-Pigeons (*Treron calvus*) measured under laboratory conditions. Error bars indicate standard deviations. The solid line in the lower panel represents a broken-stick regression model fitted to the raw data, not the mean values plotted here. Samples sizes for RMR varied from six to ten per T_a, but intermittent PIT tag reception resulted in incomplete T_b records for some birds, and thus sample sizes of T_b varied from one to seven.

Figure 2 Relationships between total thermal conductance (top panel; filled symbols), dry heat transfer coefficient (top panel; clear symbols) and evaporative water loss (EWL; bottom panel) and air temperature (T_a) in African Green-Pigeons (*Treron calvus*) measured under laboratory conditions. Error bars indicate standard deviations. The solid lines represent broken-stick regression models fitted to the raw data, not the mean values plotted here. Samples sizes for EWL varied from six to ten per T_a, but intermittent PIT tag reception resulted in incomplete body temperature records for some birds, and sample sizes of conductance values thus varied from one to seven.

Figure 3. Resting metabolic rate (RMR) of African Green-Pigeons (*Treron calvus*) significantly increased with air temperature (T_a) under laboratory conditions (upper panel), whereas body temperature (T_b; °C) significantly decreased as T_a decreased (lower panel). These trends were observed in both well-fed (clear symbols) and food-restricted (filled symbols) green-pigeons

kept overnight within metabolic chambers in a temperature-controlled cabinet. Both RMR and T_b were significantly lower in food-restricted compared to well-fed birds, regardless of T_a. Error bars indicate standard deviations. Sample sizes for RMR were constant at ten per T_a, but intermittent PIT tag reception resulted in incomplete T_b records for some birds, and thus sample sizes of T_b varied from seven to nine.

Figure 4. Body temperature (T_b; solid lines) cycles of African Green-Pigeons (*Treron calvus*) showed typical avian circadian rhythms over a 20 day period (24 August – 12 September 2012) in outdoor aviaries. The amplitude of circadian T_b rhythms (R_T) significantly increased as air temperature (dashed lines) decreased. Restricted feeding, during which green-pigeons received 20g of food on the first day (filled block) and no food on the second (clear block), resulted in significantly higher R_T values. These three T_b traces are representative of common patterns observed in individuals, and boxes in the full traces (a,c,e) indicate sections that have been enlarged in b,d and f respectively.

Figure 5. Amplitudes of circadian body temperature cycles (R_T; °C) of African Green-Pigeons (*Treron calvus*; n = 9) in outdoor aviaries significantly increased with a decrease in mean daily air temperature (T_a; a) and a continuation of restricted feeding (b; filled symbols). However, the daily heterothermy index (HI; °C), an integrated metric of the magnitude of heterothermy, did not significantly change with mean daily T_a (c) or a continuation of fasting (d). Error bars indicate standard deviations. Only well-fed birds (clear symbols) are presented in comparison to mean daily T_a (a,c).

Figure 6. The basal metabolic rate (BMR; W) of island columbid species (clear symbols) and mainland species (filled symbols). Data and sources are provided in the Electronic Supplementary Material.
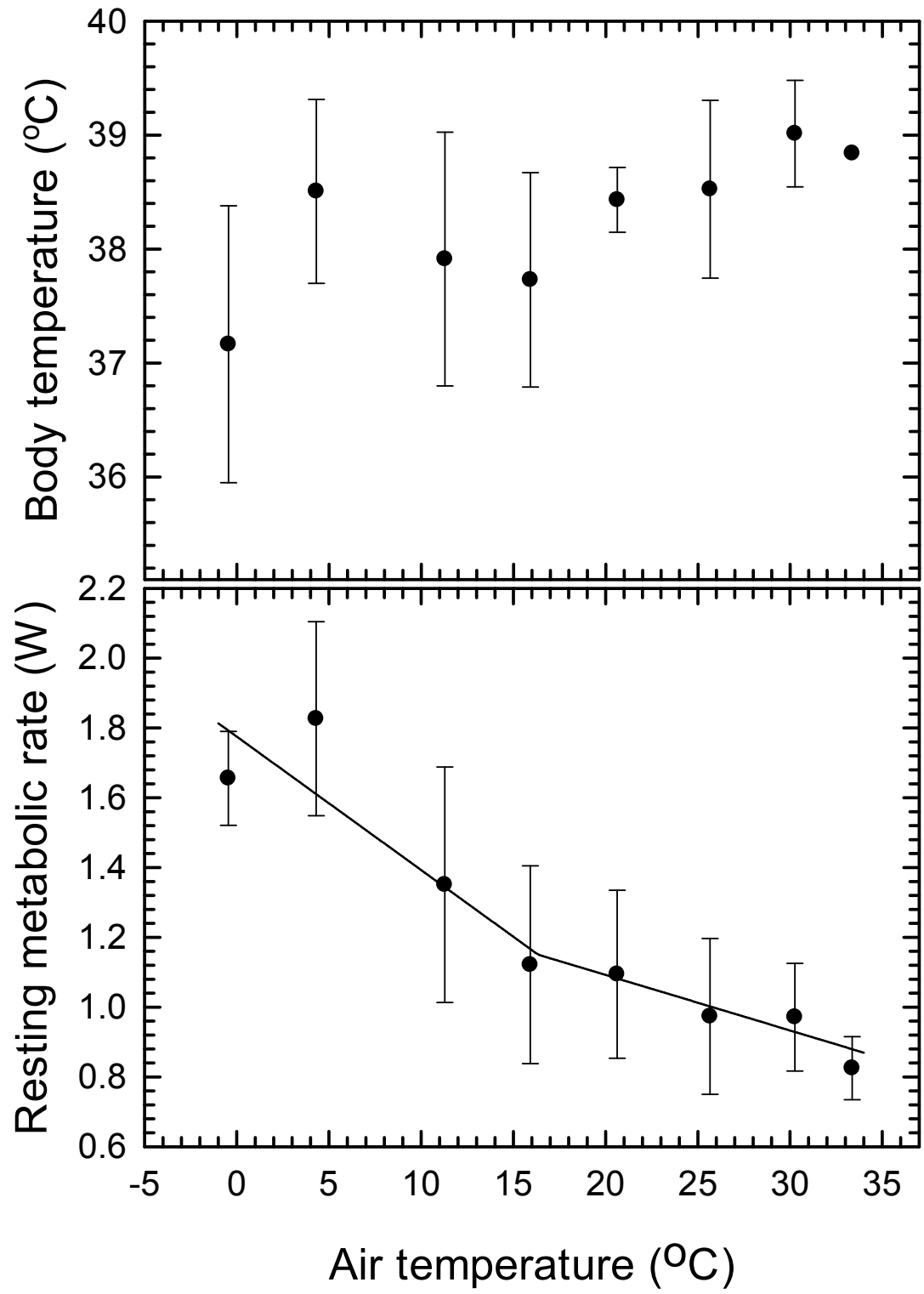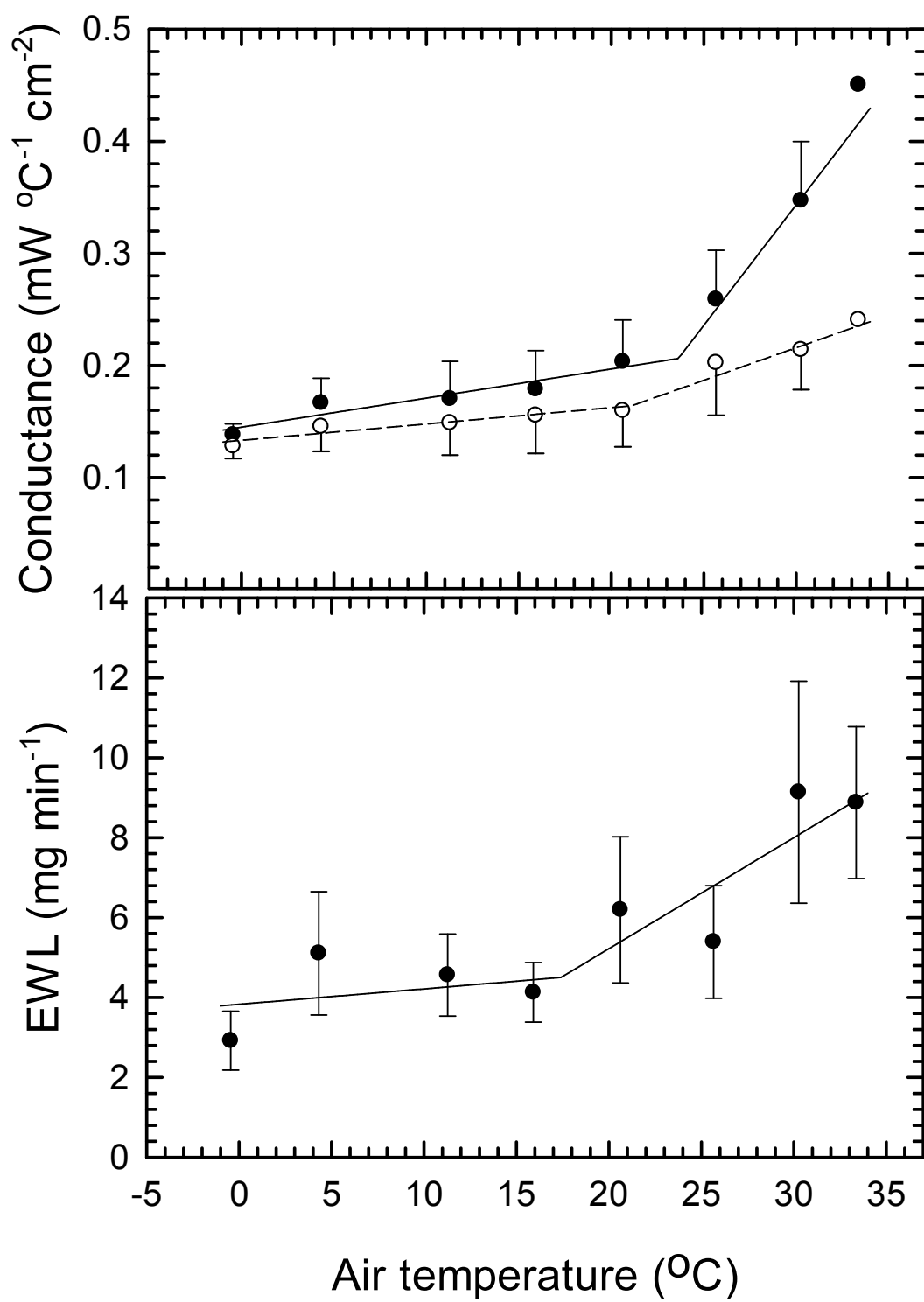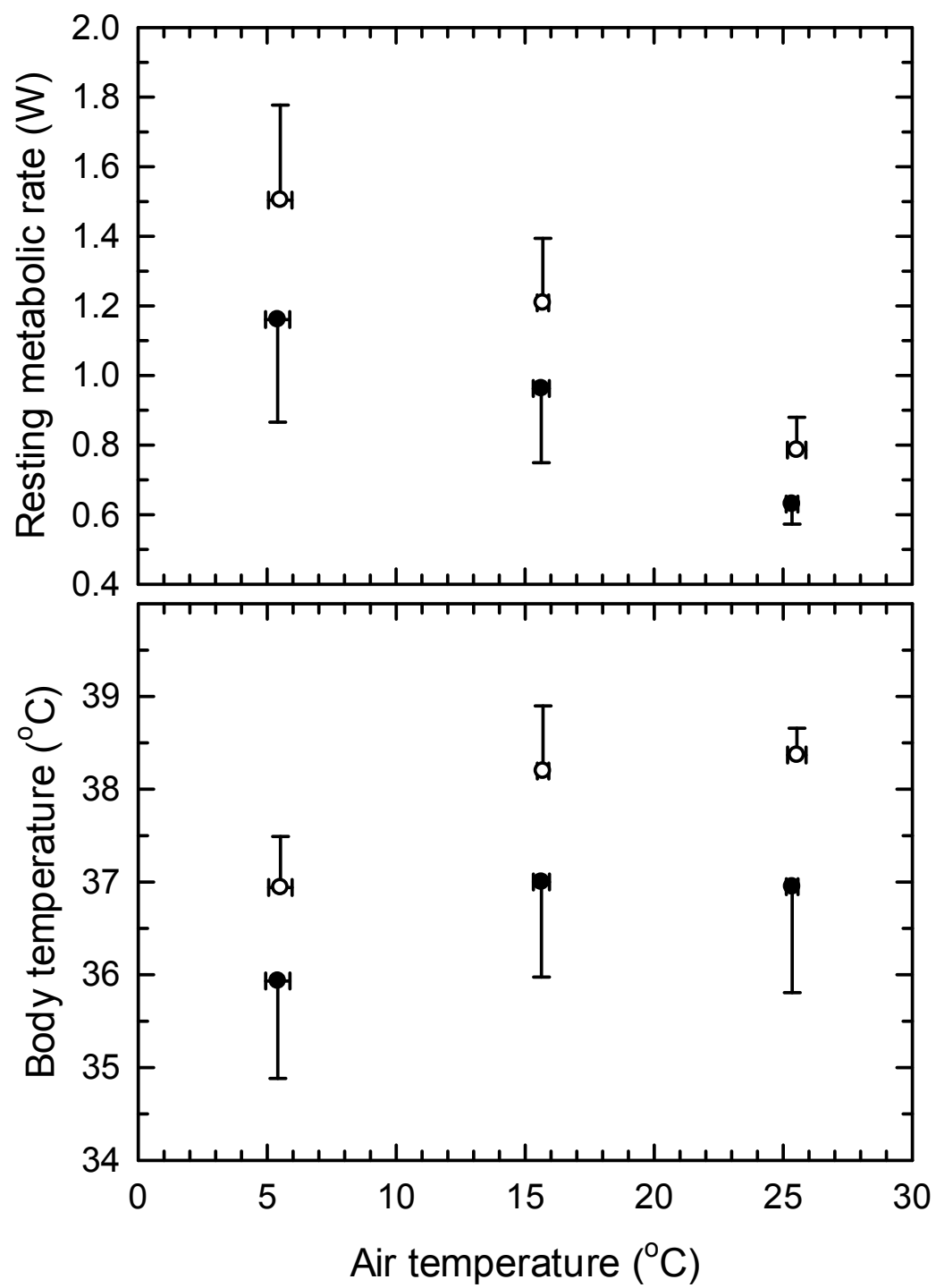
Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5

Figure 6.