

Lean-season primary productivity and heat dissipation as key drivers of geographic body-size variation in a widespread marsupial

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Geographic body-size variation characterises many mammal species. Hypotheses centring around heat conservation, heat dissipation, primary productivity and seasonality have been advanced to explain geographic body-size patterns. However, identification of the primary body-size drivers has often been hampered by a paucity of data for broadly distributed species and the application of regression models that have not explicitly accounted for the spatial clustering inherent in such datasets. We used Australia's most widespread marsupial, the common brushtail possum *Trichosurus vulpecula*, as a model species with which to test five proposed drivers of geographic body-size variation. Using geo-referenced skull measurements from 588 specimens and a suite of putative environmental covariates, we employed spatial simultaneous autoregressive models, together with information criteria, to evaluate these different hypotheses. Our analysis identified a strong, positive relationship between possum body size and primary productivity during the least productive season, whereas the relationship with mean annual productivity received less support. Consistent with the heat-dissipation hypothesis, *T. vulpecula* body size also decreased with increasing mean summer maximum temperature. Spatial autoregression coefficients estimated from the simultaneous autoregressive models were always high, suggesting that additional abiotic or biotic factors might contribute to the spatial patterns observed. We argue that the analysis of geographic body-size variation should consider multi-causal possibilities rather than treating the numerous hypotheses as competing, mutually exclusive alternatives.

Body size is perhaps the most important character affecting the morphology, life history, physiology, behaviour, ecology, evolution and extinction probability of animal species (Haldane 1928, Peters 1983, Schmidt-Nielsen 1984, Cardillo et al. 2005). It is also one of the most prominent and readily measurable phenotypic attributes responsive to environmental conditions. Spatial and temporal patterns of body-size variation have been well documented in many endotherms, particularly within mammals (Rosenzweig 1968, Boyce 1978, Yom-Tov and Nix 1986, Dayan et al. 1989, Smith et al. 1995, Wigginton and Dobson 1999, Ashton et al. 2000, Ashton 2002, Meiri et al. 2004, Blois et al. 2007, Mukherjee and Groves 2007, Gür and Gür 2012, Orcutt and Hopkins 2013, Briscoe et al. 2014, Prowse et al. 2014). The most familiar pattern of body-size variation is Bergmann's rule which posits that, within taxa of endothermic animals, larger-bodied forms are found in cooler regions (Bergmann 1847). Originally defined to apply both intra- and inter-specifically (see Clauss et al. 2013 [Appendix 1] for a translation of Bergmann's original manuscript), the rule was recast by Rensch (1938) to apply strictly at the intraspecific level. More recently, Clauss et al. (2013) demonstrated a significant interspecific pattern. Blackburn et al. (1999) reformulated the rule again by recognising temperature rather than latitude per se as the key predictor of Bergmannian body-size patterns. Most hypotheses proposed to explain such patterns

centre around heat conservation, heat dissipation, seasonality or primary productivity (Smith et al. 1995, Wigginton and Dobson 1999). However, much past research has been either largely theoretical, or empirical but not designed to test each of the hypotheses simultaneously.

Bergmann hypothesised that heat conservation requirements drive spatial and environmental patterns in body size. That is, individuals should be larger in cooler regions because of their lower surface-area-to-volume ratios, thereby minimising heat loss (Bergmann 1847). Viewed from the opposite thermal extreme, however, spatial body-size patterns might arise from the need to dissipate heat in warmer areas, with increased surface-area-to-volume ratios and hence reduced body sizes favoured (Brown and Lee 1969, James 1970, Smith et al. 1995). Within warmer regions, individuals living in dry environments can more easily lower their body temperature via evaporative cooling, whereas those occupying moist environments can only keep cool by lowering their rate of heat production, such as by being smaller bodied (James 1970). Similarly, Speakman and Król (2010) suggest that smaller individuals in warmer areas would be selectively advantaged by having a higher-surface-to-volume ratio than their larger conspecifics to promote greater heat dissipation, regardless of ambient moisture.

The ability to survive in environments with high climatic variability, such as those at high latitudes, has also

been coupled with spatial body-size differences (Boyce 1978). Because energy stores increase with body size faster than energy requirements (Lindstedt and Boyce 1985), the seasonality hypothesis proposes that larger individuals are more likely to survive food shortages because of their greater capacity for adipose tissue (fat) storage (Lindsey 1966). Thus, larger body size should be more evident in more seasonal environments.

A fundamental requirement of body-size maintenance is that of energy (food) input. Food availability is influenced by biotic and abiotic predictors and fluctuates in time and space making it very difficult to quantify. Studies of the effects of food availability on body size therefore often use net primary productivity (NPP) as a proxy for food availability (Yom-Tov and Geffen 2011). The primary productivity hypothesis therefore predicts that body size may shift with food supply (i.e. body size increases with primary productivity) (Rosenzweig 1968, see also McNab 2010). Primary productivity has received strong support as a key driver of spatial body-size variation in numerous species of mammals (Rosenzweig 1968, Kolb 1978, Yom-Tov and Nix 1986, Blois et al. 2007, Gür and Gür 2012).

An alternative explanation for geographic body-size variation based on food availability posits that body size is regulated by the NPP during the growing season of plants when many animals are reproducing and growing (Huston and Wolverton 2009, 2011). This concept, termed 'ecologically and evolutionarily relevant' NPP (eNPP), differs from NPP which is conventionally interpreted as the annual rate of plant growth. The 'eNPP rule' (Huston and Wolverton 2011) has been proposed to explain the lack of latitudinal body-size patterns observed within the tropics and the decline in body size in regions above approximately 60°N. Body-size patterns in mammals are further complicated by the Island rule, which posits that when mainland animals colonize islands, small species tend to evolve larger bodies, and large species tend to evolve smaller bodies (Foster 1964, Lomolino 2005).

Study of geographic body-size variation in mammals, particularly in relation to Bergmann's rule, has been intense in Eurasia and North America, but not in the Southern Hemisphere. Australia has a diverse array of mammals found nowhere else in the world, most notably marsupials and monotremes. Australia's climate exhibits extensive variation through space, between seasons, and in its relative predictability. Northern tropical regions with summer rains grade into the southern temperate regions where rainfall is concentrated in winter. A substantial decline in rainfall also occurs from near the coast to the arid interior (Australian Bureau of Meteorology 2008). This marked latitudinal and longitudinal variation makes Australia an ideal platform for examining which environmental factors affect mammalian body size.

Yom-Tov and Nix (1986) first examined the effects of a range of climatic variables on body size in five species of Australian mammals. Using scatter diagrams with regression equations, they found that although body size in four of the species (including the common brushtail possum *Trichosurus vulpecula*) best correlated with productivity, they were unable to separate the effects of productivity and temperature (n specimens = 227; n sites = 89). In a systematic analysis of *T. vulpecula*, Kerle et al. (1991) used a simple linear plot

to show an overall increase in body size (n specimens = 185) with an increase in latitude (n sites = 16). We use *T. vulpecula*, which is widespread across the 7.7 million square-kilometre Australian continent, as a model species to refine the study of Yom-Tov and Nix by investigating which of the proposed body-size drivers are best supported by Australian data. We compile a continent-wide dataset of skull measurements from 588 specimens, more than double that used in previous analyses, to analyse spatial body-size variation in relation to Bergmann's rule and to test the hypothesis that *T. vulpecula* body size is primarily driven by primary productivity rather than heat conservation, heat dissipation or seasonality. We also test the eNPP hypothesis specifically by determining whether productivity over the growing season can best explain geographic body-size patterns. Discriminating between the proposed hypotheses (Table 1) poses a dilemma to researchers because, as Yom-Tov and Nix (1986) and others (Gür 2010) point out, each hypothesis pertains to changes in environmental variables that are often highly correlated. We consider this problem, in part, by comparing candidate regression models that accommodate both single-cause and multi-causal explanations for spatial body-size variation in *T. vulpecula*. Importantly, we evaluate 'aspatial' regression models as well as simultaneous autoregressive (SAR) models that explicitly account for spatially autocorrelative patterns in the data. We also examine whether island populations of *T. vulpecula* were larger or smaller than might be predicted were those areas contiguous with the mainland.

Material and methods

Study species

Trichosurus vulpecula is a nocturnal, arboreal phalangerid marsupial with adult weight ranges in Australia of 2.6–4.2 kg (Kerle and How 2008). It is primarily folivorous, but also consumes flowers and fruit. Its pre-European distribution spanned almost the entire continent, but it has since vanished from the majority of central and western regions. Nevertheless, *T. vulpecula* still has a more extensive distribution, including Tasmania and several smaller offshore islands, and occupies a more diverse array of habitats than any other Australian marsupial (Kerle and How 2008). Extensive geographic variation in both size and pelage has led to prior separation of *T. vulpecula* into different species or subspecies (Kerle et al. 1991). However, genetic and taxonomically reliable morphological evidence (Taylor and Foulkes 2004) indicates that there are insufficient differences between populations to justify recognition of more than one species.

Cranial parameters

Three cranial parameters, condylobasal length (CBL) (von den Driesch 1976), total jaw length (TJL) (Myers 2001) and greatest zygomatic breadth (ZB), were measured (± 0.01 mm), using Mitutoyo digital calipers from 670 adult *T. vulpecula* specimens (m = 261, f = 237, sex unknown = 172) housed in nine Australian wildlife collections.

Table 1. Proposed mechanism and predicted pattern for hypotheses that explain patterns of spatial and temporal body-size variation as well as environmental variables used in the current study to examine the hypothesised mechanisms.

Hypothesis	Mechanism	Predicted pattern	Reference	Environmental variables
Heat conservation	Reduced surface to volume ratios of larger individuals increases heat conservation in colder environments	Body size decreases with temperature	Bergmann (1847)	Mean winter/annual minimum temperature
Heat dissipation	Increased surface to volume ratio of smaller individuals facilitates heat dissipation in warm humid environments (James) or with higher temperature (Speakman and Król)	Body size decreases with humidity in warm environments/with temperature	James (1970), Speakman and Król (2010)	Summer/annual wet-bulb temperature; mean summer/annual maximum temperature
Seasonality	Large individuals have greater fasting endurance during periods of food shortage in more seasonal environments because of their greater relative and absolute capacity for fat storage	Body size increases with seasonality	Lindsey (1966), Boyce (1978)	Seasonal coefficient of variation for climatic and primary productivity variables; primary productivity variables for the least productive season
Productivity	Body size depends on the availability of food resources (primary productivity)	Body size increases with productivity	Rosenzweig (1968), McNab (2010)	Total annual rainfall; precipitation minus potential evapotranspiration; areal actual evapotranspiration; mean normalised difference vegetation index; Australian continental net primary productivity estimate based on fluxes of carbon/nutrients and CO ₂ /water
Ecologically and evolutionarily relevant net primary productivity (eNPP)	Animal body size is regulated by the net primary productivity of plants during the growing season	Body size increases with productivity during the growing season	Huston and Wolverton (2011)	Primary productivity variables calculated over the growing seasons

Specimens with fully erupted fourth molars and/or fused skull sutures were recognised as adults (Kirkpatrick 1964) and only these specimens with known geo-reference (longitude and latitude) were sampled. Sub-fossils were excluded from the sample, which represents the time period 1923–2005. We postulate that environmental parameters used in this study (see below) have remained relatively constant during this period or aptly represent this time period. After evaluating the correlation between each cranial measurement and known body weight, we chose CBL as the best body-size representative (Supplementary material Appendix 1). Since CBL did not differ between sexes for the subset of specimens of known sex (Supplementary material Appendix 2), data for both sexes were pooled thereby allowing 172 specimens of unknown sex to be included in all analyses.

Environmental variables and covariate extraction

Gridded environmental covariates for Australia were sourced or derived from datasets obtained from the Australian Bureau of Meteorology (BoM) (2010; <www.bom.gov.au>) and the British Atmospheric Data Centre (BADC) (2008; <www.badc.nerc.ac.uk>) as well as Australian continental Net Primary Productivity (NPP) estimates (Roxburgh et al. 2004). We collated all covariates across a common 0.05°

spatial grid to match that of the datasets for rainfall, temperature, normalised difference vegetation index (NDVI) and an Australian Continental NPP estimate. To upscale (or downscale) raster datasets, we first aggregated (or disaggregated) layers to a 0.05° grid and then rescaled datasets to a common extent using bilinear interpolation. Spatial time series data from BoM and BADC were summarised on a seasonal and annual basis by averaging over all years for which information was available (see below). The spatial data were prepared using the R computing environment (R Development Core Team) and functions within the R package ‘raster’ (Hijmans and van Etten 2012).

We aligned environmental variables with the hypothesised mechanisms driving geographic body size variation as follows (summarised in Table 1).

Heat conservation – since heat loss should be more critical during cold periods than warm periods we assessed mean minimum winter (June–August) and annual temperature (°C) calculated across years 1911–2009 (WinterMinTemp, AnnualMinTemp).

Heat dissipation – because overheating should be a more critical problem during warm moist periods than during warm dry periods, we assessed summer (December–February) and annual wet-bulb temperature (an average of data for 09:00 and 15:00 h), calculated across years 1900–2011 (Summer WetBulbTemp, Annual WetBulbTemp).

Wet-bulb temperature is the lowest temperature that can be reached under current ambient conditions by the evaporation of water only. Overheating should also be a more critical problem during warmer periods than during cooler periods and so we assessed mean maximum summer and annual temperature calculated across years 1911–2009 (SummerMaxTemp, AnnualMaxTemp).

Primary productivity – primary productivity was represented by annual calculations of the following variables: 1) rainfall (mm) (AnnualRain); 2) precipitation minus potential evapotranspiration (mm); a measure of climatic water balance (i.e. water surplus or deficit for the analysed time period) averaged across years 1911–2009 (P – PET) (PET spatial grid = 0.5°); 3) areal actual evapotranspiration (mm) based on the period 1961–1990 (aaET) (spatial grid = 0.1°) and 4) the NDVI (NDVI units 0 – 1) mean averaged across January 2008–March 2012 (NDVI). We also included an Australian Continental NPP estimate based on fluxes of carbon/nutrients and CO₂/water (gigatons of carbon per year [Gt C yr⁻¹]) (CenW), which Roxburgh et al. (2004) calculated from datasets derived from ESOCLIM (1921–1995) (McMahon et al. 1995).

eNPP – eNPP was represented by primary productivity variables calculated over the growing seasons (e.g. GrowSeasNDVI). We defined the growing season for each grid cell as the set of months with a mean temperature > 15°C, as defined by BoM (< www.bom.gov.au >). Because Australia's limited alpine areas have no seasons that meet that criterion, we also imposed a minimum growing season of December–March. Since growing season might not depend solely on temperature we also investigated the effects of maximum seasonal values of primary productivity variables on *T. vulpecula* body-size variation. These variables were not supported over equivalent productivity variables calculated on an annual basis (results not shown).

Seasonality – the seasonal coefficient of variation (CV) for climatic and primary productivity variables is typically used as a measure of the relative deviation from mean conditions throughout the year (i.e. seasonality increases with increasing CV) (Boyce 1978, Medina et al. 2007, Gür and Gür 2012). We therefore calculated the CV of seasonal environmental variables as measures of seasonal variability. However, since the seasonality hypothesis proposes that body size should increase with the increasing severity of food shortage, we also calculated primary productivity variables for the least productive season (minimum seasonal values, e.g. MinSeasP – PET).

To account for possible island effects, we classified specimens as originating from the Australian mainland (n = 437), the large island of Tasmania (64 519 km², n = 84) or from all other islands, and this was considered as a 3-level factor (Island) in subsequent analysis. The smaller island group consisted of multiple specimens from Barrow Island (202 km², n = 12), Bathurst Island (2 600 km², n = 7), Centre Island (84 km², n = 2), Flinders Island (1 367 km², n = 10), Kangaroo Island (4 400 km², n = 27) and Magnetic Island (52 km², n = 7) and single specimens from Croker Island (332 km²) and Milingimbi Island (60 km²).

We extracted covariate values for each possum sample from the 0.05°-resolution environmental layers. Specimens originated from 316 distinct grid cells ranging from latitude

11.10°S to 43.15°S and longitude 114.8°E to 153.3°E. Prior to statistical analysis, multiple CBL measurements from a single grid cell were averaged because these represented pseudoreplicated body-size observations for the same covariate values. We centred and standardised covariates by their standard deviations to facilitate comparison of statistical models involving covariates with different units.

Origin (i.e. wildlife collection) and registration numbers of all specimens used in the analyses, together with all extracted environmental covariates, are available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.gq264>.

Model fitting and selection

To test the ability of proposed drivers to explain geographic body size variation in *T. vulpecula*, both individually and in combination, we fit aspatial regression models (i.e. linear models that do not account for spatial dependence) and spatial simultaneous autoregressive (SAR) models (Bivand et al. 2008) using the R computing environment (ver. 3.0.3; R Development Core Team). SAR models extend traditional linear models by assuming that the errors involve a spatial autoregressive process. The SAR model can be written as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{u}$$

where \mathbf{X} is the matrix of explanatory variables and $\boldsymbol{\beta}$ is the vector of coefficients. The spatially dependent error term, \mathbf{u} , is decomposed as:

$$\mathbf{u} = \lambda \mathbf{W}(\mathbf{y} - \mathbf{X}\boldsymbol{\beta}) + \boldsymbol{\varepsilon}$$

where λ is the spatial autoregression coefficient (values close to 1 indicate strong positive spatial autocorrelation), \mathbf{W} is the spatial weights matrix and $\boldsymbol{\varepsilon}$ are the spatially independent residual errors. We adopted a row-standardised weighting scheme that assigned equal weights to all neighbouring sites and used a neighbourhood radius of 500 km. We fit SAR models using the function 'errorsarm' within R package 'spdep' (Bivand and Gianfranco 2015).

We used Akaike's information criterion with a correction for finite sample sizes (AICc) (Burnham and Anderson 2002) as a means to: a) identify the best predictor within each hypothesis and b) select the most supported mono-causal and multi-causal explanations for body-size variation in *T. vulpecula*. Given a candidate set of models, AICc balances the number of parameters with model fit and chooses the model that minimises the information loss (i.e. better performing models have lower AICc values) (Burnham and Anderson 2002, p. 70). We selected top-ranking mono-causal models and multi-causal models on the basis of lowest AICc values. Before running multi-causal models, we determined the degree of correlation between the relevant environmental variables by calculating Spearman's rank correlation coefficient (r) (Supplementary material Appendix 3). Environmental variables that were highly correlated ($r \geq 0.75$) were not included in the same statistical model. To determine whether the residuals from aspatial regression and spatial SAR models were spatially autocorrelated, we calculated Moran's I values for distance lags of 500 km.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.gq264>> (Correll et al. 2015).

Results

Geographical variation in possum body size

Trichosurus vulpecula specimens from the coastal habitats of southeastern Australia are markedly larger than those of the remainder of the continent (Fig. 1). However, *T. vulpecula* body-size variation does conform to Bergmann's rule and increases with latitude (Fig. 2a). The spatial SAR model fitting this latitude effect, which received strong AICc

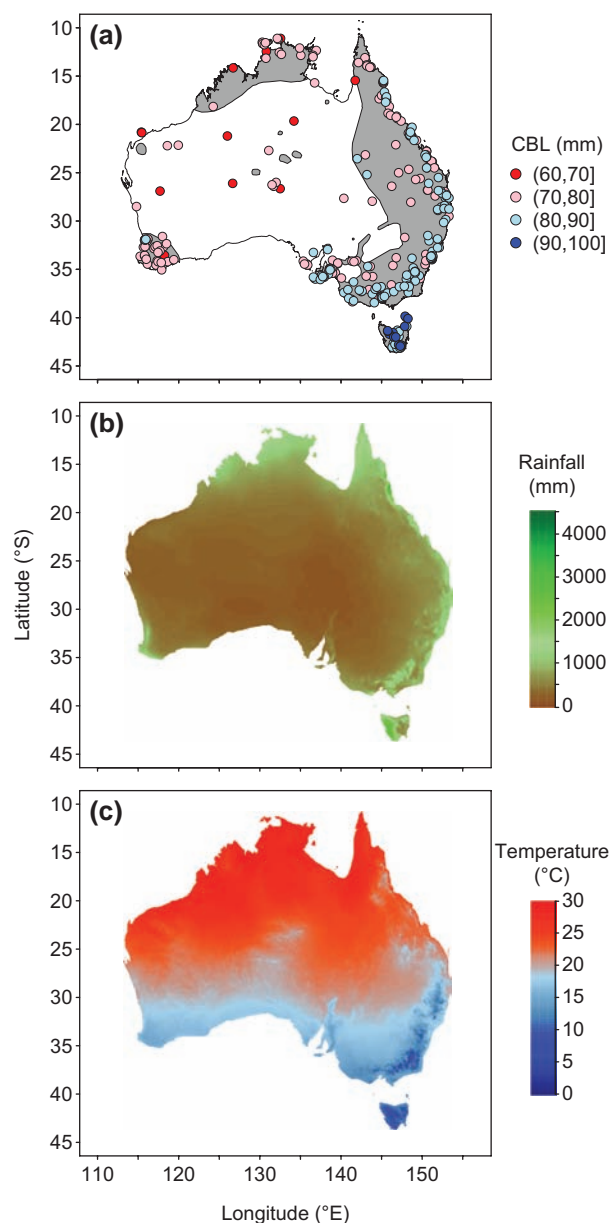


Figure 1. (a) Colour coded points represent spatial pattern of condylobasal length (CBL; mm) for *Trichosurus vulpecula*. Shaded area depicts current *T. vulpecula* distribution (International Union for Conservation of Nature [IUCN] 2013). Climatic layers are (b) annual rainfall and (c) mean annual temperature for Australia.

support relative to the equivalent aspatial model (Table 2), estimated the stronger relationship between CBL and latitude ($0.520 \pm 0.214 \text{ mm}^\circ\text{S}^{-1}$ [estimate $\pm 95\%$ confidence interval] compared to $0.398 \pm 0.062 \text{ mm}^\circ\text{S}^{-1}$).

Mono-causal environmental predictors of body size

Aspatial regression models demonstrated that *T. vulpecula* body size decreases with increasing temperature and increases with indices of primary productivity (Fig. 2b–d), which is consistent with hypotheses based on thermoregulatory responses and food availability, respectively. However, the top AICc-ranked aspatial model for the seasonality hypothesis estimated a positive relationship between body size and the average productivity of the least productive season (as represented by the variable MinSeasP – PET) (Fig. 2f). While not consistent with the seasonality hypothesis, this is consistent with the primary productivity hypothesis (i.e. body size increases as the severity of the least productive season lessens). Consequently, we rejected the seasonality hypothesis. Henceforth, we consider MinSeasP – PET to be an additional index of primary productivity. On the basis of AICc ranking and model fit (R^2), aspatial regression models clearly supported the heat dissipation and primary productivity hypotheses ($R^2 > 0.45$ for the top-performing predictor variables for both hypotheses) (Table 2, Fig. 2). In contrast, the heat conservation and eNPP hypotheses received little support (both $R^2 < 0.30$, Table 2, Fig. 2).

Equivalent spatial SAR models were strongly supported over the mono-causal models (lower AICc and higher R^2 values) (Table 2). The spatial autoregression coefficient for these spatial models was always high (all $\lambda \geq 0.75$, Table 2) demonstrating strong positive spatial autocorrelation in body size that could not be explained by single predictor variables. In all cases, spatial models estimated shallower relationships between body size and environmental covariates (i.e. all coefficients were closer to zero, Fig. 2) indicating a consistent bias in the estimates derived from the aspatial models. However, AICc rankings for the spatial models also supported the heat dissipation and primary productivity hypotheses (Table 2). Back-transformed coefficient estimates for the variables SummerMaxTemp and MinSeasP – PET were $-0.637 \pm 0.171 \text{ mm CBL per } ^\circ\text{C}$ and $0.017 \pm 0.005 \text{ mm CBL per mm P – PET}$, respectively. While those for the AnnualMinTemp, CenW and GrowSeasNDVI were $-0.136 \pm 0.194 \text{ mm CBL per } ^\circ\text{C}$, $0.004 \pm 0.002 \text{ mm CBL per Gt C yr}^{-1}$ and $7.86 \pm 4.14 \text{ mm CBL per NDVI unit}$, respectively. Wet-bulb temperature was not supported as an important body-size driver in aspatial or spatial SAR models.

Multi-causal models for possum body size

Our multi-causal models similarly supported the heat dissipation and primary productivity hypotheses (Table 2). For both the aspatial and spatial SAR analyses, the top AICc-ranked multi-causal model was of the form $\text{CBL} = \text{SummerMaxTemp} + \text{MinSeasP} - \text{PET} + \text{Island}$. However, the deviance residuals from the aspatial model of this form were spatially autocorrelated, particularly within 1000 km (Fig. 3), so we focus on the equivalent spatial

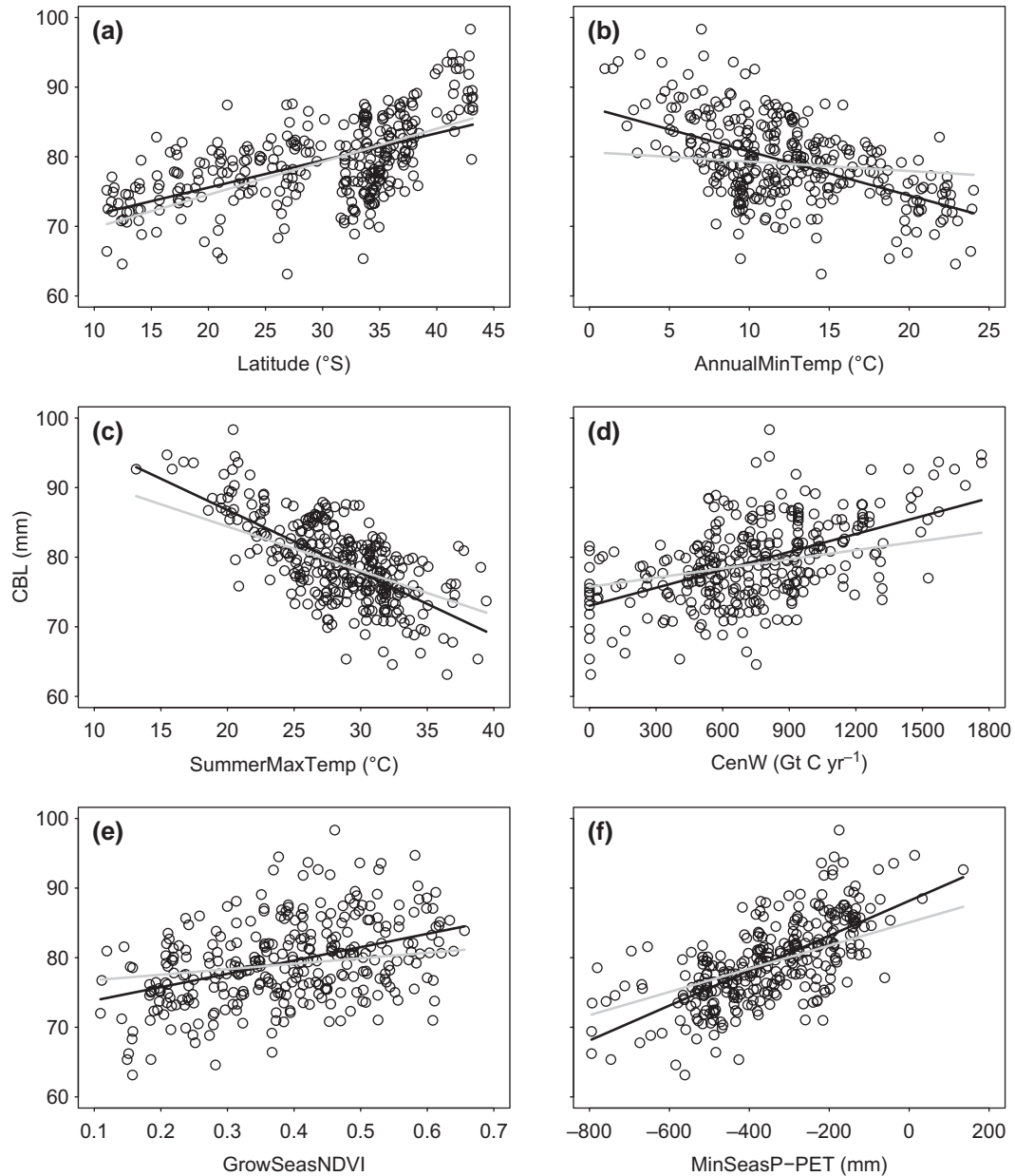


Figure 2. Fitted relationships between body size (condylobasal length [CBL]) and latitude (a) and also the top AICc-ranked predictor from each hypothesis for both aspatial models (black line) and spatial autoregressive models (grey line); (b) mean annual minimum temperature (AnnualMinTemp [heat conservation]), (c) mean summer maximum temperature (SummerMaxTemp [heat dissipation]), (d) NPP estimate based on fluxes of carbon/nutrients and CO₂/water (CenW [productivity]), (e) NDVI calculated over growing seasons (GrowSeasNDVI [eNPP]), and (f) minimum seasonal values for precipitation minus potential evapotranspiration (MinSeasP – PET [seasonality]).

model here. Despite incorporating multiple predictors, the latter model estimated a strong spatial autoregression coefficient ($\lambda = 0.627$), confirming that those predictors could only account for some of the spatial signature in the data. Coefficient estimates from this model for the variables SummerMaxTemp and MinSeasP – PET were -0.240 ± 0.267 mm °C⁻¹ and 0.012 ± 0.007 mm mm⁻¹, respectively (Fig. 4; note that the confidence intervals for SummerMaxTemp overlap zero). There was a positive effect of island isolation on possum body size, both for the large island of Tasmania (4.46 ± 2.98 mm) and for the other (smaller) islands (2.17 ± 1.85 mm) (Fig. 4).

Discussion

Our study identifies primary productivity as the most important environmental driver of *Trichosurus vulpecula* body size (Fig. 4), confirming inferences from previous work by Yom-Tov and Nix (1986). However, our results suggest that productivity during the leanest season, rather than mean annual productivity, is the primary factor controlling adult body size of this species. Specifically, we found a positive relationship between minimum seasonal precipitation minus potential evapotranspiration (an index of minimum seasonal productivity) and condylobasal length (our chosen body-size

Table 2. Model selection for aspatial and spatial SAR models of *Trichosurus vulpecula* condylobasal length (CBL). The following is shown for each candidate model: 1) the coefficient of determination (R^2), 2) Akaike's information criterion corrected for small sample sizes (AICc), and 3) the change in AICc (δ AICc) relative to the top-ranked model within each model type. The spatial autoregression coefficient (λ) is also shown for the spatial SAR models. For each of the single-causal models, multiple putatively relevant covariates were tested but only the top-ranked model for each hypothesis is shown; mean minimum annual temperature (AnnualMinTemp), mean summer maximum temperature (SummerMaxTemp), NPP estimate based on fluxes of carbon/nutrients and CO₂/water (CenW), NDVI calculated over the growing seasons (GrowSeasNDVI) (eNPP), minimum seasonal values for precipitation minus potential evapotranspiration (MinSeasP – PET). For the both aspatial and spatial SAR models, the model selected was of the form CBL ~ SummerMaxTemp + MinSeasP – PET + island effect (Island) (bold type).

Model	Aspatial models			Spatial SAR models			
	R^2	AICc	δ AICc	R^2	AICc	δ AICc	λ
Null	–	2021.0	249.2	0.554	1791.7	47.9	0.869
Latitude	0.320	1901.1	129.3	0.567	1777.4	33.6	0.792
Mono-causal models							
AnnualMinTemp (heat conservation)	0.275	1921.3	149.4	0.554	1792.1	48.3	0.852
SummerMaxTemp (heat dissipation)	0.453	1832.2	60.4	0.596	1752.8	8.9	0.754
CenW (productivity)	0.277	1920.7	148.9	0.589	1764.2	20.3	0.833
GrowSeasNDVI (eNPP)	0.174	1962.5	190.7	0.570	1780.4	36.6	0.852
MinSeasP – PET* (seasonality)	0.461	1827.8	56.0	0.589	1758.0	14.1	0.75
Multi-causal models							
AnnualMinTemp + SummerMaxTemp†	0.460	1830.4	58.5	0.597	1754.7	10.8	0.761
AnnualMinTemp + CenW	0.440	1841.9	70.1	0.588	1765.5	21.6	0.816
SummerMaxTemp + MinSeasP – PET*	0.530	1786.6	14.8	0.598	1750.1	6.2	0.691
AnnualMinTemp + SummerMaxTemp + Island†	0.480	1822.4	50.6	0.603	1752.9	9.1	0.74
AnnualMinTemp + CenW + Island	0.498	1811.7	39.9	0.599	1757.2	13.3	0.761
SummerMaxTemp + CenW + Island	0.491	1815.5	43.7	0.609	1747.6	3.8	0.731
SummerMaxTemp + MinSeasP – PET + Island*	0.557	1771.8	0	0.608	1743.9	0	0.627

*For these models, the parameter estimate for MinSeasP – PET was positive in all cases which, while not consistent with the seasonality hypothesis, is consistent with the productivity hypothesis (i.e. body size increases as the severity of the least productive season lessens).

†For the spatial SAR models of this form, the parameter estimate for AnnualMinTemp was positive which is not consistent with the heat-conservation hypothesis.

representative). Notably, this result is in the opposite direction to the pattern predicted by the seasonality hypothesis, which posits that body size should increase (not decrease) as the severity of food shortages increases. This is not surprising given that the magnitude of fat storage in mammal species increases with absolute size (Lindstedt and Boyce 1985). It is likely not evolutionarily feasible for smaller mammals to store sufficient fat during more productive seasons to rely on this strategy for survival during leaner seasons. Thus, the seasonality hypothesis might not be applicable to *T. vulpecula*.

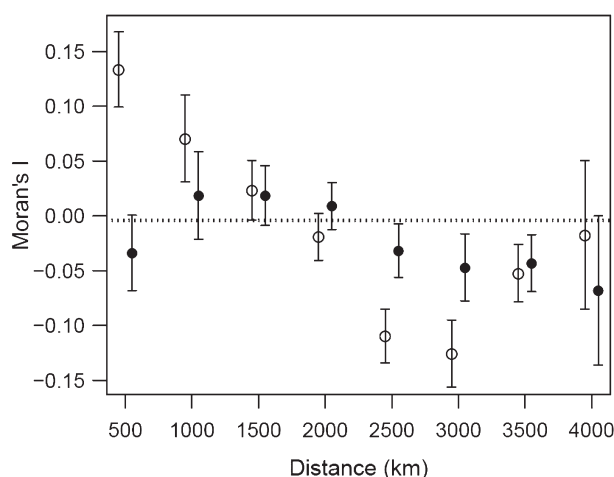


Figure 3. Plot of Moran's I values of both aspatial (open circles) and spatial SAR models (closed circles) at 500 km intervals. Values near +1.0 indicate positive spatial autocorrelation while values near –1.0 indicate negative spatial autocorrelation. Values near zero indicate a random spatial pattern.

Growing season NDVI was positively correlated with body size, which is predicted by Huston and Wolverton's eNPP hypothesis, but support for this relationship was very weak (Table 2, Fig. 2). Furthermore, our support for lean season

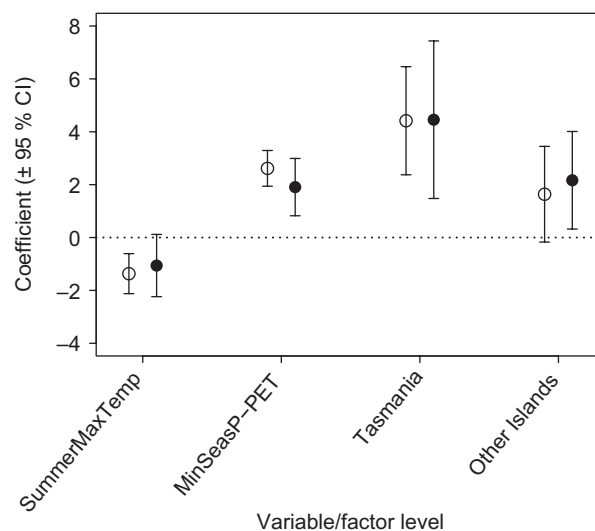


Figure 4. Plot of coefficients (\pm 95% CI) for each variable/factor level in the selected aspatial (open circles) and spatial SAR (closed circles) multi-causal model; mean summer maximum temperature (SummerMaxTemp), minimum seasonal values for precipitation minus potential evapotranspiration (MinSeasP – PET), Tasmania and all other islands. Note that the coefficients presented for the environmental covariates have been standardised to facilitate comparison (i.e. they represent the expected change in body size per unit change in standard deviation of the given covariate).

productivity is counter to the predictions of *eNPP*; where body size should increase with the productivity of the most (not least) productive season.

The negative relationship between summer maximum temperature and body size is consistent with the heat dissipation hypothesis, where body size decreases with increasing temperature to facilitate heat loss. Heat dissipation has been proposed to explain body-size differences in the eastern grey kangaroo *Macropus giganteus* (Prowse et al. 2014), in the male koala *Phascolarctos cinereus* (Briscoe et al. 2014) and within species of the North American woodrat genus *Neotoma* (Brown and Lee 1969, Smith et al. 1995). Our support for this hypothesis as an explanation for spatial body-size variation in *T. vulpecula* suggests smaller individuals occupying warmer environments are better able to facilitate heat loss giving them greater fitness than their larger conspecifics (James 1970, Speakman and Król 2010). Increased food availability and cooler temperatures therefore most likely explain increased body size of populations occurring in southeastern Australia (Fig. 1).

Bergmann's original heat-conservation hypothesis suggests that larger individuals are better able to conserve heat because of their lower surface-area-to-volume ratios. Annual minimum temperature showed a negative relationship with body size which follows that predicted by the heat-conservation hypothesis, where individuals should be larger in cooler regions. However, we did not find strong support for this hypothesis as a key explanation for spatial body-size variation in *T. vulpecula*. Our findings concur with those of Ashton et al. (2000) who reanalysed data from studies that included extensive samples and found no support for the hypothesis that smaller mammals conform more strongly to Bergmann's rule than larger mammals (Steudel et al. 1994), which would be expected if heat conservation were a key driver.

Trichosurus vulpecula exhibits a Bergmannian trend where body size increases with latitude and decreases with temperature, confirming previous studies (Yom-Tov and Nix 1986, Kerle et al. 1991). *Trichosurus vulpecula* in southwestern Australia is an exception to this rule, however, with body sizes in this temperate region more similar to those of the arid central and tropical northern populations than those of temperate southeastern Australia (Fig. 1). Today, the southwest is a habitat 'island' enclosed by ocean and the arid zone. Island dwarfing has previously been proposed to explain the diminutive size of isolated southwest populations of several large-bodied and wide-ranging Pleistocene mammals (Prideaux 2004). However, our analysis demonstrates that insular isolation positively influences body size in *T. vulpecula*. Body size in the southwest populations may instead be limited by factors such as high summer maximum temperatures or food quality potentially correlated with the low-nutrient soils of the region (Hopper and Gioia 2004). Alternatively, the smaller size in the southwest may merely be a product of declining productivity across southern Australia from east to west. *T. vulpecula* maintained a patchy if not continuous distribution across southern Australia until European settlement 200 yr ago (van Dyck and Strahan 2008). Future research could investigate the size of pre-European specimens from arid south-central Australia to assess whether these are similar in size to southwestern individuals.

Soil quality and/or soil nutrient availability have been proposed to play a significant role in primary productivity (Yom-Tov and Nix 1986, Huston and Wolverton 2011). Soil variables derived from datasets sourced from the Australian Soil Resource Information System (spatial grid = 0.0025°) (2012; <www.asris.csiro.au>) and the Food and Agriculture Organisation of the United Nations (2008; <www.fao.org>) (spatial grid = 0.083°) were included in our initial choice of environmental variables, but ranked poorly (Supplementary material Appendix 4). However, current soil datasets for Australia might not be reliable enough to rigorously test primary productivity related hypotheses because those datasets remain largely unvalidated (Roxburgh et al. 2004).

An increase in *T. vulpecula* body size on offshore islands is consistent with past observations based on much smaller sample sizes (Kerle et al. 1991). The results clearly demonstrate that *T. vulpecula* is larger on Tasmania and other islands than would be predicted by minP – PET and summermax-temp were they contiguous with the mainland. Traditional explanations for such patterns include reduced competition for food resources and/or reduced pressure from predation or parasitism (Lomolino 2005). In New Zealand, where *T. vulpecula* was introduced in 1837, in the absence of natural competitors and predators, individuals have been reported to weigh up to 6.3 kg (Fraser 1979).

Identifying the drivers of geographic body-size variation from a set of putative, correlated environmental covariates is challenging (Gür 2010, Yom-Tov and Geffen 2011). We have shown here that spatial SAR models and model selection criteria can help separate the effects of correlated environmental variables, thus shedding more light on the primary body-size drivers at hand. Spatial SAR models formulated within the maximum-likelihood framework are amenable to model comparison using standard information criteria (e.g. AIC, BIC) and also provide a direct measure of the strength of unexplained spatial autocorrelation in the response variable. For example, the top-ranked spatial SAR model for possum body size estimated a strong spatial autoregression coefficient ($\lambda = 0.627$), indicating that environmental drivers included in this study could only account for some of the spatial pattern in the data. Biotic variables not considered here may explain some of this shortfall. Predation has been suggested to influence body size in some species (Yom-Tov and Yom-Tov 2005), as have human impacts (Rowe-Rowe and Crafford 1992). Additionally, competition with sympatric species (Mukherjee and Groves 2007) may affect food availability which in turn can influence body size, but overall, competition has been found to be less important than environmental variables in explaining body-size gradients (Rosenzweig 1968, Blois et al. 2007).

Whether body-size patterns are ontogenetic (phenotypically plastic) or result from selection (genetically coded) or a combination of the two remains unclear. Possible experiments to test this might include: a) feeding captive animals different amounts of food to determine whether differences in growth endpoints (using skeletal parameters) result, and b) translocating individuals from one population to another in a different environment to investigate whether offspring more closely match the size of the parents or that of non-transferred conspecifics. Such experiments, however, may be

fraught with impracticalities, i.e. they require large sample sizes and long-term monitoring of individuals (Van Buskirk et al. 2010). Underlying genetic components accountable for body-size differences are however irrespective in terms of the outcomes of this study.

Conclusions

The relative importance of mechanisms driving geographic body-size variation in endotherms has long been a topic of debate in evolutionary ecology. In particular, much emphasis has been placed on the relative importance of either food availability (i.e. primary productivity) or thermoregulatory requirements. In this study, aspatial and spatial SAR models supported both lean-season primary productivity and heat dissipation as key explanations for geographic body-size variation in the common brushtail possum *Trichosurus vulpecula* Australia's most widespread marsupial. We therefore argue that hypotheses explaining body-size variation in endotherms should not be viewed as mutually exclusive and suggest that the forces of productivity and thermoregulatory requirements most likely interact or counteract to influence body size. The importance of either is undoubtedly dependent upon environmental circumstances, and may vary considerably between regions. For example, in the tropics, where we might expect food availability to be less restricted than in temperate regions, the ability to disperse heat (through being smaller bodied) might be more important in determining body size than food availability. Testing for the primacy of individual drivers between regions characterised by varying environmental conditions should be a key goal of future studies.

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Supplementary material (Appendix ECOG-01243 at <www.ecography.org/appendix/ecog-01243>). Appendix 1–4.