

SHORT COMMUNICATION

Facultative hyperthermia during a heatwave delays injurious dehydration of an arboreal marsupial

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ABSTRACT

Heatwaves negatively impact wildlife populations and their effects are predicted to worsen with ongoing global warming. Animal mass mortality at extremely high ambient temperature (T_a) is evidence for physiological dysfunction and, to aid conservation efforts, improving our understanding of animal responses to environmental heat is crucial. To address this, I measured the water loss, body temperature and metabolism of an Australian marsupial during a simulated heatwave. The body temperature of the common ringtail possum *Pseudocheirus peregrinus* increased passively by $\sim 3^\circ\text{C}$ over a T_a of $29\text{--}39^\circ\text{C}$, conveying water savings of 9.6 ml h^{-1} . When T_a crossed a threshold of $35\text{--}36^\circ\text{C}$, possums began actively cooling by increasing evaporative water loss and thermal conductance. It is clear that facultative hyperthermia is effective up to a point, but once this point is surpassed – the frequency and duration of which are increasing with climate change – body water would rapidly deplete, placing possums in danger of injury or death from dehydration.

KEY WORDS: Water loss, Metabolism, Energetics, Thermal tolerance, Pseudocheiridae, Climate change

INTRODUCTION

As the world's climates warm, heatwaves are predicted to increase in intensity, frequency and duration (Cowan et al., 2014; IPCC, 2013; Meehl and Tebaldi, 2004). Although relatively brief, heatwaves can bear long-lasting ecological consequences as they are associated with both sub-lethal (e.g. reduced body condition: Gardner et al., 2016) and lethal effects (Bird, 2009; Bondarenko et al., 2014; Finlayson, 1932; Kunkel et al., 1996; McKechnie et al., 2012; Saunders et al., 2011). As such, heatwaves will increasingly pose a globally significant problem for animal species.

Animals possess adaptations to persist despite fluctuations in the environment, from daily weather variability to seasonal patterns and long-term climatic trends (Norin and Metcalfe, 2019; Turner et al., 2017). However, there are limits to the breadth of conditions that animals can withstand (McKechnie and Wolf, 2010; Sergio et al., 2017). During heatwaves, as body temperature (T_b) increases and approaches ambient temperature (T_a), mammals and birds can dissipate some metabolic heat passively but will reach a T_a threshold where they must actively cool themselves via evaporative water loss (Briscoe et al., 2014; Speakman and Król, 2010; Welbergen et al., 2007). This rapidly heightens the risk of dehydration and hyperthermia, and surpassing this T_a threshold – even if only for a

few hours – can result in mortality (McKechnie and Wolf, 2010; Ratnayake et al., 2019; Welbergen et al., 2007). Both individual and mass mortality events pose a threat to many species – one that will worsen with more frequent extreme weather events (Meade et al., 2018; Ratnayake et al., 2019).

Die-offs are indicative of abiotic conditions stretching animals beyond their physiological limits. Extreme weather events jeopardise normally secure thermal refugia and an inability to escape excess heat can result in population crashes and changes in geographic distribution over time, as areas with tolerable climates shrink and shift (Briscoe et al., 2016; Kearney and Porter, 2017). Of the recent mass wildlife die-offs recorded worldwide, those caused by extreme heat were most conspicuous among Australia's arboreal fauna including ringtail possums, flying-foxes, koalas and birds (Cox, 2019; Gordon et al., 1988; Saunders et al., 2011; Towie, 2009; Welbergen et al., 2014, 2007). In most cases, dehydration, or a lack of access to water, was implicated as the driver of mortality. In fact, if body water cannot be replenished during prolonged heat exposure, rapid water loss via active cooling is likely to be the most significant factor causing animal death and injury at high T_a , not high T_a per se (McKechnie and Wolf, 2010; Riddell et al., 2019). Therefore, understanding the physiological responses of wildlife to the detrimental environmental conditions predicted to occur in the future will provide insight into how and where survival of these species is possible.

The common ringtail possum *Pseudocheirus peregrinus* (Boddaert 1785) is an arboreal marsupial that nests in spherical dreys in a range of forest types across multiple different climate zones in Australia, but is susceptible to extreme heat. I hypothesised that summer-acclimatised possums from a hot temperate climate would show physiological phenotypes conducive to survival at high temperature. To test this, I measured the metabolic, hygric and thermal biology of wild-caught possums exposed to a simulated heatwave.

MATERIALS AND METHODS

After sunset in late summer (18 March to 1 April 2019), common ringtail possums were found in Nine Mile Hill Travelling Stock Reserve (35.98°S , 146.98°E), New South Wales, using spotlights. Individuals were captured by hand, weighed and sexed. A small patch of fur ($\sim 20 \times 20\text{ mm}$) was trimmed from the right hind flank to calculate hair area density. Only adult males ($n=5$) and non-reproductive females ($n=5$) were studied and I measured one or two possums per night.

The study was approved by the Charles Sturt University Animal Care and Ethics Committee (Animal Research Authority no. A19003) and permission to capture and study possums on managed land was granted by the NSW Office of Environment and Heritage (licence no. SL102119) and NSW Local Land Services, Murray region, who generously waived the permit fee (permit no. 0064).

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Respirometry and heatwave treatment

Possums were transported ~10 km to Charles Sturt University and placed in a respirometry chamber [either a 16 l food storage container (HPL890; LOCK&LOCK Co. Ltd, Seoul, Gyeonggi, South Korea) or a custom-made 15 l acrylic tank (Blaze Displays, Albury, NSW, Australia)] in an open-flow respirometry system. Possums sat on a wire mesh platform above a thin layer of vegetable oil, which removed the effects of urine and faeces evaporation from water loss measurements. Respirometry chambers were placed inside a temperature-controlled cabinet (Westinghouse WRM1400, Electrolux Home Products Pty Ltd, Mascot, NSW, Australia), dimly illuminated by a red LED, and possums were observed using a low-light webcam (ELP-USBFHD06H-BL180, Ailipu Technology Co., Ltd, Shenzhen, Guangdong, China). Air was pumped into the system using an aquarium pump (SONIC P-85), dried using Drierite (W. A. Hammond Drierite Co. Ltd, Xenia, OH, USA) and sent to either (1) a gas pressure regulator/gauge (G261, Qubit Systems Inc., Kingston, ON, Canada) and a gas controller and monitor (G248, Qubit Systems Inc.) or (2) a rotameter (FLDA3420C, OMEGA Engineering Singapore, Singapore) and a mass flow meter (FMA-A2310, OMEGA Engineering Singapore). I used Bev-A-Line IV tubing throughout the system with some short sections of Tygon tubing (Saint-Gobain, Courbevoie, Île-de-France, France). Air entered the metabolic chambers at ~5–6.5 l min⁻¹; brass inlet and outlet connections were vertically and diagonally unaligned and located at opposite ends of the chambers to facilitate air mixing. Excurrent air was subsampled via a syringe barrel manifold by a gas switcher (G243, Qubit Systems Inc.) at ~200 ml min⁻¹. Subsampled air was measured for water vapour pressure by a dewpoint hygrometer (RH-300, Sable Systems International, Las Vegas, NV, USA), dried using Drierite and analysed for CO₂ then O₂ using a gas analysis system (S500, Qubit Systems Inc.). Gas analysers were zeroed before most measurements using compressed N₂ (BOC Ltd, North Ryde, NSW, Australia) and spanned against compressed 0.5% CO₂ in N₂ (CO₂ analyser), ambient air (O₂ analyser) or N₂ pushed through a bubbler flask (H₂O analyser), as recommended by the manufacturers. Flow meters were factory calibrated. A chamber containing only vegetable oil was measured at 34°C to quantify its water content; this value was subtracted from possum water loss calculations.

During measurements, possums were exposed to a simulated heatwave. Overnight (from 23:23 h ±56 min), possums were held at 20°C and allowed to become accustomed to the system. At 07:00 h, T_a was increased to 25°C, within the thermal neutral zone of *P. peregrinus* (Munks, 1991). Animals were briefly removed from respirometry chambers at 09:00 h and, to monitor T_b for the rest of the measurement, a fine wire thermocouple connected to a digital thermometer (SDL200, Extech Instruments, Boston, MA, USA) was inserted 5–6 cm into the cloaca and taped to the base of the tail. At 10:00 h, T_a was increased in 2°C increments from 30 to 38°C at hourly intervals before being returned to 20°C at 15:00 h to facilitate cooling. This ramped T_a design meant measurements were not made of steady-state possums; instead, my aim was to replicate physiological responses to a natural heatwave as closely as possible. The rationale for not exposing possums to the higher T_a expected during a heatwave is related to the likelihood of exposure in the wild. Ringtail possums nest in dreys constructed on branches or within tree hollows. While no information on the internal temperature of dreys is available, they are similar in size and structure to the dreys of Eurasian red squirrels *Sciurus vulgaris*, which buffer T_a by up to 30°C in winter (Pulliainen, 1973; Thomson and Owen, 1964). In hot weather, possum dreys located in trunks are cooler than T_a (Jones et al., 1994;

Thomson and Owen, 1964) and tree hollows potentially used by ringtail possums provide considerable T_a buffering; hollow temperature in summer was predicted to reach only 26.1°C at a T_a of 40°C and an overall maximum of 38.1°C (Rowland et al., 2017). Additionally, possum behaviour suggests dreys built on branches also buffer T_a (Munks, 1991). Hence, during a heatwave, possums in dreys are unlikely to be exposed to T_a much above 38°C. I did not actively search for dreys; however, none were seen in the study site and ringtails were observed entering and leaving tree hollows on several occasions, suggesting that they may use hollows more often than dreys in this forest.

To prevent injury from hyperthermia, I used a hypothetical non-lethal thermal tolerance limit of 2°C above the reported daily maximum T_b (after Whitfield et al., 2015), which was approximately 39°C for *P. peregrinus* (Kinnear and Shield, 1975; Krockenberger et al., 2012; Munks, 1991). If any individuals reached this T_b , measurements were immediately stopped and the possum was cooled using a fan. Possums were measured once each, offered water from a syringe before and after measurements, and released at their point of capture during the ensuing evening; all animals were in captivity <24 h.

I measured metabolic rate (oxygen consumption, \dot{V}_{O_2} ; and carbon dioxide production, \dot{V}_{CO_2}) and evaporative water loss (EWL; calculated after Withers, 2001), averaged during 20 min periods when values were low and stable. Metabolic heat production (MHP) and metabolic water production (MWP) were calculated using oxy-calorific and hygric coefficients for the measured respiratory exchange ratio and EWL was converted to evaporative heat loss (EHL) assuming a latent heat of evaporation of 2.4 J mg⁻¹ H₂O (McNab, 2002). Wet (C_{wet}) and dry (C_{dry}) thermal conductance were calculated as MHP/($T_b - T_a$) and (MHP - EHL)/($T_b - T_a$), respectively (McNab, 2002), where T_b is body temperature and T_a is ambient temperature. Relative water economy (RWE) was calculated as MWP/EWL (Withers et al., 2016) and evaporative cooling capacity (ECC) as EHL/MHP (Smith et al., 2015). Possums were weighed immediately before and after measurements and a linear rate of mass loss was assumed for metabolic rate calculations.

When a single possum was measured, animal air and reference air were sampled alternately for 54 and 6 min, respectively, using Qubit C950 version 3.8.9 (\dot{V}_{O_2} and \dot{V}_{CO_2}) and Sable Systems ExpeData release 1.9.22 (EWL). When two possums were in the system, I measured each animal for either 4.5 or 9 min, cycled in sequence for 54 min, followed by reference air for 6 min. Therefore, reference air was measured once per hour and this was used to drift-correct traces in ExpeData.

Statistical analysis

Data were recorded using Qubit C950 version 3.8.9 and ExpeData release 1.9.22. To allow for non-linear relationships, the effect of predictor variable T_a on response variables T_b , \dot{V}_{O_2} , \dot{V}_{CO_2} , C_{wet} , C_{dry} , EWL, RWE and ECC was examined using generalised additive mixed models in RStudio v1.2.1335 (using R version 3.5.0) with package ‘*gam4*’ (<https://CRAN.R-project.org/package=gam4>). Sex, body mass and hair area density were included as fixed factors alongside individual as a random factor. Residuals were examined visually for departure from a normal distribution. Subsequently, I calculated inflection points for C_{wet} and EWL curves to estimate a threshold T_a initiating rapid increases in physiological cooling using the package ‘*segmented*’ (<https://CRAN.R-project.org/package=segmented>) in RStudio. Data are presented as means ± s.e.m., n = number of individuals.

RESULTS AND DISCUSSION

Possum body mass was 771.5 ± 16.5 g ($n=10$) and hair area density was 0.19 ± 0.02 mg mm⁻² ($n=10$).

T_a before and during the heatwave had a significant effect on six out of eight measured or calculated variables (Table 1); the remaining two (\dot{V}_{CO_2} and C_{dry}) were non-significant ($P \leq 0.099$; Table 1). T_b during measurements ranged from 34.7 to 39.2°C; one possum was removed from the system and cooled when its T_b exceeded 39°C after ~30 min of exposure to $T_a > 37^\circ\text{C}$. At high T_a , individuals lay on their backs or sides, spread their limbs and licked their fur, presumably to expedite cooling. Mean T_b before and after the heatwave ($T_a = 19.4\text{--}27.3^\circ\text{C}$) was $36.1 \pm 0.01^\circ\text{C}$ ($n=10$). During the heatwave ($T_a = 23.0\text{--}39.0^\circ\text{C}$), T_b increased almost linearly by ~3°C (Fig. 1A, Table 1). T_b equalled T_a at 38.6°C. \dot{V}_{O_2} had a slightly curvilinear response to T_a but remained reasonably stable over the measured T_a range (Fig. 1B, Table 1). It is therefore difficult to estimate the thermal neutral zone; however, the lowest point on the curve was at $T_a = 26.4^\circ\text{C}$, where $\dot{V}_{O_2} = 0.53$ ml O₂ g⁻¹ h⁻¹.

C_{wet} increased slowly with increasing T_a before increasing rapidly as T_a approached T_b (Fig. 1C, Table 1); the inflection point was estimated at a T_a of $36.0 \pm 0.6^\circ\text{C}$, when T_b was 37.9°C . A similar pattern was observed for EWL (Fig. 1D, Table 1) and the estimated inflection point, where EWL began to rise sharply, was $34.7 \pm 0.9^\circ\text{C}$. RWE remained below 0.5 over the T_a range measured, indicating

that possums were in a constant water deficit (EWL exceeds metabolic water production when $RWE < 1$). RWE decreased as T_a increased (Fig. 1E, Table 1) and $RWE = 1$ at $T_a = -26.0^\circ\text{C}$. ECC also increased at high T_a (Fig. 1F, Table 1) and $ECC = 1$ (i.e. where $MHP = EHL$) at $T_a = 38.4^\circ\text{C}$.

When T_a exceeds T_b , the only method of cooling available to endothermic animals is EWL, which places them at risk of becoming rapidly dehydrated. The common ringtail possums in this study used facultative hyperthermia to delay EWL, thereby conserving water at high T_a during a heatwave. By allowing T_b to increase with T_a to ~3°C above the baseline level, they maintained a positive thermal gradient with the environment (i.e. $T_b > T_a$), facilitating passive heat loss via convection. Such a strategy is likely to prove vital for surviving increasingly frequent extreme weather events. Using equations in Tieleman and Williams (1999), at a T_a of 39°C, possums can save 9.6 ml of water every hour using facultative hyperthermia.

Metabolic rate, and thereby metabolic heat production, remained low and stable during the heatwave experiment. This indicates that it was reasonably energetically inexpensive for possums to warm themselves at low T_a , and to cool at high T_a , across this T_a range. Because endogenous metabolic heat production and thermal conductance (C_{wet} and C_{dry}) remained quite stable as T_a increased, the accumulating heat load from the air contributed to

Table 1. Results of generalised additive mixed models describing the relationship between predictor variable T_a and common ringtail possum response variables measured (T_b , \dot{V}_{O_2} , \dot{V}_{CO_2} , EWL) or calculated (C_{wet} , C_{dry} , RWE, ECC) during a simulated heatwave

Response variable	Smoothed terms				Linear terms				
	edf	<i>F</i>	<i>P</i>	<i>R</i> ² (adj.)	Factor	Coefficient	s.e.	<i>t</i>	<i>P</i>
T_b	2.428	127.80	<0.001	0.718	Intercept (T_a)	40.736	2.505	16.259	<0.001
					Sex	0.016	0.338	0.046	0.963
					Mass	-0.004	0.003	-1.362	0.183
					Hair	-0.721	2.328	-0.310	0.759
					Intercept (T_a)	0.1934	1.690	0.115	0.909
\dot{V}_{O_2}	2.105	3.25	0.0412	0.237	Sex	-0.292	0.218	-1.338	0.188
					Mass	0.0005	0.002	0.245	0.808
					Hair	0.7021	1.411	0.498	0.621
					Intercept (T_a)	-0.124	0.593	-0.210	0.835
					Sex	-0.142	0.077	-1.857	0.070
\dot{V}_{CO_2}	2.279	2.74	0.0577	0.394	Mass	0.0004	0.0008	0.568	0.573
					Hair	0.816	0.494	1.651	0.106
					Intercept (T_a)	-12.143	22.257	-0.546	0.591
					Sex	1.429	2.991	0.478	0.638
					Mass	0.018	0.029	0.644	0.526
C_{wet}	2.953	12.83	<0.001	0.595	Hair	26.217	18.404	1.425	0.168
					Intercept (T_a)	-22.395	14.058	-1.593	0.124
					Sex	1.814	1.902	0.954	0.349
					Mass	0.028	0.018	1.534	0.136
					Hair	16.963	11.753	1.443	0.161
C_{dry}	1	2.995	0.096	0.137	Intercept (T_a)	6.916	5.540	1.248	0.218
					Sex	-0.835	0.719	-1.161	0.251
					Mass	-0.006	0.007	-0.775	0.442
					Hair	-0.176	5.035	-0.035	0.972
					Intercept (T_a)	-0.423	0.413	-1.025	0.311
EWL	3.043	25.58	<0.001	0.510	Sex	-0.101	0.053	-1.892	0.065
					Mass	0.001	0.001	1.589	0.120
					Hair	0.191	0.343	0.556	0.581
					Intercept (T_a)	2.348	1.280	1.834	0.074
					Sex	0.248	0.166	1.495	0.143
RWE	1.974	50.02	<0.001	0.660	Mass	-0.002	0.002	-1.418	0.164
					Hair	-0.713	1.064	-0.670	0.506
					Intercept (T_a)	-0.423	0.413	-1.025	0.311
					Sex	-0.101	0.053	-1.892	0.065
					Mass	0.001	0.001	1.589	0.120
ECC	2.976	26.44	<0.001	0.564	Hair	0.191	0.343	0.556	0.581
					Intercept (T_a)	2.348	1.280	1.834	0.074
					Sex	0.248	0.166	1.495	0.143
					Mass	-0.002	0.002	-1.418	0.164
					Hair	-0.713	1.064	-0.670	0.506

T_a , ambient temperature; T_b , body temperature; \dot{V}_{O_2} , oxygen consumption; \dot{V}_{CO_2} , CO₂ production; EWL, evaporative water loss; C_{wet} , wet thermal conductance; C_{dry} , dry thermal conductance; RWE, relative water economy; ECC, evaporative cooling capacity. Bold values indicate a significant relationship ($P < 0.05$). Smoothed terms show the effect of T_a on each response variable (edf, estimated degrees of freedom), accounting for non-linear relationships. Linear terms show whether fixed factors sex, body mass and hair area density affected the response variable.

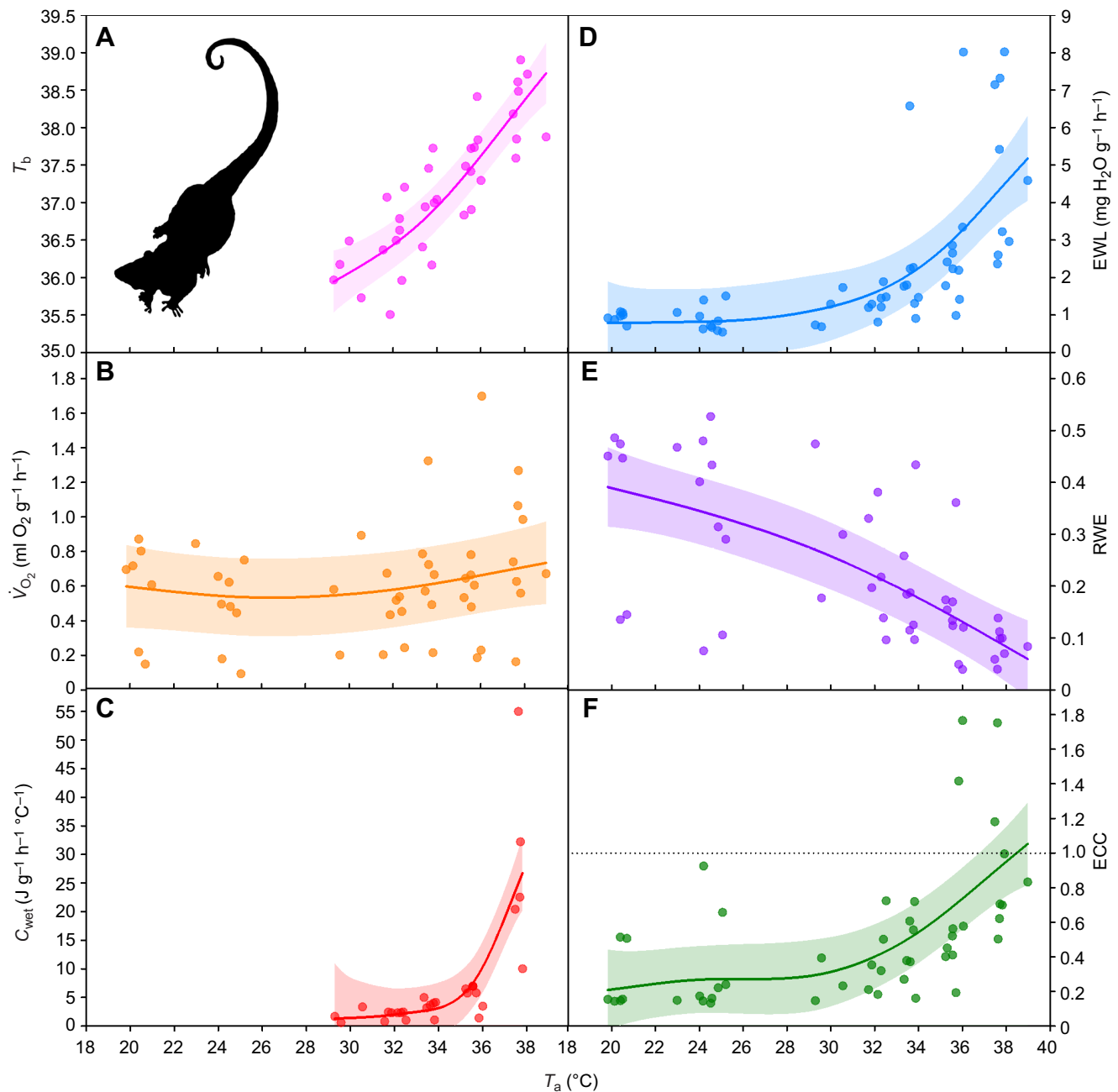


Fig. 1. Physiological responses of 10 common ringtail possums to a simulated heatwave. Variables are body temperature (T_b ; A), metabolic rate (\dot{V}_{O_2} ; B), wet thermal conductance (C_{wet} ; C), evaporative water loss (EWL; D), relative water economy (RWE; E) and evaporative cooling capacity (ECC; F) as a function of ambient temperature (T_a). Filled circles are individual means, curves represent significant relationships predicted by generalised additive mixed models and the shaded areas are bounded within 95% confidence intervals. The horizontal dotted line where $ECC=1$ indicates the point where metabolic heat production equals evaporative heat loss (i.e. when $ECC<1$, heat production exceeds heat loss; when $ECC>1$, heat loss exceeds heat production).

the observed increase in T_b . When T_a was about 35–36°C, possums began actively cooling themselves at a much higher rate, reflected in the rapid increase in EWL and C_{wet} (Fig. 1). The capacity for EWL is possibly limited because heat loss exceeded heat production (i.e. $ECC<1$) until $T_a=38.4^\circ\text{C}$, and the scope for facultative hyperthermia is probably limited by the ability of a small possum to replenish sufficient water to maintain high rates of EWL (Krockenberger et al., 2012). However, independent of water replenishment, the water-saving effects of facultative hyperthermia have been shown for 33 bird species over a 36-fold body mass range (Gerson et al., 2019).

Possums lost more water than they produced over the entire measured T_a range (i.e. $RWE<1$) and the rate of loss was positively correlated with T_a (Fig. 1). This shows that ringtail possums are perhaps particularly susceptible to water stress and the ability to replenish lost body water will be the primary factor limiting their survival during heatwaves. Theoretically, if animals are able to remain hydrated, they can persist for extended periods at high T_a without injury (McKechnie and Wolf, 2019; Mitchell et al., 2018). However, possums must contend with dietary plant secondary metabolites – naturally occurring toxins that limit the type and amount of food folivores can consume – and the ability of animals to

process these compounds decreases with increasing T_a (Beale et al., 2018; Moore et al., 2015). Given that 55% of a ringtail possum's water intake comes from leaves (Munks, 1991), these toxins are likely to constrain rehydration and survival with projected global warming in general, and during heatwaves in particular (Mella et al., 2019; Moore et al., 2015). Possums can avoid consuming leaves at high T_a , but reduced foraging will lead to decreased body condition and dehydration (Conradie et al., 2019; Mella et al., 2019), and may impact the growth of young (Cunningham et al., 2013). Provision of free water to offset reduced intake of leaf water has been trialled for the arboreal and folivorous koala *Phascolarctos cinereus*, which increased use of supplemented water at high T_a (Mella et al., 2019), but such strategies are still impractical beyond a local scale. It has been suggested that water loss would become physiologically limiting when green ringtail possums *Pseudochirops archeri* are exposed to $T_a > 30^\circ\text{C}$ for > 5 h per day during heatwaves of 4–6 days, the effect of which would be exacerbated with climate change (Krockenberger et al., 2012; Meade et al., 2018). Even with the water savings of 9.6 ml h^{-1} achieved by facultative hyperthermia, *P. peregrinus* could lose 11% of its mass in body water, a point of significant physiological impairment (McKechnie and Wolf, 2010; Patton and Thibodeau, 2013), as quickly as 17.5 h at 39°C . This point would be reached after 14.1 h at 43.3°C , the average daily maximum T_a of a 5 day heatwave that occurred at the field site in January 2019 (Australian Bureau of Meteorology). T_a stayed above 35°C , *P. peregrinus*' threshold for rapid evaporative cooling, for 10.2 h every day during this heatwave.

The slow change in metabolic and hygric variables when T_b warms towards T_a indicates that facultative hyperthermia is an adaptive response that common ringtail possums use to contend with high T_a . This response is potentially common among mammals (Withers, 1992) and has been documented for a number of marsupials, including other possums (Robinson and Morrison, 1957), and birds (Gerson et al., 2019). While this may indicate a level of resilience to heatwaves, the threshold T_a is most likely species specific (McKechnie and Wolf, 2019) and may vary with body size and condition among individuals (Gerson et al., 2019). Its success will also rely on the ability of animals to replace lost water and behaviourally thermoregulate by, for example, seeking shade or cooler microclimates within a habitat. Ultimately, facultative hyperthermia is an unstable physiological state, which relies on T_a staying below a critical threshold. It is clear that when the threshold is surpassed, animals must respond rapidly by employing evaporative cooling to avoid death, but it is this very process which imperils them further and accelerates dehydration.

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Competing interests

The author declares no competing or financial interests.

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Data availability

Data are available from figshare (Turner, 2020): <https://doi.org/10.6084/m9.figshare.11900295.v1>.

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