

Geographical variation in the standard physiology of brushtail possums (*Trichosurus*): implications for conservation translocations

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Identifying spatial patterns in the variation of physiological traits that occur within and between species is a fundamental goal of comparative physiology. There has been a focus on identifying and explaining this variation at broad taxonomic scales, but more recently attention has shifted to examining patterns of intra-specific physiological variation. Here we examine geographic variation in the physiology of brushtail possums (*Trichosurus*), widely distributed Australian marsupials, and discuss how pertinent intra-specific variation may be to conservation physiology. We found significant geographical patterns in metabolism, body temperature, evaporative water loss and relative water economy. These patterns suggest that possums from warmer, drier habitats have more frugal energy and water use and increased capacity for heat loss at high ambient temperatures. Our results are consistent with environmental correlates for broad-scale macro-physiological studies, and most intra-generic and intra-specific studies of marsupials and other mammals. Most translocations of brushtail possums occur into Australia's arid zone, where the distribution and abundance of possums and other native mammals have declined since European settlement, leading to reintroduction programmes aiming to re-establish functional mammal communities. We suggest that the sub-species *T. vulpecula hypoleucus* from Western Australia would be the most physiologically appropriate for translocation to these arid habitats, having physiological traits most favourable for the extreme T_a , low and variable water availability and low productivity that characterize arid environments. Our findings demonstrate that geographically widespread populations can differ physiologically, and as a consequence some populations are more suitable for translocation to particular habitats than others. Consideration of these differences will likely improve the success and welfare outcomes of translocation, reintroduction and management programmes.

Key words: Basal metabolic rate, evaporative water loss, thermal conductance, wildlife management

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Introduction

A fundamental goal of comparative physiology is to determine how variation in physiological traits and processes differs spatially and/or temporally between and within species (Feder and Block, 1991; Bozinovic *et al.*, 2011). Macro-physiological studies have commonly focused on broad inter-specific comparisons to achieve a wide geographical and taxonomic perspective for environmental or life history influences on a particular variable (Chown *et al.*, 2004; Bozinovic and Naya, 2015). However, this approach generally ignores potential variation within a particular taxonomic group, assuming that the trait(s) in question are fixed for each species being studied (Bozinovic *et al.*, 2009). Variation in physiological traits between spatially separated populations of a single or closely related species has been relatively understudied (Bozinovic and Naya, 2015; McClelland *et al.*, 2016), but recognition of lower-taxonomic-level physiological variation is gaining prominence along with attempts to identify the underlying mechanisms and functional significance when such variability is found (Bozinovic *et al.*, 2009).

Studies of low-level taxonomic variation over a wide spatial scale not only have application to theoretical considerations of physiological function, evolutionary processes, ecological interactions and species assemblages (Chown *et al.*, 2004; Bozinovic *et al.*, 2009; Chown and Gaston, 2016), but they can also address more applied questions concerning impacts of human-induced habitat modification on biodiversity, and of global climate change (Bozinovic *et al.*, 2011). These two key environmental perturbations of the Anthropocene are gaining ever more social, economic and political attention (Feder and Block, 1991; Steffen *et al.*, 2007). We consider here whether there is sufficient spatial variation in the physiology of a widely distributed mammal to warrant consideration in conservation translocation programmes. More broadly, we consider how studies of comparative physiology can enhance the success of wildlife management and ecosystem conservation in a changing environment.

Translocation of species is a widely used conservation tool, but the success rate of translocations is very low worldwide, with only one third to one half of translocation programmes deemed successful. Translocation outcomes in Australia are particularly poor (Griffith *et al.*, 1989; Wolf *et al.*, 1996; Fischer and Lindenmayer, 2000). The appropriateness of the new habitat and characteristics of a translocated species affect the success of these programmes (Sarrazin and Barbault, 1996; Armstrong and Seddon, 2007), and we posit that characterizing the environmental physiology of the animals to be translocated will further improve their chances for survival. Wildlife managers commonly consider factors such as predation, competition, genetics, habitat, reproductive biology, behaviour and disease as influencing the success of conservation measures (Griffith *et al.*, 1989; Sarrazin and Barbault, 1996; Snyder *et al.*,

1996; Fischer and Lindenmayer, 2000), but basic environmental physiology is generally overlooked (Tarsisz *et al.*, 2014). This is despite the IUCN Guidelines for conservation translocations clearly indicating that the biotic and abiotic habitat needs and basic biology of a species should be known prior to planning a translocation, and specifically recognizing that an assessment of physiological suitability should be made (IUCN/SSC 2013). Physiological assessment can predict a mammal's likely capacity for survival and reproduction in a particular environment, and therefore evaluation of pertinent physiological variables should improve the success of conservation translocations beyond that achieved with current ecological, behavioural, health and genetic considerations (Tarsisz *et al.*, 2014).

Environmental conditions directly affect an animal's energy, water and thermal requirements and whether it can successfully survive and reproduce (Wikelski and Cooke, 2006). It is therefore not surprising that there are significant correlations between metabolic, thermal and hygric physiological traits and environmental factors such as temperature and rainfall at a broad inter-specific level for endotherms (e.g. Tieleman and Williams, 2000; Schleucher and Withers, 2001; Lovegrove, 2003; Rezende *et al.*, 2004; Withers *et al.*, 2006; White *et al.*, 2007; van Sant *et al.*, 2012), suggesting that these physiological characteristics are under environmental selection. However, few studies have examined such correlations at lower taxonomic levels, and even fewer describe intra-specific physiological variation, although there is some evidence that geographic variation in physiological traits is consistent with accommodating environmental variables (e.g. Tracy and Walsberg, 2000; Mueller and Diamond, 2001; Tieleman and Williams, 2002; Williams *et al.*, 2004; Careau *et al.*, 2007; Bozinovic *et al.*, 2009; Cooper and Withers, 2010). These studies suggest that it is inappropriate to consider a physiological variable as a fixed species-wide trait, and that intra-specific variation may play an important role in determining the potential survival of individuals translocated to a new geographical location. Translocated individuals must have physiological traits that are appropriate for survival and subsequent reproduction in their new environment, or they must have the phenotypic flexibility to quickly acclimatize. Environmental conditions such as drought have been implicated in the decline of populations of re-introduced species (e.g. Winnard and Coulson, 2008; Facka *et al.*, 2010), thus identifying intra-specific differences among individuals from different geographical locations most likely to physiologically cope with environmental conditions will aid in planning for more successful translocations.

The common brushtail possum (*Trichosurus vulpecula*) is the mostly widely distributed Australian marsupial, with a historical distribution throughout Australia (How, 1983; How and Hillcox, 2000). Despite it being one of the most successful marsupial urban adaptors, the distribution and abundance of the brushtail possum has declined post-European settlement.

Declines are particularly prominent in the arid zone where the brushtail possum has disappeared from much of its former range (Kerle *et al.*, 1992; How and Hillcox, 2000). Increasing environmental aridity, compounded by other anthropogenic impacts such as hunting, predation by introduced mammals and land clearing have been implicated in its decline (Kerle *et al.*, 1992). As a consequence of this decline and its wide geographical distribution across the Australian continent, the brushtail possum features in many of the conservation translocation programmes that aim to re-establish functional mammal communities on the Australian mainland, particularly in the arid zone. There are a number of such programmes currently planned or in the early stages of implementation by government and non-government conservation agencies (Short and Hide, 2014; Natural Resource Management South Australia Arid Lands, 2017; Department of Biodiversity, Conservation and Attractions, 2017; Australian Wildlife Conservancy, 2018; Threatened Species Recovery Hub, 2017) and so quantifying the physiological characteristics of brushtail possums on a broad spatial scale, and assessing potential for variation consistent with local environmental conditions, is a timely contribution to these ambitious conservation initiatives.

There is considerable variation in size and colour of brushtail possums, and this has led to the recognition of various sub-species, and in some cases new species, each with distinct geographical ranges (Kerle *et al.*, 1991; Lindenmayer *et al.*, 2002). Body size variation is related to environmental aridity and food availability, with possums from more arid regions having a smaller body size than those from mesic areas (Yom Tov and Nix, 1986). We examine here if this observed anatomical variation is accompanied by physiological variation on a large spatial scale, from south-west Western Australia to north-east Queensland. If pertinent physiological traits are found to vary geographically within this species, then this has important implications for the success of translocation programmes.

Methods

Brushtail possums were captured in wire cage traps baited with a rolled oat, peanut butter and sardine mixture. Possums were captured and held under licence from the relevant state wildlife authorities, and experiments followed the Australian code of practice for the care and use of animals

for scientific purposes, approved by the animal ethics committees of Curtin University, University of Western Australia, James Cook University, University of New England and University of Wollongong.

Six common brushtail possums were caught at Mt Caroline near Kellerberrin, south-west Western Australia (WA, 31.6°S 117.7°E; *Trichosurus vulpecula hypoleucus*), six at Wilton, near Wollongong, New South Wales (NSW, 34.4°S 150.9°E; *Trichosurus vulpecula vulpecula*), and eight were captured near Ayr, northern Queensland (Qld, 19.6°S 147.4°E; *Trichosurus vulpecula johnstonii*). Six short-eared brushtail possums (*Trichosurus caninus*) were captured at Washpool National Park (Northern Tablelands, NSW, 29.3°S 152.3°E). All possums were adult and no females were lactating. The total annual rainfall, mean number of rainy days, and mean minimum and maximum ambient temperatures of the capture locations are presented in Table 1, with the WA site characterized by a warm and dry climate, the two NSW sites cool and moist, and the QLD site being hot and wet (Australian Bureau of Meteorology, 2017). Brushtail possums were held in captivity for several weeks, fed on an *ad libitum* diet of fresh fruit and vegetables, cheese, *Eucalyptus* leaves, small animal muesli and rodent cubes, with *ad libitum* drinking water.

Metabolic rate (MR), as determined by rates of oxygen consumption (VO₂) and carbon dioxide production (VCO₂), and evaporative water loss (EWL), were measured using standard flow-through respirometry after Withers (2001). Measurements were made, in random order, at ambient temperatures (T_a) ranging from 6°C to 35°C; not all possums were measured at all T_a for logistical and ethical reasons. Data for *T. v. hypoleucus* at 26°C and 30°C have been published by Cooper and Withers (2008). Possums were fasted overnight, then measured during their inactive phase (day) for ~8 h, except at $T_a = 34^\circ\text{C}$ where experiments were no longer than 6 h to avoid potential adverse effects of heat exposure and dehydration. Possums were measured at only a single T_a per day, with at least three days between successive measurements. Body temperature (T_b) was measured using a Radiospares (Smithfield, New South Wales Australia) thermocouple metre ($\pm 0.1^\circ\text{C}$), with a plastic-tipped thermocouple inserted ~2–3 cm into the cloaca immediately after the possum was removed from the chamber at the conclusion of each experiment. Possums were weighed to the nearest

Table 1: Climate variables for the capture locations of brushtail possums used in this study

Climate variable	Kellerberrin WA	Wilton NSW	Ayr QLD	Washpool NSW
Mean maximum temperature (°C)	25.2	23.4	29.4	24.9
Mean minimum temperature (°C)	10.8	8.9	17.8	6
Total annual rainfall (mm)	330	805	1060	891
Mean number of rainy days	48	71	52	79

Data from the Australian Bureau of Meteorology (2017).

gram before and after each experiment, and the mean of the two measures used in calculations.

The respirometry system consisted of an 8000 cm³ metabolic chamber placed in a controlled temperature cabinet or room ($\pm 2^\circ\text{C}$). Airflow through the chamber was achieved via a variety of pumps or a compressed air line; water vapour was removed using Drierite (W.A. Hammond Drierite Co. Ltd, Xenia, OH, USA), and flow rate regulated by a mass flow controller (Aalborg GFC171 or Omega FMAA2412; Orangeburg, NY, USA and Stamford, CT, USA respectively) at 2.5–4.6 l min⁻¹ (dependent on T_a and animal mass). A subsample of excurrent air passed through a Vaisala HMP45A (Helsinki, Finland) relative humidity (RH) and T_a probe, then through Drierite to carbon dioxide and oxygen analysers (Leybold–Heraeus Binos-C Cologne, Germany, Qubit S153 Kingston, Ontario, or Sable Systems CA-2A Las Vegas, NV, USA CO₂ analysers; Sable Systems Foxbox or Servomex 572, 574 or OA184 Crowborough, East Sussex, UK, O₂ analysers). A PC running a custom-written Visual Basic (V6; Microsoft, Redmond, WA, USA) programme recorded the voltage outputs of the analysers every 10–30 s. A baseline of background O₂, CO₂ and RH was established for at least 20 min before and after each experiment.

The mass flowmeters were calibrated using a Gilian Gilibrator (Sensidyne, St Petersburg, Florida, USA), traceable to a national standard, or a bubble flowmeter, corrected to standard temperature and pressure dry (STPD). Gas analysers were calibrated using room air (20.95% O₂), nitrogen (0% O₂ and CO₂) and a precision gas mix (0.53% CO₂, BOC Gases, Perth, Western Australia) and/or a butane flame after Withers (2001). Calibration of the RH probes, achieved by saturating air at a known temperature and then warming to T_a after Cooper and Withers (2008), was routinely confirmed using 2 points, 1% RH (dried with Drierite) and 100% RH (saturated; by breathing on the probe). A mercury thermometer, traceable to a national standard, was used for temperature calibration.

Respirometry calculations were made after Withers (2001) using a custom-written Visual Basic programme, and resting VO₂, VCO₂ and EWL were calculated for a period of at least 20 min during each experiment when values were steady and minimal, indicating the possums were at rest. Respiratory exchange ratio (RER) for each experiment was calculated as VCO₂/VO₂, and was used to convert MR to metabolic heat production (MHP) and metabolic water production (MWP) using oxy-calorific and hygric conversion coefficients at the measured RER (Withers *et al.*, 2016). EWL was converted to evaporative heat loss (EHL) using 2.4 J mg⁻¹ H₂O (Withers *et al.* 2016). Wet (C_{wet}) and dry (C_{dry}) thermal conductance (J g⁻¹ h⁻¹ °C⁻¹) were calculated as $C_{\text{wet}} = \text{MHP}/(T_b - T_a)$, and $C_{\text{dry}} = (\text{MHP} - \text{EHL})/(T_b - T_a)$. Relative water economy (RWE) was calculated as MWP/EWL and the point of relative water economy (PRWE) as the T_a where RWE was calculated to be 1.

We used generalized linear mixed effect models (GLMM) to examine T_a and geographic location effects, while accounting for repeated measurements of individuals as a random factor, using the lmer function in library lme4 (Bates *et al.* 2014) and lmerTest (Kuznetsova *et al.* 2014), in RStudio (RStudio Team, 2015), with Satterthwaite's approximations for calculation of degrees of freedom. Individual differences between possums were examined with a likelihood ratio test of the random effect. We examined the physiological response to T_a for each species, with T_a as a polynomial fixed factor and individual as a random factor. To compare between locations, MR, EWL and C_{wet} were expressed as mass-independent values using the marsupial scaling exponents of 0.74, 0.68, 0.57, respectively (Withers *et al.*, 2006). We then compared body mass and physiological responses to T_a among locations, with T_a as a polynomial function, location as a fixed factor, and individual as a random factor. Pair-wise location comparisons were made with the most arid habitat sub-species (*T. v. hypoleucus* from WA) as the reference category. Finally, we compared mass-independent standard physiological variables (measured at basal MR; $T_a \sim 26^\circ\text{C}$) among possums from each location using a one-way ANOVA with Student–Newman–Keuls post-hoc tests, in Statistix (v2.1, Nedlands, Western Australia). Values are presented as mean \pm standard error (SE), with N = number of individuals and n = number of measurements.

Results

Body mass of brushtail possums differed at the various locations ($F_{3,40} = 5.42$, $P = 0.004$); short-eared brushtails (*T. caninus*; 2370 ± 24.8 g, $N = 6$, $n = 28$) were heavier than *T. v. hypoleucus* from WA (1787 ± 22.4 g, $N = 6$, $n = 41$; $t_{30} = 3.14$, $P = 0.003$), and the other sub-species of common brushtail were of intermediate body mass (*T. v. vulpecula* 1992 ± 129.1 g, $N = 6$, $n = 15$; *T. v. johnstonii* 2011 ± 48.1 g, $N = 8$, $n = 37$). There were overall significant differences for individuals within sub-species/species with respect to body mass ($\chi^2_1 = 108$, $P < 0.001$) and all physiological variables ($\chi^2_1 \geq 5.47$, $P < 0.019$).

Body temperature of all brushtail possums was positively influenced by T_a ($F_{1,15-41} \geq 7.18$, $P \leq 0.002$; Fig. 1; Table 2). There was a significant location effect ($F_{3,121} = 11.6$, $P < 0.001$) and interaction with T_a ($F_{3,121} = 3.68$, $P = 0.014$) for the different taxa. Common brushtail possums from WA had a lower T_b than short-eared brushtails ($T_{121} = 2.61$, $P = 0.010$), but a higher T_b than the other sub-species of common brushtail ($t_{121} \geq 2.26$, $P \leq 0.028$). The influence of T_a on T_b was more pronounced for common brushtail possums from NSW and QLD ($t_{121} \geq 2.26$, $P \leq 0.026$) than it was for those from WA and for the short-eared brushtail (Fig. 1). Significant differences between the taxa were apparent for standard T_b ($F_{3,22} = 13.8$, $P < 0.001$; Fig. 2), which was significantly higher ($36.2 \pm 0.17^\circ\text{C}$; $N = 6$) for the short-eared brushtail than for common brushtail possums from all locations ($34.8\text{--}34.9^\circ\text{C}$; $P < 0.001$; $N = 6\text{--}8$).

Table 2: Summary of the coefficients for the quadratic equation of a GLMM (with individual as a random factor) of ambient temperature (T_a) on physiological variables (T_b , body temperature; VO_2 , oxygen consumption rate; VCO_2 , carbon dioxide production rate; EWL, evaporative water loss; C_{wet} , wet thermal conductance; C_{dry} , dry thermal conductance; RWE, relative water economy) for brushtail possums from Kellerberrin Western Australia (*Trichosurus vulpecula hypoleucus*), Wilton New South Wales (*T. v. vulpecula*), Washpool New South Wales (*T. caninus*) and Ayr Queensland (*T. v. johnstonii*). Individual is included in the GLMM model as a random factor

Variable	Coefficients	<i>T. v. hypoleucus</i> for Kellerberrin	<i>T. v. vulpecula</i> for Wilton	<i>T. caninus</i> for Washpool	<i>T. v. johnstonii</i> for Ayr
T_b (°C)	Intercept	$34.5 \pm 0.19^{***}$	$33.4 \pm 0.10^{***}$	$36.0 \pm 0.20^{***}$	$37.8 \pm 0.12^{***}$
	T_a	$4.08 \pm 1.19^{**}$	$4.52 \pm 0.39^{***}$	$4.02 \pm 0.47^{***}$	$6.31 \pm 0.60^{***}$
	T_a^2	1.93 ± 1.19^{ns}	-0.07 ± 0.39^{ns}	$1.50 \pm 0.46^{**}$	$2.95 \pm 0.61^{***}$
VO_2 (ml O_2 h ⁻¹)	Intercept	$0.404 \pm 0.007^{***}$	$0.364 \pm 0.024^{***}$	$0.428 \pm 0.014^{***}$	$0.418 \pm 0.015^{***}$
	T_a	$-0.592 \pm 0.046^{***}$	$-0.410 \pm 0.036^{***}$	$-0.395 \pm 0.041^{***}$	$-0.480 \pm 0.058^{***}$
	T_a^2	$0.346 \pm 0.046^{***}$	$0.209 \pm 0.036^{**}$	$0.140 \pm 0.040^{**}$	$0.374 \pm 0.059^{***}$
VCO_2 (ml CO_2 h ⁻¹)	Intercept	$0.339 \pm 0.008^{***}$	$0.309 \pm 0.027^{**}$	$0.375 \pm 0.032^{***}$	$0.296 \pm 0.015^{***}$
	T_a	$-0.465 \pm 0.053^{***}$	$-0.285 \pm 0.084^*$	$-0.342 \pm 0.101^{**}$	$-0.196 \pm 0.043^{***}$
	T_a^2	$0.226 \pm 0.053^{***}$	0.137 ± 0.084^{ns}	$0.242 \pm 0.100^*$	$0.224 \pm 0.043^{***}$
EWL (mg H_2O h ⁻¹)	Intercept	$0.564 \pm 0.049^{***}$	$0.332 \pm 0.022^{***}$	$0.674 \pm 0.044^{***}$	$0.795 \pm 0.055^{***}$
	T_a	$2.574 \pm 0.315^{***}$	0.123 ± 0.049^{ns}	$1.665 \pm 0.233^{***}$	$2.839 \pm 0.330^{***}$
	T_a^2	$2.380 \pm 0.315^{***}$	0.109 ± 0.049^{ns}	$1.278 \pm 0.233^{***}$	$2.740 \pm 0.330^{***}$
C_{wet} (J g ⁻¹ h ⁻¹ °C ⁻¹)	Intercept	$1.133 \pm 0.131^{***}$	$0.572 \pm 0.041^{***}$	$1.009 \pm 0.049^{***}$	$1.390 \pm 0.115^{***}$
	T_a	$5.926 \pm 0.829^{***}$	$0.444 \pm 0.073^{***}$	$3.192 \pm 0.257^{***}$	$5.910 \pm 0.688^{***}$
	T_a^2	$5.184 \pm 0.829^{***}$	$0.197 \pm 0.072^*$	$2.043 \pm 0.257^{***}$	$4.569 \pm 0.688^{***}$
C_{dry} (J g ⁻¹ h ⁻¹ °C ⁻¹)	Intercept	$0.643 \pm 0.048^{***}$	$0.501 \pm 0.039^{***}$	$0.699 \pm 0.045^{***}$	$1.349 \pm 0.111^{***}$
	T_a	$1.586 \pm 0.301^{***}$	$0.282 \pm 0.060^{**}$	$1.560 \pm 0.173^{***}$	$5.735 \pm 0.668^{***}$
	T_a^2	$1.008 \pm 0.301^{**}$	$0.163 \pm 0.060^*$	$0.668 \pm 0.172^{**}$	$4.434 \pm 0.668^{***}$
RWE	Intercept	$0.766 \pm 0.042^{***}$	$0.720 \pm 0.042^{***}$	$0.545 \pm 0.032^{***}$	$0.481 \pm 0.035^{***}$
	T_a	$-2.412 \pm 0.169^{***}$	$-0.950 \pm 0.107^{***}$	$-1.567 \pm 0.160^{***}$	$-1.474 \pm 0.104^{***}$
	T_a^2	$-0.437 \pm 0.169^*$	0.184 ± 0.107^{ns}	0.072 ± 0.159^{ns}	-0.168 ± 0.106^{ns}

Values are mean \pm standard error. ns, not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Strong T_a effects were found for MR (VO_2) of all brushtail possums ($F_{2,9-41} \geq 53.5$, $P \leq 0.001$; Fig. 3; Table 2), with MR decreasing with increasing T_a to $T_a \sim 26^\circ\text{C}$, before stabilizing or increasing at higher T_a . Patterns of VCO_2 essentially mirrored VO_2 . Brushtail possums from the various locations differed with respect to MR ($F_{3,29} = 8.3$, $P < 0.001$) and there was a significant interaction between T_a and location ($F_{6,97} = 7.1$, $P < 0.001$). The short-eared brushtail possum and common brushtail from QLD had overall higher MRs ($t_{18} \geq 3.34$, $P < 0.004$) and a less pronounced response to T_a , than common brushtails from WA, which did not differ from NSW brushtails ($t_{71} = 0.512$, $P = 0.610$). Basal metabolic rate (BMR; at $T_a \sim 26^\circ\text{C}$) differed between possums from the various locations ($F_{3,22} = 9.13$, $P < 0.001$), with those from WA (2.02 ± 0.112 ml O_2 g^{-0.75} h⁻¹; $N = 6$) and NSW (1.81 ± 0.149 ml O_2 g^{-0.75} h⁻¹; $N = 6$) significantly lower than those from QLD (2.47 ± 0.353 ml O_2 g^{-0.75} h⁻¹; $N = 8$) and the short-eared brushtail (2.83 ± 0.198 ml O_2 g^{-0.75} h⁻¹; $P < 0.037$, $N = 6$; Fig. 2).

Conductance remained low and relatively constant at T_a below thermoneutrality, and increased at high T_a (Fig. 4), C_{wet} by 6.1–10.7 times and C_{dry} by 3.2–7.4 times at $T_a = 35^\circ\text{C}$ compared to $T_a = 6^\circ\text{C}$, reflecting the highly significant effects of T_a for both C_{wet} ($F_{2,9-40} \geq 21.8$, $P < 0.002$) and C_{dry} ($F_{2,9-40} \geq 41.2$, $P \leq 0.001$; Table 2). There were no over-all location ($F_{3,120} = 1.19$, $P = 0.316$), T_a ($F_{2,120} = 1.46$, $P = 0.237$) or interaction ($F_{6,120} = 1.82$, $P = 0.010$) effects for mass-independent C_{wet} , and no location differences ($F_{3,21} = 2.85$, $P < 0.061$; Fig. 2) for standard mass-independent C_{wet} .

For all brushtail possums, T_a affected EWL ($F_{10-41} \geq 5.4$, $P < 0.025$; Fig. 5; Table 2). EWL was relatively constant at T_a below thermoneutrality, but increased by 4.3–6.6 times from $T_a \sim 10^\circ\text{C}$ to 36°C ; EHL was 50–73% of MHP at $T_a = 36^\circ\text{C}$. Location ($F_{3,120} = 4.9$, $P = 0.003$), and its interaction with T_a ($F_{6,120} = 5.7$, $P < 0.001$), were significant. Brushtail possums from WA differed from those from NSW and QLD ($P \leq 0.032$), with a

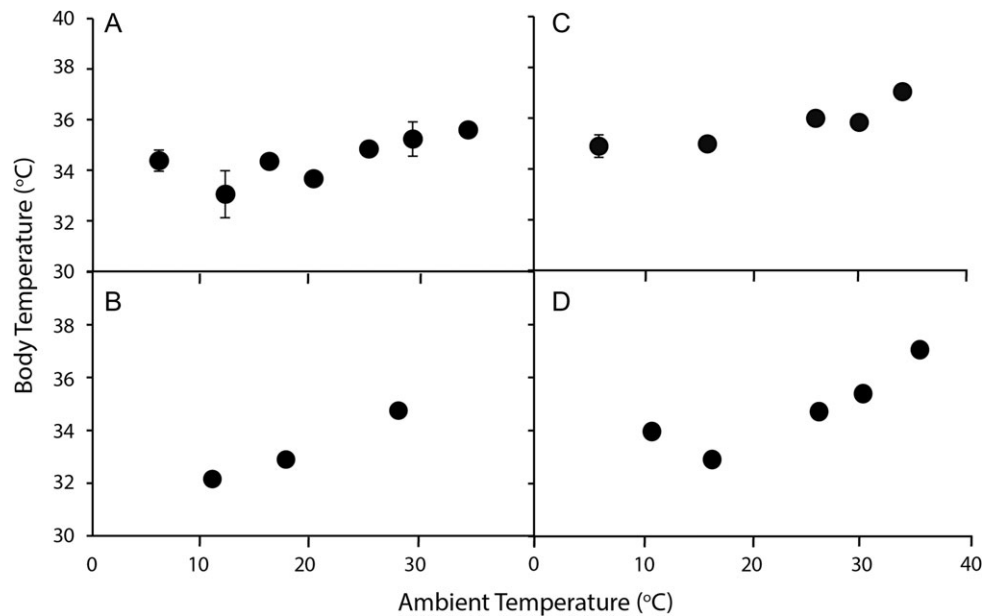


Figure 1: Body temperature of brushtail possums (**A:** *Trichosurus vulpecula hypoleucus*, Western Australia; **B:** *T. v. vulpecula*, New South Wales; **C:** *Trichosurus caninus*, Tablelands, New South Wales; **D:** *T. v. johnstonii*, Queensland) at a range of ambient temperatures. Values are mean \pm SE, $N = 6-8$.

lower EWL at low to moderate T_a and a greater increase at the highest T_a . Standard EWL at $T_a \sim 26^\circ\text{C}$ was influenced by location ($F_{3,22} = 5.02$, $P = 0.008$), with common brushtail possums from WA having a lower standard EWL ($3.09 \pm 0.197 \text{ mg O}_2 \text{ g}^{-0.68} \text{ h}^{-1}$) than short-eared brushtail possums ($6.49 \pm 0.412 \text{ mg O}_2 \text{ g}^{-0.68} \text{ h}^{-1}$) and common brushtails from QLD ($5.36 \pm 0.870 \text{ mg O}_2 \text{ g}^{-0.68} \text{ h}^{-1}$; Fig. 2). Common brushtail possums from NSW also had lower EWL ($4.13 \pm 0.805 \text{ mg O}_2 \text{ g}^{-0.68} \text{ h}^{-1}$) than the short-eared brushtail possum. The PRWE ranged from 5.9°C (QLD and the short-eared brushtail) to 10.4°C (NSW) and 15.0°C (WA; Fig. 6).

Discussion

We have quantified significant variation in the physiological traits of spatially separated populations of brushtail possums, marsupials with a wide geographical distribution throughout the Australian continent. This variation was consistent with environmental patterns of inter-specific variation for marsupials (Withers *et al.*, 2006) and other endotherms (e.g. Tieleman and Williams, 2000; Schleucher and Withers, 2001; Lovegrove, 2003; Rezende *et al.*, 2004; White *et al.*, 2007; van Sant *et al.*, 2012), and with anatomical differences identified previously for brushtail possums (Yom Tov and Nix, 1986). We discuss here potential environmental drivers of this geographic variability and then assess the likely impacts of these patterns on management and conservation actions, particularly conservation translocations, for this species and for mammals in general.

Possums from all locations had typical endothermic responses to T_a . Possums were thermoneutral at 26°C , MR

increased at lower T_a while T_b , EWL and C remained relatively constant, and all variables increased at higher T_a . This pattern was consistent with previous observations for *T. v. vulpecula* from NSW (Dawson, 1969; Dawson and Hulbert, 1970), although our measures of BMR and EWL were 16–24% lower, and our standard T_b was 1.3°C lower (despite almost identical body masses). These differences are presumably due to possums in the earlier studies being restrained and having a thermocouple inserted in the cloaca throughout measurement.

Various macro-physiological studies have reported environmental influences on standard physiological variables that highlight the important role of these factors on the physiological phenotype of mammals. Smaller body mass is well described for many other mammalian species from hot compared to colder habitats (i.e. Bergmann's rule; reviewed by Meiri and Dayan, 2003). There are a number of environmental correlates with standard physiological variables for marsupials (Withers *et al.* 2006) that are broadly consistent with patterns for mammals (e.g. Lovegrove, 2003; Rezende *et al.*, 2004; Van Sant *et al.*, 2012). Inter-specific environmental correlates for standard marsupial T_b , BMR and EWL indicated that species from arid environments with high rainfall variability have lower values than species from mesic environments with more reliable rainfall.

Broad environmental patterns are also apparent at lower taxonomic levels, although there is a paucity of such studies at broad spatial scales, and some inconsistencies between studies (Bozinovic *et al.*, 2009, 2011). Within genera, species from mesic, cold-climate and high productivity habitats typically

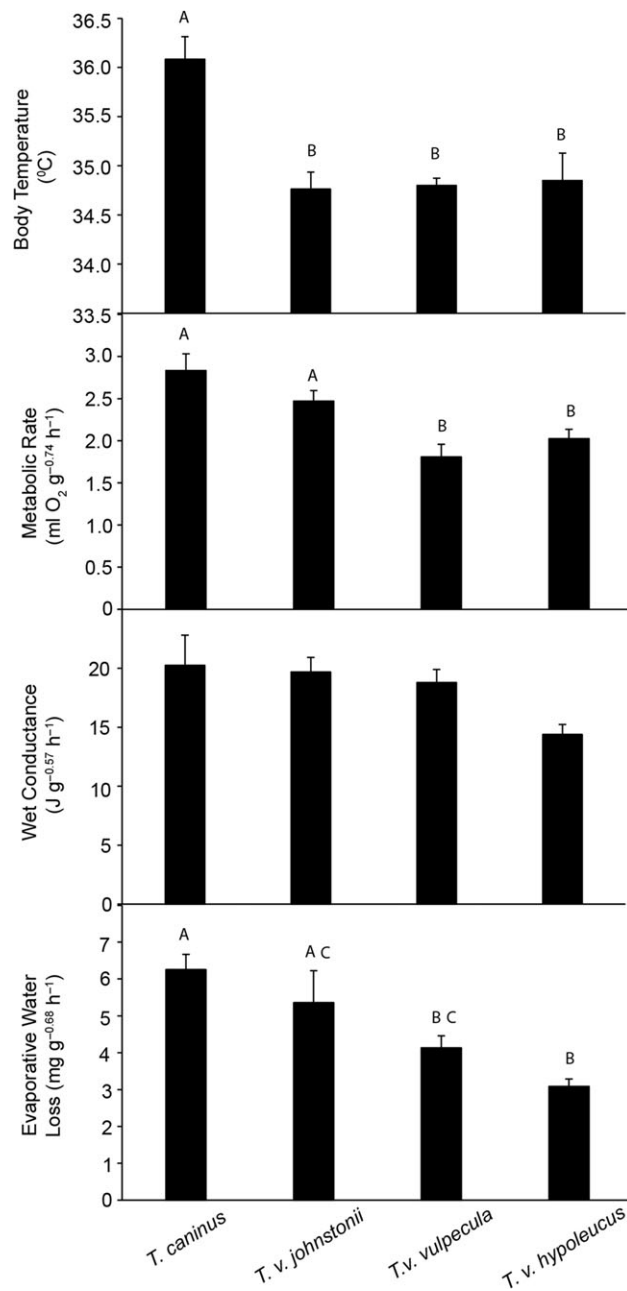


Figure 2: Mass-independent standard physiological variables, measured at an ambient temperature of ~26°C, of brushtail possums from four geographical regions; *Trichosurus caninus* from the northern tablelands of New South Wales ($N = 6$), *T. vulpecula johnstonii* from north Queensland ($N = 8$), *T. v. vulpecula* from New South Wales ($N = 6$) and *T. v. hypoleucus* from Western Australia ($N = 6$). Different letters indicate significant differences at $\alpha = 0.05$. Values are mean \pm SE.

have higher BMR and EWL, and lower PRWE, than species from arid, hot and low productivity habitats (Mueller and Diamond, 2001; Williams *et al.*, 2004; Careau *et al.*, 2007;

Cooper and Withers, 2010). Broadly, intra-specific physiological differences between populations reflect these intra-generic, and wider inter-specific, patterns for rodents, bats, marsupials and monotremes (Augee, 1978; Tracy and Walsberg, 2000; Geiser and Ferguson, 2001; Bozinovic *et al.*, 2009; Dunbar and Brigham, 2010; Stawski and Geiser, 2011), but there are exceptions. For example, there were no differences in torpor T_b for northern and southern little red bats (*Lasiurus borealis*), but there were for big brown bats (*Eptesicus fuscus*; Dunbar and Brigham, 2010), while woodrats (*Neotoma* spp.) from different environments had similar MR and T_b but different C_{wet} and body mass (Brown and Lee, 1969). There is currently no clear explanation as to why the established ecological drivers of physiology observed at higher levels of taxonomy are reflected in geographically separated populations of many, but not all, species. Presumably there are a suite of genetic, evolutionary, life history and environmental factors that determine populational differences a over broad geographic scales (Dunbar and Brigham, 2010). A much more comprehensive dataset of broad-scale intra-specific population studies is required to address this question, but it does highlight the requirement for species-specific studies to examine potential geographic effects, when the aim is to inform conservation and management actions.

Our physiological data for brushtail possums are generally consistent with the broad macro-physiological observations and lower-taxonomic level environmental patterns for other mammals. Body mass variation with T_a is well documented for brushtail possums (Yom Tov and Nix, 1986), consistent with our results. Differences in thermal, metabolic and hygric traits of brushtail possums were also generally consistent with other studies, with possums from warmer/drier habitats having more frugal energy and water use and increased capacity for EHL at T_a above thermoneutrality. The PRWE, an index of water economy and hence a measure of adaptation to aridity (MacMillen, 1990; MacMillen and Hinds, 1983; Hinds and MacMillen, 1986) provided further evidence that the physiology of *T. v. hypoleucus* from WA is more favourable for drier habitats compared to possums from other environments.

The variation we identify here for brushtail possums throughout their geographic range adds to the growing evidence that basic physiological traits are not necessarily fixed species-specific characteristics, and that local environmental conditions can be significant physiological drivers. Unfortunately, there is little evidence that translocation studies consider this variation in the planning phase. Baker and Gemmell (1999) found that possums translocated from cool-temperature Armidale (NSW) to sub-tropical Brisbane (QLD) had greater immune and hormonal responses, and mortality compared to locally captured possums. Our data, showing significant geographic variation in possum physiology, suggest that climate may have contributed to these results; possums from Armidale likely had a less favourable physiology for the Brisbane climate and this impacted on their health and survival.

Our data do not distinguish between genetic, developmental or acclimatisation differences between possum populations.

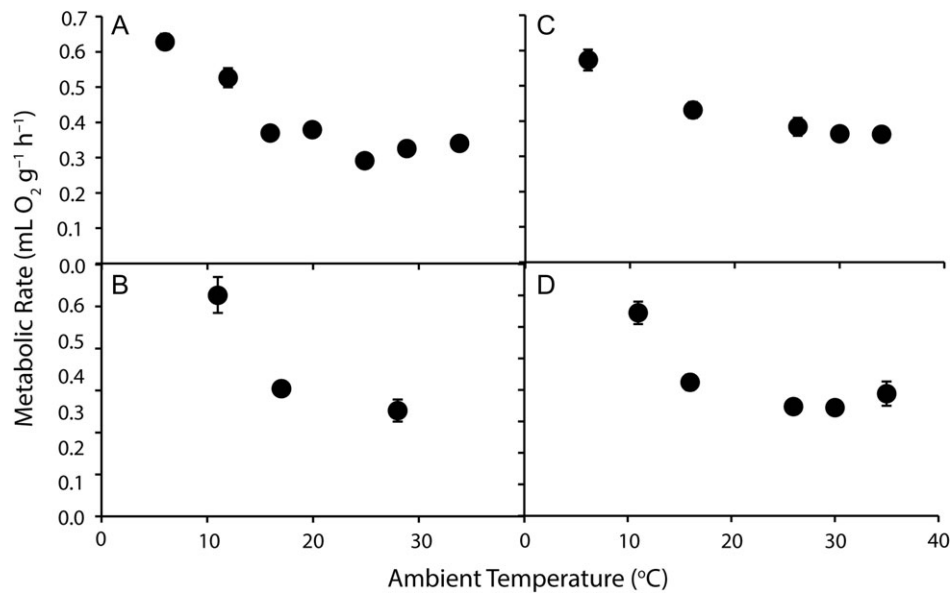


Figure 3: Metabolic rate of brushtail possums (**A:** *Trichosurus vulpecula hypoleucus*, Western Australia; **B:** *T. v. vulpecula*, New South Wales; **C:** *Trichosurus caninus*, Tablelands, New South Wales; **D:** *T. v. johnstonii*, Queensland) at a range of ambient temperatures. Values are mean ± SE, *N* = 6–8.

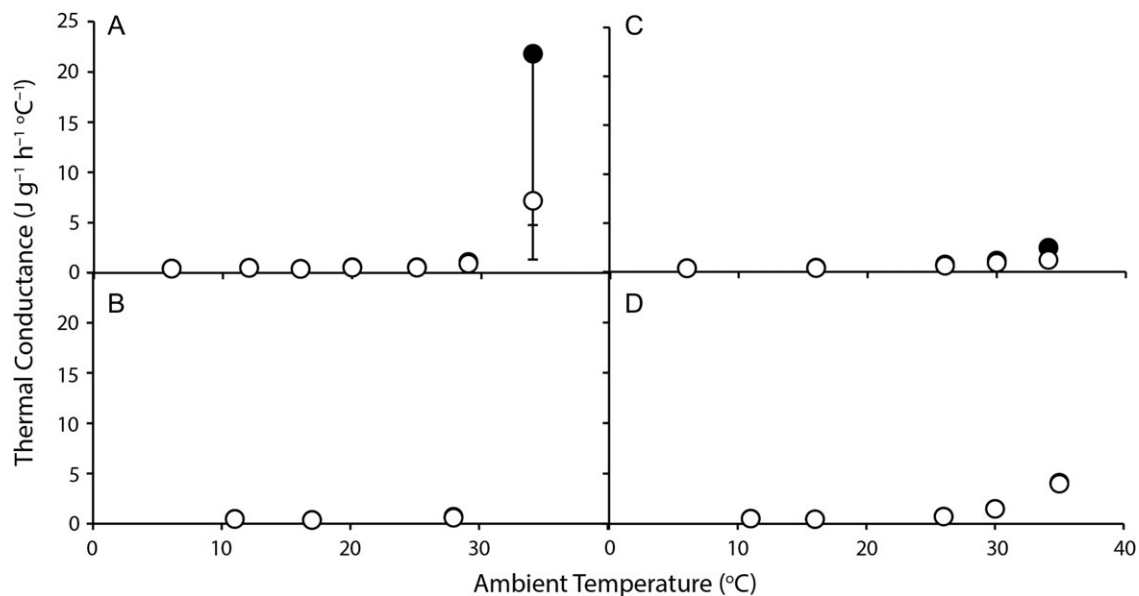


Figure 4: Wet (black symbols) and dry (white symbols) thermal conductance of brushtail possums (**A:** *Trichosurus vulpecula hypoleucus*, Western Australia; **B:** *T. v. vulpecula*, New South Wales; **C:** *Trichosurus caninus*, Tablelands, New South Wales; **D:** *T. v. johnstonii*, Queensland) at a range of ambient temperatures. Values are mean ± SE, *N* = 6–8.

Acclimation and acclimatization to changing environmental conditions, temperature in particular, have long been well documented for mammals (e.g. Chaffee and Roberts, 1971), and there is also evidence that the environment experienced during development can impact the physiological characteristics of

adult mammals (e.g. Riek and Geiser, 2012). Tracey and Walsberg (2001) found that developmental and acclimatory effects on the hygric physiology of kangaroo rats (*Dipodomys merriami*) could be as substantial as genetic differences between populations, and could occur relatively quickly. This suggests

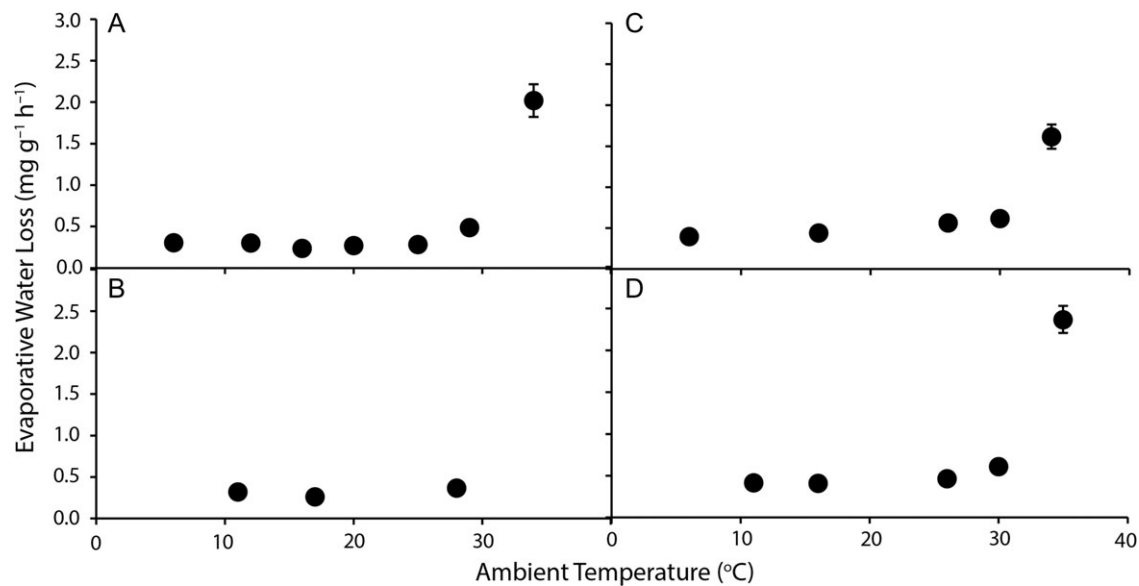


Figure 5: Evaporative water loss of brushtail possums (**A:** *Trichosurus vulpecula hypoleucus*, Western Australia; **B:** *T. v. vulpecula*, New South Wales; **C:** *Trichosurus caninus*, Tablelands, New South Wales; **D:** *T. v. johnstonii*, Queensland) at a range of ambient temperatures. Values are mean \pm SE, $N = 6-8$.

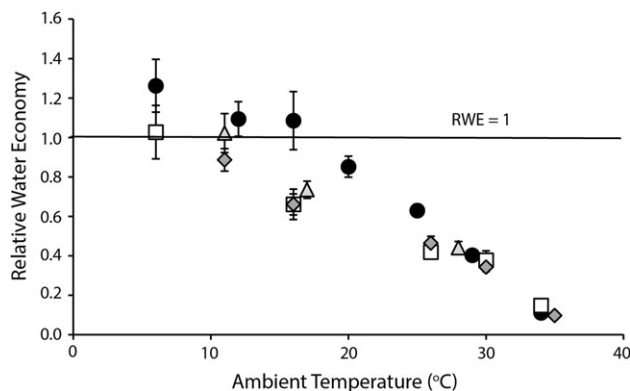


Figure 6: Relative water economy (RWE) of brushtail possums (*Trichosurus vulpecula hypoleucus*, Western Australia, black circles; *T. v. vulpecula*, New South Wales, light grey triangles; *Trichosurus caninus*, tablelands, New South Wales, white squares; *T. v. johnstonii*, Queensland, dark grey diamonds) at a range of ambient temperatures. Values are mean \pm SE, $N = 6-8$.

that translocated individuals have the potential to adjust to their new environment via phenotypic plasticity, but given the considerable stress experienced by animals prior to, during and after translocation, and their vulnerability immediately post-translocation (Waas *et al.*, 1999; Teixeira *et al.*, 2007; Dickens *et al.*, 2010), it is undesirable to impose the added stressor of a sub-optimal physiology that could reduce an individual's immediate fitness (e.g. Baker and Gemmell, 1999). In addition, the extreme environmental conditions characteristic of arid habitats are likely to be closer to species' tolerance limits than more

mesic environments (Fuller *et al.*, 2010), so species translocated to these environments from milder habitats may be less able to accommodate their new environment. Appreciating geographic patterns in physiological variation is also likely to improve animal welfare outcomes during translocation programmes. Selection of the most appropriate individuals for translation is recognized as one of the first steps in maximizing animal welfare, including assessing if individuals are suited to their new environment (Harrington *et al.*, 2013).

Despite the potential for acclimatization to account for geographic patterns observed here for brushtail possums, data of Cooper and Withers (2010), which approximated a common garden design for another widespread genus of marsupial (*Dasyurus*), suggests a strong genetic basis to their physiology, reflecting environmental conditions. Even if there are significant genetic differences between brushtail possum populations, with sufficient time, re-introduced populations could respond to a new environment by adaptation (evolution, micro-evolution or epigenetic control of gene expression; Hetem *et al.*, 2014). However, re-introduced populations are by necessity small and may not have the capacity to survive because of the reduced fitness of less-suited individuals, and the variation in the founder population might not provide sufficient adaptive scope.

Recommendations

Given our observed differences in brushtail possum physiology, together with the findings of Baker and Gemmell (1999) concerning translocation responses of brushtail possums from cool-temperature to sub-tropical environments,

we recommend that possums involved in translocation programmes should be sourced from areas with the most similar environmental conditions to the proposed release site, not necessarily possums from the closest geographical location. As it is the arid zone where brushtail possum re-introductions are most desirable (Kerle *et al.*, 1992), then the sub-species *T. v. hypoleucus* would be most physiologically appropriate for these translocations, having physiological traits most favourable for the low productivity, low and variable water availability and extreme T_a of arid environments.

Implications for conservation translocations

Similar intra-specific geographic variability in physiological traits for an array of other species (e.g. Tracey and Walsberg, 2000; Mueller and Diamond, 2001; Williams *et al.*, 2004; Bozinovic *et al.*, 2009; Dunbar and Brigham, 2010; Stawski and Geiser, 2011) suggest that our recommendation regarding the physiological suitability for translocation of brushtail possums has general significance to translocation, reintroduction and management programmes for other mammals. Tarszisz *et al.*'s (2014) review of 120 translocation programmes found that only 11 programmes (9%) considered aspects of 'traditional' physiology in any way. Even for these, the vast majority involved only clinical health checks or post-release monitoring. Traditional physiological variables are not usually considered as part of initial pre-translocation planning (Tarszisz *et al.*, 2014). Our study of brushtail possums is the first to our knowledge that has assessed basic physiological variation of geographically separated populations of a mammal as a consideration in terms of their suitability for translocation. Our data provide a physiological explanation for previous observations of responses by brushtail possums to translocation (Baker and Gemmel, 1999) and support the suggestion of Cooke *et al.* (2013) that individual variation in physiology and environmental tolerance can potentially impact on long-term translocation success. We conclude from our study that widespread mammals can have considerable geographic variation in basic physiological variables, and that knowledge of location-dependence of thermal, metabolic and hygric physiology is a potentially useful tool in selection of which populations would be most suitable to source individuals for conservation translocations.

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