Avian thermoregulation in the heat: phylogenetic variation among avian orders in evaporative cooling capacity and heat tolerance

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ABSTRACT

Little is known about phylogenetic variation in avian evaporative cooling efficiency and heat tolerance of birds in hot environments. We quantified thermoregulatory responses to high air temperature (T_a) in ~100-g representatives of three orders: African cuckoo (*Cuculus gularis*, Cuculiformes), lilac-breasted roller (*Coracias caudatus*, Coraciiformes), and Burchell's starling (*Lamprotornis australis*, Passeriformes). All three species initiated respiratory mechanisms to elevate evaporative heat dissipation when body temperature (T_b) approached 41.5°C in response to increasing T_a, with gular flutter observed in cuckoos and panting in rollers and starlings. Resting metabolic rate (RMR) and evaporative water loss (EWL) increased by quantitatively similar magnitudes in all three species, although maximum EWL was proportionately lower in starlings. Evaporative cooling efficiency—defined as the ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) —generally remained below 2.0 in cuckoos and starlings, but reached a maximum of ~3.5 in rollers. The high value for rollers reveals a very efficient evaporative cooling mechanism, and is similar to EHL/MHP maxima for similarly sized columbids which rapidly dissipate heat via cutaneous evaporation. These findings shed new light on the ecology, physiology and evolution of birds that routinely have to maintain T_b below environmental temperature.

Keywords: evaporative heat loss, heat dissipation, upper critical limits of thermoneutrality, panting, gular flutter

Summary statement

Avian evaporative cooling efficiency and heat tolerance show substantial taxonomic variation. We show that a 100-g coraciiform shows highly efficient evaporative cooling capacity and tolerates higher air temperatures, compared with a similar sized cuculiform and passerine. These findings highlight that we currently have a poor understanding of the mechanisms underpinning taxonomic variation in avian thermoregulation under hot conditions.

Introduction

Evaporative heat loss (EHL) is the only mechanism whereby birds can maintain body temperature (T_b) below lethal limits in hot environments where environmental temperature exceeds T_b. Rapid increases in evaporative water loss (EWL) are a ubiquitous avian response to such temperatures (Bartholomew and Cade, 1963; Dawson and Bartholomew, 1968; Smith et al., 2015; Whitfield et al., 2015). Water requirements for thermoregulation have thus shaped the ecology and evolution of birds living in hot environments, and lead to important trade-offs between dehydration and hyperthermia avoidance in arid-zone species (Smit et al., 2013; Tieleman and Williams, 2000; Tieleman and Williams, 2002; Tieleman et al., 2003).

Avian heat tolerance and evaporative cooling efficiency (quantified as the maximum ratio of heat dissipated evaporatively, EHL, to that generated metabolically, MHP) appears to vary substantially among orders (Lasiewski and Seymour, 1972; Smith et al., 2015), within orders (McKechnie et al., 2016a; McKechnie et al., 2017), and even within species (Noakes et al., 2016). For example, recent studies have shown that the efficiency of evaporative cooling is generally very high (EHL/MHP > 2.0) in members from the order Columbiformes

73 and Caprimulgiformes (McKechnie et al., 2016a; O'Connor et al., 2017; Smith et al., 2015;
74 Talbot et al., 2017) where efficiency of evaporative cooling regularly exceeds 2.0, and less so
75 in Passeriformes, Pteroclidiformes, Galliformes and Strigiformes, where efficiency rarely
76 exceeds 2.0 (Bartholomew et al., 1968; McKechnie et al., 2016b; McKechnie et al., 2017;
77 Smith et al., 2015; Whitfield et al., 2015). Many avian taxa also allow their T_b to increase in a
78 controlled manner (described as facultative hyperthermia), which reduces water
79 expenditure but increases the risk of reaching lethal limits during heat exposure. Narrow
80 phylogenetic sampling means we have an incomplete understanding of the diversity of avian
81 EHL mechanisms and their functional significance for heat tolerance.

82 Body mass represents one of the most prominent sources of variation in heat stress
83 tolerance and the efficiency of EHL (McKechnie and Wolf, 2010), but even species of similar
84 size can still show substantial variation. For example, Lasiewski and Seymore (1972) showed
85 that four similarly sized species from different avian orders (*Ploceus cucullatus, o*rder
86 Passeriformes; *Excalfactoria chinensis*, order Galliformes; *Scardafella inca*, order
87 Columbiformes; *Phalaenoptilus nuttallii*, order Caprimulgiformes) show substantial variation
88 (in terms of magnitude of elevations in T_b, metabolism, EWL, and EHL/MHP) in their
89 responses to heat. Recent studies have suggested that some of the underlying mechanisms
90 explaining this variation may include differential reliance on respiratory versus cutaneous
91 pathways of evaporative cooling (McKechnie et al., 2016a), and also morphological variation
92 (e.g. bill size) (Danner et al., 2016; Tattersall et al., 2009; van de Ven et al., 2016). Variation
93 in the rate and efficiency of evaporative cooling in avian taxa may reflect physiological costs,
94 such as risk of dehydration and hyperthermia (McKechnie and Wolf, 2010), but may also
95 reflect behavioural [e.g. reduced foraging efficiency correlated with heat dissipation efforts
96 (du Plessis et al., 2012)] and ecological costs [e.g. reliance of surface water sources (Smit et

97 al., 2016)]. Thus far, evaporative cooling efficiency and heat tolerance are most studied in
98 the orders Passeriformes and Columbiformes, and data from more unrepresented avian
99 orders are needed to further our understanding of the evolutionary drivers and mechanisms
100 involved in thermoregulation in the heat.

101 Here we present data on thermoregulation under hot conditions in three 100-g avian
102 species representing three orders: Cuculiformes, Coraciiformes and Passeriformes. The
103 Cuculiformes and Coraciiformes remain largely unstudied in terms of thermoregulation at
104 high temperatures; both represent diverse taxa that include many species occurring in hot,
105 arid regions. To the best of our knowledge, the only thermoregulatory data from a
106 cuculiform under hot conditions is for the roadrunner (Calder and Schmidt-Nielsen, 1967). In
107 the latter study, high humidity levels may have confounded the efficiency of EHL at
108 experimental temperatures (T_a) below T_b. Recent advances in carbon dioxide and water
109 analysers have allowed us to maintain low humidity levels during testing by utilising high
110 flow rates, thus avoiding the complications associated with high humidity that plagued early
111 studies (Gerson et al., 2014; Lasiewski et al., 1966; Smith et al., 2015; Whitfield et al., 2015).
112 In addition, our inclusion of a large passerine (>100g) allows for more rigorous analyses of
113 the scaling of traits related to heat tolerance and evaporative cooling in this speciose taxon
114 (McKechnie et al., 2017).

115

116

117 **Methods**

118 *Study species and study sites*

119 We measured resting metabolic rate (RMR), evaporative water loss (EWL), and T_b in species
120 representing three avian orders in the southern Kalahari Desert in the Northern Cape

121 province of South Africa, an arid area with a mean annual rainfall of ~200 mm and summer
122 daily maximum T_a ranging from ~20-43°C (Whitfield et al., 2015). We followed the
123 methodology of Whitfield et al. (2015) to quantify thermoregulatory responses to high T_a in
124 a field laboratory from January to April 2012 at Wildsgenot Game Ranch (27°04´S, 21°23´E),
125 and from January to March 2013 at Leeupan Game Ranch (26°58´S, 21°50´E).

126 We trapped six African cuckoos (*Cuculus gularis*, order Cuculiformes, hereafter
127 cuckoos) with a mean ± SD body mass (M_b) of 109.6 ± 5.6 g at Leeupan Game Ranch during
128 early 2013 (austral summer) using mist nets. We trapped 10 lilac-breasted rollers (*Coracias*
129 *caudatus*; Order Coraciiformes, hereafter rollers) with a M_b of 95.4 ± 8.5g; two individuals
130 were trapped in February 2012 at Wildsgenot Game Ranch, and the remaining individuals
131 were trapped at Leeupan Game Ranch between January 2013 and March 2013. We trapped
132 seven Burchell's starlings (*Lamprotornis australis*; order Passeriformes, hereafter starlings)
133 with a M_b of 109.1 ± 9.3g using mist nets and/or flap traps baited with tenebrionid beetle
134 larvae on Wildsgenot Game Ranch in February 2012, and Leeupan Game Ranch from
135 December 2013 to February 2013. Measurements were carried out on the same day of
136 capture. If birds were not tested within the first three hours after being trapped, they were
137 housed in cages constructed of shade-cloth, and were provided with tenebrionid beetle
138 larvae and water ad libitum, until physiological measurements commenced.

139 Birds were held in respirometry chambers for 2-3 hr, a period that typically limited
140 M_b loss to <5% of initial M_b (mean M_b loss during measurements was 4.0 ± 1.8 % of initial
141 values) and time in captivity did not exceed 24 hr, after which birds were released at the site
142 of capture following Whitfield et al. (2015). All experimental procedures were approved by
143 the Animal Ethics Committee of the University of Pretoria (protocol EC071-11) and the
144 Institutional Animal Care and Use Committee of the University of New Mexico (12-1005370-

145 MCC). A permit to trap the birds was issued by the Northern Cape Department of
146 Environmental Affairs (ODB 008/2013).
147
148 *Gas exchange and temperature measurements*
149 We used the same experimental set-up as described by Whitfield et al. (2015) to obtain gas
150 exchange, T_a and T_b measurements. We measured T_b using calibrated temperature-sensitive
151 passive integrated transponder (PIT) tags (Biomark, Boise, ID, USA) which were injected
152 intraperitoneally into the abdominal cavity of each bird shortly after capture. We monitored
153 T_b throughout gas exchange measurements, using a reader and transceiver system (model
154 FS2001, Biomark, Boise, ID, USA). We obtained carbon dioxide production ($\dot{V}_{CO_2}$) and EWL
155 measurements over the T_a range of 25-56°C (depending on the species), also using the same
156 experimental setup as described by Whitfield et al. (2015). All three species were placed
157 individually in 9-L plastic chambers, and stood on a platform of plastic mesh 10 cm above a
158 1-cm layer of mineral oil to trap excreta. We used flow rates between 9 and 30L min^{-1} for
159 cuckoos; 9 and 70 L min^{-1} for rollers, and 10 and 55 L min^{-1} for starlings, depending on the
160 experimental T_a, in order to keep chamber humidity below 5 ppt. As was the case in
161 previous studies using the same methodology (Smith et al. 2015, Whitfield et al. 2015,
162 McKechnie et al. 2016a, McKechnie et al. 2016b), birds remained calmer at very high T_a
163 when we increased flow rate (and hence decreased humidity).
164
165 *Experimental protocol*
166 Following the protocol described by Whitfield et al. (2015), we exposed birds to
167 progressively higher T_a, with increments of approximately 5°C between 25 and 40°C, and 2°C
168 increments between 40°C and the maximum T_a (ranging from 48 to 56°C depending on the

species). Tests were conducted during the day, as this was the active phase of all three species. Birds spent between 10 and 30 min at each T_a value. We continually monitored birds during measurements using a live video feed and an infrared light source (Whitfield et al., 2015). We recorded behavioural responses of birds within the respirometry chambers every two minutes; an activity state score of the individual (e.g. calm, turning around or jumping) was recorded, as well as respiratory EHL mechanisms, including panting (defined as gaping) and gular flutter (defined as an obvious pulsation of hyoid bone in the gular area while gaping). For each individual, we recorded the air temperature and body temperature at which heat dissipation behaviour was initiated.

We followed Whitfield et al. (2015) in terminating test runs when a bird a) exhibited prolonged escape behaviour such as agitated jumping, pecking and/or wing flapping), b) showed signs of a loss of coordination or balance accompanied by T_b > 44°C, or c) exhibited a decrease in EWL and RMR accompanied by an uncontrolled increase in T_b. In the last instance, a bird was considered to have reached its upper limit of heat tolerance, and the T_a associated with the onset of these signs of heat stress was considered the thermal endpoint for that individual. When a bird reached any the conditions described above, we removed the individual from the chamber by hand, gently rubbed a cotton pad soaked in ethanol onto its body, and held it in front of an air-conditioner producing chilled air in order to facilitate rapid heat loss (Whitfield et al., 2015).

$\dot{V}_{CO_2}$

Data analyses

Data were analysed following Whitfield et al.(2015). We calculated physiological estimates by extracting, EWL and T_b as the lowest 5 min mean at each T_a using Expedata (Sable Systems, Las Vegas NV, USA). We present whole-animal values, although we also calculated

193 the slope of mass-specific EWL vs. T_a to compare our values with the allometric equation
194 presented by McKechnie and Wolf (2010). We converted rates of EWL to evaporative heat
195 loss (W) assuming a latent heat of vaporisation of water of 2.406 J mg^{-1} at 40°C (Tracy et al.
196 2010). Since none of our study species display crops we assumed all birds were post-
197 absorptive at the time of measurements, but we were unable to confirm this.
198 Measurements typically took place more than 1 hr after capture, and food (mealworm
199 larvae) was only offered to individuals not tested within 3 hrs of capture. We therefore
200 assumed a respiratory exchange ratio of 0.85, representative of a mix of carbohydrate and
201 lipid metabolism in post-absorptive birds (Walsberg and Wolf 1995), and converted rates of
202 $\dot{V}_{CO_2}$ to metabolic rate (Watt, W) using 24.4 J mL^{-1} CO_2 (Withers 1992).

203 We used segmented linear regression models fitted in the *R* package *segmented*
204 (Muggeo, 2009) to estimate inflection T_a in the physiological data. Although our use of these
205 models violates assumptions of independent samples, we used segmented models purely to
206 aid us in identifying inflection T_a values in physiological variables. We subsequently used
207 linear mixed effects models that included individual identity as a random factor in the *R*
208 package *nlme* (Pinheiro et al., 2009), to obtain estimates of physiological variables as a
209 function of T_a, using subsets of the data above respective inflection T_a. We contrasted the
210 slopes of physiological parameters obtained from these mixed effects models among
211 species, by including data previously collected from laughing doves (*Stigmatopelia*
212 *senegalensis*, 89.4 ± 13.0, hereafter doves) studied at the same time and site as our species
213 (McKechnie et al., 2016a), and freckled nightjars (*Caprimulgus tristigma*, 64.7 ± 6.3,
214 hereafter nightjars) studied from a desert site in Namaqualand, South Africa (O'Connor et
215 al., 2017). Thermoregulatory data in the doves and nightjars were collected in the same

216 manner as described here, although we recalculated physiological estimates of $\dot{V}_{CO_2}$, EWL
217 and T_b in the dove, as the lowest 5 min mean at each T_a, to facilitate comparison with our
218 study species and the nightjar. Our small sample size of species prevented us from
219 conducting more rigorous statistical analyses that test phylogenetic inertia and, if necessary,
220 account for phylogenetic relatedness. However, the five avian orders representing these
221 taxa all diverged from a common ancestor between 71.5 and 79.6 million years ago (Jetz et
222 al., 2012), and given the current uncertainty of the fine-scale relatedness of these avian
223 orders, we argue that it will be difficult to obtain an accurate phylogenetic signal at this
224 level. We therefore calculated the upper and lower 95% confidence limits (CL) of each
225 coefficient, and considered species to differ quantitatively in the parameters when there
226 was no overlap in the 95% CL.
227
228 **Results**
229 *Body temperature*
230 Normothermic T_b measured at T_a < 35°C, or the respective T_{uc} of each species, varied by
231 0.7°C in the three species, from a mean of 40.0 ± 0.6°C in cuckoos to 40.7 ± 0.8°C in rollers
232 (Table 1). The inflection T_a above which T_b increased was below 37°C in all three species
233 (Table 1), and in all three species T_b increased linearly and significantly above the inflection
234 T_a (cuckoo, $t_{1,26}$=14.275, p<0.001; rollers, $t_{1,56}$= 12.10, p<0.001; starlings, $t_{1,28}$=7.71, p<0.001)
235 (Fig. 1). The maximum T_a reached was 50°C for both cuckoos and starlings, and 56°C for
236 rollers. Any further increases in T_a resulted in these individuals becoming severely agitated.
237 Average maximum T_b ranged between 42.8° and 44.0°C in the three species at the highest
238 T_as tested. In two calm cuckoos, T_b exceeded 44°C at T_a = 46° and 48°C, respectively,
239 whereupon they lost their ability to right themselves and the experiment was terminated

240 immediately. With the exception of T_b exceeding 44°C in one roller individual (with no ill-
241 effects), T_b remained <44°C in calm rollers and starlings at the maximum T_as. At the highest
242 T_a (46°C) shared among the three species, rollers regulated a lower T_b than cuckoos and
243 starlings (Table 1). The mean T_a where birds initiated respiratory EHL mechanisms varied
244 from 35.9°C in starlings to ~41°C in cuckoos and rollers, typically as T_b approached 41.5°C in
245 all three species (Table 1). Our observations of the cuckoos revealed that gaping was always
246 accompanied by gular flutter, which was visibly evident from the pulsating throat and
247 moving hyoid apparatus. Rollers and starlings panted while gaping (the gape is wide in
248 rollers) and we did not observe gular flutter (hyoid movement) in either species.
249
250 *Resting metabolic rate*
251 One cuckoo showed abnormally high RMR values (ranging from 1.03W at T_a = 30°C, to
252 5.20W at T_a = 50°C, i.e. > 6 x SD greater than the mean for the remaining cuckoos), and we
253 excluded data from this individual from our RMR analyses and descriptive statistics.
254 Minimum RMR values measured at T_a < 35°C, or the respective T_{uc} of each species, varied
255 from 0.64 ± 0.20W and 0.69 ± 0.13W in cuckoos and rollers, respectively, to 1.19 ± 0.31W in
256 starlings (Table 1). Minimum mass-specific RMR ranged from 5.85 ± 1.79 mW g^{-1} in cuckoos
257 to 10.76 ± 1.98 mW g^{-1} in starlings (Table 2). In rollers and starlings T_{uc} (T_a inflection) ranged
258 from 31°C in starlings to 47.5°C in rollers. No clear inflection point could be identified for
259 cuckoos, and RMR increased across the entire range of T_a tested (Fig. 2). In all three species,
260 RMR increased linearly and significantly at $T_a > T_{uc}$ (cuckoo, $t_{1,23}$=2.67, $p<0.05$; rollers, $t_{1,25}$ =
261 2.5866, $p<0.05$; starlings, $t_{1,29}$=4.13, $p<0.001$) (Fig. 2). Maximum RMR observed at maximum
262 T_a was higher in the starlings, at an average of 1.91W, and lowest in the rollers at ~ 1.10W.
263 Maximum RMR was 0.96W and 2.77W in two cuckoo individuals, respectively (Table 1). The

average magnitudes of RMR elevations above estimated thermoneutral levels (max. RMR / min. RMR) were generally below 1.6, with the exception of a single cuckoo that showed a 3-fold increase in RMR (Table 1). At the highest test T_a shared among the three species, RMR was quantitatively similar in cuckoos and rollers, but ~2-fold higher in the starlings (Table 1).

Evaporative water loss

Minimum EWL values measured at T_a < 35°C, or the respective T_{uc} of each species ranged from 0.48 ± 0.14 g h^{-1} in cuckoos to 1.00 ± 0.67 g h^{-1} in starlings (Table 1). Similarly, mass-specific EWL was lowest in cuckoos and highest in starlings (Table 2). The inflection T_a varied by more than 10°C among the three species; inflection T_a was 33.3°C in starlings and greater than 42°C in cuckoos and rollers (Table 1). Whereas cuckoos and starlings showed stable EWL rates below their respective inflection T_as, rollers showed a shallow but significant increase in EWL to 1.65 ± 0.35 g h^{-1} at T_a = 44.7 °C ($t_{1,22}$=3.22, p<0.01; Fig. 3). Above the inflection T_a EWL increased linearly and significantly in all three species (cuckoo, $t_{1,20}$=13.22, p<0.001; rollers $t_{1,33}$=11.64, p<0.001; starlings, $t_{1,28}$=11.133, p<0.001; Fig. 3). Mass-specific slopes varied from around 2.1 mg g^{-1} h^{-1} °C^{-1} in cuckoos and starlings to >4 mg g^{-1} h^{-1} °C^{-1} in rollers (Table 2). Maximum elevations in EWL were around 5-fold (>5.5-fold in cuckoos and rollers) above thermoneutral values in the three species (Fig. 3, Table 1). Whereas rollers showed maximum EHL/MHP ratios exceeding 3 at the maximum T_as tested, cuckoos and starlings generally showed values below 2 (Fig. 3). At the highest shared T_a cuckoos and rollers showed similar EWL rates and evaporative efficiencies (Table 1). In contrast, starlings showed EWL of ~ 3.40 g h^{-1}, and a slightly lower efficiency compared to the former species (Table 1).

288

289

290 *Variation in thermoregulation at high air temperatures*

291 Our data, combined with those for doves and nightjars, provide an opportunity to compare
292 heat tolerance and evaporative cooling capacity among five avian orders. The T_b of cuckoos
293 and doves increased more rapidly compared to those of the remaining species, although the
294 95% CL overlapped largely in most species (Fig. 5, Table 3). The slope of RMR at T_a above
295 thermoneutrality in doves was similar to those of our three present study species, with
296 overlapping 95% confidence intervals. In contrast, nightjars showed almost no increase in
297 RMR above 40°C and no overlap in 95% CL with any of the other species (Fig. 5, Table 3).
298 Similarly, the slope of EWL above the inflection T_a was also lower in nightjars compared to
299 the other four species (no overlap in 95% CL). Rollers showed a higher slope in EWL above
300 the inflection T_a compared to the cuckoos, starlings and the dove (Fig. 5, Table 3). Nightjars
301 achieved more rapid increases in EHL/MHP at T_a above the inflection, compared to our
302 three study species and doves (Fig. 5; Table 3); whereas nightjars showed a higher EHL/
303 MHP values compared to rollers and cuckoos, the 95% CL overlapped marginally (Table 3).
304 Unexpectedly, the slopes of EHL/MHP were similar in doves and starlings, both lower than in
305 cuckoos and rollers showing no overlap in 95% CL (Table 3).

306

307 **Discussion**

308 All three species studied here showed elevations in T_b, RMR and EWL at T_a above 40°C,
309 which is qualitatively consistent with typical avian patterns. Despite their similarity in M_b,
310 they showed substantial variation in patterns of T_b, RMR and EWL at high T_a. The
311 comparatively shallow elevations in RMR in rollers were associated with the highest

312 evaporative efficiency, and this species tolerated the highest T_a among the three species.
313 Rollers showed very small elevations in T_b, associated with high evaporative efficiency. In
314 contrast, at lower T_as both starlings and cuckoos showed sharp elevations in T_b, rapid
315 elevations in RMR, and lower evaporative efficiencies. Yet, the T_a at which these responses
316 were initiated, patterns of T_b regulation, and EWL elevations, were strikingly different
317 between these taxa. Additionally, our five-order comparison reveals that all species, with
318 the exception of caprimulgids (O'Connor et al., 2017), clearly showed elevated metabolic
319 costs of heat dissipation (as defined by the slope of RMR above the inflection point) (Fig. 5).
320 These findings illustrate how little we know about the phylogenetic variation in avian
321 evaporative cooling pathways, and specifically the functional significance, selective
322 pressures and evolution of these seemingly diverse pathways for heat tolerance.
323
324 *Body temperature and heat tolerance limits*
325 The mean T_b of cuckoos at T_a below 35°C (39.8 ± 0.30°C) was 1.5 °C lower than the mean
326 active phase T_b values for Cuculiformes (41.3°C), but the mean T_bs of starlings and rollers
327 were within 0.5°C of the mean values reported for Passeriformes and Coraciiformes,
328 respectively (Prinzinger et al., 1991). In all three species, the inflection T_a for T_b was below
329 40°C (Fig. 1). This is lower than the inflection T_a recorded previously in columbids, quail, and
330 smaller passerines (generally T_a ~ 40°C) (McKechnie et al., 2016a; Smith et al., 2015;
331 Whitfield et al., 2015). Two species of Caprimulgiform also show a T_b inflection at T_a below
332 40°C (O'Connor et al., 2017).
333 In calm birds, maximum T_b was >44.5°C in a cuckoo at T_a = 49.6°C, 44.1°C in a starling
334 at T_a = 49.2°C and 44.6°C in a roller at T_a = 53°C (Fig. 1). The two cuckoos lost coordination at
335 T_b > 44°C, which suggests this taxon may have lower critical thermal limits than

336 Passeriformes and Columbiforms, where several species have been shown to tolerate
337 T_b>45°C (Dawson, 1954; McKechnie et al., 2016a; Whitfield et al., 2015). Several smaller
338 passerines also reached thermal limits as T_a approached 50°C (McKechnie et al., 2017;
339 Whitfield et al., 2015). However, T_a = 50°C is probably an underestimation of the heat
340 tolerance limits of cuckoos and starlings, as we did not reach the T_as at which calm
341 individuals showed a plateau in EWL accompanied by an increasing T_b (Whitfield et al.,
342 2015). In contrast to cuckoos and starlings, rollers defended their T_b over a much larger T_a-T_b
343 gradient, tolerating T_a ~ 56°C, with a mean T_b of ~ 43°C (Fig. 1). The T_b patterns of the
344 coraciiform in our study at T_a approaching 60°C was therefore quantitatively similar to the
345 thermoregulatory patterns observed in Columbiformes (McKechnie et al., 2016a; Smith et
346 al., 2015).
347
348 *Resting metabolic rate*
349 The upper inflection T_a in RMR versus T_a, i.e., the T_{uc} indicating increased energetic costs of
350 respiratory EHL, generally occurs at T_{air} < 40°C (Calder and Schmidt-Nielsen, 1967; Dawson
351 and Bennett, 1973; McNab and Bonaccorso, 1995; Tieleman and Williams, 2002; Whitfield
352 et al., 2015). In all three species studied here, T_{uc} was not clearly related to increased efforts
353 of respiratory EHL, unlike the case in Burchell's sandgrouse (McKechnie et al. 2016a). Our
354 data suggest that the initiation of gular flutter or panting was related to a threshold T_b of
355 ~41.5°C, rather than a threshold T_a (Table 1). The cuckoos in our study did not show a clear
356 upper inflection T_a, contrasting with the marked T_{uc} associated with the onset of gular
357 flutter in Burchell's sandgrouse (*Pterocles burchelli*) (McKechnie et al., 2016b). At the T_a
358 value at which we observed cuckoos to initiate gular flutter (~42°C, Table 1), RMR had
359 already increased significantly by more than 50% above minimum resting levels. Similarly,

360 in the starlings, the inflection T_a for RMR was well below the T_a at which this species
361 initiated gaping behaviour, and lower than recorded in smaller passerines (Whitfield et al.
362 2015). The patterns in these two species are perhaps explained by a Q_{10} effect associated
363 with T_b elevations, but our small sample sizes precluded us from making any firm
364 conclusions; it is noteworthy that Weathers (1981) has shown that elevations in body
365 temperature do not affect RMR in a number of passerines, but this idea has not been
366 rigorously tested. In contrast to the starlings and cuckoos, rollers maintained a low and
367 stable RMR up to T_a = 47°C (Fig. 2), much higher than the T_a associated with gaping. This
368 suggests that rollers kept metabolic heat loads low during the initial stages of panting. Our
369 estimate of the upper T_{uc} in rollers is thus substantially higher than typically observed in
370 passerines, which also make use of panting (McKechnie et al., 2017; Weathers, 1981;
371 Whitfield et al., 2015).

372 Our data reveal considerable overlap in the slope of RMR increases above the T_{uc} in
373 all three species studied here when compared to a similar-sized dove (*S. senegalensis*) (Fig.
374 5, Table 3). Our estimate of the slope of RMR *vs.* T_a above the inflection T_a was higher than
375 reported for this species of dove (same data) by McKechnie et al., (2016a), as we calculated
376 RMR over a 5-min period, instead of the 1-minute period used by the latter authors. This
377 discrepancy does not influence our conclusions; doves showed quantitatively similar
378 metabolic elevations at high T_as to cuckoos, rollers and starlings (Fig 5, Table 3). At least one
379 previous study noted that the metabolic costs in species that pant (e.g. village weavers,
380 *Ploceus cucullatus*) are similar to those in species which supplement panting with gular
381 fluttering (e.g. Chinese painted quails, *Excalfactoria chinensis*), and additionally cutaneous
382 EHL [e.g. Inca doves, *Scardafella inca* (Lasiewski and Seymour, 1972)]. However, one striking

383 difference among the species we compare here is that doves and rollers reached maximum
384 RMR at higher T_as and maintained lower T_bs compared with cuckoos and starlings.
385 The fractional elevations in RMR at T_a up to 50°C were lower in cuckoos (~24% above
386 thermoneutral values) compared to starlings (~60%); in the latter species values were
387 quantitatively similar to those recorded in passerines [30-90%; (McKechnie et al., 2017;
388 Whitfield et al., 2015)]. However, fractional RMR elevations at T_a up to 50°C in cuckoos and
389 starlings were higher than those observed in the roller (~10% higher; this study), and
390 Columbiformes (approximately 7% higher than in seven species; (McKechnie et al., 2016a),
391 over a similar T_a range (30°C to 50°C). The lack of metabolic elevations at T_as above those
392 where gular flutter was initiated in the nightjars (T_a ~ 40°C) contrasts strongly with all the
393 above-mentioned species (Fig. 5). O'Connor et al. (2017) argued that the low RMR of
394 nightjars contributes to low metabolic heat load at high T_a s. However, the negligible
395 metabolic increases at high T_a previously also observed in the common poorwill [linked to
396 the unique mode of gular flutter (Bartholomew et al. 1968, Lasiewski and Seymour 1972)],
397 strongly suggest that this is characteristic of caprimulgids in general (O'Connor et al., 2017;
398 Talbot et al., 2017).
399
400 *Evaporative heat loss*
401 Patterns of EWL followed the typical trend observed in birds, where EWL was minimal at T_as
402 around 25-35°C and increased approximately linearly at T_as approaching or exceeding 40°C.
403 Average minimum EWL rates recorded in our three study species were higher than those
404 predicted by Williams (1996) for all birds (eqn. 2) at T_a = 25°C, at 124%, 153%, and 169% of
405 expected values for the cuckoos, rollers, and starlings, respectively, when compared to the
406 expected values for arid-zone species (Williams, 1996); these discrepancies may reflect the

407 fact that most of our minimum measurements of calm individuals were obtained at T_a >
408 30°C, as opposed to T_a = 25°C in the latter study. The inflection T_as above which we observed
409 rapid elevations in EWL in the three species studied here varied by > 10°C. McKechnie and
410 Wolf (2010) showed that inflection T_as vary with body mass, and show large inter-specific
411 variation of a quantitatively similar magnitude to what we observed here. McKechnie and
412 Wolf (2010) found that the slope of mass-specific EWL *versus* T_a scales negatively with body
413 mass, explaining ~90% of variation. However, we observed substantial variation in the
414 slopes of EWL above the respective inflection T_as, among the species we studied (Fig. 3).
415 This variation in the sensitivity of EWL to T_a is difficult to explain. Comparisons of slopes in
416 EWL with other species are also not feasible as the data from the literature analysed by
417 McKechnie and Wolf (2010) were obtained under different experimental conditions, most
418 notably varying chamber humidity levels, which has been shown to influence evaporative
419 cooling efficiency (Gerson et al., 2014).

420 The capacity for evaporative cooling, expressed as maximum EHL/MHP, was
421 qualitatively related to the maximum T_a reached by our three study species. On average,
422 cuckoos and starlings evaporated less than 200% of metabolic heat production at the
423 maximum T_a reached (Fig. 4) – patterns similar to those observed in passerines (McKechnie
424 et al., 2017; Whitfield et al., 2015). The comparatively high RMR of starlings likely
425 constrained their evaporative cooling efficiency as they had to evaporate water almost
426 twice as rapidly (compared to the other species) to dissipate 100% of their metabolic heat.
427 This may have broad-scale implications for heat loss in the order Passeriformes, especially
428 considering a recent study which demonstrated its comparatively high energy demands as
429 an order (Londoño et al., 2015). Cuckoos showed a slope of EHL/MHP versus T_a only
430 marginally lower than rollers, but despite their low RMR at T_a < 35°C, they did not reach a

431 very high efficiency (Fig. 4); even though a very calm cuckoo dissipated 200% of its
432 metabolic heat load at T_a = 50°C, the T_b of this individual was already ~ 43°C.
433 Rollers showed a mean maximum EHL/MHP of 3.64 (> 4 in one individual) (Fig. 4),
434 quantitatively similar to values reported in Columbiformes (ranging from 2.27 to 4.66), a
435 taxon in which we expect significant reliance on cutaneous EHL (McKechnie et al., 2016a;
436 Smith et al., 2015). In fact, at T_a > 50°C rollers evaporated much more of their metabolic
437 heat compared to medium-sized columbids (the 140-g *S. capicola*, and 90-g *S. senegalensis*)
438 occupying the same habitat in the Kalahari Desert (McKechnie et al. 2016b). We do not
439 know if rollers rely on cutaneous evaporation at high T_a, although we propose that
440 evaporative cooling may be enhanced by the large gape of rollers increasing the surface
441 area of EWL over the respiratory region (personal observation); the large gape and high
442 evaporative efficiency is also seen Caprimulgids, but it would be interesting to investigate
443 the contribution of CEWL to overall water loss.Our understanding of the capacity for
444 different avian taxa to partition EWL into cutaneous and respiratory pathways remains very
445 poorly studied, and besides for a few studies focussing on Columbiformes and
446 Passeriformes, we have limited empirical data on how increased reliance on CEWL at high T_a
447 would reduce the energetic demands for respiratory heat dissipation.
448
449 *Phylogenetic variation in thermoregulation under hot conditions: ecological and evolutionary*
450 *consequences*
451 The metabolic cost of heat dissipation seems to vary widely amongst avian orders. With the
452 exception of the patterns of RMR observed in nightjars, the other four species discussed
453 here show elevations in RMR, apparently correlated with phylogenetic variation in the use
454 of gular flutter and/or panting. Similar variation was observed by Lasiewski and Seymour

455 (1972), using four taxa from different orders with varying modes of respiratory EHL, from
456 panting only in a passerine, to varying modes of gular flutter and panting in a galliform,
457 columbid, and caprimulgid, respectively. All species, except the caprimulgid, showed
458 elevations in RMR at high T_a.

459 Although our study was not designed to directly quantify the relative importance of
460 gular flutter versus panting in our study species, we suspect that variation in the relative
461 importance of these processes may explain some of the taxonomic patterns observed here.
462 Calder and Schmidt-Nielson (Calder and Schmidt-Nielsen, 1967) categorised variation in
463 respiratory EHL pathways among avian orders as 1) a combination of panting and gular
464 flutter, where gular flutter and panting/breathing rates are synchronised [e.g. Strigiformes,
465 Columbiformes and Cuculiformes [(Bartholomew et al., 1968)], 2) strictly gular flutter where
466 the frequency and amplitude of breathing cycles are generally significantly lower, and
467 generally asynchronous with gular flutter rates [e.g. some Pelicaniformes and some
468 Caprimulgiformes (Bartholomew et al., 1968; Lasiewski and Bartholomew, 1966; Lasiewski
469 and Seymour, 1972)], or 3) panting only [e.g. Passeriformes ((Calder and Schmidt-Nielsen,
470 1967)]. Bartholomew et al. (1968) further suggested that variation in the two primary
471 modes of gular flutter may have consequences for the energetic costs of ventilating the
472 buccal region, with species that maintain rapid gular flutter rates accompanied by slow
473 breathing rates (Caprimulgiforms, and some Pelicanifroms) achieving very high evaporative
474 cooling efficiencies compared to species where panting frequency and amplitude is
475 completely synchronised with gular fluttering. To the best of our knowledge, the role these
476 different modes of gular flutter play in the efficiency of EHL has not been further
477 investigated.

478 The phylogenetic variation in modes of avian respiratory EHL pathways is interesting,
479 and there is no clear explanation for the dichotomy between gular flutter and/or panting
480 among avian taxa. One potential physiological cost of respiratory EHL (other than the
481 supposed energetic cost) is an elevated risk of alkalosis during severe heat stress (Calder
482 and Schmidt-Nielsen, 1966; Calder and Schmidt-Nielsen, 1968), and at least one field
483 behavioural study demonstrated that reliance on panting could carry fitness costs when
484 birds are exposed to high air temperatures (du Plessis et al., 2012). Some authors have
485 argued that gular fluttering reduces the risks of alkalosis, compared to panting, since CO_2
486 levels are likely to be higher over gas-exchange tissues (Schmidt-Nielsen, 1990). The
487 prevalence of gular flutter in phylogenetically older taxa, such as Paleognathae and most
488 basal Neognathae, suggests it is a plesiomorphic trait. This may indicate that the function of
489 the hyoid bone, which ventilates the gular area, was modified in some clades of the
490 Neognathae (e.g. Corraciiformes and Passeriformes). Interestingly, Psitticiformes [parrots,
491 which are closely related to Passeriformes, (Hackett et al., 2008) are the only avian taxon in
492 which lingual flutter (movement of tongue) is known to supplement panting to ventilate the
493 buccal area (Bucher, 1981; Bucher, 1985). However, to the best of our knowledge no studies
494 have determined if the latter mode of respiratory EHL is any different in efficiency to
495 panting alone.

496 In conclusion, substantial phylogenetic variation exists in avian heat tolerance and
497 evaporative cooling capacity, an observation reiterated by our comparative analysis of
498 representatives of five orders. These patterns may have far-reaching implications for the
499 ecology and evolution of birds that routinely have to maintain T_b below environmental
500 temperature. The consequences of this variation for water balance and risk of hyperthermia
501 during very hot weather are strikingly illustrated by the observation that, among the species

502 considered here at T_a ~50°C, rates of EWL expressed in term of body mass loss vary ~2-fold;
503 from an equivalent of 2.3 % M_b h^{-1} in nightjars to 4.6 % M_b h^{-1} in starlings. Moreover, at the
504 same T_a the T_b of starlings is ~3 °C higher than that of nightjars. Quantifying phylogenetic
505 diversity in avian thermal physiology under hot conditions is critical for testing hypotheses
506 regarding physiological adaptation, and predicting vulnerability to the higher T_a and more
507 frequent and intense heat waves associated with anthropogenic climate change (Albright et
508 al., 2017). For instance, the 140-fold (from 0.0003 mW °C^{-1} in nightjars to 0.0417 mW °C^{-1} in
509 starlings) and 3.6-fold (0.093 g h^{-1} °C^{-1} in nightjars to 0.337 g h^{-1} °C^{-1} in rollers) differences in
510 slopes of RMR and EWL vs T_a, respectively, suggests that, even within similarly-sized species,
511 the consequences of the predicted 4 °C increase in extreme T_a maxima for the 21st Century
512 will vary substantially. The current phylogenetic sampling of data on avian thermoregulatory
513 patterns in the heat is poor, and a thorough review of the functional role that these
514 mechanisms play in the efficiency of evaporative cooling will require sampling more avian
515 taxa from unstudied orders.
516
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522 **Competing interests**
523 The authors declare no competing financial interests.
524
525

Author contributions

B.O.W., A.E.M. and B.S. designed the study. M.C.W., B.S., W.A.T. and B.O.W. collected data, B.S. and A.R.G. analysed the data. B.S. and A.E.M. wrote the manuscript.

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Tables:

Table 1: Physiological variables (mean ± SD, n) related to thermoregulation at the air temperature (T_a) range we tested African cuckoo (*Cuculus gularis*; cuckoo), lilac-breasted roller (*Coracias caudatus*; roller), and Burchell's starling (*Lamprotornis australis*; starling). Minimum values represent lowest value for each individual at T_a < 35°C, or the upper critical limit of thermoneutrality (T_{uc}) for each species. Maximum values where obtained at the highest T_a tested; when n<3, we also show average values at the second highest T_a tested. We further indicate mean values for the highest T_a (n≥3), i.e. T_a = 46°C, shared by the three species.

Physiological variable	cuckoo	roller	starling
Body mass (g)	110.00 ± 0.02 (5)	94.50 ± 8.50	109.10 ± 9.30 (5)
Body temperature (T_b)			
Minimum T_b (°C)	40.04 ± 0.57 (6)	40.69 ± 0.82 (11)	40.65 ± 0.75 (5)
Inflection T_a (°C)	32.8	36.7	34.2
T_b vs T_a slope	0.2790	0.1613	0.1843
Maximum T_b (°C)	44.0 (2)	43.58 ± 0.84 (5)	42.81 ± 1.03 (3)
	43.7 (2)	43.40 ± 0.68 (2)	43.18 (2)
Maximum T_a (°C)	48 (2)	54 (5)	48 (3)
	50 (2)	56 (2)	50 (2)
T_b at onset of panting/gular flutter (°C)	41.56 ± 0.57 (5)	41.31 ± 0.53 (9)	41.46 ± 0.23 (5)
T_a at onset of panting/gular flutter (°C)	40.89 ± 0.79 (5)	41.18 ± 1.94 (9)	35.92 ± 4.45 (5)
Resting metabolic rate (RMR)			
Minimum RMR (W)	0.643 ± 0.198 (5)	0.69 ± 0.13 (8)	1.189 ± 0.311 (5)
T_{uc} (°C)	na	47.5	31
RMR slope (mW °C^{-1})	0.0224	0.0396	0.0417
Maximum RMR (W)	2.773 (1)	1.00 ± 0.24 (4)	1.538 ± 0.215 (3)
	0.955 (1)	1.07 ± 0.17 (2)	1.913 (2)
Max. RMR / Min. RMR	3.06 (1)	1.45 (4)	1.29 (3)
	1.24 (1)	1.55 (2)	1.61 (2)
Evaporative water loss (EWL)			
Minimum EWL (g h^{-1})	0.481 ± 0.144 (6)	0.85 ± 0.38 (8)	1.00 ± 0.67
Inflection T_a (°C)	42.7	44.7	33.3
EWL slope (g h^{-1} °C^{-1})	0.2383	0.3370	0.2306
Maximum EWL (g h^{-1})	2.72 (2)	4.81± (4)	3.33 ± 0.51 (3)
	3.09 (2)	5.41± (2)	4.97 (2)
Max. EWL / Min. EWL	5.66 (2)	5.66 (4)	3.33 (3)
	6.57 (2)	6.36 (2)	4.97 (2)
Minimum EHL/MHP	0.382 ± 0.157 (5)	0.72 ± 0.43 (8)	0.29 ± 0.29
Maximum EHL/MHP	0.80 (1)	3.35 ± 0.75 (4)	1.70 ± 0.280 (3)
	2.13 (1)	3.48 ± 0.85 (2)	1.90 (2)
EHL/MHP vs Ta slope	0.1590	0.1709	0.0704
Shared T_a = 46°C			
T_b (°C)	43.00 ± 0.95 (5)	41.96 ± 1.30 (8)	42.61 ± 0.36 (4)
RMR (W)	0.857 ± 0.111 (4)	0.830 ± 0.333 (8)	1.700 ± 0.378 (4)

EWL (g hr^{-1})	1.88 ± 0.28 (5)	1.86 ± 0.38 (8)	3.40 ± 1.15 (4)
EHL/MHP (W)	1.49 ± 0.24 (4)	1.57 ± 0.32 (8)	1.31 ± 0.20 (4)

Table 2: Mass-specific values for resting metabolic rate (RMR) and evaporative water loss (EWL) related to thermoregulation at the air temperature (T_a) range we tested African cuckoo (*Cuculus gularis*; cuckoo), lilac-breasted roller (*Coracias caudatus*; roller), and Burchell's starling (*Lamprotornis australis*; starling). Minimum values represent lowest value for each individual at T_a < 35°C, or the upper critical limit of thermoneutrality (T_{uc}) for each species. Maximum values where obtained at the highest T_a tested; when n<3, we also show average values at the second highest T_a tested. We also indicate mean values for the highest T_a (n≥3), i.e. T_a = 46°C, shared by the three species.

Physiological variable	**Cuckoo**	**Roller**	**starling**
Resting metabolic rate (RMR)			
Minimum RMR (mW g^{-1})	5.85 ± 1.79 (5)	8.91 ± 1.11 (6)	10.76 ± 1.98 (5)
Maximum RMR (mW g^{-1})	25.37 (1) 8.62 (1)	10.55 ± 3.61 (3) 11.32 (2)	14.15 ± 3.45 (3) 16.39 (2)
Evaporative water loss (EWL)			
Minimum EWL (mg g^{-1} h^{-1})	4.45 ± 1.45 (6)	8.28 ± 2.82 (6)	8.92 ± 5.67 (5)
EWL slope (mg g^{-1} h^{-1} °C^{-1})	2.10	4.03	2.07
Maximum EWL (mg g^{-1} h^{-1})	30.09 (1) 27.14 (1)	52.91 ± 8.95 (3) 57.36 (	30.19 ± 3.36 (3) 42.41 (2)

Table 3: Slopes and upper and lower 95% confidence intervals (CI) for African cuckoos (cuckoo; *Cuculus gularis*, this study), Lilac-breasted rollers (roller; *Coracias caudatus,* this study), Burchell's starlings (starling; *Lamprotornis australis*, this study), laughing doves [dove; *Spilopelia senegalensis* (McKechnie et al. 2016b)], and Freckled nightjars [nightjar; *Caprimulgis tristigma* (O'Connor et al., 2017)] derived from linear mixed effects models. Non-overlapping 95% CI are indicated by different symbols.

Species	RMR (mW °C^{-1})	EWL (g h^{-1} °C^{-1})	EHL/MHP (mW/°C^{-1})	T_b (°C °C^{-1})
Cuckoo	0.0224 [0.0059, 0.0389][a]	0.2383 [0.2030, 0.2736][a]	0.1590 [0.1041, 0.2139] [a]	0.2790 [0.2408, 0.3172][a,b]
Roller	0.0396 [0.0096, 0.0696][a]	0.3370 [0.2802, 0.3938][b]	0.1709 [0.1342, 0.2076] [a]	0.1613 [0.1353, 0.1874][c,d]
Starling	0.0417 [0.0220, 0.0613][a]	0.2306 [0.1900, 0.2712][a]	0.0704 [0.0610, 0.0798][b]	0.1843 [0.1375, 0.2311][b,c,d]
Dove	0.0382 [0.0190, 0.0574][a]	0.1999 [0.1583, 0.2415][a]	0.0803 [0.0687, 0.0919][b]	0.2367 [0.1920, 0.2814][a,b]
Nightjar	0.0003 [-0.0015, 0.0021][b]	0.093 [0.0812, 0.1048][c]	0.224 [0.2044, 0.2436][a]	0.151 [0.1334, 0.1687][d]

Figure legends:

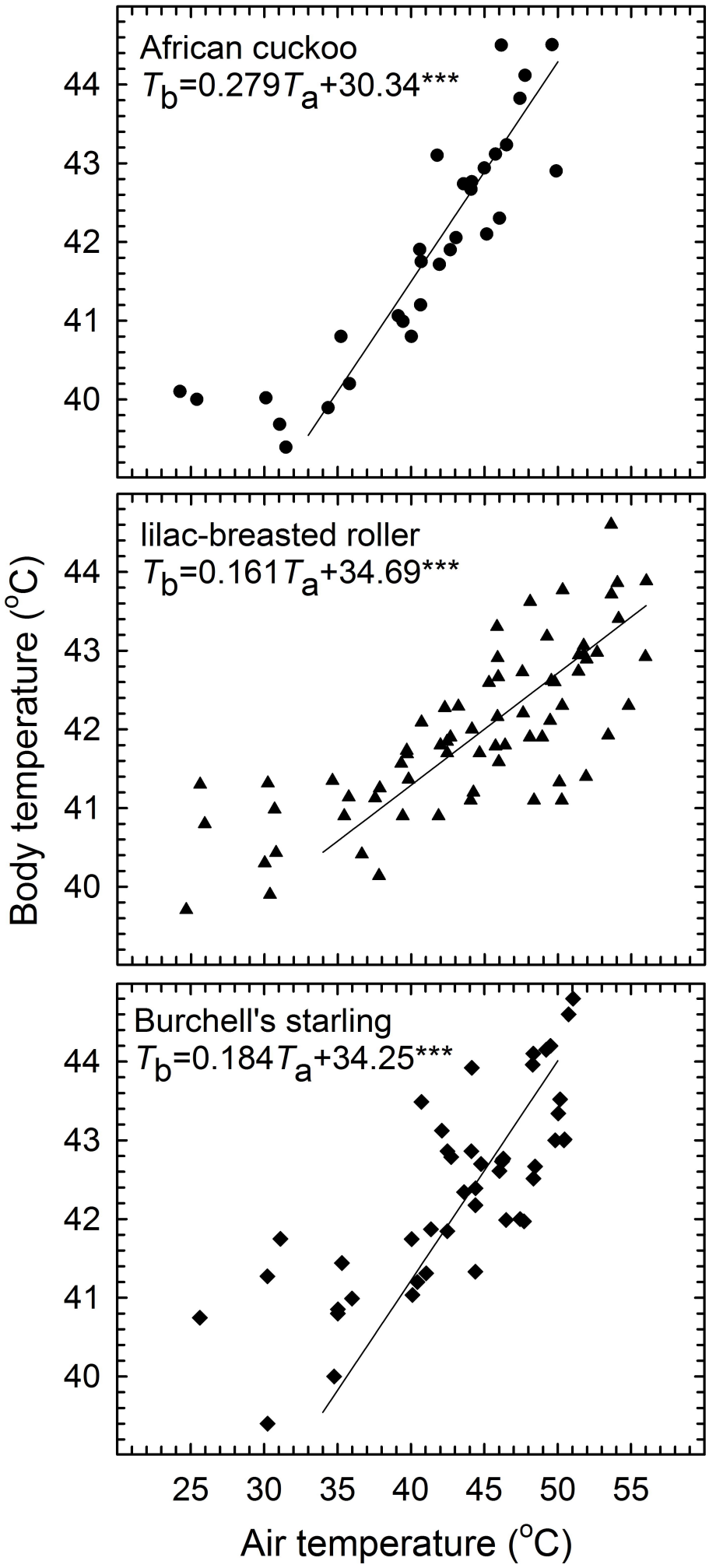
Figure 1: **Body temperature (T_b) in African cuckoos (*Cuculus gularis*; n=6), lilac-breasted rollers (*Coracias caudatus*; n=10), and Burchell's starlings (*Lamprotornis australis*; n=7) as a result of air temperature (T_a).** The trendlines represent relationships between T_b and T_a above an upper inflection T_a (see methods). The slopes and intercepts were calculated using linear mixed-effects models. Significant relationships are represented by asterisks: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

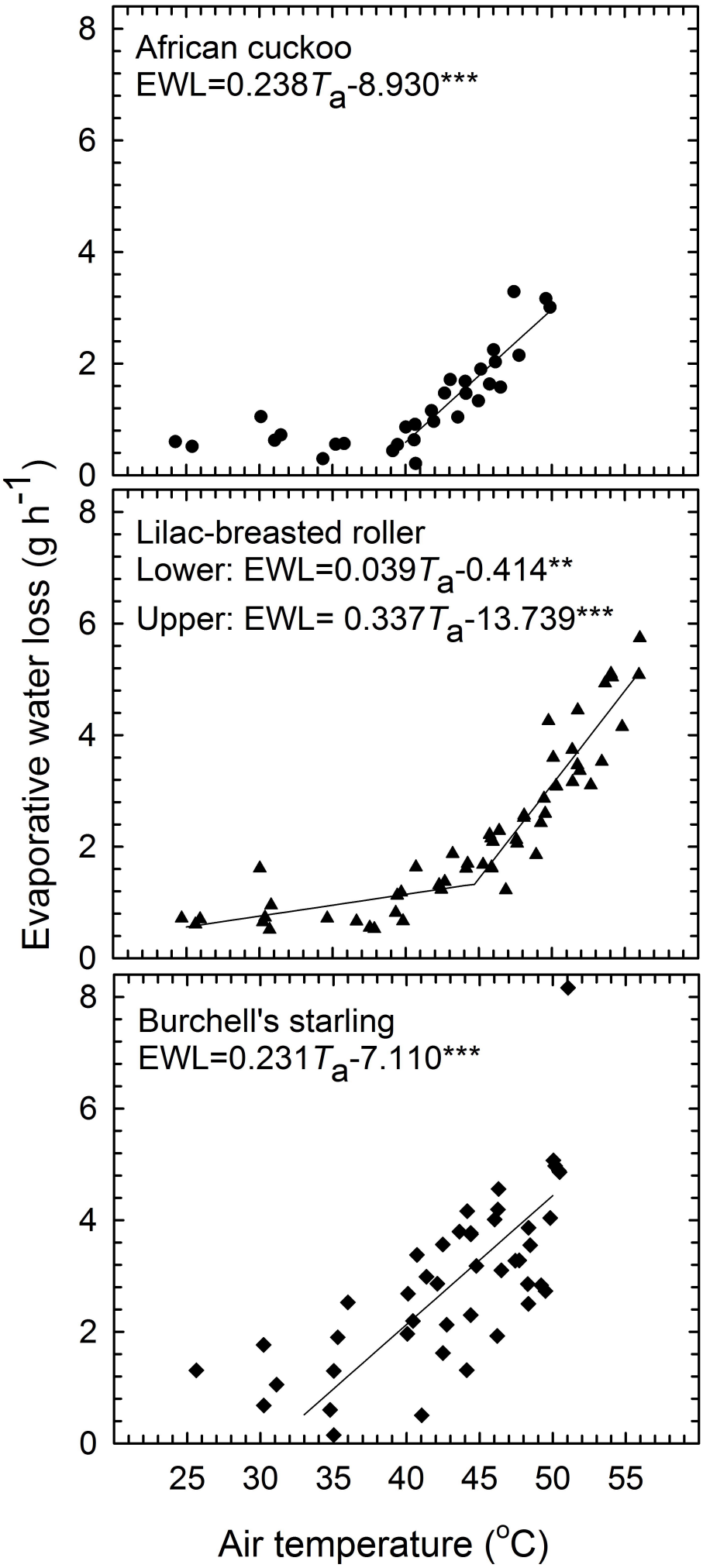
Figure 2: **Resting metabolic rate (RMR) in African cuckoos (*Cuculus gularis*; n=5), lilac-breasted rollers (*Coracias caudatus*; n=10), and Burchell's starlings (*Lamprotornis australis*; n=7) as a result of air temperature (T_a).** The trendlines represent relationships between T_b and T_a above an upper inflection T_a (see methods). The slopes and intercepts were calculated using linear mixed-effects models. Significant relationships are represented by asterisks: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

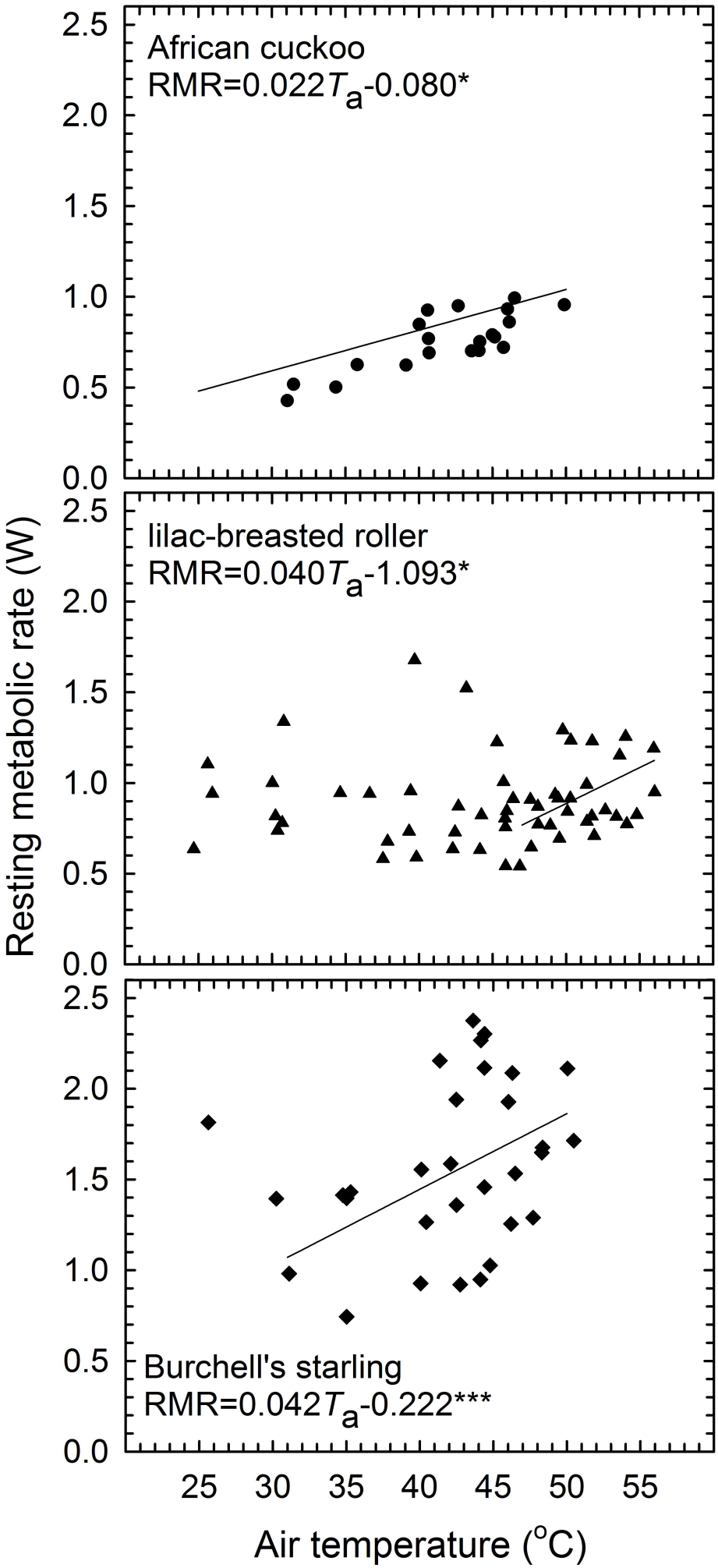
Figure 3: **Evaporative water loss (EWL) in African cuckoos (*Cuculus gularis*; n=6), lilac-breasted rollers (*Coracias caudatus*; n=10), and Burchell's starlings (*Lamprotornis australis*; n=7) as a result of air temperature (T_a).** The trendlines represent relationships between T_b and T_a above an upper inflection T_a (see methods). The slopes and intercepts were calculated using linear mixed-effects models. For lilac-breasted rollers two significant relationships are shown (25 °C < T_a < 44.7 °C; and T_a > 44.7 °C). Significant relationships are represented by asterisks: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

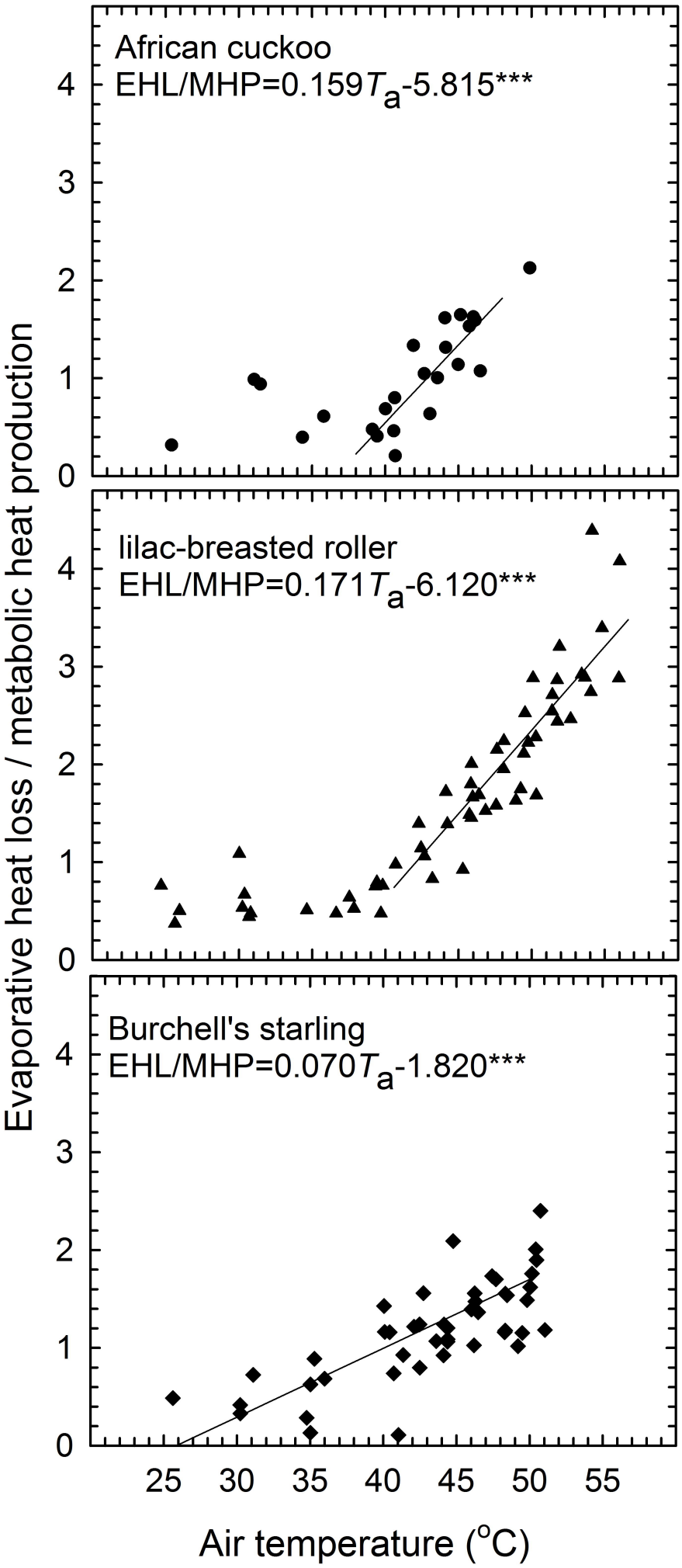
Figure 4: **Ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) in African cuckoos (*Cuculus gularis*; n=6), lilac-breasted rollers (*Coracias caudatus*; n=10), and Burchell's starlings (*Lamprotornis australis*; n=7) as a result of air temperature (T_a).** The trendlines represent relationships between T_b and T_a above an upper inflection T_a (see methods). The slopes and intercepts were calculated using linear mixed-effects models. Significant relationships are represented by asterisks: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

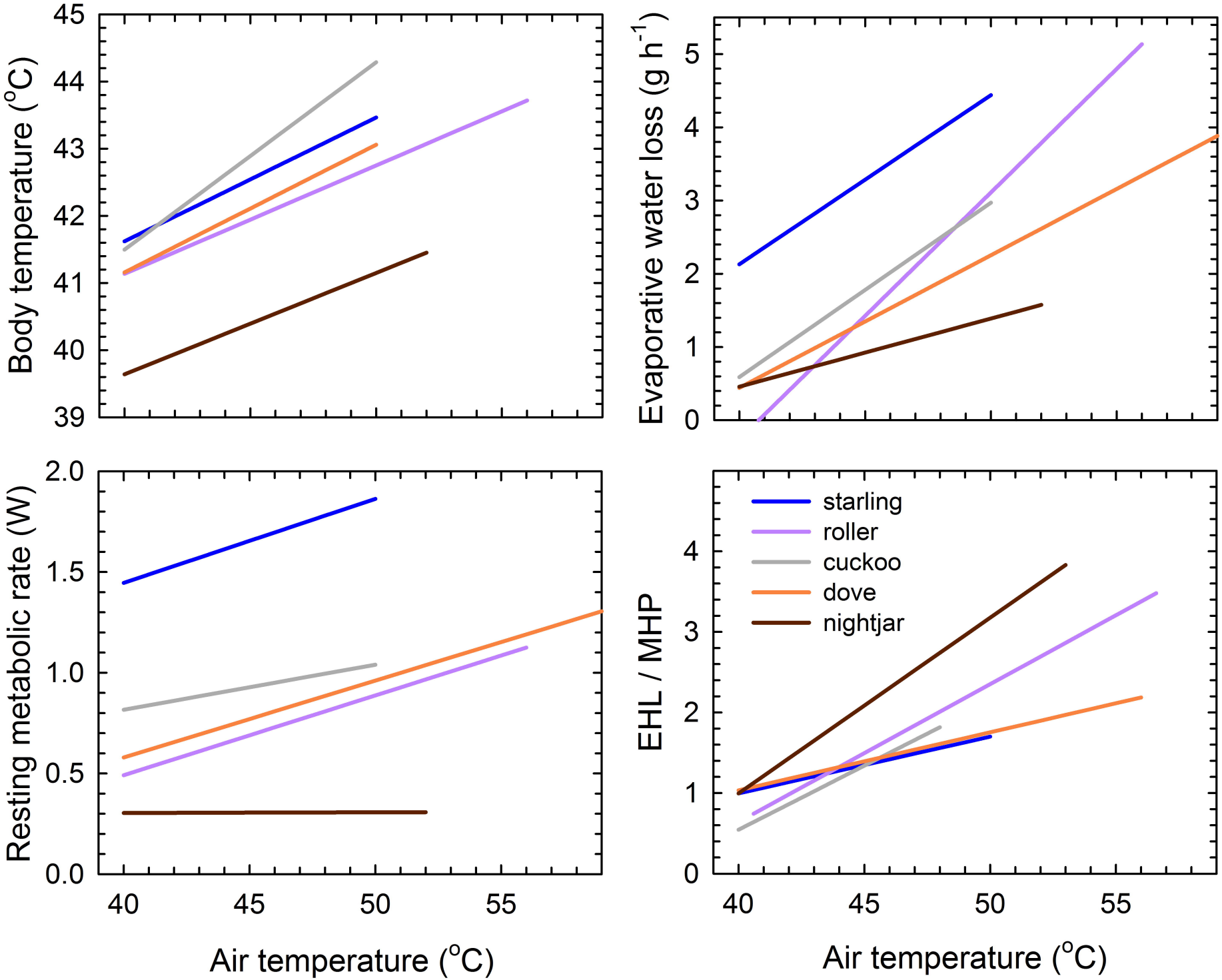
Figure 5: Physiological responses as a result of temperature in five desert species making use of varying modes of respiratory heat dissipation. These include African cuckoos (cuckoo; *Cuculus gularis*, this study) and laughing doves [dove; *Spilopelia senegalensis* (McKechnie et al. 2016b)] make use of gular flutter probably synchronised with panting. Lilac-breasted rollers (roller; *Coracias caudatus,* this study) and Burchell's starlings (starling; *Lamprotornis australis*, this study) make use of panting only. Freckled nightjars [nightjar; *Caprimulgis tristigma* (O'Connor et al. in press)] make use of rapid gular, but probably asynchronously to breathing rates. The slopes and 95% confidence levels of the relationship for each species are displayed in Table 3).


African cuckoo
T_b=0.279T_a+30.34***
lilac-breasted roller
T_b=0.161T_a+34.69***
Burchell's starling
T_b=0.184T_a+34.25***
Body temperature (°C)
Air temperature (°C)
40
41
42
43
44
25
30
35
40
45
50
55


African cuckoo
EWL=0.238T_a-8.930***
Lilac-breasted roller
Lower: EWL=0.039T_a-0.414**
Upper: EWL= 0.337T_a-13.739***
Burchell's starling
EWL=0.231T_a-7.110***
Evaporative water loss (g h^{-1})
Air temperature (°C)
0
2
4
6
8
25
30
35
40
45
50
55


African cuckoo
RMR=0.022T_a-0.080*
lilac-breasted roller
RMR=0.040T_a-1.093*
Burchell's starling
RMR=0.042T_a-0.222***
Resting metabolic rate (W)
Air temperature (°C)
0.0
0.5
1.0
1.5
2.0
2.5
25
30
35
40
45
50
55


African cuckoo
EHL/MHP=0.159T_a-5.815***
lilac-breasted roller
EHL/MHP=0.171T_a-6.120***
Burchell's starling
EHL/MHP=0.070T_a-1.820***
Evaporative heat loss / metabolic heat production
Air temperature (°C)
0
1
2
3
4
25
30
35
40
45
50
55


Body temperature (°C)
45
44
43
42
41
40
39
Evaporative water loss (g h-1)
5
4
3
2
1
0
Resting metabolic rate (W)
2.0
1.5
1.0
0.5
0.0
EHL / MHP
4
3
2
1
0
starling
roller
cuckoo
dove
nightjar
40
45
50
55
Air temperature (°C)
Air temperature (°C)