RESEARCH ARTICLE

Avian thermoregulation in the heat: metabolism, evaporative cooling and gular flutter in two small owls

William A. Talbot[1],*, Alexander R. Gerson[2], Eric Krabbe Smith[1], Andrew E. McKechnie[3] and Blair O. Wolf[1]

ABSTRACT

The thermoregulatory responses of owls to heat stress have been the subject of few studies. Although nocturnality buffers desert-dwelling owls from significant heat stress during activity, roost sites in tree and cactus cavities or in deep shade provide only limited refuge from high environmental temperatures during the day. We measured thermoregulatory responses to acute heat stress in two species of small owls, the elf owl (*Micrathene whitneyi*) and the western screech-owl (*Megascops kennicottii*), which occupy the Sonoran Desert of southwestern North America, an area of extreme heat and aridity. 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 limits (HTL; the maximum T_a reached). Comparatively low RMR values were observed in both species, T_b approximated T_a at 40°C and mild hyperthermia occurred as T_a was increased toward the HTL. Elf owls and screech-owls reached HTLs of 48 and 52°C, respectively, and RMR increased to 1.5 and 1.9 times thermoneutral values. Rates of EWL at the HTL allowed for the dissipation of 167–198% of metabolic heat production (MHP). Gular flutter was used as the primary means of evaporative heat dissipation and produced large increases in evaporative heat loss (44–100%), accompanied by only small increases (<5%) in RMR. These small, cavity-nesting owls have thermoregulatory capacities that are intermediate between those of the open-ground nesting nightjars and the passerines that occupy the same ecosystem.

KEY WORDS: Strigiformes, Respirometry, Evaporative water loss, Resting metabolic rate, Body temperature, Heat tolerance limit

INTRODUCTION

The thermoregulatory physiology of birds in the heat has received increased attention as the impact of a warming climate on animal populations becomes more evident (e.g. Albright et al., 2016; McKechnie et al., 2015, 2016, 2017; Smith et al., 2015). For birds in the deserts of North America, heat waves are predicted to increase in frequency, intensity and duration and the region will be increasingly subjected to severe drought events (IPCC, 2011, 2014). These conditions are likely to impact the abundance and distribution of birds, through both direct effects on survival (McKechnie and Wolf, 2010; Albright et al., 2016) and indirect effects on reproductive performance (du Plessis et al., 2012; Cunningham et al., 2013;

[1]Department of Biology, University of New Mexico, MSC03-2020, Albuquerque, NM 87131-0001, USA. [2]Department of Biology, University of Massachusetts, Amherst, MA 01003, USA. [3]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

Cruz-McDonnell and Wolf, 2016; Borgman and Wolf, 2016). Birds inhabiting hot, dry deserts must regularly contend with high ambient temperatures as well as intense solar heat loads. Evaporative cooling is the only avenue for heat dissipation when air temperature (T_a) exceeds body temperature (T_b); therefore, a trade-off exists between the avoidance of lethal hyperthermia and the avoidance of lethal dehydration (Wolf and Walsberg, 1996; McKechnie and Wolf, 2010). Diurnal species can potentially restore body water through dietary metabolic water or flying to often scarce water sources to drink. Owls, as nocturnally active species, might be assumed to avoid these increasingly severe conditions; however, during the day they must still endure thermal conditions in their roosts that may pose significant challenges to heat and water budgets (Ganey et al., 1993; Weathers et al., 2001; Ganey, 2004). The direct effects of heat waves on mortality in some Australian birds (McKechnie et al., 2012) and in roosting bats are well known (Welbergen et al., 2008; Bondarenco et al., 2014) although such data do not exist for owls. In addition to behavioral adaptations, recent studies have explored different physiological strategies among diverse avian taxa for enhancing the efficiency of evaporative cooling. Desert passerines rely on panting to increase evaporative water loss (EWL) at the cost of increasing metabolic heat load through the use of respiratory musculature (McKechnie et al., 2017; Smith et al., 2017). Desert doves and pigeons rely on cutaneous evaporation, a passive process that does not increase metabolic heat load (McKechnie and Wolf, 2004a; Smith et al., 2015; McKechnie et al., 2016). In desert nightjars, gular flutter, the resonant movement of the hyoid apparatus, is associated with increased EWL with little or no increase in metabolic rate (O'Connor et al., 2017; Talbot et al., 2017). Our current understanding of thermoregulatory performance in owls, relative to other avian orders, is highly limited and a better understanding of their thermal constraints will aid in modeling the effects of climate change on individuals and populations (Williams et al., 2008; Fuller et al., 2010).

Information on the thermoregulatory response of all owls under conditions where T_a exceeds T_b is restricted to a small number of field and laboratory studies. Limited heat tolerance in spotted owls (*Strix occidentalis*), for example, apparently constrains their activities to dense forest cover during the summer (Barrows, 1981). Captive spotted owls from Arizona had a lower upper critical temperature (T_{uc}) and a more limited ability to dissipate heat than the wider-ranging great horned owl (*Bubo virginianus*) (Ganey et al., 1993; Weathers et al., 2001). Few data also exist on the thermoregulatory performance of small forest and woodland owls, with measurements for pygmy owls (*Glaucidium gnoma*), whiskered screech-owls (*Megascops trichopsis*), western screech-owls (*Megascops kennicottii*), saw-whet owls (*Aegolius acadicus*) and elf owls (*Micrathene whitneyi*) mostly limited to captive, hand-raised birds exposed at $T_a \leq 40°C$ (Ligon, 1969). Ligon (1969) described the occurrence and rates of gular flutter in heat-stressed owls and also

List of abbreviations

EHL	evaporative heat loss
EWL	evaporative water loss
HTL	heat tolerance limit
M_b	body mass
MHP	metabolic heat production
RH	relative humidity
RMR	resting metabolic rate
STP	standard temperature and pressure
T_a	air temperature
T_b	body temperature
T_{uc}	upper critical temperature
TNZ	thermoneutral zone

reported strong hyperthermic responses to increasing T_a, noting a doubling of metabolic rate associated with gular flutter in the elf owl. Coulombe (1970, 1971) undertook a very comprehensive study of burrowing owl (*Athene cunicularia*) energetics, behavior and thermoregulation in the Imperial Valley of southern California, where T_a can reach 50°C. This detailed and thorough study included measurements of not only resting metabolic rate (RMR), EWL and T_b, but also heart rate, respiratory rates, the efficiency of gular flutter and coat reflective properties, and notably linked data collected from captive birds at T_a as high as 45°C to the thermal and hydric environments the owls experience on the surface and in their burrows, and the role of the burrows as thermal refugia (Coulombe, 1971).

The present study followed the approach we have used previously for studies of avian thermoregulation in the heat in other desert birds (Whitfield et al., 2015; Smith et al., 2015, 2017; McKechnie et al., 2015, 2016, 2017; O'Connor et al., 2017; Talbot et al., 2017). These studies have shown that desert passerines tend to have a distinct T_{uc} above which panting is necessary for evaporative cooling, and this comes at a high metabolic cost. Nightjars and doves, in contrast, show very small increases in RMR at high temperatures (a relatively ill-defined T_{uc}), which reflects the high efficiency of evaporative cooling mechanisms that are driven by cutaneous evaporation in the doves and gular flutter in the nightjars. Here, we used the same methods to quantify thermoregulatory performance, including the upper limits of heat tolerance and evaporative cooling capacity in two sympatric small owls: the elf owl and the western screech-owl. The elf owl, *Micrathene whitneyi* (J. G. Cooper 1861), the smallest of owls (40 g), breeds in the deserts of the southwestern USA and northern Mexico and then migrates south. It shares its breeding range, habitat and many ecological characteristics with the western screech-owl (101 g), *Megascops kennicottii* (Elliot 1867), hereafter referred to as the screech-owl, a year-round resident. Both species nest in cavities, primarily in mesquite (*Prosopis* sp.) and ironwood (*Olneya tesota*) trees or in saguaro cactus (*Carnegiea gigantea*). Individuals used in this study were captured during the summer and thermoregulatory measurements were performed within 24 h of capture. We characterized the thermoregulatory performance of these small owls by asking the following questions: (1) how does RMR change with T_a within the thermoneutral zone (TNZ) and with increasing heat stress?; (2) is there a distinct T_{uc} and is it associated with the onset of panting/gular flutter?; (3) how does EWL change with T_a within the TNZ and with increasing heat stress?; (4) what is the efficiency of the gular flutter mechanism (i.e. what is the fractional increase in metabolic heat production (MHP) compared with the increase in evaporative heat loss (EHL)?; (5) how does T_b change with T_a within the TNZ and with increasing heat stress?; (6) what are the acute heat tolerance limits (HTLs) in these owls?; and

(7) how does the performance of these owls compare with that of other nocturnal and diurnal avian species?

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), the US Fish and Wildlife Service and the Arizona Game and Fish Department.

Field site, bird capture and care
Twenty-three western screech-owls and 21 elf owls were captured at night using recorded calls, mist nets and hand capture in the palo verde–cacti–mixed scrub habitat of the Sonoran Desert, Pinal Co., AZ, USA. The captures occurred within an ~8 km radius of livestock water tanks located at 32°31′N, 111°01′W and 1097 m a.s.l. Birds were transported in cloth bags to the field laboratory and were held for an average of 3.0 h (minimum 1.1 h) after capture. The birds typically required from 45 min to 1 h in the chambers to become calm and for CO_2 and H_2O levels to reach a nadir before any measurements were taken. Based on previous studies, we believe this allows for a post-absorptive state (Walsberg and Wolf, 1995). Experiments were performed on the night of capture during the active phase and coolest part of their diel cycle. Birds were released at their capture site before morning. Released birds flew away vigorously. 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. Prior to placement in the metabolic chamber, the mean body mass (M_b) of screech-owls was 101.3±8.9 g and that of elf owls was 39.7±1.8 g.

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 (4 l, 22×19×12 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 air temperature 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 with a range of 0–30 or 0–50 l min^{-1} at standard temperature and pressure (STP) and with an accuracy of ±0.8% of the reading ±0.2% of the full scale (Alicat Scientific Inc., Tucson, AZ, USA). Mean flow rate through the respirometry chamber during trials was 16.2±9.2 l min^{-1} at STP, but ranged from 5 to 48 l min^{-1} at STP. Sub-samples of incurrent and excurrent air were pulled through a CO_2/H_2O analyzer at 250 ml min^{-1} (model LI-840A, LICOR, Lincoln, NE, USA). Prior to placement in the chamber, each bird was hooded and briefly restrained 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. PIT tags measured 2.12±0.10 mm in diameter by 13±0.4 mm in length and weighed 0.109±0.030 g with a

monitoring temperature range of 33–44°C. At the beginning of the study, a representative sample of 70 PIT tags were calibrated in a circulating water bath over temperatures from 39 to 46°C against a digital thermocouple reader (model RDXL12SD, Omega, Stamford, CT, USA) with Cu–Cn thermocouples (Physitemp, Clifton, NJ, USA). The temperatures measured by PIT tags deviated from actual values by 0.02±0.09°C (mean±s.d., $n=70$). The antenna was placed next to the respirometry chamber and tuned for optimal reception according to the manufacturer's specifications. The serial number of the PIT tag records the origin of the signal. A small drop of cyanoacrylate adhesive closed the needle puncture site and the bird was released bearing the tag. As this technique involved only brief restraint (approximately 30 s), it was deemed less stressful to the bird than using anesthesia. M_b was obtained to ±0.1 g (scale model V31XH2, Ohaus, Parsippany, NJ, USA). 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. Continuous observation of the birds' behavior was possible via an infrared light and video camera mounted within the ice chest. 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 per 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) within the TNZ for these owls, as noted in earlier studies (Ligon, 1968, 1969). A constant T_a was maintained until CO_2, H_2O and T_b values were stable for at least 10 min. Thus, the bird had been held at a constant T_a for 30–60 min before subsamples were taken. The bird was then exposed to increasing 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 and Dawson, 1964). Flow rates of up to 48 l min^{-1} were required to maintain acceptable water vapor pressures 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 (Lighton, 2008). 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. 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 some individuals of each species, we were able to observe the onset of gular flutter during a period of stable T_a and changes in RMR and EWL associated with gular flutter were recorded. 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 HTL was reached, which we defined as a T_b approaching 45°C. Lutterschmidt and Hutchison (1997) considered the lethal limit for birds to be ∼46°C. As the rate of T_b increase exceeded 0.1°C min^{-1}, birds rapidly increased T_b to HTL and this became an additional criterion to end the experiment. 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. No mortality occurred during the course of these experiments.

Data analysis

$\dot{V}_{CO_2}$ was calculated using eqn 10.5 from Lighton (2008). Metabolic heat gain (W) was calculated as in Walsberg and Wolf (1995) assuming a respiratory quotient of 0.71. Metabolic heat gain so calculated is herein referred to as the RMR. Rates of EWL were calculated using eqn 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. Statistical analyses were produced in R (version 3.4.0; R Development Core Team 2017) inside RStudio (version 1.1.223). Graphs were produced in SigmaPlot 14 (Systat Software, Inc.). The R package *segmented* was used to estimate breakpoints in the rate of change in response variables (Muggeo, 2008). Data were then divided between values below and above the inflection point. Regression formulas for the relationships between EWL, RMR, EHL/MHP ratio and T_b as a function of T_a were obtained using the linear mixed effects model from R package *nlme* (https://CRAN.R-project.org/package=nlme). Values for regression slopes are given with standard errors of the mean. Values for response variables are given with standard deviations. Several measurements were made at different T_a values although each bird was only tested once. Thus, the models included individual identity of the bird as a random factor. Maximal models included T_a and M_b as predictor variables. The minimal adequate model was obtained by stepwise regression.

RESULTS
RMR

In elf owls, segmented regression identified an inflection point at $T_a=42°C$ in the slope of RMR as a function of T_a (Fig. 1). Between $T_a=30°C$ and $T_a=42°C$, the slope of the regression did not differ significantly from zero ($F_{1,6}=4.964$, $P=0.07$). The mean RMR below the inflection point was 0.46±0.07 W (11.6±1.6 mW g^{-1}). Above the inflection point, the minimum adequate model includes only T_a as a predictor. The slope of RMR as a function of T_a was 0.02±0.01 W, which does not reach significance at the α level of 0.05 ($F_{1,12}=3.765$, $P=0.08$). The mean maximum RMR of four elf owls tested at the HTL ($T_a=48°C$) was 0.58±0.03 W (Table 1). The maximum RMR in an individual elf owl was 0.69 W (17.9 mW g^{-1}) at $T_a=46°C$.

In screech-owls, the minimum adequate model for RMR included only T_a as a predictor. Between the lowest test T_a (30°C) and the inflection point (46.4°C), the slope of RMR as a function of T_a did not differ significantly from zero ($F_{1,19}=0.16$, $P=0.69$) (Fig. 1). The mean RMR below the inflection point was 0.81±0.16 W (8.0± 1.4 mW g^{-1}). The slope of RMR above the inflection point was 0.12±0.04 W ($F_{1,4}=7.87$, $P<0.05$). The mean maximum RMR of seven screech-owls tested at the HTL ($T_a=52°C$) was 1.47±0.60 W (Table 1). The maximum RMR in an individual screech-owl was 2.51 W (25.5 mW g^{-1}) at $T_a=52°C$.

EWL

The minimum adequate model for EWL included only T_a as a predictor in each species. In elf owls, between the lowest test T_a (30°C) and the inflection point (36.8°C), the slope of EWL as a function of T_a did not differ significantly from zero ($F_{1,10}=1.31$, $P=0.28$) (Fig. 2). The mean EWL below the inflection point was 0.36±0.10 g h^{-1}. The slope of EWL above the inflection point was 0.11±0.01 g h^{-1} ($F_{1,8}=146.60$, $P<0.0001$). The mean maximum EWL of four elf owls tested at the HTL ($T_a=48°C$) was 1.46
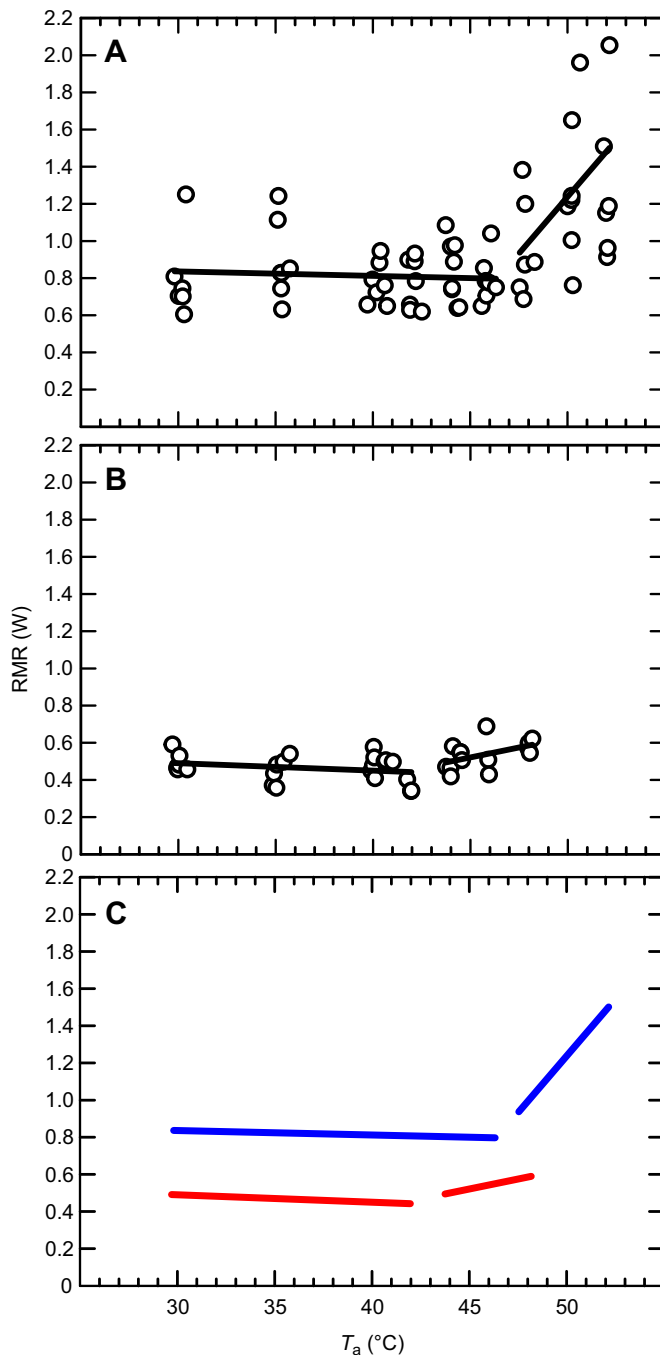
Fig. 1. Resting metabolic rate (RMR) in two species of Sonoran Desert owls over a range of air temperatures (T_a). (A) Western screech-owl. (B) Elf owl. Linear regressions above and below inflection points are shown. (C) Summary graph showing the regression lines for western screech-owls ($N=23$) in blue and elf owls ($N=19$) in red. These data represent only calm birds.

Table 1. Variables related to thermoregulation at high air temperature (T_a) in two Sonoran Desert owls

Variable	Elf owl *Micrathene whitneyi*	Western screech-owl *Megascops kennicottii*
Body mass (g)	39.7±1.8 (21)	101±8.9 (23)
Body temperature (T_b)		
$\quad$ Minimum T_b (°C)	38.8±0.7 (6)	39.1±0.4 (6)
$\quad$ T_a at minimum T_b (°C)[a]	30	30
$\quad$ Inflection T_a (°C)[c]	–	37.3
$\quad$ T_b versus T_a slope below inflection (°C °C^{-1})[b,c]	–	0.02
$\quad$ T_b versus T_a slope above inflection (°C °C^{-1})[b,c]	0.23	0.29
$\quad$ Maximum T_b (°C)	42.9±0.8 (4)	43.2±0.9 (7)
$\quad$ T_a at maximum T_b (°C)[a]	48	50
$\quad$ Heat tolerance limit (°C)[a]	48	52
Resting metabolic rate (RMR)		
$\quad$ Minimum RMR (W)	0.40±0.07 (7)	0.77±0.14 (7)
$\quad$ T_a at minimum RMR (°C)[a]	42	42
$\quad$ Inflection T_a (°C)	42.0	46.4
$\quad$ RMR slope below inflection (W °C^{-1})[b]	0.00	0.00
$\quad$ RMR slope above inflection (W °C^{-1})[b]	0.03	0.12
$\quad$ Maximum RMR (W)	0.58±0.03 (4)	1.47±0.60 (7)
$\quad$ T_a at maximum RMR (°C)[a]	48	52
$\quad$ Max. RMR/min. RMR	1.45	1.91
Evaporative water loss (EWL)		
$\quad$ Minimum EWL (g h^{-1})	0.33±0.12 (6)	0.59±0.27 (6)
$\quad$ T_a at minimum EWL (°C)[a]	35	30
$\quad$ Inflection T_a (°C)	36.8	41.5
$\quad$ EWL slope below inflection (g h^{-1} °C^{-1})[b]	0.00	0.06
$\quad$ EWL slope above inflection (g h^{-1} °C^{-1})[b]	0.11	0.28
$\quad$ Maximum EWL (g h^{-1})	1.46±0.15 (4)	4.16±1.38 (7)
$\quad$ T_a at maximum EWL (°C)[1]	48	52
$\quad$ Max. EWL/min. EWL	4.42	7.05

All response variables are means±s.d. Number of individuals is given in parentheses.
[a]Test T_a±0.5°C. [b]Slopes are derived from linear mixed models. [c]No inflection point found for elf owl T_b; slope of mixed model regression for all T_a is 0.23.

4.16±1.38 g h^{-1} (Table 1). The maximum EWL in an individual screech-owl was 6.93 g h^{-1} at $T_a=48$°C.

Gular flutter and heat dissipation
Converting water loss to watts of heat dissipated evaporatively and metabolic rate to watts of heat produced provides the ratio EHL/MHP as a measure of the effectiveness of evaporative heat dissipation (see Materials and methods, 'Data analysis', for conversion factors). The minimum adequate model for EHL/MHP included only T_a as a predictor in each species. In elf owls, between the lowest test T_a (30°C) and the inflection point (35.7°C), the slope of EHL/MHP as a function of T_a did not differ significantly from zero ($F_{1,9}=0.02$, $P=0.90$) (Fig. 3). The mean EHL/MHP below the inflection point was 0.53±0.16. The slope of EHL/MHP above the inflection point was 0.10±0.01 ($F_{1,8}=65.95$, $P<0.0001$). The mean maximum EHL/MHP of four elf owls tested at the HTL ($T_a=48$°C) was 1.67±0.09 (Table 2). The maximum EHL/MHP in an individual elf owl was 1.82 at $T_a=46$°C.

In screech-owls, between the lowest test T_a (30°C) and the inflection point (34.4°C), the slope of EHL/MHP as a function of T_a did not differ significantly from zero ($F_{1,4}=1.11$, $P=0.35$) (Fig. 3). The mean EHL/MHP below the inflection point was 0.48±0.16. The slope of EHL/MHP above the inflection point was 0.09±0.01 ($F_{1,32}=153.86$, $P<0.0001$). The mean maximum EHL/MHP of seven individual screech-owls tested at the HTL ($T_a=52$°C) was

±0.15 g h^{-1} (Table 1). The maximum EWL in an individual elf owl was 1.66 g h^{-1} at $T_a=48$°C.

In screech-owls, between the lowest test T_a (30°C) and the inflection point (41.5°C), the slope of EWL as a function of T_a did not differ significantly from zero ($F_{1,2}=15.82$, $P=0.06$) (Fig. 2). The mean EWL below the inflection point was 0.78±0.34 g h^{-1}. The slope of EWL above the inflection point was 0.28 g h^{-1} ($F_{1,21}=83.69$, $P<0.0001$). The mean maximum EWL of seven individual screech-owls tested at the HTL ($T_a=52$°C) was
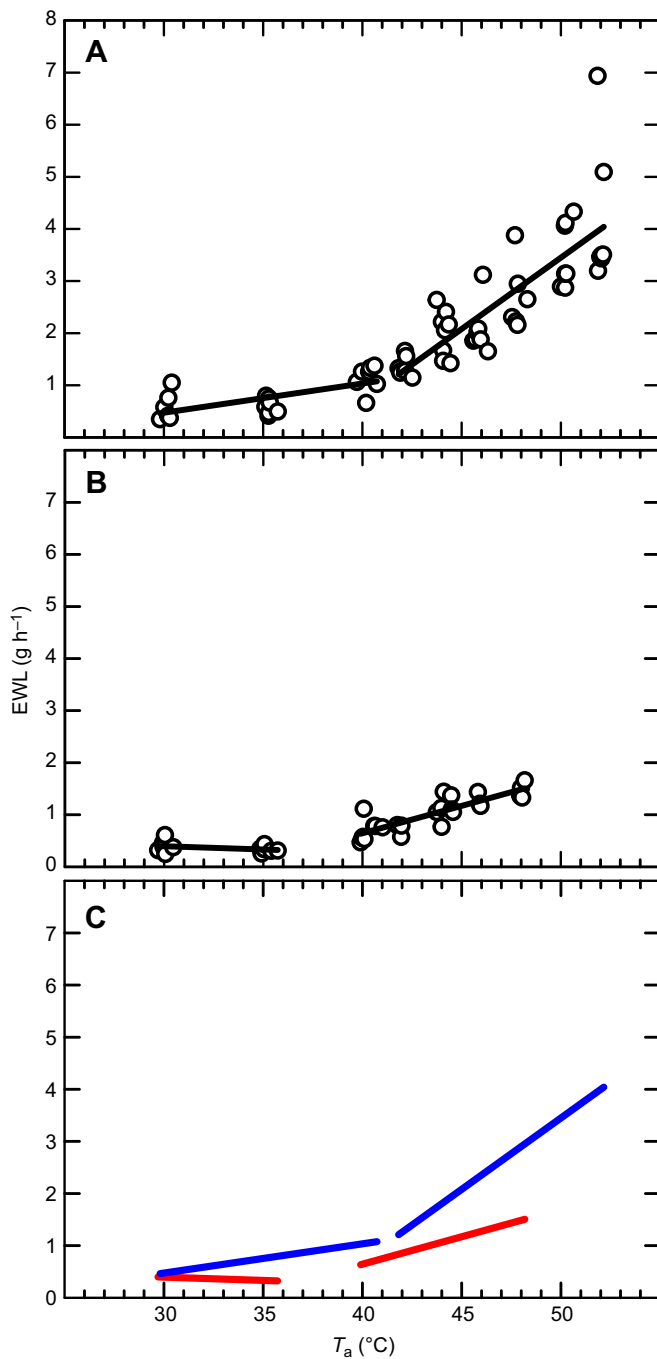
Fig. 2. Evaporative water loss (EWL) in two species of Sonoran Desert owls over a range of T_a. (A) Western screech-owl. (B) Elf owl. Linear regressions above and below inflection points are shown. (C) Summary graph showing the regression lines for western screech-owls (N=23) in blue and elf owls (N=19) in red. These data represent only calm birds.

Fig. 3. The ratio of evaporative heat loss to metabolic heat production (EHL/MHP) in two species of Sonoran Desert owls over a range of T_a. (A) Western screech-owl. (B) Elf owl. Linear regressions above and below inflection points are shown. (C) Summary graph showing the regression lines for western screech-owls (N=23) in blue and elf owls (N=19) in red. These data represent only calm birds.

1.98±0.39 (Table 2). The maximum EHL/MHP in an individual screech-owl was 2.76 at T_a=50°C.

In 6–7 individuals of each species, we were able to observe the onset of gular flutter during a period of stable T_a. The pre-gular flutter measurements were taken at an average T_a=40.7°C for elf owls and 41.9°C for screech-owls. The post-gular flutter measurements were taken at an average T_a=41.9°C for elf owls and 42.2°C for screech-owls. During the interval between pre- and post-gular flutter measurements, the average T_b of each species
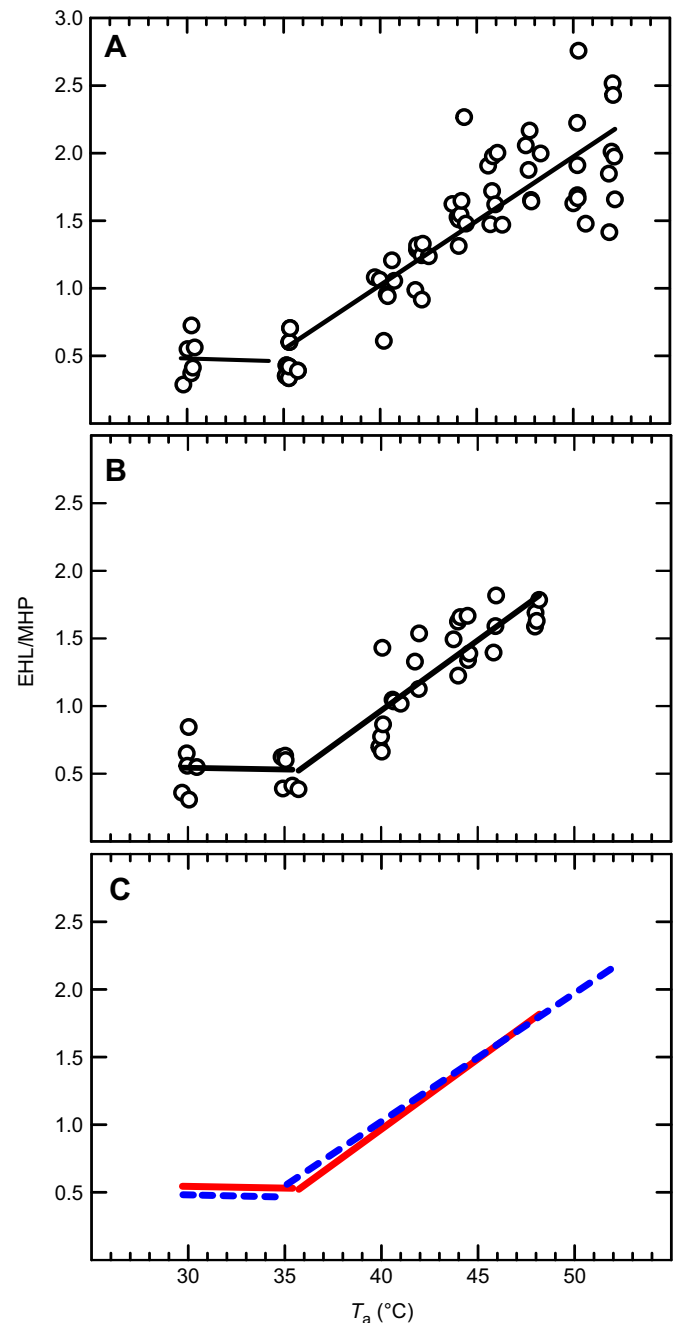
increased <1.0°C. The onset of gular flutter produced an increase in the EHL/MHP ratio of the elf owl from 0.76 to 1.07 and in the screech-owl from 0.63 to 1.23 (Table 2, Fig. 4).

T_b

The minimum adequate model for T_b included only T_a as a predictor in each species. In elf owls, at T_a=30°C, mean T_b=38.8±0.7°C (Fig. 5). No inflection point was noted on segmented regression. The slope of T_b as a function of T_a was 0.23±0.02°C °C^{-1}

Table 2. Variables related to the efficiency of evaporative cooling in two Sonoran Desert owls

Variable	Elf owl *Micrathene whitneyi*	Western screech-owl *Megascops kennicottii*
Minimum EHL/MHP	0.51±0.12 (6)	0.46±0.14 (7)
T_a at minimum EHL/MHP (°C)[a]	35	35
Inflection T_a (°C)	35.7	34.4
EHL/MHP versus T_a slope below inflection (°C °C^{-1})[b]	0.009	−0.003
EHL/MHP versus T_a slope above inflection (°C °C^{-1})[b]	0.103	0.093
Maximum EHL/MHP	1.67±0.09 (4)	1.98±0.39 (7)
T_a at maximum EHL/MHP (°C)[a]	48	52
T_b at onset of gular flutter (°C)	40.3±0.7 (16)	40.4±1.2 (19)
T_a at onset of gular flutter (°C)	41.6±1.9 (16)	41.8±1.6 (19)
Change in RMR with gular flutter (W)[c]	(i) 0.42±0.07 (7) (ii) 0.44±0.07 (7)	(i) 0.77±0.08 (6) (ii) 0.80±0.10 (6)
Change in EHL with gular flutter (W)[c]	(i) 0.32±0.12 (7) (ii) 0.46±0.11 (7)	(i) 0.49±0.19 (6) (ii) 0.98±0.15 (6)
Change in EHL/MHP with gular flutter[c]	(i) 0.76±0.25 (7) (ii) 1.07±0.27 (7)	(i) 0.63±0.22 (6) (ii) 1.23±0.18 (6)

Data are means±s.d. Number of individuals is given in parentheses.
[a]Test T_a±0.5°C. [b]Slopes are derived from linear mixed models. [c]Change in variables with onset of gular flutter: (i) before gular flutter and (ii) after the onset of gular flutter.

($F_{1,18}$=151.74, P<0.0001). The mean maximum T_b of four elf owls tested at the HTL (T_a=48°C) was 42.9±0.8°C (Table 1). The maximum sustained T_b in an individual elf owl was 44.5°C at T_a=46°C. One of eight elf owls failed to tolerate T_a=48°C and five of five owls tested at T_a=50°C failed.

In screech-owls, between the lowest test T_a (30°C) and the inflection point (37.2°C), the slope of T_b as a function of T_a did not differ significantly from zero ($F_{1,11}$=0.12, P=0.73) (Fig. 5). The mean T_b below the inflection point was 39.2±0.6°C. The slope of T_b above the inflection point was 0.29±0.0°C °C^{-1} ($F_{1,25}$=203.01, P<0.0001). The mean maximum T_b of seven individual screech-owls tested at the HTL (T_a=52°C) was 43.2±0.6°C (Table 1). The maximum sustained T_b in an individual screech-owl was 44.1°C at T_a=50°C. Four of 11 screech-owls failed to tolerate T_a=50°C and one of six failed to tolerate T_a=52°C. Two owls tested at T_a=54°C failed.

DISCUSSION
We quantified the thermoregulatory abilities of two small owls under conditions of heat and aridity similar to those that they experience during the summer in the Sonoran Desert. Elf owls (~40 g) and screech-owls (~101 g) both showed low metabolic rates within the TNZ, dissipation of as much as 167–198% of MHP via evaporation facilitated by gular flutter and mild hyperthermia in response to increasing T_a above T_b. Few studies have focused on the metabolic consequences of acute heat stress in small owls. Detailed data are limited to those reported by Ligon (1968, 1969), who provided information on the physiology and behavior of owls exposed to heat and cold stress, and Coulombe (1970, 1971), who conducted an in-depth study of the thermoregulatory biology, energetics and behavior of the burrowing owl (~150 g). In the discussion below, we examine our results in the context of these studies. We also compare our data with similar data from two sympatric nightjars, the common poorwill (*Phalaenoptilus nuttallii*) (~44 g) and the lesser nighthawk (*Chordeiles acutipennis*) (~50 g). Our results indicate that these small owls, in general, have thermoregulatory abilities intermediate between those of Sonoran Desert caprimulgids and passerines (Talbot et al., 2017; Smith et al., 2017).

RMR
Most previous reports on owl metabolic rates involve birds that have been maintained in captivity. Phenotypic plasticity in metabolic rates has been demonstrated in response to captivity (McKechnie et al., 2006), environmental factors (Tieleman et al., 2003) and habituation to handling (Jacobs and McKechnie, 2014), which calls into question the many proposals suggesting a fixed or universal allometry in metabolic scaling. Our study focused on wild-caught birds acclimatized to the most thermally challenging season of their annual cycle; that is, the very hot, dry pre-monsoon months in the Sonoran Desert. Our metabolic trials were performed within 12 h of capture and the length of time the owls were subjected to high T_a was relatively brief to avoid the confounding effect of dehydration. Because of these considerations, we did not explore the full range of the TNZ; however, the minimum stable RMR values we observed (0.40 W for elf owls; 0.77 W for screech-owls) agree nicely with the allometry of McKechnie and Wolf (2004b), which accounts for M_b, phylogeny and acclimatization. Their allometric predictions ascribe a basal metabolic rate for the elf owl of 0.41 W and for the screech-owl of 0.76 W. Sympatric avian species from other taxa have been studied under an identical protocol simultaneously with this study. Minimal RMR in doves (6.9–7.4 mW g^{-1}) (Smith et al., 2015) and nightjars (7.0–8.0 mW g^{-1}) (Talbot et al., 2017) is comparable to that for our owls (7.6–10.3 mW g^{-1}) but lower than the minimal RMR observed in passerines (Smith et al., 2017). Thus, our data agree with earlier observations that owls have relatively low metabolic rates among bird taxa (Ligon, 1969; Coulombe, 1970; Weathers et al., 2001).

Definition of a precise T_{uc} has proven difficult in some birds in hot environments showing either a high T_{uc} or no evidence of a T_{uc} (Tieleman et al., 2002; McKechnie et al., 2016). O'Connor et al. (2017) found a suggestion of increased RMR at T_a≈50°C in two South African nightjars but the inflection point was not significant. This was the case with our elf owls, where segmented regression identified an inflection point at T_a=42°C but the slope of the regression above that point was not significant. The screech-owl, in contrast, had a distinct T_{uc} at T_a=46.4°C (Table 1, Fig. 1). This is comparable to the T_{uc} found in Sonoran Desert doves (45.9–46.5°C) but higher than the T_{uc} for Sonoran Desert passerines (36.2–42.6°C). The two sympatric nightjars (Table 3) had widely differing T_{uc} (40.3 for the common poorwill and 56.2 for the lesser nighthawk). The hyperthermic response to increasing T_a and the dominant mechanism for EWL may allow some species to delay increased energy expenditure for cooling until the gradient between T_a and T_b becomes quite large (see discussion below).

EWL
Our measurements of thermoregulatory performance were carried out under conditions of low humidity (dew point <−5°C) that characterize the Sonoran Desert before the summer monsoon (May–July). This protocol provided experimental animals with conditions conducive for EHL by maximizing the vapor pressure gradient for evaporation. Many previous studies have been carried out with higher chamber relative humidity ranging from 10% to 80% (Ligon, 1968, 1969; Coulombe, 1970), which can directly impede evaporation and heat loss at high T_a (Gerson et al., 2014). Minimum rates of EWL observed (Table 3, Fig. 2) represent minimum obligatory cutaneous and respiratory water losses. Our EWL values are 2–4 four times those measured by Ligon (1969) in
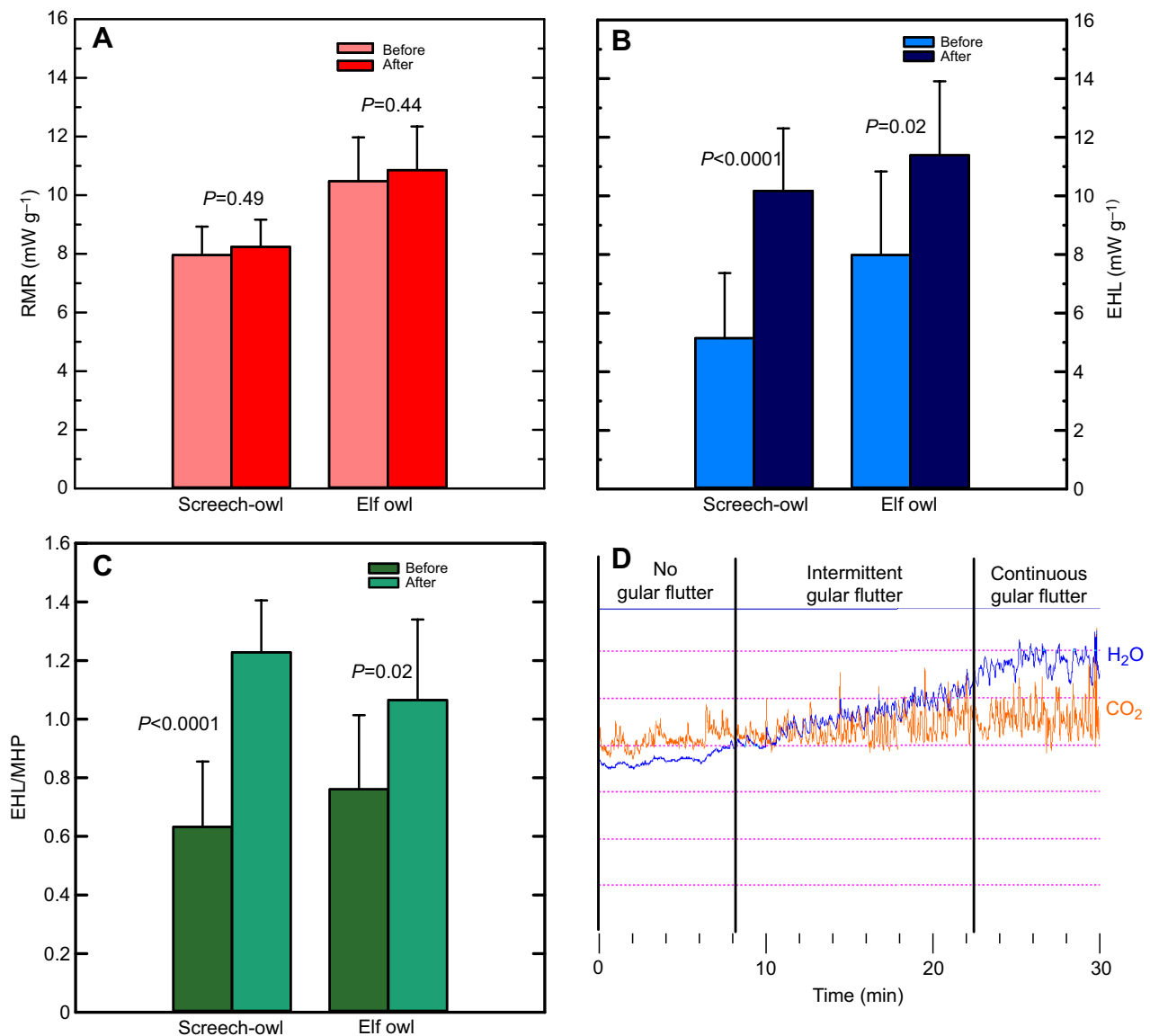
Fig. 4. Effect of gular flutter on MHP, EHL and their ratio in two species of desert owls. (A) RMR as a measure of MHP; (B) EHL and (C) EHL/MHP. Data (mass-specific means+s.e.m.) are shown before and after gular flutter. Paired t-test shows no significant difference in MHP before and after gular flutter. (D) Sample output of direct CO_2 and H_2O measurements from an elf owl showing 30 min of samples taken before and during gular flutter.

four species of small owls ($\sim$2–4 mg g^{-1} h^{-1}) at a T_a 35°C (Table 3). Chamber humidity was higher in Ligon's (1969) study (relative humidity, RH $\sim$10–14%), and the RMRs measured in these hand-raised, laboratory-housed birds were approximately half the values we observed. Rates of EWL in laboratory-housed burrowing owls at T_a=35°C reported by Coulombe (1970) were also less than half (2.4 mg g^{-1} h^{-1}) the values we observed in the smaller western screech-owl. Interestingly, rates of EWL we obtained in the sympatric common poorwill and lesser nighthawk using the same methodology and temperatures produced EWL rates comparable to those of the owls (Table 3) (Talbot et al., 2017). These observations highlight how differences in time in captivity, thermal acclimation history and the humidity of measurement conditions may confound direct comparison of thermoregulatory data from different studies and among/within species.

As T_a approaches T_b, dry heat loss through conduction, convection and radiation decreases and EHL becomes increasingly important. In some species, we have observed distinct inflection points that signal

an upregulation in rates of EWL with increased heat stress. In our owls, these inflection points for EWL occurred at T_a $\sim$5°C lower than the inflection points for RMR (36.8°C in elf owls and 41.5°C in screech-owls) (Table 1, Fig. 2). Above the inflection point, EWL increased by 2.6–2.8 mg g^{-1} h^{-1} °C^{-1}. Although other taxa show great variation in the T_a at which the upregulation of EWL occurs, the rates of EWL are similar to those seen in sympatric doves (2.0–2.6 mg g^{-1} h^{-1} °C^{-1}) (Smith et al., 2015) and nightjars (2.4–4.2 mg g^{-1} h^{-1} °C^{-1}) (Talbot et al., 2017) (Table 3). In a similar study, passerines showed rates of EWL that ranged from 3.6 to 5.4 mg g^{-1} h^{-1} °C^{-1} (Smith et al., 2017). Overall, elf owls and screech-owls were capable of increasing EWL rates by 4.4 and 7.1 times the TNZ values, respectively. Burrowing owls in Coulombe's (1970) study showed an EWL scope of $\sim$6 times the values observed at 35°C at the highest T_a=43°C with chamber RH averaging 34%. The maximum EWL scope observed in small owls is thus similar to that observed in Sonoran Desert passerines, which have maximum EWL values that are 3.3–6.6 times TNZ values
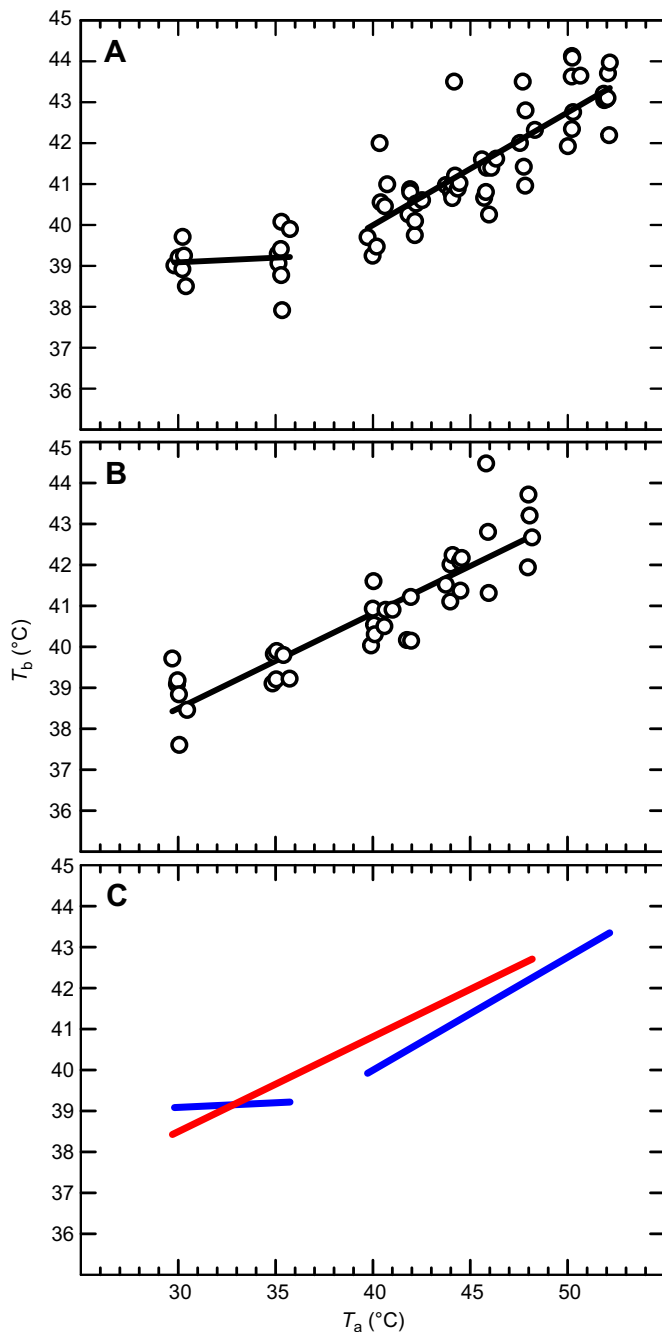
Fig. 5. Body temperature (T_b) in two species of Sonoran Desert owls over a range of T_a. (A) Western screech-owl. (B) Elf owl. Linear regressions above and below inflection points are shown. No inflection point was found for the elf owl. (C) Summary graph showing the regression lines for western screech-owls (N=23) in blue and elf owls (N=19) in red. These data represent only calm birds.

(Smith et al., 2017). In contrast, the caprimulgids show increases in EWL as much as 16.5 times thermoneutral levels (Talbot et al., 2017). Although both the owls and nightjars possess an effective gular flutter mechanism, the nightjars show a significantly greater capacity for evaporative heat loss (Table 3). Thus, elf owls and screech-owls show responses that are intermediate between the very heat-tolerant caprimulgids and passerines that have heat tolerances similar to those of owls.

Efficiency of evaporative processes: EHL/MHP

When T_a exceeds T_b, metabolic heat and increasing environmental heat loads must be either stored by allowing T_b to increase or dissipated by greatly increasing rates of evaporation (Tieleman and Williams, 1999). The EHL/MHP ratio provides a relative measure of the efficiency of evaporative cooling mechanisms by indicating the multiples of MHP that can be dissipated through EHL (Fig. 4). By definition, changes in both RMR and EHL have a direct effect on the ratio and, as a consequence, the primary pathway for evaporation (respiratory, mucosal or cutaneous surfaces) and its underlining metabolic costs have direct bearing on this ratio (McKechnie et al., 2016). Presumably, the most metabolically costly mechanism for evaporation is respiratory panting, requiring mechanical activation of a large portion of the respiratory tract, followed by gular flutter, in which increased movement of the respiratory apparatus is limited to the mucosal surfaces of the mouth and throat, and then by cutaneous evaporation, which requires no mechanical activation and lacks a detectable metabolic cost. Under conditions of increasing heat stress, the small owls in this study initiated active heat dissipation using gular flutter (Fig. 4). We observed only a small increase in MHP, accompanied by a much greater increase in EHL associated with the onset of gular flutter (Table 2, Fig. 4). In order to isolate the effect of gular flutter, the data on the change in MHP and EHL were taken during a time period when T_a was maintained at a constant level and the response T_b was stable. When gular flutter was activated, EHL/MHP increased immediately from 0.76 to 1.07, or 41%, in the elf owl and increased from 0.63 to 1.23, or 95%, in the screech-owl. Thus, activation of the gular mechanism greatly increased EHL with only a very small increase in metabolism (Table 2, Fig. 4). The elf owl and screech-owl achieved average maximal EHL/MHP ratios of 1.7 and 2.0, respectively (Table 2, Fig. 3). The highest sustained EHL/MHP value we observed was 1.8 in an individual elf owl and 2.8 in an individual screech-owl during continuous gular flutter. In the lesser nighthawk and common poorwill, low metabolic rates and high evaporative capacities drive their average values to 3.3 and 4.2, respectively. The highest EHL/MHP value reported for any bird is 5.15 in the rufous-cheeked nightjar (*Caprimulgus rufigena*) (O'Connor et al., 2017). Although we did not measure changes in respiratory rate with the onset of gular flutter, Ligon (1969) observed values in the elf owl that ranged from 135 to 160 breaths min^{-1} during panting to 176–523 flutters min^{-1} during gular flutter, suggesting these are separate processes. Large owls such as great horned owls (*B. virginianus*) and barn owls (*Tyto alba*) are known to use both gular flutter and panting simultaneously as T_a exceeds T_b (Bartholomew et al., 1968). We did not observe obvious panting activation of thoracic musculature but that could have been disguised by the depth of plumage.

T_b and HTL

Both elf owls and western screech-owls showed T_b of ∼39°C within the TNZ. These values are lower than the values we found in six species of passerines (∼41°C) (Smith et al., 2017) and very similar to the values observed in the lesser nighthawk (38.8°C) and common poorwill (38.4°C) (Talbot et al., 2017). As T_a approached T_b, owls showed modest hyperthermic responses which serve to reduce heat gain from the environment, resulting in water savings (Schleucher, 2001). Smith et al. (2017) showed that six species of sympatric desert passerines increase T_b above T_a=36°C at rates of 0.18–0.31°C °C^{-1}. Hyperthermic responses above T_a=36°C were 0.23 and 0.29°C °C^{-1} in elf owls and screech-owls, respectively (Table 1, Fig. 5), and 0.20 and 0.18°C °C^{-1} in common poorwills

Table 3. Mass-specific RMR and EWL rates for Sonoran Desert owls and nightjars

Variable	Elf owl *Micrathene whitneyi*	Western screech-owl *Megascops kennicottii*	Common poorwill[b] *Phalaenoptilus nuttallii*	Lesser nighthawk[b] *Chordeiles acutipennis*
RMR				
Minimum RMR (mW g^{-1})	10.3±2.1 (4)	7.6±1.2 (7)	8.0±2.3 (9)	7.0±0.6 (5)
RMR slope (mW g^{-1} °C^{-1})[a]	0.73	1.15	0.57	0.37
Maximum RMR (mW g^{-1})	14.5±0.5 (4)	14.5±6.3 (7)	13.6±6.9 (6)	12.4±1.6 (3)
EWL				
Minimum EWL (mg g^{-1} h^{-1})	8.5±1.7 (6)	5.8±1.4 (7)	4.5±1.7 (6)	4.4±0.8 (3)
EWL slope (mg g^{-1} h^{-1} °C^{-1})[a]	2.6	2.8	4.2	2.4
Maximum EWL (mg g^{-1} h^{-1})	36.2±2.1 (4)	40.8±14.5 (7)	75.8±36.9 (5)	60.5±4.2 (3)

Data are means±s.d. Number of individuals is given in parentheses.
[a]EWL and RMR slopes are derived from mixed models above the inflection point. [b]Data from Talbot et al. (2017).

and lesser nighthawks, respectively (Talbot et al., 2017). Thus, the rate of T_b increase at high T_a in owls falls in the upper range of that seen in passerines, while the rate of T_b increase at high T_a in nightjars falls in the lower range of that seen in passerines.

The hyperthermic response to increasing T_a was not accompanied by an increase in metabolic rate within the range of thermoneutrality. The lack of a Q_{10} effect on metabolic rate has been noted in other endotherms, bringing into question the applicability of a purely temperature-related effect on metabolic rate (Heldmaier and Ruf, 1992; Tieleman and Williams, 1999; Chaui-Berlinck et al., 2004). For example, in elf owls at T_a=30°C, T_b averaged 38.8°C and RMR averaged 0.50 W. At T_a=40°C, T_b averaged 40.7°C while RMR averaged 0.49 W. A Q_{10}=2.5 would predict a RMR=1.25 W.

A maximum T_b of 42.9°C was observed in elf owls at the HTL of T_a=48°C. In the screech-owl, the maximum T_b observed was 43.2°C at the HTL with a T_a=52°C. These values are lower than those observed in sympatric passerines, where maximum T_b ranged from 43.7 to 44.8°C at HTLs that ranged from 48 to 50°C (Smith et al., 2017). In the common poorwill and lesser nighthawk, maximum T_b was 42.6 and 43.6°C, respectively, at the HTL, which was 62°C for the common poorwill and 60°C for the lesser nighthawk (Talbot et al., 2017). Overall, we observed normothermic and maximum T_b in the owls comparable to those of the nightjars, and lower than those of sympatric passerines (Smith et al., 2017). In contrast to T_b, the HTL of the owls was most comparable to that of the passerines, with owls showing lower maximum RMR and T_b at the HTL. The HTL of nightjars stands in stark contrast to that of the owls; although they have similar T_b at the HTL (~43°C), the very large EWL scope in the nightjars allows for a HTL of 60–62°C, i.e. 10°C or more higher than that of the owls (Talbot et al., 2017).

Ecological aspects of comparative thermoregulation

How do these differences in HTL compare with the respective ecologies of the small owls and nightjars that live in the Sonoran Desert during the heat of the summer? Nightjars and owls are summer-breeding residents in the Sonoran Desert (Cannings et al., 2017; Henry and Gehlbach, 1999; Latta and Baltz, 2012; Woods et al., 2005) with nesting typically initiated during May or June, a time when air temperatures routinely exceed 40°C and often reach 48°C (National Park Service, 2016). Screech-owls and elf owls are cavity nesters (tree holes or saguaro cacti) and roost in cavities or dense foliage during the day. In contrast, both the lesser nighthawk and common poorwill nest on the ground, either open ground or under the sparse canopies of the creosote bush (*Larrea tridentata*) or other perennial shrubs. Common poorwills roost on the ground under low shrubs and lesser nighthawks may roost in trees or on the ground. Although the differences in microclimates of these disparate nesting/

roosting sites have received limited direct study (Ligon, 1968; Cannings et al., 2017; Henry and Gehlbach, 1999), the nesting and roosting microclimates of tree cavities and dense foliage of iron wood, mesquite and palo verde trees are likely to be buffered from the heat compared with the open substrates on the ground used by nightjars. Nesting and roosting sites of owls would thus be expected to be characterized by a thermal environment that is deeply shaded with an operative temperature near or mostly below that of shade air temperature (Walsberg, 1985; Wolf and Walsberg, 1996). In contrast, soil temperatures at the soil surface can often exceed 60°C during parts of the day, and direct solar heat loads can exceed 1000 W m^{-2}, thus placing extreme thermoregulatory demands on nightjars roosting on the soil surface (Tracy and Walsberg, 2002; Cowles and Dawson, 1951). These differences in microclimates appear to drive behavior in burrowing owls. Coulombe (1971) reported that the temperature within owl burrows did not differ greatly from the outside air temperature, and that during the heat of the day, burrowing owls tend to leave their burrows and seek elevated perches. These contrasting differences in thermoregulatory demands may well explain species' differences in their capacity for evaporative heat dissipation and HTLs among owls and nightjars.

Conclusions

Most earlier observations on the thermoregulatory capacity of heat-stressed owls were conducted on birds maintained or raised in captivity. In this study, our observations were on owls taken briefly from the wild and acclimated to the hot, dry conditions of the Sonoran Desert. The low metabolic rates within the TNZ, the relatively high T_{uc} and the contribution of gular flutter to the efficiency of cooling of the owls are more comparable to findings for the heat-tolerant nightjars, but their EWL slope and HTL are closer quantitatively to those of passerines. This places them in an intermediate position in thermoregulatory ability between the passerines and the nightjars. For small owls, resilience to the rapid warming in the Sonoran Desert ecosystem may well depend upon suitable thermal refugia.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.E.M., B.O.W.; Methodology: A.R.G., A.E.M., B.O.W.; Formal analysis: A.R.G.; Investigation: W.A.T., A.R.G., E.K.S., B.O.W.; Writing - original draft: W.A.T.; Writing - review & editing: W.A.T., A.R.G., E.K.S., A.E.M., B.O.W.; Visualization: W.A.T.; Supervision: B.O.W.; Funding acquisition: B.O.W.

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