The Company of Biologists

RESEARCH ARTICLE

Avian thermoregulation in the heat: evaporative cooling capacity of arid-zone Caprimulgiformes from two continents

William A. Talbot[1],*, Todd J. McWhorter[2], Alexander R. Gerson[3], Andrew E. McKechnie[4] and Blair O. Wolf[1]

ABSTRACT

Birds in the order Caprimulgiformes (nightjars and allies) have a remarkable capacity for thermoregulation over a wide range of environmental temperatures, exhibiting pronounced heterothermy in cool conditions and extreme heat tolerance at high environmental temperatures. We measured thermoregulatory responses to acute heat stress in three species of Caprimulgiformes that nest in areas of extreme heat and aridity, the common poorwill (*Phalaenoptilus nuttallii*: Caprimulgidae) and lesser nighthawk (*Chordeiles acutipennis*: Caprimulgidae) in the Sonoran Desert of Arizona, and the Australian owlet-nightjar (*Aegotheles cristatus*: Aegothelidae) in the mallee woodlands of South Australia. We exposed wild-caught birds to progressively increasing air temperatures (T_a) and measured resting metabolic rate (RMR), evaporative water loss (EWL), body temperature (T_b) and heat tolerance limit (HTL; the maximum T_a reached). Comparatively low RMR values were observed in all species (0.35, 0.36 and 0.40 W for the poorwill, nighthawk and owlet-nightjar, respectively), with T_b approximating T_a at 40°C and mild hyperthermia occurring as T_a reached the HTL. Nighthawks and poorwills reached HTLs of 60 and 62°C, respectively, whereas the owlet-nightjar had a HTL of 52°C. RMR increased gradually above minima at T_a of 42, 42 and 35°C, and reached 1.7, 1.9 and 2.0 times minimum resting values at HTLs in the poorwill, nighthawk and owlet-nightjar, respectively. EWL increased rapidly and linearly as T_a exceeded T_b and resulted in maximum rates of evaporative heat dissipation equivalent to 237–424% of metabolic heat production. Bouts of gular flutter resulted in large transient increases in evaporative heat loss (50–123%) accompanied by only small increments in RMR (<5%). The cavity-nesting/roosting owlet-nightjar had a lower HTL and less efficient evaporative cooling compared with the species that nest and/or roost on open desert surfaces. The high efficiency of gular flutter for evaporative cooling, combined with mild hyperthermia, provides the physiological basis for defending T_b well below T_a in extreme heat and is comparable to the efficient cooling observed in arid-zone columbids in which cutaneous EWL is the predominant cooling pathway.

KEY WORDS: Caprimulgiformes, Hyperthermia, Respirometry, Evaporative water loss, Resting metabolic rate, Heat tolerance limit

INTRODUCTION

Birds inhabiting hot subtropical deserts face significant physiological challenges on account of regular exposure to intense solar radiation and high air temperatures (T_a). Maintenance of normothermic body temperature (T_b) under such conditions requires a trade-off between evaporative heat dissipation to avoid hyperthermia and conservation of body water to avoid dehydration. When environmental temperature exceeds T_b, evaporative heat loss (EHL) is the only mechanism whereby birds, like other animals, can defend T_b at sub-lethal levels. The need to reduce activity and seek cool microsites at high T_a, and associated behaviors such as panting, can severely constrain the time available for foraging and activities such as provisioning chicks (Williams and Tieleman, 2005; Cunningham et al., 2013a,b), resulting in periods of very hot weather potentially having far-reaching effects for several components of avian fitness. Mild hyperthermia can mitigate some of the water requirements necessary for evaporative cooling, but as T_a increases, so does the risk of lethal dehydration (Albright et al., 2017).

Many of the nocturnal/crepuscular birds of the order Caprimulgiformes are remarkable for their ability to tolerate a wide range of environmental temperatures (Bartholomew et al., 1962; Lasiewski, 1969). They possess lower basal metabolic rates (BMRs) than most birds of similar body mass (Bennett and Harvey, 1987; Lane et al., 2004) and many species routinely use heterothermy, energy-conserving reductions in T_b and metabolic rate, when cold or inclement weather reduces the availability of aerial insects, their primary prey (e.g. Bartholomew et al., 1957; Howell and Bartholomew, 1959; Brigham, 1992, 2012; Woods et al., 2005; Lane et al., 2004; Doucette and Geiser, 2008; Smit et al., 2011). Although less well studied, many species in this group also exhibit a remarkable capacity to tolerate extreme heat (Lasiewski, 1969; Grant, 1982). How these capacities will be challenged by future climates is a question of considerable conservation interest. In Australia, the biological costs of heat waves are already becoming apparent, with recent heat events causing mass mortality in a variety of arid zone bird species as well as in populations of flying foxes (Welbergen et al., 2008). Current climate models suggest, with high certainty, that future climates will involve longer, more frequent and more intense heat waves as global surface temperatures increase (IPCC, 2012). The deserts of North America and Australia are expected to warm by >4°C by the end of this century (IPCC, 2014). How bird communities will respond to a hotter and drier environment is of significant interest for understanding the consequences to biodiversity of a rapidly warming planet (McKechnie and Wolf, 2010). Here, we examined the thermoregulatory capacities of three species of caprimulgiform birds exposed to levels of heat stress typical of their natural habitats, where operative temperatures can approach or even exceed 60°C (Grant, 1982; O'Connor et al., 2017). The two North American species, the common poorwill (*Phalaenoptilus*

[1]Department of Biology, University of New Mexico, MSC03-2020, Albuquerque, NM 87131-0001, USA. [2]School of Animal & Veterinary Sciences, University of Adelaide, Roseworthy Campus, SA 5371, Australia. [3]Department of Biology, University of Massachusetts, Amherst, MA 01003, USA. [4]DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa.

*Author for correspondence (wtalbot@unm.edu)

W.A.T., 0000-0003-4717-3454

Abbreviations

BMR	basal metabolic rate
EHL	evaporative heat loss
EWL	evaporative water loss
HTL	heat tolerance limit
M_b	body mass
MHP	metabolic heat production
RMR	resting metabolic rate
SLMP	standard liters per minute
T_a	air temperature
T_b	body temperature
T_{uc}	upper critical temperature

nuttallii Audubon 1844) and lesser nighthawk [*Chordeiles acutipennis* (Hermann 1783)], hereafter referred to as 'poorwill' and 'nighthawk', are in the family Caprimulgidae and are common inhabitants of the Sonoran Desert of Arizona. Poorwills are year-round residents whereas nighthawks are migratory and reside in this region from April to September. Both species roost and nest on bare, open ground with access to only scant shade, and so are often exposed to very high T_a combined with intense solar heat loads (Woods et al., 2005; Latta and Baltz, 2012). Ground surface temperatures in the Sonoran desert can reach 70°C (Nobel, 1984) and black-bulb temperatures as high as 60°C have been recorded near nighthawk nests at the edge of the Salton Sea, CA, USA (Grant, 1982). We also examined thermoregulation in the Australian owlet-nightjar [*Aegotheles cristatus* (Shaw, 1790)] of the family Aegothelidae, hereafter referred to as 'owlet-nightjar', which has a widespread distribution in Australia including mallee scrub regions that also experience extreme heat. The owlet-nightjar is a non-migratory species and air temperatures in the daytime over much of its habitat can reach 48–50°C during the summer months (Australian Government Bureau of Meteorology, http://www.bom.gov.au, 2016). Owlet-nightjars avoid some of the extreme heat experienced by the North American species by roosting and nesting in tree cavities (Brigham and Geiser, 1997; Doucette and Geiser, 2008). All three of these species appear well adapted to cope with hot, dry climates by virtue of their low resting metabolic rates, their use of a gular flutter mechanism that appears to provide very efficient EHL, and their relatively low and labile T_b (Calder and Schmidt-Nielsen, 1967; Bartholomew et al., 1962; Brigham et al., 2012).

There appear to be three major mechanisms whereby birds increase rates of evaporative heat dissipation in response to rapid heat gain. Two of these involve elevated rates of respiratory heat loss, the first via panting and the second via gular flutter, achieved via rapid pulsation of the hyoid bone (Calder and Schmidt-Nielsen, 1967). In the context of avian heat dissipation, the gular flutter mechanism may be of particular interest because observations suggest that it is a highly efficient mechanism that maximizes evaporative water loss (EWL) without greatly elevating resting metabolic rates and thus internal heat loads, as is commonly observed in passerine birds that rely on panting to enhance respiratory evaporation (McKechnie et al., 2017). The large and highly vascular surface area of the mouth and throat pouch and a fluttering rate that apparently matches the resonant frequency of the tissues in this area contributes to this efficiency (Bartholomew et al., 1968; Baumel et al., 1983). Although few data exist on the efficiency of this mechanism, in a study of three captive poorwills, oxygen consumption rose by only 12.5% between ambient temperatures of 35 and 47°C, whereas EWL increased by 750%

(Lasiewski, 1969). Cowles and Dawson (1951) prevented a Texas nighthawk (*Chordeiles acutipennis*), sitting on the ground at a T_a of 50°C, from using the gular surfaces for evaporative cooling by holding the bill closed. When the bill was released, the bird immediately resumed gular fluttering and within 5 min its T_b had decreased by 0.6°C. In the rufous-cheeked nightjar (*Caprimulgus rufigena*), which also uses gular flutter, O'Connor et al. (2017) reported the highest ratio of EHL to metabolic heat production (EHL/MHP) yet recorded in birds.

This study builds on the very limited, opportunistic research of the past to more fully characterize the thermoregulatory responses of these arid-zone Caprimulgiformes to extreme heat stress. We used heat acclimatized, wild birds to ask: (1) what are the metabolic and EWL rates in these desert-dwelling nightjars and how do they respond to increasing T_a and during extreme heat stress?; (2) what is the maximum thermal gradient ($T_a - T_b$) that these species can maintain during heat exposure and how is this related to their nesting and roosting habits?; (3) what is the magnitude of hyperthermic responses and what are the limits of heat tolerance in these Caprimulgiformes?; (4) what is the risk of dehydration during prolonged exposure to heat stress as experienced by the nightjars continuously sitting on exposed nest sites during the day?; and (5) to what degree does gular flutter enhance the efficiency of heat dissipation?

MATERIALS AND METHODS

Permits and approval of the experimental protocol were obtained from the Institutional Animal Care and Use Committees of the University of New Mexico (protocol no. 12-100537-MCC) and the University of Adelaide (S-2013-151A), the Animal Ethics Committee of the University of Pretoria (protocol EC054-16), the US Fish and Wildlife Service, the Arizona Game and Fish Department and the South Australian Department of Environment, Water and Natural Resources.

Values for variables are given as means±s.d. and values for slopes are given with confidence intervals.

Field site, bird capture and care

Twenty-two nighthawks and 36 poorwills were captured in the early evening near livestock water tanks in the palo verde cacti–mixed scrub habitat of the Sonoran Desert (Pinal Co., AZ, USA; 32°31′N 111°01′ W 1097 m a.s.l.). Prior to placement in the chamber, the mean body mass (M_b) of poorwills was 44.1±4.1 g and that of nighthawks 50.6 ±5.6 g. Recaptured poorwills were not used in analysis. The study took place during the months of June to September in both 2012 and 2013. Maximal T_a reported from nearby weather stations during this period was 42.2°C. Birds were captured in mist nets and transported in cloth bags to the field laboratory. The birds were held an average of 4.1 h (minimum 1.2 h) after capture without supplemental food or water to allow for a post-absorptive state. Experiments were performed the night of capture during the active phase and coolest part of their diel cycle. Birds were released at their capture site in the early morning. Released birds flew away vigorously.

Twenty-three owlet-nightjars were captured in mallee woodlands on the Gluepot Reserve (SA, Australia; 33°46′S 140°07′E 61 m a.s.l.). Prior to placement in the chamber, the mean M_b of owlet-nightjars was 44.2±3.2 g. Captures occurred in February and March 2014. Maximal T_a recorded at the reserve during this period was 44.4°C. A recaptured bird was not used in analysis. Birds were captured in mist nets using playback within 2 h of dawn and transported to the field laboratory in cloth bags. They were held for an average of 5.9 h (minimum 2.4 h) after capture without supplemental food or water

to allow for a post-absorptive state. Experiments were performed on the day of capture and the birds were released at the capture site at dusk. Released birds flew away vigorously. The measurements on the owlet-nightjars were made during the rest phase of their circadian cycle whereas the measurements on the nighthawks and poorwills were made during the active phase of their circadian cycle. As a part of a larger suite of studies, data were obtained from diurnal birds during the day and nocturnal birds during the night. The photoperiod under which studies were undertaken on the owlet-nightjars was entirely a logistical issue related to the availability of power discovered only after we were afield. All individuals held longer than 4 h were given approximately 4 ml of water by gavage prior to being placed in the metabolic chamber and again prior to their release.

Measurements of metabolism, EWL and T_b

Rates of CO_2 production and EWL were determined using a flow-through respirometry system. The respirometry chamber was a transparent plastic container (5 l with maximal external dimensions approximately 22 cm×25 cm×12 cm, Rubbermaid, Atlanta, GA, USA) modified by the addition of ports for incurrent and excurrent air flow and a thermocouple. The bird rested on a plastic mesh platform 5 cm above a 2 cm layer of medium weight mineral oil, an arrangement that trapped excreta and prevented oiling of feather surfaces. The chamber was housed in an insulated ice chest in which T_a was controlled to within ±0.5°C with a Peltier unit (AC-162 Peltier-Thermoelectric Air Cooler and TC-36-25-rs232 controller, TE Technology, Traverse City, MI, USA). Dry air was produced by pushing compressed air through a membrane air dryer (Champion® CMD3 air dryer and filter, Champion Pneumatic, Quincy, IL, USA) or calcium sulfate desiccant column (W. A. Hammond Drierite Co., Xenia, OH, USA). The dry air stream pushed into the respirometry chamber was regulated using mass flow controllers (30 or 50 standard liters per minute, SLPM, range) with an accuracy of ±0.8% of the reading ±0.2% of the full scale (Alicat Scientific Inc., Tuscon, AZ, USA). Mean flow rate at which samples were obtained was 15.5± 9.3 SLPM, but ranged from 4 to 40 SLPM. Sub-samples of incurrent and excurrent air were directed through a CO_2/H_2O analyzer (model LI-840A, LICOR, Lincoln, NE, USA) calibrated as described in Whitfield et al. (2015). Prior to placement in the chamber, each bird was hooded and briefly restrained (approximately 20 s) while a temperature-sensitive PIT (passive integrated transponder) tag (model TX1411BBT, Biomark, Boise, ID, USA) was injected into the abdominal cavity through an antiseptically prepared skin site. A droplet of cyanoacrylate adhesive closed the needle puncture site and the bird was released bearing the tag. The technique involved brief restraint (approximately 30 s), and was deemed less stressful to the bird than employing anesthesia. Mass was obtained to ±0.1 g (scale model V31XH2, Ohaus, Parsippany, NJ, USA). An infrared light and video camera allowed continuous observation of the subject bird in the darkened ice chest. A bird was considered to have tolerated this intervention well if it demonstrated escape attempts while being placed into the chamber, engaged in exploration of the chamber, then settled into quiet, but alert posture with eyes open and only shifted position slightly or moved its head to look about the chamber. Core T_b was recorded every 10 s from a transceiver, placed within the ice chest, that interrogated the PIT tag (Biomark FS2001). Chamber temperature (T_a) was continuously monitored with a type T thermocouple (TC-2000 thermocouple reader, Sable Systems International, Las Vegas, NV, USA). Respirometry chamber CO_2 and humidity values were recorded once each second via an A-D converter (UI-2, Sable

Systems International) and data were captured on a laptop computer using Expedata (version 1.4.15, Sable Systems International).

During each trial the bird was exposed initially to a T_a (30–35°C) approximating thermoneutrality as defined in earlier studies (Doucette and Geiser, 2008; Bartholomew et al., 1962; Lasiewski and Dawson, 1964). When the bird was calm as indicated by CO_2/H_2O values that had reached a nadir and T_b and T_a were stable for approximately 10 min, the bird was exposed to higher T_a from 40°C or higher upward in 2°C increments over a period of 1–3 h. Dry air flow rate was adjusted to maintain chamber water vapor values <5.0 ppt (dew point <−5°C) to avoid impairing EWL because of increased chamber humidity (Lasiewski et al., 1966). Flow rates of up to 40 SLPM were required to maintain acceptable water vapor pressure levels as the birds increased evaporation with rising T_a. Calculation of metabolic rate from CO_2 production rather than O_2 utilization is more reliable with higher flow rates. The data used for analysis were taken after 5–10 min of stable T_b at a stable T_a and from birds at rest showing no evidence of flight attempts or escape behavior at the time. A trial was terminated if the bird demonstrated continuous active escape behavior or evidence of neurological impairment by loss of balance or righting reflex. Trials were also terminated if a heat tolerance limit (HTL) was reached, which we defined as a T_b approaching 45°C close to lethal limits of ~46°C (Lutterschmidt and Hutchinson, 1997) or, as this T_b was approached, a rate of T_b increase greater than 0.1°C min⁻¹. The bird was then removed from the chamber, cooled, given additional water by gavage, and observed for thermoneutral T_b and normal behavior before release. Only one instance of mortality occurred during the course of these experiments.

Calculations and statistical analysis

CO_2 production ($\dot{V}_{CO_2}$) was calculated using equation 10.5 from Lighton (2008). Metabolic heat gain (W) was calculated as in Walsberg and Wolf (1995) assuming a respiratory quotient (RQ) of 0.71; metabolic heat gain so calculated is herein referred to as the resting metabolic rate (RMR). Rates of EWL were calculated using equation 10.9 from Lighton (2008), assuming 0.803 mg H_2O per ml of water vapor. The calculation for EHL was based on 2.406 J mg⁻¹ H_2O. Statistical analyses were performed on data obtained from birds that remained calm or resting during the temperature trials. One poorwill and two nighthawks were excluded from the analysis as outliers because RMR values varied erratically to 3.6 times the mean RMR of the remaining birds. Graphs and statistical analyses were produced in R (v3.1; R Development Core Team 2011) inside RStudio (v0.98.932). The R package *segmented* was used to estimate breakpoints in the rate of change in response variables (Muggeo, 2008). Regression formulas for the relationships between EWL, RMR, EHL/MHP and T_b as a function of T_a were obtained using the linear mixed effects model from R package *lme4* (version 1.1-13, https://CRAN.R-project.org/package=lme4).

RESULTS
RMR
Minimum RMR values varied from 0.35 to 0.40 W and were found at test T_a=42°C in the poorwill and nighthawk and test T_a=35°C in the owlet-nightjar (Table 1). Segmented regressions indicate inflection points from T_a=40.3 to 50.2°C at which the slope of the RMR as a function of T_a changes. Below this point, the slope is zero or slightly negative, and above this point, it increases to 0.01–0.02 W °C⁻¹ in poorwills and nightjars but shows a sharp increase in the owlet-nightjar (Table 1, Fig. 1). The breadth of regression line confidence intervals was quite narrow except for high variability in the owlet-nightjar at high T_a (Table 2). Maximum average RMRs

Table 1. Variables related to thermoregulation at high air temperature in three arid-zone Caprimulgiformes

Variable	Common poorwill	Lesser nighthawk	Australian owlet-nightjar
M_b (g)	44.1±4.1 (34)	50.6±5.6 (21)	44.2±3.2 (23)
T_b			
Min. T_b (°C)	38.4±0.8 (6)	38.8±0.18 (3)	37.7±1.4 (7)
T_a at min. T_b (°C)*	30	30	30
Inflection T_a (°C)	48	52.1	47.2
T_b versus T_a slope below inflection (°C °C^{-1})‡	0.09	0.11	0.22
T_b versus T_a slope above inflection (°C °C^{-1})‡	0.24	0.33	0.47
Max. T_b (°C)	42.6±0.8 (5)	43.6±0.4 (3)	43.7±0.7 (5)
T_a at max. T_b (°C)*	62	60	52
HTL (°C)*	62	60	52
RMR			
Min. RMR (W)	0.35±0.12 (9)	0.36±0.06 (5)	0.40±0.07 (9)
T_a at min. RMR (°C)*	42	42	35
Inflection T_a (°C)	40.3	56.2	50.7
RMR slope below inflection (W °C^{-1})‡	−0.01	0.00	0.00
RMR slope above inflection (W °C^{-1})‡	0.01	0.02	0.21
Max. RMR (W)	0.59±0.22 (5)	0.68±0.08 (3)	0.79±0.34 (5)
T_a at max. RMR (°C)*	62	60	52
Max. RMR/min. RMR	1.69	1.89	1.98
EWL			
Min. EWL (g h^{-1})	0.21±0.08 (6)	0.20±0.04 (3)	0.21±0.03 (8)
T_a at min. EWL (°C)*	30	30	30.0
Inflection T_a (°C)	48.2	42.9	45.3
EWL slope below inflection (g h^{-1} °C^{-1})‡	0.07	0.04	0.05
EWL slope above inflection (g h^{-1} °C^{-1})‡	0.15	0.11	0.21
Max. EWL (g h^{-1})	3.24±0.76 (5)	3.29±0.27 (3)	2.51±0.69 (5)
T_a at max. EWL (°C)*	62	60	52
Max. EWL/min. EWL	15.43	16.45	11.95

Data are means±s.d.; number of individuals is in parentheses. M_b, body mass; T_b, body temperature; T_a, air temperature; HTL, heat tolerance limit; RMR, resting metabolic rate; EWL, evaporative water loss.
*Test T_a±0.5°C. ‡Slopes are derived from linear mixed models.

coincided with the heat tolerance limits in all three species; however, some individuals at the highest T_a exceeded those rates. Maximum RMR for individual poorwills, nighthawks and owlet-nightjars was 1.09, 0.75 and 1.19 W, respectively.

EWL
Minimal EWL values occurred at the lowest test T_a (~30°C) in each species and increased significantly with increasing T_a (Table 1, Fig. 2). Above inflection points, which varied among species from T_a=45.3 to 48.2°C, EWL increased from 0.04–0.07 to 0.11–0.21 g h^{-1} °C^{-1} (Table 2). The breadth of the regression line confidence intervals was greater above the inflection point than below in all species. Maximum EWL occurred at each species' HTL and was equivalent to 12–16 times minimal values. In individual poorwills, nighthawks and owlet-nightjars, maximal EWLs of 5.8, 3.5 and 3.6 g h^{-1} °C^{-1} were recorded, respectively.

T_b
From the lowest test T_a (~30°C), T_b increased significantly to the HTL (Table 1, Fig. 3). Above an inflection point that varied among species from T_a=47.2 to 52.1°C, the rates of increase in T_b

approximately tripled (Table 2). The breadth of the regression line confidence limits ranged between 0.1 and 0.3°C (Table 2). At the HTL, an average T_b of 42.6–43.7°C was maintained with stable RMR and EWL values for at least 10 min. Maximum T_b sustained in an individual poorwill, nighthawk and owlet-nightjar was 44.0, 44.1 and 44.0°C, respectively. These T_b were reached without distress in only a single bird of each species at test T_a=62, 62 and 54°C, respectively. Failure to tolerate a given T_a (see Materials and methods) occurred in three of six poorwills at T_a=62°C, five of six nighthawks at T_a=60°C and four of eight owlet-nightjars at T_a=52°C.

Gular flutter and heat dissipation
EHL/MHP increased linearly with no evidence of an inflection point from the lowest T_a to the HTL (Table 3, Fig. 4). At the highest T_a, which only a single nighthawk and a single owlet-nightjar were able to tolerate, the EHL/MHP was actually 15–25% lower than the EHL/MHP at that species' HTL. Maximum EHL/MHP ranged from 2.4 (owlet-nightjar) to 4.2 (poorwill; Table 3). In most cases, the onset of gular flutter coincided with an increasing T_a as the chamber temperature was adjusted to the next test T_a; however, in 5–8 individuals of each species, we were able to observe the onset of

Table 2. Slopes of variables as a function of T_a derived from linear mixed effects models in arid-zone Caprimulgiformes

Species		RMR (W °C^{-1})	EWL (g h^{-1} °C^{-1})	EHL/MHP	T_b (°C °C^{-1})
Common poorwill	(a)	−0.01 (−0.02,0.12)	0.07 (0.06,0.08)	0. 0.13 (0.11,0.14)	0.09 (0.06,0.12)
	(b)	0.01 (0.00,0.01)	0.15 (0.10,0.19)	No inflection point	0.24 (0.20,0.28)
Lesser nighthawk	(a)	0.00 (0.00,0.01)	0.04 (0.02,0.06)	0.11 (0.10,0.12)	0.11 (0.08,0.15)
	(b)	0.02 (0.01,0.04)	0.11 (0.11,0.14)	No inflection point	0.33 (0.23,0.44)
Australian owlet-nightjar	(a)	0.00 (0.00,0.01)	0.05 (0.04,0.06)	0.10 (0.09,0.11)	0.22 (0.18,0.25)
	(b)	0.29 (0.29,0.29)	0.21 (0.15,0.26)	No inflection point	0.47 (0.28,0.67)

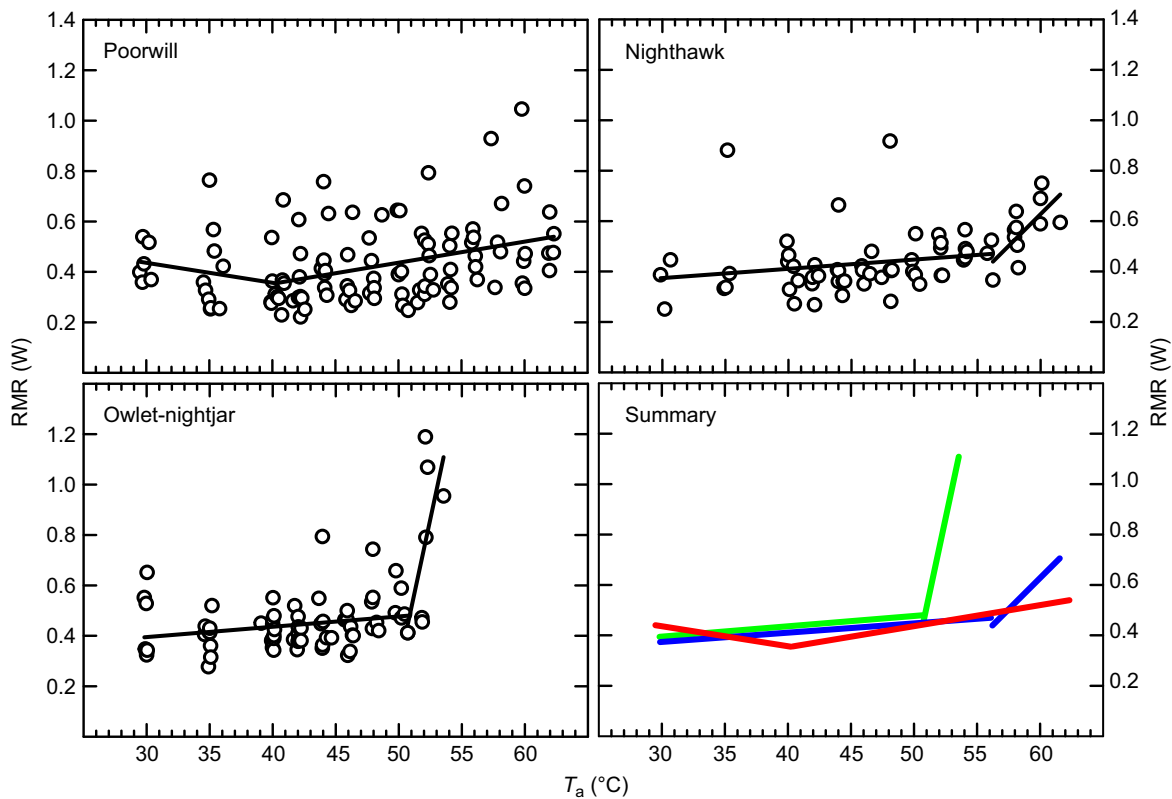Slopes below (a) and above (b) the inflection T_a are given with 95% confidence intervals.

Fig. 1. Resting metabolic rate (RMR) in three species of caprimulgiform birds over a range of air temperatures (T_a). Linear regressions above and below inflection points are shown. In the lower right-hand corner, a summary graph shows the regression lines for common poorwills (N=34, red), lesser nighthawks (N=22, blue) and Australian owlet-nightjars (N=23, green). These data represent only calm birds.

gular flutter during a period of stable T_a. Thus, we have a record of the changes in RMR and EWL that occur abruptly as gular flutter commences (Table 3, Fig. 5). The onset of gular flutter was associated with an increase in the proportion of MHP dissipated by evaporation from 0.91 to 2.09, from 1.15 to 1.67 and from 0.80 to 1.32 in the poorwill, nighthawk and owlet-nightjar, respectively.

DISCUSSION

Our data for two North American caprimulgids and one Australasian aegothelid reveal efficient evaporative cooling in all three species, providing the capacity for defending T_b between 10

and 20°C below T_a. These findings support the notion that members of the Caprimulgiformes have evolved heat tolerance and evaporative cooling abilities that are unusual among birds (Dawson and Fisher, 1969; O'Connor et al., 2017). Our data also reveal considerable variation within this order; maximum EHL/MHP in the three species we examined here varied from 2.4 (owlet-nightjar), a value not far above the range typical for passerines (Whitfield et al., 2015; McKechnie et al., 2017), up to 4.2, one of the highest avian values yet documented (Smith et al., 2015; McKechnie et al., 2016a,b; O'Connor et al., 2017). In the following discussion, we address the performance of each of these

Table 3. Variables related to the efficiency of evaporative cooling in three arid-zone Caprimulgiformes

Variable	Common poorwill	Lesser nighthawk	Australian owlet-nightjar
Min. EHL/MHP	0.33±0.13 (6)	0.38±0.06 (3)	0.33±0.10 (7)
T_a at min. EHL/MHP (°C)*	30	30	30
Slope of EHL/MHP versus T_a[‡]	0.13	0.11	0.10
Max. EHL/MHP	4.24±0.44 (5)	3.30±0.7 (3)	2.37±0.22 (6)
T_a at max. EHL/MHP (°C)*	62	60	52
T_b at onset of gular flutter (°C)	39.2±1.2 (33)	39.8±1.2 (19)	40.1±0.9 (20)
T_a at onset of gular flutter (°C)	42.2±3.3 (33)	42.7±3.4 (19)	40.8±1.7 (20)
Change in RMR with gular flutter (W)[§]	(a) 0.33±0.04 (8)	(a) 0.37±0.09 (8)	(a) 0.42±0.06 (5)
	(b) 0.33±0.05 (8)	(b) 0.39±0.08 (8)	(b) 0.39±0.05 (5)
Change in EHL with gular flutter (W)[§]	(a) 0.30±0.11 (8)	(a) 0.42±0.17 (8)	(a) 0.33±0.08 (5)
	(b) 0.66±0.19 (8)	(b) 0.64±0.21 (8)	(b) 0.52±0.14 (5)
Change in EHL/MHP with gular flutter[§]	(a) 0.91±0.31 (8)	(a) 1.15±0.43 (8)	(a) 0.80±0.17 (5)
	(b) 2.09±0.83 (8)	(b) 1.67±0.60 (8)	(b) 1.32±0.25 (5)

Data are means±s.d.; number of individuals is in parentheses. EHL, evaporative heat loss; MHP, metabolic heat production; T_a, air temperature; T_b, body temperature; RMR, resting metabolic rate.
*Test T_a±0.5°C. [‡]Slopes are derived from linear mixed models. [§]Change in variables with onset of gular flutter: (a) before gular flutter and (b) after the onset of gular flutter.
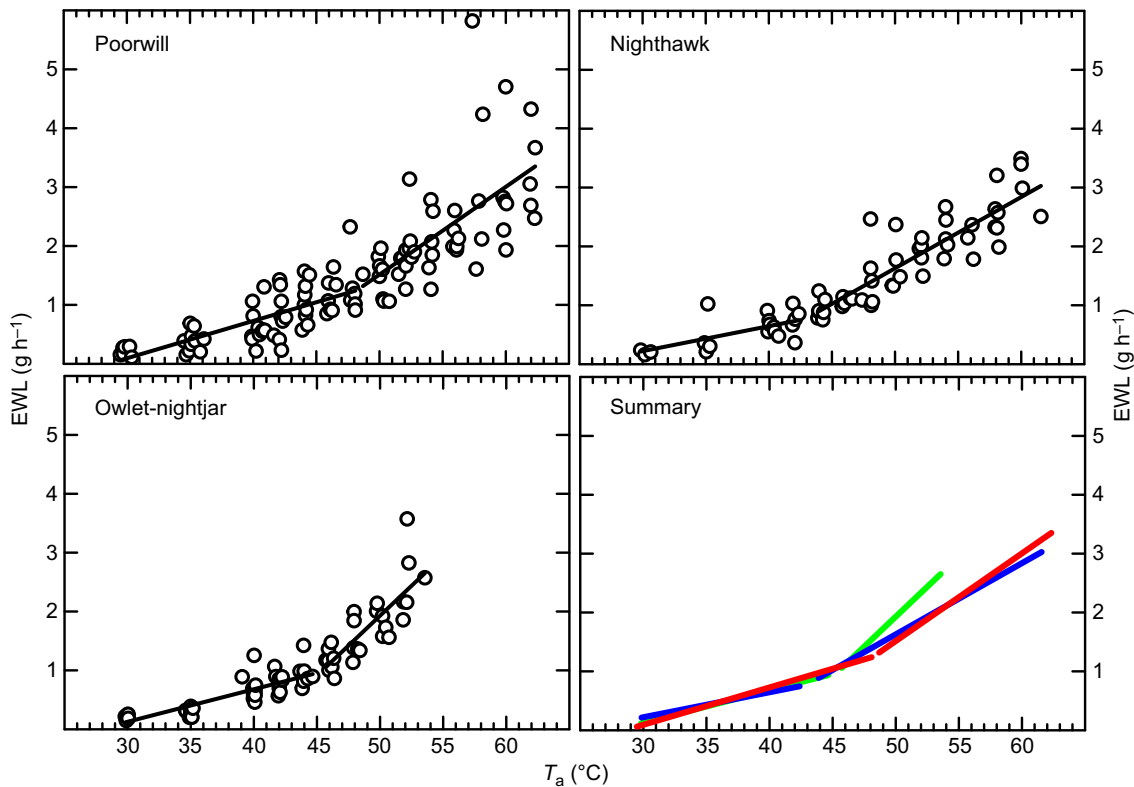
Fig. 2. Evaporative water loss (EWL) in three species of caprimulgiform birds over a range of T_a. Linear regressions above and below inflection points are shown. In the lower right-hand corner, a composite graph shows the regression lines for common poorwills (N=34, red), lesser nighthawks (N=22, blue) and Australian owlet-nightjars (N=23, green). These data represent only calm birds.

species in detail, comparing our results with those from other avian taxa and the existing nightjar literature.

RMR

Measurements of RMR provide insight into the minimum heat load animals experience as a function of T_a and how internally produced heat contributes to the total heat load during periods of heat stress. Our measurements of RMR are broadly similar to those reported previously, with differences that likely reflect variation in measurement conditions. Our measurements on poorwills and nighthawks were conducted on the night of capture during the active phase of their diel cycle. In our wild-caught poorwills, the lowest RMR was ~65% greater than RMRs found in previous studies using captive poorwills, acclimated to laboratory conditions (Bartholomew et al., 1962; Lasiewski, 1969), but was comparable to values observed in wild-caught South African nightjars (O'Connor et al., 2017). The lowest mass-specific RMR observed in our wild-caught lesser nighthawks was 25% higher than that of the larger common nighthawk (*Chordeiles minor*) acclimated to laboratory conditions (Lasiewski and Dawson, 1964). In our study, the lowest RMR observed in the owlet-nightjar averaged 0.40± 0.07 W compared with 0.32 W measured by Doucette and Geiser (2008). In the latter study, birds were captured before dawn and studied during the rest phase of their diel cycle.

As expected, our RMR values are considerably lower than those measured for passerines; RMRs in passerines of similar mass were approximately 1.5–2.0 times higher than those we observed in the nightjars. For example, two 40 g desert passerines, the white-browed sparrow-weaver of South Africa (Whitfield et al., 2015) and the chestnut-crowned babbler of Australia (McKechnie et al., 2017) showed average minimal RMRs of 0.54 and 0.59 W. In contrast,

desert-nesting Columbiformes showed very similar RMRs to those of the Caprimulgiformes, with the 37 g Namaqua dove (*Oena capensis*) exhibiting an average RMR of 0.31 W (McKechnie et al., 2016b). The RMR values obtained in this study correspond well to the low metabolic rates noted in caprimulgiform birds in general relative to other taxa (Lane et al., 2004), a trait that importantly reduces the contribution of metabolic heat to the total heat load that the bird must dissipate via evaporation at high T_a.

Passerine birds have higher resting metabolic rates than caprimulgids. When T_a increases and active heat dissipation (panting) begins, there is a more rapid increase in RMR in passerines than in caprimulgids. Increases in RMR with increasing heat stress add to the total heat load that must be dissipated through evaporation. The high metabolic costs of respiratory evaporative heat dissipation via panting contrast sharply with the negligible energetic costs of gular flutter in the nighthawks. Cowles and Dawson (1951) commented on the highly effective nature of evaporative cooling via the gular apparatus in the Texas nighthawk and urged further study. Bartholomew et al. (1962) noted that the large highly vascularized mouth and gular area in the common poorwill and other nightjars provides a large, effective surface for evaporation, and vigorous gular flutter increases evaporation with little observed increase in metabolism. This highly vascularized mouth of nightjars was clearly illustrated in Audubon's (1830) print of a whip-poor-will pursuing a moth. Bartholomew et al. (1962) found no increase in RMR at T_a as high as 44°C, concluding that an upper critical temperature (T_{uc}) must lie above 44°C. Work by Lasiewski and Dawson (1964) on common nighthawks also failed to identify a clearly discernible T_{uc} and found only gradual increases in RMR over T_a ranging from 35 to 45°C. Doucette and Geiser (2008), in contrast, estimated the T_{uc} for owlet nightjars at 34.8°C during the
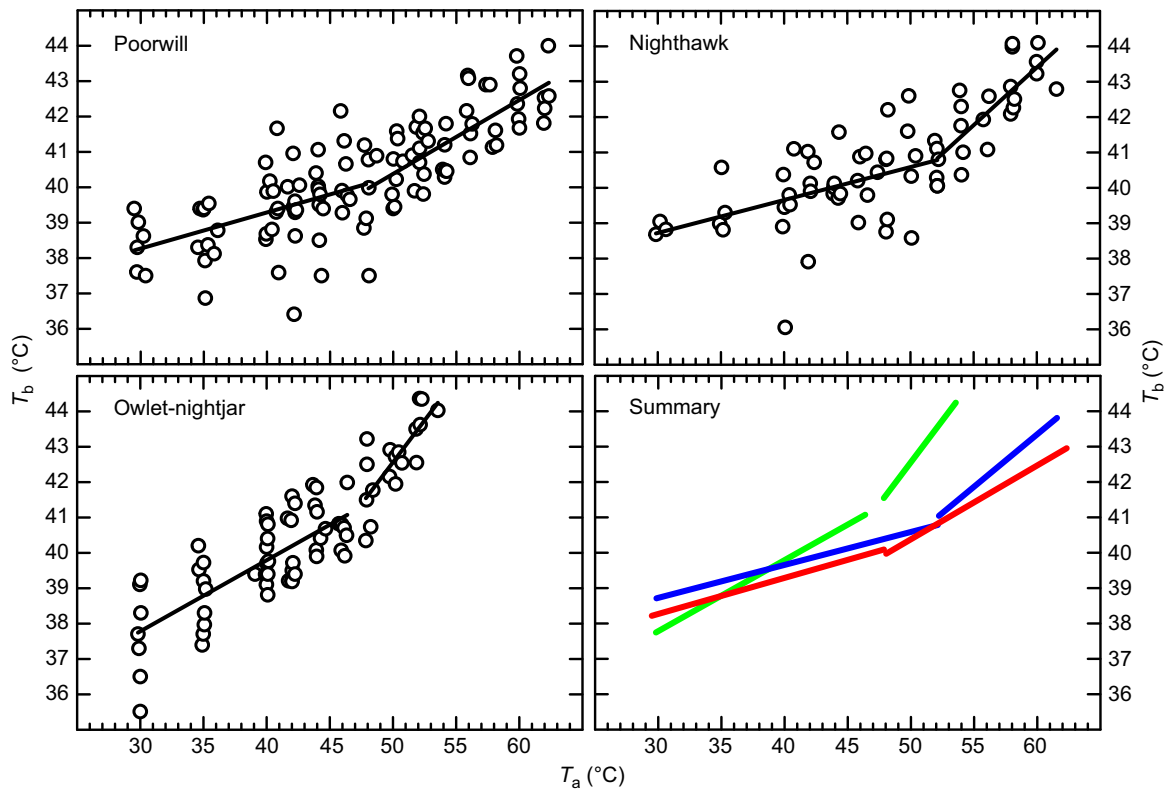
Fig. 3. Body temperature (T_b) in three species of caprimulgiform birds over a range of T_a. Linear regressions above and below inflection points are shown. In the lower right-hand corner, a composite graph shows the regression lines for common poorwills ($N=34$, red), lesser nighthawks ($N=22$, blue) and Australian owlet-nightjars ($N=23$, green). These data represent only calm birds.

summer, but based this value on few data points. Most recently, O'Connor et al. (2017) found low stable RMRs across a wide range of high temperatures with no apparent T_{uc} in rufous-cheeked and freckled nightjars in South Africa. In the present study, we found gradual increases in RMR from the minimal observed values to a point ranging from 40.3 to 56.2°C (identified by segmented regressions) at which there is an abrupt increase in the slope of the RMR as a function of T_a. We do not define a thermoneutral zone in our birds because the criteria suggested by Scholander et al. (1950) are not met. Instead of a range of T_a at which RMR remains stable, our birds showed decreasing RMR from $T_a=30$°C to a minimal value, then a subtle increase in RMR until T_a neared the HTL. It is likely that birds in the wild, which are not experiencing additional stress from handling or the experimental conditions, might more closely reflect the findings of O'Connor et al. (2017) and not show significant metabolic responses to heat stress until reaching the limits of heat tolerance. Other researchers have noted the low metabolic costs of gular flutter and associated it with the small mass of the gular area and the apparent resonant frequency at which the gular area moves, irrespective of temperature (Lasiewski and Bartholomew, 1966; Bartholomew et al., 1968). They found that common poorwills did not change the frequency of gular flutter, but birds increased the amplitude and the area of the gular apparatus engaged with increasing heat stress.

To gain further insight into the effectiveness of the gular flutter process in our species, we quantified the costs (increases in RMR) versus the benefits (increases in EHL) where gular flutter occurred intermittently and other variables were stable but before increasing heat stress produced continuous gular flutter. Over a series of 5–10 bouts of gular flutter, we measured changes in metabolic rate and

rates of evaporation immediately before gular flutter commenced, and then during the gular flutter bout that followed. Strikingly, common poorwills showed a 123% increase in EWL when gular flutter commenced, with no concomitant increase in RMR (Fig. 5). Lesser nighthawks showed a somewhat less effective pattern, with a 50% increase in EWL and a 5% increase in RMR. The cavity-nesting owlet-nightjar's responses were intermediate to those of the other species and showed a 57% increase in EHL and a 6% decrease in RMR. From a practical standpoint, the very low metabolic cost of the gular flutter apparatus (see discussion below) allows for increasing rates of EWL as heat stress increases, without additional metabolic heat contributing to the total heat load, thus saving water and allowing for high heat tolerance. These data indicate that the effectiveness of the gular flutter system used for evaporative heat dissipation by nightjars clearly rivals that found in Columbiformes (Smith et al., 2015; McKechnie et al., 2016b), where cutaneous evaporation is paramount, and is far more effective then respiratory evaporation driven by panting observed in most small passerine birds (Whitfield et al., 2015; McKechnie et al., 2017). The differences in evaporative mechanisms among orders clearly affect individual HTLs and the trajectory of T_b with increasing heat stress, as well as overall water balance during chronic heat stress.

EWL

As T_a increases, all birds become increasingly reliant on EWL for heat dissipation as the gradient between T_a and T_b decreases. In nightjars, as T_a increased, birds transitioned from modest increases in EWL from cutaneous and respiratory surfaces (Lasiewski et al., 1971) to activation of the gular flutter apparatus, which greatly increased rates of EWL. In our species, minimum values for EWL
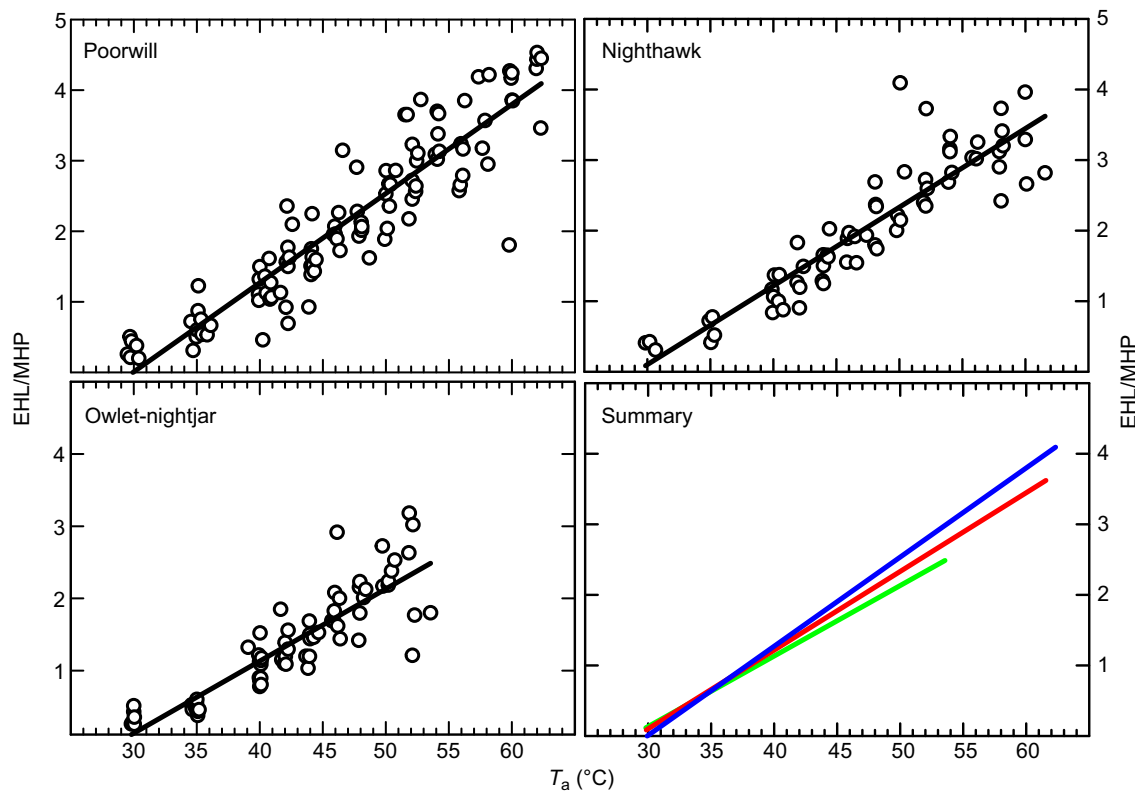
Fig. 4. The ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) in three species of caprimulgiform birds over a range of T_a. Linear regressions above and below inflection points are shown. In the lower right-hand corner a composite graph shows the regression lines for common poorwills (N=34, red), lesser nighthawks (N=22, blue) and Australian owlet-nightjars (N=23, green). These data represent only calm birds.

ranged from 0.20 to 0.21 g h^{-1} at T_a=30°C, the lowest test T_a in our study. These rates are ∼50% higher than the minimal EWL values measured by Bartholomew et al. (1962) in captive poorwills, but are very similar to EWL of wild-caught South African nightjars studied by O'Connor et al. (2017). As T_a increased, EWL increased gradually to an inflection point, varying among our species over T_a≈43–48°C, at which EWL increased markedly and reached ∼12–16 times the minimal values at the birds' thermal limits (HTL). Above this inflection point, EWL increased at 0.11–0.21 g^{-1} h^{-1} °C^{-1}. O'Connor et al. (2017) reported a relatively low and stable EWL in South African nightjars that increased rapidly starting at T_a≈38–39°C at rates of 0.093–0.099 g^{-1} h^{-1} °C^{-1}. Other taxa studied at the same sites and times and by the same techniques show similar values but differences in the inflection point at which there was an abrupt uptick in the rate of water loss. McKechnie et al. (2017) in a study of Australian desert passerines found that the spiny-cheeked honeyeater (∼42 g) and the chestnut-crowned babbler (∼52 g) increased EWL at rates of 0.18 and 0.23 g^{-1} h^{-1} °C^{-1} above inflection points at 38.1 and 42.2°C. The slope of EWL for the South African Namaqua dove (∼37 g) was 0.096 g^{-1} h^{-1} °C^{-1} (McKechnie et al., 2016b). Overall, rates of EWL did not differ greatly among these arid-zone taxa; however, inflection points marking a significant increase in EWL vary.

Efficiency of evaporative processes: EHL/MHP
We can use the ratio of EHL/MHP to examine the relative efficiency of different evaporative pathways as individuals become reliant on evaporative pathways for heat dissipation when T_a approaches and exceeds T_b. Pathways of EWL vary greatly among different taxa and the relative efficiency of these pathways varies within and among

groups. In general, EWL occurs by means of the respiratory surfaces or skin and the relative importance of these pathways in heat-stressed birds differs greatly (McKechnie et al., 2016a,b). In passerine birds, the dominant pathway for evaporative heat dissipation is through respiratory panting, where individuals ventilate the full respiratory surfaces to varying degrees, which results in significant increases in RMR with increasing heat stress and an increased demand for EHL (Whittow, 1976; Wolf and Walsberg, 1996).

EHL/MHP values in the thermoneutral zone are typically <1 and provide insight into the relative EHL compared with total heat loss as denoted by metabolic rate. When T_a>T_b, the maintenance of a stable T_b demands that EHL/MHP>1 and in birds that tolerate very high temperatures (many Columbiformes), these values can exceed 4.0 (Smith et al., 2015; McKechnie et al., 2016a,b). Columbiform birds studied to date rely primarily on cutaneous EWL during periods of heat stress, which appears to have little or no metabolic cost associated with evaporation from skin surfaces (McKechnie and Wolf, 2004). A number of researchers have commented on the efficiency of the gular flutter apparatus for evaporative cooling in caprimulgiform birds (Lasiewski and Seymour, 1972; Grant, 1982; Cowles and Dawson, 1951). The highest EHL/MHP (5.15) recorded for any bird was noted in the rufous-cheeked nightjar, which employs the gular flutter mechanism during heat exposure (O'Connor et al., 2017). The highly vascular and capacious oral cavity is a constant feature of nightjar anatomy and in the lesser nighthawk, for example, this area is equivalent to 15% of the total body surface area (Cowles and Dawson, 1951). Cowles and Dawson (1951) showed the efficacy of gular flutter by observing increases in T_b in Texas nighthawks when the bill was held closed, thus preventing gular flutter. We found
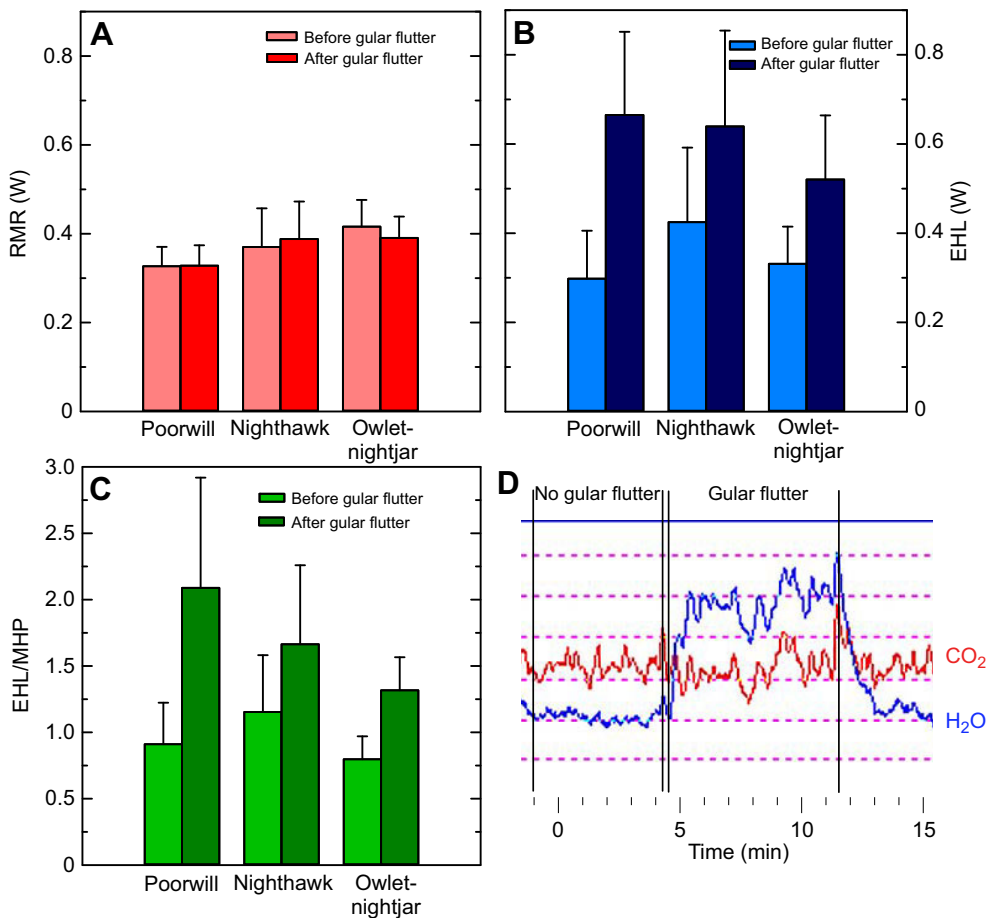
Fig. 5. Effect of gular flutter on RMR, EHL and EHL/MHP ratio in three species of nightjars. (A) RMR; (B) EHL; and (C) EHL/MHP for common poorwills (N=8), lesser nighthawks (N=8) and Australian owlet-nightjars (N=5). (D) Sample output of direct CO_2 and H_2O measurements from an Australian owlet-nightjar showing 5 min samples taken before and during gular flutter.

that at $T_a{\approx}40°C$, the onset of gular flutter resulted in increases in EHL/MHP ratios of 44–129% (Fig. 5). We speculate that increases in the depth of gular flutter and the surface area employed with increasing heat stress probably allow our species to increase EHL/MHP to maximal values comparable to those found in the South African nightjars (O'Connor et al., 2017). As a consequence, very low RMRs combined with high rates of EWL provide a highly effective system for heat dissipation, which we believe is responsible for the very high heat tolerance limits in our nightjars.

Hyperthermic responses and HTLs

When T_a approaches T_b, birds typically respond by increasing EWL and T_b. Hyperthermic responses to $T_a>T_b$ can serve to minimize the heat gain from the environment and thus reduce the EWL necessary for thermoregulation. Early research by Lasiewski and Seymour (1972) showed that common poorwills exhibit modest hyperthermic responses to increasing heat stress, with T_b increasing by 0.13°C per 1°C change in T_a to 41.6°C at a T_a of 45°C. O'Connor et al. (2017) found increases in T_b of 0.12 and 0.14°C per 1°C change in T_a in rufous-cheeked and freckled nightjars, with T_b reaching 41.5 and 40.1°C, respectively, at $T_a=52°C$. The rate of T_b increase in our North American nightjars is similar to that found in the African nightjars studied by O'Connor et al. (2017), with increases of 0.09 and 0.11°C per 1°C change in T_a for the poorwill and nighthawk, respectively, and 0.22°C per 1°C change in T_a in the owlet-nightjar. In contrast to the nightjars, heat-stressed passerines showed increases in T_b of 0.23–0.58°C per 1°C change in T_a (Whitfield et al., 2015; McKechnie et al., 2017), while T_b of the similar-sized Namaqua dove (~40 g) increased by 0.11°C per 1°C change in T_a

(McKechnie et al., 2016a,b). The observed hyperthermic responses led to maximum T_b in individual birds of 44.0, 44.1 and 44.4°C for poorwills ($T_a=62°C$), nighthawks ($T_a=60°C$) and owlet nightjars ($T_a=52°C$), respectively. Even at these high T_b, poorwills and nighthawks were able to maintain a $T_a–T_b$ gradient of 17.3 and 15.1°C, respectively, whereas the tree cavity-roosting owlet-nightjar maintained a maximal $T_a–T_b$ gradient of 7.7°C. The maximal gradients observed in comparably sized passerines are in the 2.4–5.4°C range (Whitfield et al., 2015; Smith et al., 2017; McKechnie et al., 2017). The performance of nightjars in the heat is currently only rivaled by doves and pigeons; Smith et al. (2015), for example, found that mourning doves and white-winged doves can maintain a maximal $T_a–T_b$ gradient of 14.1 and 15.3°C, respectively. These differences in performance among avian orders translate directly into overall heat tolerance.

During high-temperature events, birds may be severely challenged to evaporate sufficient water to maintain a stable T_b and thus be subject to overheating and death. We wanted to establish baseline performance values for heat tolerance in the Caprimulgiformes, as earlier researchers (Lasiewski, 1969; Grant, 1982) have suggested that this group shows exceptional heat tolerance compared with most other birds. We thus estimated the HTL of nightjars to acute exposure to high T_a. We defined the HTL as the T_a at which birds showed rapidly increasing T_b approaching or reaching a sub-lethal endpoint of $T_b=45°C$. We chose $T_b=45°C$ because the limited data on lethal temperatures suggest that the avian lethal range is from 45.7 to 47.8°C (Arad and Marder, 1982; Brush, 1965; Randall, 1943). For the ground-nesting/roosting common poorwill and the lesser nighthawk, we observed HTLs

of $T_a\approx62$–64°C and 60–62°C, respectively. These values are comparable to the performance observed (58–64°C) in a variety of Columbiformes (McKechnie et al., 2016a,b; Smith et al., 2015). For the Australian owlet-nightjar, which nests/roosts in tree cavities and experiences less extreme heat exposure, the observed HTL was $T_a\approx52$–54°C. Thus, we found that the HTLs of the owlet-nightjar were closer to the HTLs of passerines (HTL $T_a\approx48$–52°C) tested under similar conditions (Whitfield et al., 2015; McKechnie et al., 2017; Smith et al., 2017).

Conclusions

This study builds on earlier seminal studies on nightjars, which recorded their remarkable ability to tolerate heat (Bartholomew et al., 1962; Lasiewski and Dawson, 1964). We worked on heat-acclimated, recently captured birds and found that the low resting metabolic rate observed in all species reduces the contribution of metabolic heat to the overall heat load. The use of gular flutter increases evaporative cooling with little metabolic cost compared with the large increases in metabolic heat production associated with panting used by passerines, thus increasing heat tolerance limits and conserving water. This mechanism rivals the performance found in doves and pigeons that primarily rely on cutaneous evaporation for cooling, which also has negligible metabolic costs. Although we present the data for North American nightjars with the Australian owlet nightjar together, their relative performances are in part a function of the differing measurement conditions (active versus rest phase measurements) among species, and differences in their ecologies (ground dwelling versus cavity roosting). All species, however, demonstrate HTLs and capacities for thermoregulation that greatly exceed those of sympatric passerines, potentially making them more resilient to the rapid warming that is occurring in their current distributions.

References
Albright, T. P., Multibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E. and Wolf, B. O. (2017) Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proc. Natl. Acad. Sci. USA.* **114**, 2283-2288.
Arad, Z. and Marder, J. (1982). Effect of long-term heat acclimatization on the thermoregulatory mechanisms of the desert sinai and white leghorn fowls (*Gallus domesticus*) *Comp. Biochem. Physiol. A* **72**, 185-190.
Audubon, J. J. (1830). *Whip-poor-will. Birds of America, no.82.* The Collection, National Gallery of Art, Washington, D. C.
Bartholomew, G. A., Howell, T. R. and Cade, T. J. (1957). Torpidity in the white-throated swift, Anna hummingbird and poor-will. *Condor* **59**, 145-155.
Bartholomew, G. A., Hudson, J. W. and Howell, T. R. (1962). Body temperature, oxygen consumption, evaporative water loss and heart rate in the poor-will. *Condor* **64**, 117-125.
Bartholomew, G. A., Lasiewski, R. C. and Crawford, E. C., Jr. (1968). Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. *Condor* **70**, 31-34.
Baumel, J. J., Dalley, A. F. and Quinn, T. H. (1983). The collar plexus of subcutaneous thermoregulatory veins in the pigeon, *Columba livia*; its association with esophageal pulsation and gular flutter. *Zoomorphology* **102**, 215-239.
Bennett, P. M. and Harvey, P. H. (1987). Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool.* **213**, 327-344.
Brigham, R. M. (1992). Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). *Physiol. Zool.* **65**, 457-472.
Brigham, R. M. and Geiser, F. (1997). Breeding biology of Australian owlet-nightjars *Aegotheles cristatus* in Eucalypt woodland. *Emu* **97**, 316-321.
Brigham, R. M., McKechnie, A. E., Doucette, L. I. and Geiser, F. (2012). Heterothermy in caprimulgid birds: a review of inter- and intraspecific variation in free-ranging populations. In *Living in a Seasonal World: Thermoregulation and Metabolic Adaptation* (ed. T. Ruf, C. Bieber, W. Arnold and E. Millesi), pp. 175-187. Berlin, Heidelberg: Springer.
Brush, A. H. (1965). Energetics, temperature regulation and circulation in resting, active, and defeathered California quail, *Lophortyx californicus. Comp. Biochem. Physiol.* **15**, 399-421.
Calder, W. A. and Schmidt-Nielsen, K. (1967). Temperature regulation and evaporation in the pigeon and the roadrunner. *Am. J. Physiol.* **213**, 883-889.
Cowles, R. B. and Dawson, W. R. (1951). A cooling mechanism of the Texas nighthawk. *Condor* **53**, 19-22.
Cunningham, S. J., Martin, R. O., Hojem, C. L. and Hockey, P. A. R. (2013a). Temperatures in savanna: a study of common fiscals. *PLoS ONE* **8**, e74613.
Cunningham, S. J., Kruger, A. C., Nxumalo, M. P. and Hockey, P. A. R. (2013b). Identifying biologically meaningful hot-weather events using threshold temperatures that affect life-history. *PLoS ONE* **8**, e82492.
Dawson, W. R. and Fisher, C. D. (1969). Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* **71**, 49-53.
Doucette, L. I. and Geiser, F. (2008). Seasonal variation in thermal energetics of the Australian owlet-nightjar (*Aegotheles cristatus*). *Comp Biochem Phys A* **151**, 615-620.
Grant, G. S. (1982). Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithol. Monogr.* **30**, 1-100.
Howell, T. R. and Bartholomew, G. A. (1959). Further experiments on torpidity in the poor-will. *Condor* **61**, 180-185.
IPCC (2012). Intergovernmental Panel on Climate Change. *Special Report on Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation (SREX).* Cambridge: Cambridge University Press.
IPCC (2014). Intergovernmental Panel on Climate Change. *Climate Change 2014: Synthesis Report.* Cambridge: Cambridge University Press.
Lane, J. E., Swanson, D. L., Brigham, R. M. and McKechnie, A. E. (2004). Physiological responses to temperature by whip-poor-wills: more evidence for the evolution of low metabolic rates in Caprimulgiformes. *Condor* **106**, 921-925.
Lasiewski, R. C. (1969). Physiological responses to heat stress in the poorwill. *Am. J. Physiol.* **217**, 1504-1509.
Lasiewski, R. C. and Bartholomew, G. A. (1966). Evaporative cooling in the poor-will and the tawny frogmouth. *Condor* **68**, 253-262.
Lasiewski, R. C. and Dawson, W. R. (1964). Physiological responses to temperature in the common nighthawk. *Condor* **66**, 477-490.
Lasiewski, R. C. and Seymour, R. S. (1972). Thermoregulatory responses to heat stress in four species of birds weighing approximately 40 grams. *Physiol. Zool.* **45**, 106-118.
Lasiewski, R. C., Acosta, A. L. and Bernstein, M. H. (1966). Evaporative water loss in birds–I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* **19**, 445-457.
Lasiewski, R. C., Bernstein, M. H. and Ohmart, R. D. (1971). Cutaneous water loss in the roadrunner and poor-will. *Condor* **73**, 470-472.
Latta, S. C. and Baltz, M. E. (2012). Lesser Nighthawk (*Chordeiles acutipennis*). In *The Birds of North America* (ed. P. G. Rodewald). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/lesnig.
Lighton, J. R. B. (2008). *Measuring Metabolic Rates: A Manual for Scientists.* Oxford: Oxford University Press.
Lutterschmidt, W. I. and Hutchison, V. H. (1997). The critical thermal maximum: history and critique. *Can. J. Zool.* **75**, 1561-1574.
McKechnie, A. E. and Wolf, B. O. (2004). Partitioning of evaporative water loss in white-winged doves: plasticity in response to short-term thermal acclimation. *J. Exp. Biol.* **207**, 203-210.
McKechnie, A. E. and Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biol. Lett.* **6**, 253-256.

McKechnie, A. E., Smit, B., Whitfield, M. C., Noakes, M. J., Talbot, W. A., Garcia, M., Gerson, A. R. and Wolf, B. O. (2016a). Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell's sandgrouse (*Pterocles burchelli*). *J. Exp. Biol.* **219**, 2137-2144.

McKechnie, A. E., Whitfield, M. C., Smit, B., Gerson, A. R., Smith, E. K., Talbot, W. A., McWhorter, T. J. and Wolf, B. O. (2016b). Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids. *J. Exp. Biol.* **219**, 2145-2155.

McKechnie, A. E., Gerson, A. R., McWhorter, T. J., Smith, E. K., Talbot, W. A. and Wolf, B. O. (2017). Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation in heat tolerance. *J. Exp. Biol.* **220**, 2436-2444.

Muggeo, V. M. R. (2008). Segmented: an R package to fit regression models with broken-line relationships. *R News* **8**, 20-25.

Nobel, P. S. (1984). Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia* **62**, 310-317.

O'Connor, R. S., Wolf, B. O., Brigham, R. M. and McKechnie, A. E. (2017). Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *J. Comp. Physiol. B* **187**, 477-491.

Randall, W. C. (1943). Factors influencing the temperature regulation of birds. *Am. J. Physiol.* **139**, 56-63.

Scholander, P. F., Hock, R., Walters, V., Johnson, F. and Irving, L. (1950). Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* **99**, 237-258.

Smit, B., Boyles, J. G., Brigham, R. M. and McKechnie, A. E. (2011). Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. *J. Biol. Rhythm* **26**, 241-248.

Smith, E. K., O'Neill, J., Gerson, A. R. and Wolf, B. O. (2015). Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail. *J. Exp. Biol.* **218**, 3636-3646.

Smith, E. K., O'Neill, J. J., Gerson, A. R., McKechnie, A. E. and Wolf, B. O. (2017). Avian thermoregulation in the heat: resting metabolism, evaporative cooling, and heat tolerance in Sonoran Desert songbirds. *J. Exp. Biol.* **220**, 3290-3300.

Walsberg, G. E. and Wolf, B. O. (1995). Variation in the respirometry quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. *J. Exp. Biol.* **198**, 213-219.

Welbergen, J. A., Klose, S. M., Markus, N. and Eby, P. (2008). Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc. R. Soc. B* **275**, 419-425.

Whitfield, M. C., Smit, B., McKechnie, A. E. and Wolf, B. O. (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* **218**, 1705-1714.

Williams, J. B. and Tieleman, B. I. (2005). Physiological adaptation in desert birds. *Bioscience* **55**, 416-425.

Whittow, G. C. (1976). Regulation of body temperature. In *Avian Physiology* (ed. P. D. Sturkie), pp. 147-170. Berlin Heidelberg: Springer.

Wolf, B. O. and Walsberg, G. E. (1996). Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. *J. Exp. Biol.* **199**, 451-457.

Woods, C. P., Csada, R. D. and Brigham, R. M. (2005). Common Poorwill (*Phalaenoptilus nuttallii*). Common Poorwill (*Phalaenoptilus nuttallii*), *The Birds of North America* (ed. P. G. Rodewald). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/compoo DOI: 10.2173/bna.32.