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The limit to the distribution of a rainforest marsupial folivore is consistent with the thermal intolerance hypothesis

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Abstract Models of impacts of climate change on species are generally based on correlations between current distributions and climatic variables, rather than a detailed understanding of the mechanisms that actually limit distribution. Many of the vertebrates endemic to rainforests of north-eastern Australia are restricted to upland forests and considered to be threatened by climate change. However, for most of these species, the factors controlling their distributions are unknown. We examined the role of thermal intolerance as a possible mechanism limiting the distribution of *Pseudochirops archeri* (green ringtail possum), a specialist arboreal folivore restricted to rainforests above an altitude of 300 m in Australia's Wet Tropics. We measured short-term metabolic responses to a range of ambient temperatures, and found that *P. archeri* stores heat when ambient temperatures exceed 30°C, reducing water requirements for evaporative cooling. Due to the rate at which body temperature increases with ambient temperatures >30°C, this strategy is not effective over periods longer than 5 h. We hypothesise that the distribution of *P. archeri* is limited by interactions between (i) the duration and severity of extreme ambient temperatures (over 30°C), (ii) the scarcity of free water in the rainforest canopy in the dry season, and (iii) constraints on water intake from foliage imposed by plant secondary metabolites and fibre. We predict that dehydration becomes limiting for *P. archeri* where extreme ambient temperatures (>30°C) persist for more than 5 h per day over 4–6 days or more. Consistent with our hypothesis, the abundance of *P. archeri* in the field is correlated with the occurrence of extreme temperatures, declining markedly at sites where the average maximum temperature of the warmest week of the year is above 30°C. Assuming the mechanism of limitation is based on extreme temperatures, we expect impacts of climate change on *P. archeri* to occur in discrete, rapid events rather than as a slow contraction in range.

Keywords Climate change · Limits to distribution · Metabolic rate · Plant secondary metabolites · Temperature extremes · Water availability

Introduction

Worldwide, animals and plants that are restricted to cool upland habitats are considered to be particularly vulnerable to the effects of climate change (Thomas et al. 2004; Pounds et al. 2006). In northeastern Australia, a 1°C increase in average temperature is predicted to reduce the extent of the environments presently supporting high-elevation rainforests by 40–50% (Hilbert et al. 2001), while a 3.5°C increase is predicted to eliminate the core climatic habitat of 30 of 65 vertebrates endemic to the region, and reduce the core climatic habitat of the remaining species by nearly 90% (Williams et al. 2003). However, most of these predictions are based on correlations between current distributions and

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climatic parameters, rather than on a detailed understanding of the ecological factors and physiological processes that actually limit distributions (Berteaux et al. 2006). Predictions based entirely on extrapolating from correlative relationships that are reliant on statistically capturing implicit ecological relationships to describe current distributions also rely on those relationships being relevant in the new environment. This is potentially prone to inaccuracy, particularly under changing and non-steady state conditions such as those expected under many climate change scenarios (Kearney et al. 2010). Mechanistic or process-driven approaches can be used to provide further confidence in predictions, particularly when the results are congruent with the correlative models (Kearney et al. 2010).

The vertebrates endemic to the rainforests of north-eastern Australia include four species of ringtail possum (Pseudocheiridae). All are restricted to upland forests, have small geographical ranges, and exhibit patterns of distribution that reflect alternate contraction and expansion of rainforest habitat through the Pleistocene (Winter 1997). A plausible explanation for the upland distribution of these possums is that they are adapted to a cool climate (Nix 1991; Winter 1997). Several alternative hypotheses have recently been dismissed, including altitudinal variation in the floristic composition of forests, foliar chemistry and predation (Kanowski et al. 2003; Kanowski 2004). Briefly, many of the plant taxa that are known to be important in the diet of the ringtail possums occur in lowland forests; none of the known or likely predators of the ringtail possums are restricted to lowland forests; and foliar chemistry (defined in terms of nutrients such as nitrogen or tannins) does not explain altitudinal variation in possum abundance.

In this study, we examine the hypothesis that the upland distribution of rainforest ringtail possums reflects their intolerance of hot temperatures experienced in the lowlands. Specifically, we examine (i) the metabolic responses of individuals of *Pseudocheirus archeri* Collett (green ringtail possum) to a range of temperatures, particularly to short-term periods of high temperature, and (ii) the relationship between the abundance of *P. archeri* and the occurrence of high temperatures throughout its range. *P. archeri* is a specialist arboreal folivore restricted to rainforests above 300 m elevation in the Australian Wet Tropics (Winter 1997; Jones et al. 2006). Unlike other Australian rainforest ringtail possums, *P. archeri* does not den in hollow trees or dreys (nests), but spends daylight hours curled up on a branch in the canopy (Winter et al. 2008), and hence is exposed to temperatures prevailing in the forest canopy. Having determined the metabolic responses of green ringtail possums to variation in temperature, and the relationship between their distribution and the occurrence of extreme temperature, we proceed to develop a hypothesis for the mechanism of intolerance of temperature extremes, linking limits on intake imposed by plant secondary metabolites with demands for evaporative cooling during extreme temperature events.

Materials and methods

Metabolic responses to temperature

Seven individuals of *P. archeri* were collected during the dry season (July–October) from two sites in complex notophyll vine forest at 740–780 m elevation on the Atherton Tableland, North Queensland, Australia (17°15′S, 145°30′E). Possums were located at night (19:00–24:00) using spotlights from the edge of the forest, and captured using a gas-powered tranquiliser dart-gun (Montech Black Wolf; Tranquil Arms Company, VIC, Australia) and 0.5 ml darts (Minidarts; Tranquil Arms Company) containing 30 mg Zoletil (zolazepam and tiletamine 50:50; Virbac Pty Ltd). Tranquillised possums were weighed and transported 5–10 km to the laboratory, where they were held overnight in a small cage (500 × 400 × 400 mm) before measuring metabolism as oxygen consumption. In our previous work with this species, we have found that possums are fully alert and active around 2 h after being tranquilised in this way, and, although there have been no pharmacokinetic studies of these drugs in a herbivore or any marsupial, plasma half-lives for the clearance of these drugs of between 1 and 5 h have been reported across a range of mammals (cat, dog, monkey, rat, Lin et al. 1993; polar bear, Semple et al. 2000). Consequently, at least 2 and up to 10 plasma half-lives elapsed between capture and energetic measurements, giving us confidence that there was little if any effect of the tranquilisation on the following measurements. To allow for the possibility that there was some residual effect of tranquiliser on the results, time since tranquilisation was included as a factor in the statistical analysis. The possums were released after dark at the point of capture and no more than 24 h after capture.

Oxygen consumption was measured by positive pressure, flow-through respirometry starting at 07:00 the morning after capture and finishing by 17:00 that day. This is the normal resting phase for these possums. Each possum was held in a metabolism chamber (300 × 300 × 300 mm) containing a branch for a perch over wire mesh and a layer of vegetable oil to prevent evaporation from faeces or urine produced during the measurement. The metabolism chamber was placed inside a temperature-controlled cabinet. The possum's body temperature was measured using a fine (32 gauge) thermocouple (Type T) inserted approximately 50 mm into the rectum and held in place by taping to the tail. Chamber temperature was measured using another (8 gauge) thermocouple protruding approximately 50 mm into the chamber. These thermocouples exited the metabolism chamber through a gas-tight cable gland to a thermocouple reader (TC-1000; Sable Systems International, NV, USA). Possums were allowed to adjust to the chamber for 1 h, then exposed for 90 min to each of six temperatures sequentially (5, 12, 18, 24, 30 and 35°C). After allowing 60 min for the metabolism to reach a steady state at each temperature, measurements were taken for the final 30 min of exposure to determine the response of possums to that temperature. At the highest temperature (35°C), possums were monitored constantly and removed from the chamber when their body temperature reached 39°C or when they became agitated, to avoid excessive heat stress. In this case, measurements were averaged from the final 30 min of exposure. Measurements never included substantial activity, since possums were generally inactive and all animals that became agitated at the highest temperature were immediately removed from the chamber.

Air was pumped (3–4 l min^{-1}) from outside the laboratory through a desiccant (Drierite, anhydrous Na_2SO_4, Hammond Drierite Co., OH, USA), then a mass-flow controller/meter (Sidetrak 840L-2-0V1-SV1-E-V1-S1, Sierra Instruments Inc., CA, USA, with a Sable Systems mass flow controller v. 1.0), a copper coil within the cabinet to equilibrate its temperature with that of the cabinet, and then into the chamber. Excurrent air from the chamber was subsampled (100 ml min^{-1}) via a manifold and passed through a humidity sensor (HMP-45A, Viasala Oy, Finland), a desiccant scrubber (Drierite), then a carbon dioxide scrubber (Ascarite; sodium hydroxide coated silica, Sigma Chemicals USA, followed by desiccant, Drierite, to redry the air) and the oxygen analyser (Sable Systems FC-2 Oxzilla). The oxygen analyser was set up for differential gas analysis, continually comparing the excurrent air with incurrent air subsampled after the dessicant but before the flow meter. At the start of each measurement, and periodically (at least every 60 min), a baseline was recorded by manually switching from the excurrent air to a subsample of the incurrent air. Output from all sensors were acquired every 5 s onto a personal computer using a 12-bit analog to digital converter (Lab-NB; National Instruments Corp., TX, USA) and Labhelper software (Warthog Systems; http://www.warthog.ucr.edu). Oxygen consumption was estimated according to Withers (1977) using LabAnalyst software (Warthog Systems) and converted to energy equivalents using the value provided by Gessaman and Nagy (1988) for the metabolism of lipid (19.8 kJ.l O_2^{-1}). The oxygen analyser was standardised with dry, carbon dioxide free air before commencing each day's measurements. The respirometry system was calibrated using the iron-burn method of Young et al. (1984).

Respiration rate and tidal volume were measured by whole-body plethysmography according to the method described by Dawson et al. (2000b). Pressure fluctuations caused by warming and wetting inspired air were measured using a pressure transducer (Sable Systems PT-100) and acquired at 20–60 Hz using the system described above. Volume change equivalents of the pressure fluctuations were calibrated by recording pressure fluctuations associated with injecting a known volume of air (25 ml) into the chamber after each recording of ventilation. The injection procedure was repeated ten times at rates such that deflection kinetics were similar to those recorded from the possums at that temperature, and the mean deflection of those repeats was used in calculations. Ventilatory frequency was determined directly from the average period of pressure fluctuations recorded, and tidal volume (V_T) was estimated using the method of Malan (1973; Eq. 6), assuming that lung temperature was equal to body temperature.

To determine the influence of temperature on metabolic rate, body temperature, evaporative water loss, respiratory rate, and tidal volume and minute volume, we fitted a nonlinear mixed effects model with temperature, temperature^2, $\log_e$(mass), time since tranquilisation, time in chamber and time of day fitted as fixed effects, and animal ID treated as a random factor. Temperature^2 was included based on theoretical expectations that response to varying temperature would not be linear across the measurement range (Withers 1992); confirmed via the existence of a parabolic scatter of residuals against temperature in all initial diagnostic plots. To account for potential temporal nonindependence, we implemented an autoregressive correlation structure (AR1) at the lowest level (i.e., to allow for the possibility that there were differences in correlation structure between individuals) using a dummy time variable in each model (Zurr et al. 2009). The order in which the explanatory variables were entered was chosen to reflect our expectation of their biological importance. There are strong theoretical reasons to suggest that temperature, temperature^2 (because the effect of temperature is curvilinear) and body mass will be influential in determining all response variables (Withers 1992). Thus, these factors were fitted first and in this order. The three remaining explanatory variables were fitted to the model in the following order: time since tranquilisation, time spent in chamber, and time of day. For each response variable, we began by fitting the full model (including all main effects), and examined the significance of all terms in the overall fit. When main effects were not significant ($P > 0.05$), we removed the term with least explanatory power (the least significant in its contribution to describing the data) and refitted the model. We repeated this process until all remaining terms were significant and no further terms could be removed (Zurr et al. 2009). We deemed the final result of the sequential term deletion process to represent the minimum adequate model required to describe the data. Model fitting was performed in the NMLE package in R (R Development Core Team 2010). In the case of respiration rate, residuals from the final linear mixed model (dependent on temperature and temperature^2) were not normally distributed, and we were unable to transform the data to find an appropriate model. Consequently, we have analysed the data using a repeated measures analysis of variance with temperature as a repeated measure, followed by post-hoc paired *t* tests with Bonferroni corrections. This approach assumes that time itself was not a significant factor, which we feel is reasonable given that it was not significant (Table 1) for any other variable considered.

Abundance of possums in relation to temperature

The abundance of *P. archeri* was surveyed by spotlight at 50 sites in rainforests on the Atherton Tablelands and adjacent lowlands, North Queensland (Kanowski et al. 2001). For each site, an index of the occurrence of extreme temperatures, the average temperature of the hottest week of the year, was estimated from an interpolation of climatic data using ANUCLIM software (see the "Acknowledgments").

Results

Metabolic responses to temperature

The seven individuals of *P. archeri* measured in this experiment ranged from 1.04 to 1.55 kg in mass, with a mean mass of 1.17 ± 0.07 (SE) kg. Resting metabolic rate was strongly related to ambient temperature (Table 1; Fig. 1a). The minimum of the modelled rate of metabolism was 231 kJ d^{-1} at an ambient temperature of 27.1°C and the average mass of 1.17 kg. Below this thermoneutral zone, the metabolic rate rose (Fig. 1a), indicating thermoregulatory heat production. Body temperature was also dependent on ambient temperature (Table 1; Fig. 1b) and increased significantly from a modelled minimum of 35.8°C at $T_a = 16.6$°C to 38°C at $T_a = 35$°C (Fig. 1b). Body temperature rose monotonically as a function of the time (up to 145 min) the possum was exposed to temperatures greater than 30°C (Fig. 2; Body temperature

Table 1 Significant factors in final nonlinear mixed effects model analyses of the effect of temperature on the metabolic physiology of green ringtail possums, *Pseudochirops archeri*

Factor	$F_{1,33}$	P	Estimate	SE	$\hat{d}$[a]	ϕ[b]
Metabolic rate (kJ/day)						
Intercept	276.38	<0.0001	486.3	24.2	0.0213	0.899
Temperature^2	23.01	<0.0001	0.3461	0.0421		
Temperature	114.36	<0.0001	−18.79	1.76		
Oxygen consumption (ml/min)						
Intercept	276.38	<0.0001	17.06	0.85	0.000395	0.899
Temperature^2	23.01	<0.0001	0.01214	0.00148		
Temperature	114.36	<0.0001	−0.6589	0.0616		
Body temperature (°C)						
Intercept	44421.39	<0.0001	37.50	0.28	0.00004	0.783
Temperature^2	53.47	<0.0001	0.00623	0.00064		
Temperature	60.54	<0.0001	−0.2067	0.0266		
Evaporative water loss (mg/min)						
Intercept	199.94	0.00011	15.07	2.29	2.798	0.665
Temperature^2	132.39	<0.0001	0.03122	0.0051		
Temperature	7.98	0.0079	−0.5958	0.2109		
Tidal volume (ml)						
Intercept	127.56[c]	<0.0001	9.396	0.732	0.000255	0.755
Temperature^2	40.04[c]	<0.0001	−0.004715	0.000745		

Results are from model fitting performed for seven individual possums measured at six temperatures using an autoregressive correlation structure (CorAR1) with individual treated as a random factor

[a] Estimate of standard deviation of the random effect intercept

[b] Correlation between sequential measures in an individual

[c] DF = 1,34

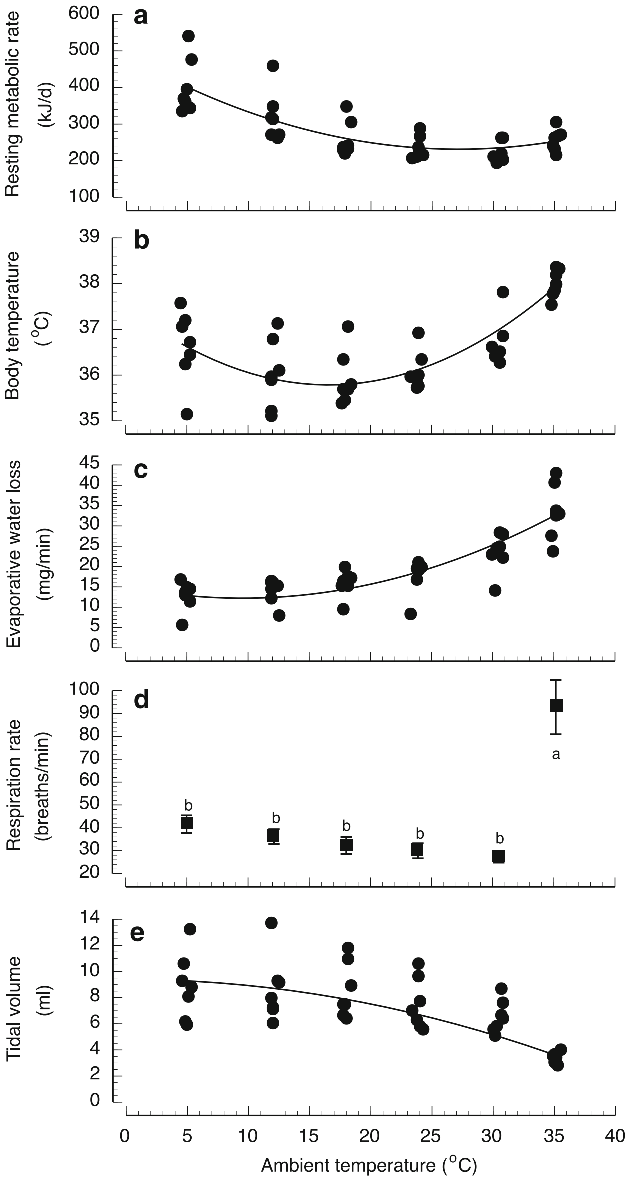

Fig. 1 The effect of ambient temperature on the metabolic physiology of the green ringtail possum, *Pseudochirops archeri*. The curves indicate the final mixed effects models fitted to the data. **a** Resting metabolic rate (kJ/day), **b** body temperature (°C), **c** evaporative water loss (mg/min), **d** respiration rate (breaths/min) (means ± SE, $n = 7$; *letters* indicate statistically similar means), **e** respiratory tidal volume (ml)

[°C] = 36.5 + 0.01439 × Time [mins]; $F_{1,13} = 11657$, $P < 0.001$, $r^2 = 0.999$). It should be noted that responses were not measured beyond 145 min, and the relationship could change after that time. The sample size represented in this relationship also declined after 85 min of exposure as possums either reached body temperatures of 39°C (which was set as a conservative limit for body temperature due to animal welfare considerations) or became agitated and dislodged the thermocouple, necessitating the termination of the experiment.

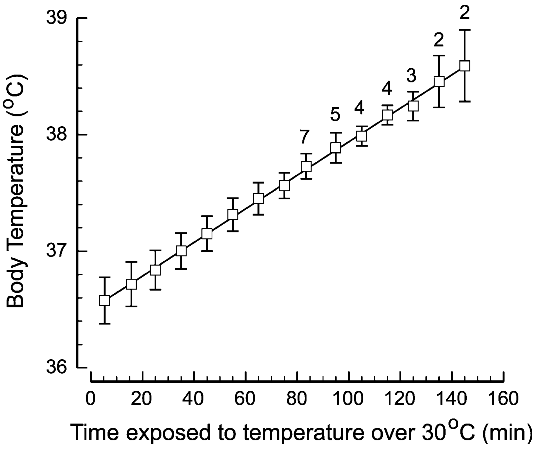

Fig. 2 Body temperatures of green ringtail possums, *Pseudochirops archeri*, at 10 min intervals from 5 to 145 min after they were exposed to ambient temperatures that were greater than 30°C and increased over time to 35°C (means ± SE, $n = 7$ for times from 5 to 84 min after the temperature of 30°C was reached; thereafter sample size is marked above the data point). Prior to the period represented here, they had undergone an acclimatisation period of 90 min at 30°C during the measurement of resting metabolism at that temperature. The linear least-squares line of best fit to those means is displayed (body temperature [°C] = 36.5 + 0.01439 × time [mins]; $F_{1,13} = 11657$, $P < 0.001$, $r^2 = 0.999$)

Evaporative water loss accelerated with increasing ambient temperature above 10°C (Table 1; Fig. 1c). Respiration rate tended to decline slightly as ambient temperature rose, but then rose sharply at higher temperatures (Table 1; Fig. 1d), and tidal volume fell slowly at first but increasingly rapidly as the ambient temperature rose (Table 1; Fig. 1e); at 35°C was only 37% of the tidal volume at 5°C.

Abundance of possums in relation to temperature

The abundance of *P. archeri* was negatively correlated with the mean maximum temperature of the hottest week (Spearman rank correlation, $r_s = -0.45$, $P = 0.001$, Fig. 3). The relationship was not linear. Possums were on average an order of magnitude more abundant at sites where the mean maximum temperature of the warmest week was less than 30°C (0.38 ± 0.05 (SE) individuals ha^{-1}) than at sites which experienced higher temperatures (0.03 ± 0.02 (SE) individuals ha^{-1}) (t test on $\ln(x + 1)$ transformed data, P (determined from randomisation) = 0.001).

Discussion

Metabolic responses of *P. archeri* to temperature

At low ambient temperatures, *P. archeri* displayed a predictable mammalian pattern of metabolism (Fig. 1a). The

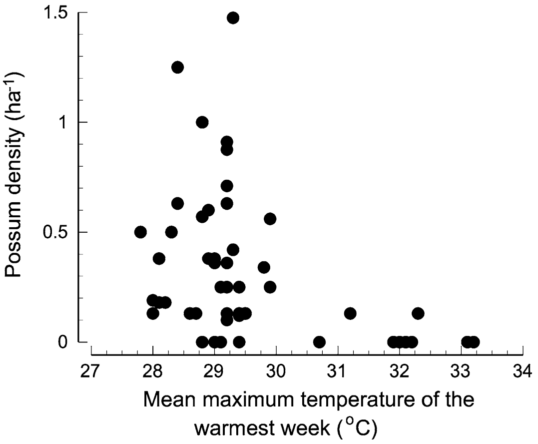

Fig. 3 Abundance of the green ringtail possum *Pseudochirops archeri* in relation to the mean maximum temperature of the warmest week, an index of extreme temperatures, at 50 sites in rainforest on the Atherton Tablelands and adjacent lowlands

minimum resting metabolic rate in the thermoneutral zone at 27°C was 100–110% of the level expected for a marsupial of the same mass (Dawson and Hulbert 1970; Withers et al. 2000, 2006) and rose rapidly as temperatures dropped below 20°C, indicative of possums increasing metabolism to maintain body temperature. This was accompanied by slow deep breathing at low temperatures, with ventilation rate and tidal volume changing relatively little across the range of lower temperatures. At temperatures above 30°C, the body temperature of the possums rose rapidly. Over the range of ambient temperatures examined, body temperature rose as a linear function of the time they were exposed to temperatures above 30°C (up to 145 min of exposure). This was initially evident as an increase in body temperature at the ambient temperature of 30°C (Fig. 1b). Critical thermal maxima vary substantially from species to species (Adolph 1947; Robinson and Morrison 1957; Maloney et al. 1999), but body temperature rises of around 4–6°C are sufficient to impair function in most birds and mammals (Cossins and Bowler 1987). A mid-range estimate of a lethal body temperature rise of 5°C above the minimum of 35.8°C for *P. archeri* (Fig. 1b) to 40.8°C matches the single record of lethal body temperature in the quokka (40.9°C; Robinson and Morrison 1957), and approaches the LD_{50} body temperature of dogs (Adolph 1947), giving us some confidence in adopting 40.8°C as a putative limit in *P. archeri*. Extrapolating from the rate of increase in body temperature (Fig. 2), possums would reach lethal body temperatures after 5 h of exposure to temperatures over 30°C unless they substantially increased their evaporative heat loss at those high temperatures.

The response of *P. archeri* to high temperature (a 2.1°C increase in body temperature with an increase in ambient temperatures from 18–35°C) is similar to the 2.3°C increase reported for the greater glider, *Petauroides volans* (Pseudocheiridae), over the same range of temperatures (Rubsamen et al. 1984). Withers (1992) suggests that heat storage is a relatively common characteristic of mammals, taken to its extreme in the strategy of “adaptive heterothermy” exhibited by some large-bodied arid-zone herbivores (Schmidt-Nielsen et al. 1957; Bartholomew and Rainy 1971; Mitchell et al. 2002; Ostrowski and Williams 2006). A number of other small marsupials show similar rises in body temperature when exposed to high ambient temperatures (mainly stabilising after about an hour; Robinson and Morrison (1957)). Adaptive heterothermy is most strongly exhibited in dehydrated individuals, and the extent of temperature change seen in *P. archeri* is similar to that found in much larger, dehydrated grey kangaroos (Dawson et al. 2007). The alternative is to maintain stable body temperature at high ambient temperatures by increasing evaporative cooling, through panting, increased ventilation frequency and reduced tidal volume, and, in some species, licking well-vascularised portions of the skin (Needham et al. 1974; Dawson et al. 2000a, b; Jessen 2001). Consequently, heterothermy serves to reduce both evaporative water loss in cooling and heat gain from the environment (Schmidt-Nielsen et al. 1957; Bartholomew and Rainy 1971; Withers 1992; Mitchell et al. 2002; Ostrowski and Williams 2006). At the highest ambient temperature measured in this study, individuals of *P. archeri* did increase evaporative water loss through increased ventilation frequency and reduced tidal volume, but this was insufficient (within the time of the measurements) to maintain a stable body temperature. Individuals were not observed licking their skin, but may have done so if their body temperatures continued to rise. In contrast to possums in this study, Robinson and Morrison (1957) described “possums” (*Trichosurus, Petaurus* and *Petauroides*) as the most active “coat-licking” marsupials, and Rubsamen et al. (1984) reported that *P. volans* intensively licked its limbs, but only when body temperature exceeded 38°C.

An important caveat to this study is that responses of captive and free-ranging animals can be different. Nychthemeral body temperature cycles of captive and free-ranging bandicoots vary in timing and intensity (Warnecke et al. 2007), and captive sugar gliders become less likely to enter torpor (Geiser et al. 2007). However, in these cases, captive animals had been captive for substantial periods and displayed less variability in body temperature than free-ranging animals, making it less likely that the body temperature variability observed in this study was exaggerated by captivity.

Heterothermy as a water conservation strategy in *P. archeri*

We hypothesize that heterothermy in *P. archeri* is a strategy for minimising water intake requirements during the hot, dry conditions experienced seasonally in the rainforest canopy, and enhances their ability to tolerate temperature extremes. This hypothesis is based on the following premises: (i) free water is seasonally scarce in the canopy of Australian tropical rainforests; (ii) rainforest ringtail possums are likely to have difficulty satisfying their water requirements from foliage alone, particularly at high temperatures, and (iii) the water savings provided by heterothermy are likely to be ecologically significant.

Seasonal scarcity of free water in the rainforest canopy

Australia's tropical rainforests are subject to marked seasonality of rainfall. For example, median monthly precipitation in the driest quarter (August–October) is around 17 mm at Kairi Research Station, the closest weather station to the study area providing daily data (11 km away at 697 m in elevation; Bureau of Meteorology 2011). For extended periods during the dry season, there may be no free water in the rainforest canopy, apart from dew and mist in forests within the cloud layer (McJannet et al. 2007). Extreme temperatures in Australia's wet tropical rainforests tend to occur during the late dry season before cloud cover increases, particularly during El Nino years with a late onset of the wet season (Tracey 1982). In 2002 at Kairi Research station, the hottest daily maximum temperatures of the year were recorded during October, which had no rainfall (Bureau of Meteorology 2011). Maximum temperatures also occur mid-afternoon, and rainforest ringtail possums do not feed during daylight (Winter et al. 2008), so they experience the hottest conditions during the time when water is least readily available to them.

Water intake requirements of rainforest ringtail possums

Observations of water flux in wild Pseudocheirids indicate that all rely on free water to meet part of their water requirements (Foley et al. 1990; Goudberg 1990; Munks and Green 1995). This is also likely to be true for *P. archeri*. An average-sized individual (1,170 g) *P. archeri* is predicted to require 172 ml d^{-1} of water (Nagy and Bradshaw 2000). To satisfy predicted water requirements from foliage alone, an average-sized individual of *P. archeri* would have to consume 65–82 g d^{-1} DW foliage (assuming a water content of 65–70% for preferred foliage: Goudberg 1990; Jones and Krockenberger, unpublished data; and 20 ml d^{-1} metabolic water production: Munks and Green 1995; Foley et al. 1990). Adjusted for mass this is up to 70% higher than intake rates for other pseudocheirids (Foley et al. 1990; Marsh et al. 2003b), and may not be feasible. However, the water intake requirements of *P. archeri* may be comparatively low, as it has a relatively long distal colon and may have more efficient water reabsorption than other pseudocheirids (Crowe and Hume 1997).

Constraints on foliage intake

Even if the water requirements of *P. archeri* can be met by foliage intake under "normal" conditions, it is unlikely that *P. archeri* could meet elevated water requirements such as those imposed by active thermoregulation or lactation (Green 1997) by increasing foliage intake. Rates of food intake by other small folivorous mammals are strongly constrained by the gut-filling effects of fibre (Cork and Foley 1991) and various physiological effects of plant secondary metabolites (PSMs) (Torregrossa and Dearing 2009), including toxicity (McLean et al. 2004), acidosis (Foley et al. 1995), depletion of energy and nutrients used to eliminate PSMs from the body (Foley 1992; Sorensen et al. 2005) and diuresis (Dearing et al. 2001, 2002). Although folivores have evolved sophisticated mechanisms for detoxifying and excreting PSMs, these are rate limited (Foley et al. 1995; Marsh et al. 2006a, b). There is considerable evidence that folivores regulate intake of PSMs below physiological thresholds (Lawler et al. 2000; Marsh et al. 2003a; Scrivener et al. 2004; Foley and Moore 2005; Moore et al. 2005; Iason and Villalba 2006). These constraints on intake can be sufficiently strong to override elevated demands for nutrients and energy (Torregrossa and Dearing 2009), including those from active thermoregulation (Stapley et al. 2000). Under this scenario, the most vulnerable individuals in the population are likely to be lactating females, whose food intake would be the highest of any individuals in the population (Gittleman and Thompson 1988; Krockenberger 2003; Krockenberger and Hume 2007; Kearney et al. 2010). Given that the limited evidence shows no reproductive seasonality in this species (Krockenberger, unpublished data), it is feasible that lactating females are exposed to hot, dry conditions. This potential vulnerability assumes that extra water intake by lactating females is exported in milk and is not available for evaporative cooling, as in common ringtail possums, *Pseudocheirus peregrinus*, where close to 90% of the increased water intake at peak lactation is exported in milk (Munks 1990; Munks and Green 1995). However, if lactating females increase foliage water intake for the energetic requirements of milk production by more than what they export in milk, then lactating female *P. archeri* would not be as vulnerable to impacts of heatwave events.

There is no reason to believe that rainforest ringtail possums can escape these constraints on intake. Rainforest ringtail possums tend to avoid foliage with high concentrations of condensed tannins (Goudberg 1990). Compared with sympatric ringtail possums, *P. archeri* selects foliage with a relatively high fibre content (Goudberg 1990), but this does not mean that overall levels of food intake by *P. archeri* are unconstrained by fibre (Cork 1994). Herbivores can attempt to circumvent constraints on fibre intake by feeding on young leaves, which have higher water content and lower fibre content than mature foliage (Coley and Barone 1996), but young leaves are often strongly defended by PSMs such as cyanogenic glycosides (Coley and Barone 1996; Miller et al. 2006). *P. archeri* does not eat young leaves of *Aleurites rockinghamensis* (Procter-Gray 1985; Jones et al. 2006), which typically have concentrations of cyanogenic glycosides an order of magnitude higher than mature foliage (Jones and Krockenberger, unpublished data), and it also avoids individual trees with high concentrations of cyanogenic glycosides within that species (Jones and Krockenberger, unpublished data).

Water conservation provided by heterothermy

We argue that water savings due to heterothermy could be significant to water conservation by *P. archeri*, as follows. If an average-sized possum (1.17 kg) stored metabolic heat equivalent to a 5°C rise in body temperature over a 5 h period at high ambient temperatures, 19.9 kJ of heat energy would be stored. This would otherwise have taken 8.3 g water to shed by evaporation (heat capacity of tissue = 3.4 J g^{-1}°C^{-1}, latent heat of vaporisation of water at 40°C is 2400 J/g; Withers 1992). A strategy of maintaining constant body temperature at an ambient temperature of 35°C would raise evaporative water loss across that 5 h by 85%, resulting in an extra loss of 8.3 g of water, or 1% of the body water content of *P. archeri* (average mass 1170 g and 73.5% body water content; Krockenberger, unpublished data) compared with the strategy adopted by *P. archeri* (32 mg/min evaporative water loss at 35°C, see Fig. 1c, while storing heat at 0.86°C/h, see Fig. 2—a total of 9.7 g water loss over 5 h). Most mammals are relatively intolerant of dehydration, with negative effects on physiological function occurring at just 4–6% dehydration (Thibodeau and Patton 2006), so the water conservation represented by heterothermy is likely to be significant over an extended period of extreme temperature, such as a heatwave lasting 4–6 days. Because another consequence of elevated body temperature is that metabolic heat production rises (Q_{10} effect), body temperature would rise progressively more quickly if evaporative water loss did not increase, although the rise in dry heat loss rate as the temperature gradient between the possum and its environment increased could partially compensate. At a Q_{10} of 2.3 (Dawson et al. 2007), a possum at a body temperature of 40.8°C would have to dissipate 44% more metabolic heat than at its resting metabolism. This would ultimately shorten the time taken to reach lethal limits unless evaporative heat loss increased to compensate. This 44% increase in metabolism due to a rise in body temperature substantially reduces or negates the water savings of the strategy if the individual is eventually forced to evaporate water to control body temperature (Dawson et al. 2007), so the greatest water savings occur if the ambient temperature declines before an upper body temperature limit is reached, and heat can be shed by dry means. Similarly, if our hypothesis of heat storage breaks down at body temperatures above 39°C and *P. archeri* defends a lower body temperature than 40.8°C, the limit due to either dehydration or intoxication that we propose still applies. However, under these circumstances the mechanism would operate at a shorter time threshold, because possums would be forced to substantially increase evaporative water loss to defend that temperature, particularly as metabolic heat production rises (Dawson et al. 2007).

In summary, the use of heat storage means that *P. archeri* would be tolerant of extreme temperatures that were around 30–35°C for up to 5 h a day without having to markedly increase water intake. If temperatures remained above 30°C for over 5 h a day, however, it is likely that possums would be forced to increase evaporative cooling. In situations where free water is unavailable, we argue that *P. archeri* is likely to have difficulty meeting elevated water requirements from foliage alone. In these circumstances, dehydration would become biologically limiting where extreme temperatures (>30°C) persisted for more than 5 h per day over 4–6 days or more. This is concordant with the observed pattern of distribution of *P. archeri* in relation to the occurrence of extreme temperatures (Fig. 3). Given that lactating females have the highest intake of any individuals in the population (Gittleman and Thompson 1988; Krockenberger 2003; Krockenberger and Hume 2007), we expect this effect to be most marked in lactating females, and may act to reduce reproductive success in marginal habitat, as suggested for greater gliders (Kearney et al. 2010).

Limitations on water intake may also account for the upland distribution of other rainforest ringtail possums in northeastern Australia, which show similar threshold responses to extreme temperatures (Kanowski 2004), and for the montane distribution of most rainforest ringtail possum species in New Guinea (Flannery 1994). The mechanism of limitation that we have proposed is also relevant to the eucalypt-feeding marsupial folivores and other folivores more generally, as long as intake is limited by fibre or PSMs. Indeed, Kearney et al.'s (2010) mechanistic model suggested that the northern and inland limits to the distribution of greater gliders were set by water requirements for cooling and/or lactation.

Predicted impacts of climate change

If our hypothesis is correct, then predictions of the impacts of climate change on the range of *P. archeri* and the other rainforest ringtail possums (Williams et al. 2003; Kanowski 2004) are likely to be underestimates, as the correlative models used in these predictions are based largely on climatic averages, rather than extremes. Extreme thermal stresses (heat and cold) along with average summer temperature provided the best descriptors of local extinctions of pikas, *Ochotona princeps*, in America's Great Basin over the last 60 years (Beever et al. 2010). The frequency and severity of extreme temperature events are expected to increase markedly under enhanced greenhouse conditions (IPCC 2007). In northeastern Australia (Cairns), the frequency of hot summer days (>35°C) is predicted to increase by 47–150% by 2030 (CSIRO and Bureau of Meteorology 2007). In addition, current predictions cannot consider synergistic effects of climate change, such as the lifting of the cloud base (Still et al. 1999), or increases in the production of PSMs by rainforest trees under enhanced carbon dioxide concentrations (Kanowski 2001). Because the proposed mechanism limiting the distribution of *P. archeri* involves interactions with plant defenses, elevated levels of PSMs may further constrain foliage intake and exacerbate the effects of high temperatures on water requirements.

Our hypothesis provides a testable mechanism linking strongly supported predictions of changes in the physical climate (IPCC 2007) to often poorly understood impacts on fauna (Berteaux et al. 2006; Parmesan 2006). We predict that range contractions of *P. archeri* are likely to follow long dry seasons with periods of extreme temperatures where daily temperatures exceed 30°C for five or more hours over a period of 4–6 consecutive days. Under these conditions, we expect populations of *P. archeri* at sites close to threshold maximum temperatures to decline or disappear. Lastly, because the mechanism is based on extremes rather than slow accumulation of warming, we can expect impacts of climate change on *P. archeri* to occur in discrete events rather than as a slow contraction in range. Given the increasing frequency of extremely hot years, we may soon be accorded the opportunity to test these predictions in the field.

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