Determinants of body-size variation within Australian mammal species

by

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Dedicated to the memory of Donovan H. Correll (19/10/1928 – 23/03/2015), who never tired of responding to relentless questions from his young children about the sun and the clouds, the sheep and the dogs, the dirt and the rain. Thanks, Dad.

“The most obvious differences between different animals

are differences of size…”

J.B.S. Haldane (1928)

CONTENTS

ABSTRACT

Body size is arguably the most important character affecting the morphology, life history, physiology, behaviour, ecology, evolution and extinction probability of animal species. Spatial and temporal patterns of body-size variation have been well documented in many endotherms, particularly mammals. The most familiar pattern of body-size variation is Bergmann’s rule, which posits that, within endotherms, larger-bodied forms are found in cooler regions. Several hypotheses centring around thermoregulatory response, primary productivity (food availability) and seasonality, have been advanced to explain geographic body-size patterns, including Bergmann’s rule. The relative importance of various drivers within different taxa and regions has been the topic of much debate. To a significant degree this is due to biases in sampling, comparisons of varying geographic scales, and a lack of consideration of the potential impacts of, and interactions between, different potential drivers.

This study uses measurements from around 5,000 specimens representing seven Australian mammal species with continental distributions to examine spatial body-size patterns and explicitly test each of the major hypotheses typically advanced to explain such patterns. Highly correlated environmental variables were dealt with, in part, a) by comparing ‘aspatial’ regression models as well as spatial autoregression models that accommodate both single-cause and multi-causal explanations for spatial body-size variation within a species, b) using model selection procedure based on information criteria (AIC/DIC) to tease apart the best-supported body-size drivers, and c) excluding highly correlated environmental variables from the same fitted model. Moran’s I spatial

autocorrelation coefficients showed that spatial models were less spatially autocorrelated than the aspatial models. Thus, focus was placed on the spatial models. Spatial autoregression coefficients also indicated that environmental drivers included in those studies could only account for some of the spatial pattern in the data. Bayesian models were used to impute missing sex data, fit non-linear growth models and account for non-random spatial sampling methods.

Bergmann's rule, as a generalised pattern, is revealed within Australian marsupials that occupy a broad latitudinal / temperature range. Primary productivity and thermoregulatory requirements are evidently key counterparts in driving body-size evolution in the Common Brushtail Possum, *Trichosurus vulpecula,* and species of kangaroo (genus *Macropus*). These findings are consistent with a recent review (Yom-Tov & Geffen 2011), which concludes that food availability and ambient temperature are the principal predictors of body size. This thesis highlights the importance of multi-causal variables responsible for spatial body-size variation; i.e., body size is not driven by a single mechanism. Thus, hypotheses explaining body-size variation in endotherms should not be viewed as mutually exclusive.

Life-history theory predicts the progressive dwarfing of animal populations that are subjected to chronic mortality stress, but the evolutionary impact of harvesting terrestrial herbivores has seldom been tested. In Australia, marsupials of the genus *Macropus* (kangaroos and wallabies) are subjected to size-selective commercial harvesting. Contrary to expectation, skull measurements from wildlife collections spanning the last 150 years demonstrate a slight increase in body size in the Eastern and Western Grey Kangaroos, *Macropus giganteus* and *M. fuliginosus*, Red-necked Wallaby, *M. rufogriseus*, and Common Wallaroo, *M. robustus*. This may be in response to increased food and water availability due to European pastoral activities. Little evidence of temporal body-size change occurs in the Red Kangaroo, *M. rufus*, over this time period.

The island rule is a recognised pattern of body-size evolution, most often noted in mammals, where larger species are held to become smaller bodied and smaller species larger on islands. However, recent research has suggested that the island rule may not hold in most mammal groups. Using body-size measurements from mainland and island populations of *T. vulpecula* and the Australian Bush Rat, *Rattus fuscipes*, two fundamental features of the rule are refuted by showing that a) size shifts within a species are not unidirectional, and b) species with a larger initial (mainland) body mass can actually increase in size instead of decreasing in size, contrary to a core prediction of the island rule. Moreover, the absence of any detectable overall global island effect shows that the island rule is upheld in neither species. Island area, distance from mainland, interval of isolation, and numbers of competitors or predators exert no influence on island body-size patterns in these species. Rather, temperature is the best predictor of *T. vulpecula* island body size followed by productivity. However, predictors of *R. fuscipes* body size were unable to be demonstrated. Including covariates in model analyses and sampling from islands within distinct climatic zones likely has a critical bearing on the identification of island body-size patterns and their determinants.

In summary, productivity and thermoregulatory requirements appear to be the key drivers of spatial (including island–mainland) and temporal body-size evolution in several Australian marsupials and a rodent. Future studies might fruitfully extend the approaches employed here to other species within Australia and elsewhere. It would also be worth explicitly testing the degree to which Bergmann’s rule, as a pattern, is scale dependent through space and in relation to temperature, and whether environmental determinants of body size vary in their relative influence between regions. Studies of body-size patterns through the late Quaternary hold potential for exploring past influences of climatic and pre-European hunting practises on Australian mammals, which could provide an improved platform for refined predictions of the likely future impacts of changes in rainfall and temperature. Exploring the degree to which body-size patterns are phenotypically plastic or genetically coded should be another target of future studies. All in all, despite two millennia of pondering why animals are the size they are, it is clear that body-size studies still hold great potential for addressing key questions in ecology and evolution.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

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Rachel Correll

2 July 2015

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LIST OF PUBLISHED PAPERS AND MANUSCRIPTS

Chapters 2–5 are either published papers or manuscripts intended for publication in scientific journals as stand-alone pieces of work. For continuity, Chapters 2–3 (*Papers* 1–2) have been formatted in accordance with the other thesis chapters. Thus, there are subtle formatting differences between Chapters 2–3 and their published form.

Chapter 2

Paper 1. Correll, R.A., Prowse, T.A.A. and Prideaux, G.J. (2015) Lean-season primary productivity and heat dissipation as key drivers of geographic body-size variation in a widespread marsupial. *Ecography*, **38**, doi:10.1111/ecog.01243.

Chapter 3

Paper 2. Prowse, T.A.A., Correll, R.A., Johnson, C.N., Prideaux, G.J. and Brook, B.W. (2015) Empirical tests of harvest-induced body-size evolution along a geographic gradient in Australian macropods. *Journal of Animal Ecology*, **84**, 299–309.

Chapter 4

Paper 3. Correll, R.A., Prowse, T.A.A. and Prideaux, G.J. (in preparation). Environmental and human-induced body-size evolution in two widespread kangaroos with largely overlapping distributions

Chapter 5

Paper 4. Correll, R.A., Prowse, T.A.A., Gardner, M.G. and Prideaux, G.J. (in preparation). Is there really an island rule? An autecological approach reveals that determinants of mainland body size also rule on islands

PREFACE

Body size is arguably the single most obvious and fundamental character of an animal. It affects most aspects of physiology, morphology and life-history traits, and is strongly correlated with numerous other behavioural and ecological factors (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown *et al.* 2013). The study of body size has a long history in scientific discourse (Smith & Lyons 2013). Some of the earliest scientific essays date back to Aristotle (384−322 BC) and other ancient Greeks who speculated on factors underlying the body mass of organisms. Later, philosophers of the scientific revolution, e.g., Galileo (1564−1642), pondered why organisms are the size they are and the consequences of larger or smaller size. During the latter part of the 19th century, body size was considered within an evolutionary framework with particular interest in why body size evolved in certain trajectories (e.g., Darwin 1859; Wallace 1876). Since then, the study of body size evolution has become a major area within the fields of evolutionary and ecological biology.

Body-size evolution within species may be evident in spatial and or temporal dimensions and can be overlayed by factors such as anthropogenic practices, insularity (island rule) (Van Valen 1973) and sexual size dimorphism (Rensch's rule) (Rensch 1936). In recent decades, considerable research has gone into understanding patterns and determinants of body-size evolution within and across these systems; much of which has centred on how and why body size varies spatially. In particular, much emphasis has been placed on the relative importance of numerous factors including food availability (e.g., McNab 2010), thermoregulatory requirements (e.g., Speakman & Król 2010; Briscoe *et* *al.* 2015), selection against desirable phenotypes by humans (e.g., Allendorf *et al.* 2008), competition (e.g., Mukherjee & Groves 2007), predation (e.g., Yom-Tov & Yom-Tov 2005), and land-mass characteristics (i.e., island-specific traits) (e.g., Heaney 1978).

Despite extensive research on spatial body-size variation in mammals in North America and Eurasia, relatively little has been undertaken in Australia which has a unique mammalian fauna unlike those found elsewhere in the world, most notably marsupials and monotremes.

The overarching aim of this thesis is to examine spatial body size-variation in Australian mammals. Additionally, it examines body-size variation in a temporal dimension. Body-size observations from several species are used to examine generalised spatial, insular or temporal patterns within these species and to test several pivotal hypotheses proposed to explain such patterns.

CHAPTER 1

GENERAL INTRODUCTION

This introduction provides a detailed overview of background information underpinning the data chapters (2–5) and is subdivided into Aims; Part 1: Spatial body-size variation; Part 2: Human-induced body-size evolution; and Part 3: The island rule.

AIMS

The aims of this thesis are to investigate geographic (spatial) body-size patterns (e.g., Bergmann's rule) and determinants using skull measurements from seven Australian mammal species with continental distributions. Emphasis is placed on testing several well established hypotheses proposed to explain spatial body-size patterns, including those that centre around food availability and thermoregulatory requirements. Additionally, temporal body-size trends are explored in species of kangaroo post-European arrival in Australia (late 19th Century through 2009) and the potential effect of human-induced activities such as commercial harvesting practices and or increased food and water availability due to European pastoral activities are examined. Finally, body-size measurements from mainland and island populations of the Common Brushtail Possum, *Trichosurus vulpecula*, and the Australian Bush Rat, *Rattus fuscipes*, are used to test fundamental features of the island rule; e.g., do 'small' species get larger and 'large' species get smaller when isolated on islands?

PART 1: SPATIAL BODY-SIZE VARIATION

Historical account of biological interest in geographic variation of animal traits

Geographic variation of animal traits has long interested biologists given its central role in the evolution of species (e.g., Darwin 1859; Wallace 1876). Such variation was defined by Mayr (1963) as "the occurrence of differences among spatially segregated populations of a species". Ecogeographic rules describe similar patterns of variation within and across species and their relationship with geographic variables, particularly latitude and temperature. Several well-established ecogeographic rules have been formulated to explain spatial and environmental patterns between populations and within species (Mayr 1956). These include: Gloger's rule, which predicts that individuals living in warm, humid environments are darker in colour than those living in cold, dry environments (Gloger 1833); Allen's rule, which predicts that organisms from colder environments usually have shorter limbs or appendages than organisms from warmer environments (Allen 1877); and Bergmann's rule, which predicts that, within species of endothermic animals, larger-bodied individuals are found in cooler regions (Bergmann 1847).

Differentiation in body size is the most widely-studied form of geographic variation, probably because it is the single most obvious and fundamental character affecting morphology, life history, physiology, behaviour, ecology, evolution and extinction probability of animal species (Haldane 1928; Stanley 1973; Peters 1983; Schmidt-Nielsen 1984; Cardillo *et al.* 2005). Moreover, body size is one of the most prominent and readily measurable phenotypic attributes responsive to environmental changes through both space (e.g., Ashton *et al.* 2000; Meiri 2011) and time (e.g., Smith *et al.* 1995; Blois *et al.* 2007). Study of geographic, or spatial, body-size variation, particularly in relation to Bergmann's rule, has been well studied in Eurasia and North America, but not so in the Southern Hemisphere, including Australia.

How body size is measured

Defining body size, however, is not as straightforward as it may initially sound. Researchers generally equate body size with body mass, which can be measured directly or by proxy. The latter can either be a part or parts of the body (e.g., skull length) or a product (e.g., faecal pellets). However, body size and body mass need not mean the same thing. For example, within a species, a long, gracile individual might have a similar mass to a comparatively short, robust individual. Nonetheless, it is generally accepted that for comparative purposes relative measures should be acceptable as long as one compares the same character or element (see *Strength of body-size measures*).

Establishment of Bergmann's rule

Originally defined to apply both intra- and inter-specifically (see Clauss *et al.* 2013 *Appendix 1* for a translation of Bergmann's original manuscript), Bergmann's rule was recast by Rensch (1938), and later Mayr (1956, 1963), to apply only at the intraspecific level. More recently, Clauss *et al.* (2013) demonstrated a significant interspecific pattern. Nonetheless, the most widely used definition of the rule pertains to the intraspecific level (Medina *et al.* 2007). In the original paper, Bergmann (1847) concluded that "although it is not as clear as we would like, it is obvious that on the whole the larger individuals live farther north and the smaller ones farther south" (translated in James 1970). Bergmann treated latitude as a proxy for environmental temperature and, because of a general lack of detailed climatic measures until recent decades, many workers have essentially done the same in relation to temperature and also other environmental factors when investigating body-size variation (e.g., Langvatn & Albon 1986; Blackburn & Gaston 1996a). The rule was later reformulated again with the recognition of temperature rather than latitude *per se* as the key predictor of Bergmannian body-size patterns (Blackburn *et al.* 1999). Recently, it has been argued that Bergmann's rule is a pattern to be applied to studies of size variation with temperature or latitude in any taxon, and that the rule should be simply defined as "a tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes" (Meiri 2011, p. 205). Major advances in climatic assessment over the past decade, in particular, have allowed recent studies to more directly relate body size to climatic and environmental parameters (e.g., White & Searle 2007; Gür & Gür 2012).

Evidence for Bergmann's rule

A negative relationship between temperature and body size and/or a positive relationship between latitude and body size has been documented intraspecifically and/or interspecifically in invertebrates (e.g., Cushman *et al.* 1993; Van Voorhies 1996; Ho *et al.* 2010; Shelomi 2012; Manyak-Davis *et al.* 2013; Hassall *et al.* 2014), some ectothermic vertebrates, such as amphibians (Ashton 2002, 2004), fishes (Lindsey 1966; Fisher *et al.* 2010; Rypel 2014), turtles and lizards (Ashton & Feldman 2003; Olalla-Tárraga *et al.* 2006), and in birds (e.g., Kendeigh 1969; James 1970; Murphy 1985; Graves 1991, Yom-Tov 2001; Ashton 2002; Ramirez *et al.* 2008; Teplitsky *et al.* 2008; Olsen *et al.* 2009; Husby *et al.* 2011; Brommer *et al.* 2014). Bergmann's rule has been documented most widely, though, among mammals (e.g., Rosenzweig 1968; Brown & Lee 1969; Rees 1969; Kennedy 1984; Langvatn & Albon 1986; Yom-Tov & Nix 1986; Sharples *et al.*

1996; Ravosa 1998; Smith & Betancourt 1998; Wigginton & Dobson 1999; Ashton *et al.* 2000; Storz *et al.* 2001; Freckleton *et al.* 2003; Meiri & Dayan 2003; Blackburn & Hawkins 2004; Yom-Tov *et al.* 2006; Blois *et al.* 2007; Diniz-Filho *et al.* 2007; Ravosa 2007; White & Searle 2007; Lin *et al.* 2008; Harcourt & Schreier 2009; Schillaci *et al.* 2009; Smith *et al.* 2009; Tomlinson & Withers 2009; Fernandez-Duque 2011; Viranta & Kauhala 2011; Gür & Gür 2012; Zhang *et al.* 2012; Orcutt & Hopkins 2013; Briscoe *et al.* 2015).

Despite extensive evidence for Bergmannian body-size patterns across numerous taxa the validity of the rule has long been discussed. The following section focuses on the generalisation of the rule within mammal species.

Generalisation of Bergmann's rule

Mayr (1956, p.105) defined ecogeographic rules as "…purely empirical generalisations describing parallelism between morphological variation and physiogeographical features" and argued that if the majority, i.e., over 50%, of species studied conform to an ecogeographic rule, its validity should not be questioned (Mayr 1956, 1963). Although agreeing that recognition of a rule should at the very least imply that a pattern is seen more often than not, Blackburn *et al.* (1999 p. 166) suggested that Mayr's concept "is rather generous in respect of a "rule"".

Early support for the validity of Bergmann's rule comes from Rensch (1936), who concluded that the majority of North American and European mammals, 81% and 60% respectively, conform to the rule. However, the strength of Rensch's (1936) data has been criticized because they were taken from a field guide rather than from measurements of individuals from different localities (Scholander 1955; McNab 1971). McNab (1971) demonstrated that only 32% of 47 North American species of mammals show a positive relationship between body size and latitude. He argued that most mammals in North America do not follow the rule and those that do are usually carnivores or granivores. But a more recent review on the occurrence of Bergmann's rule by Ashton *et al.* (2000) criticizes McNab's method by pointing out that it limited sample size and geographic range over which a correlation between size and latitude was sought. Ashton and colleagues analysed data from the literature and found that 71% of 110 mammal species showed a positive correlation between size and latitude and that 75% of 64 mammal species showed a negative correlation between size and temperature. Similarly, Meiri and Dayan (2003) found that 65% of 149 mammal species follow the rule.

Some studies suggest that Carnivora is one of the mammalian orders in which the percentage of species obeying the rule is highest (Ashton *et al.* 2000; Meiri & Dayan, 2003). However, when Meiri *et al.* (2004) tested the validity of Bergmann's rule in 44 species of Carnivora using an unbiased sample and a liberal mode of vote counting (from data on patterns of correlation between skull length and geographical latitude), they found a significant positive correlation between body size and latitude in 50% of the species and a significant negative correlation in 11%. The occurrence of Bergmann's rule in carnivorous mammals might be less frequent than previously published data suggest (Meiri *et al.* 2004). Furthermore, species included in published studies of spatial body-size variation are argued to represent a biased selection of taxa chosen for study. Patterns of spatial size variation are more likely to be studied in cases where it is suspected beforehand, thus, Bergmann's rule could be viewed as an artefact of non-random sampling and submission of publication (Meiri *et al.* 2004).

A lack of evidence for Bergmann's rule, including evidence for converse patterns, has been observed intra- and inter-specifically in some mammals (e.g., Geist 1987; Cotgreave & Stockley 1994; Kamilar *et al.* 2012). Converse Bergmannian patterns, i.e., a negative correlation between body size and latitude, are evident within some carnivorans (Meiri *et al.* 2004). One example is that of hunter-killed Brown Bears, *Ursus arctos*, within the latitude range 60–68º N in Finland, where male body size decreases towards the North (Kojola & Laitala 2001). Further evidence for decreasing body size with increasing latitude has been observed in studies of rodents across three continents. Intraspecific analyses of body-size variation in two species of subterranean rodents (Tuco-tucos), *Ctenomys talarum* and *C. perrensi*, in Argentina show that Tuco-tuco body size decreases from 15.0º to 48.2º S (Medina *et al.* 2007). Similarly, Wood Mice, *Apodemus sylvaticus*, apparently increase from north to south across south-western Europe (Renaud & Michaux 2007). A converse Bergmannian pattern has also been reported in the Australian Sandy Inland Mouse, *Pseudomys hermannsburgensis* (Tomlinson & Withers 2009).

Body-size patterns opposite to those predicted by Bergmann's rule have also been reported in *Sorex* shrews (Mezhzherin 1964). Palearctic shrews from colder regions were found to be smaller than those from warmer regions. Similarly, in three of the five shrews, body size was negatively correlated with latitude, and the same trend, although not statistically significant, was also found in the fourth species (Ochocinska & Taylor 2003). Other examples of converse patterns come from Daurian Pikas, *Ochotona daurica*, of the Tibetan Plateau (Liao *et al.* 2006), Red Foxes, *Vulpes vulpes*, and Eurasian Badgers, *Meles meles*, in Denmark (Yom-Tov *et al.* 2003), and Southern Brown Bandicoots, *Isoodon obesulus*, in Australia (Cooper 1998).

Other studies suggest seemingly conflicting or ambiguous examples of Bergmannian patterns. Decreased body size from north to south has been demonstrated in Jungle Cats (*Felis chaus*) in the Palearctic region (Meiri *et al.* 2004), but Bergmann's rule is largely not observed in India and part of Israel between latitudes 24º and 34º N (Mukherjee & Groves 2007). Similarly, Red Fox body size increases with latitude in the Palearctic region, but little change of body size occurs in the Saharo–Arabian region (Dayan *et al.* 1989). Bergmann's rule is evident in Ermine Weasels, *Mustela ermine*, of North America (Ralls & Harvey 1985), but weasel body size does not increase with latitude in Ireland (Fairly 1981) or Russia (Petrov 1962). Least Weasels, *M. nivalis*, of North America and most of Europe do not increase in size with latitude (Kratochvil 1977a, b) and, in fact, decrease with latitude in Sweden (Stolt 1981). Ambiguous Bergmannian patterns are also evident in the Eastern Cottontail, *Sylvilagus floridanus*, which follows Bergmann's rule in the northeastern USA and southern Canada, but not in southeastern USA. Furthermore, in southwestern USA and northern Mexico, Cottontail body-size decreases with increasing latitude (the reverse of Bergmann's rule), but increases with cooler summer environment (Olcott & Barry 2000).

In summary, the validity of Bergmann's rule in mammals remains unresolved. Many individual, autecological and synthetic studies, and reviews have apparent analytical flaws, e.g., limited sample size and limited measurements of individuals from different localities (i.e., poor sampling in space). Furthermore, non-random sampling of study species and their geographic range, as well as a tendency to focus on species wherein Bergmannian patterns are already suspected, have combined to hinder validation of the rule (Meiri *et al.* 2004). However, despite examples of deviations from the rule, there is general support at the intraspecific level, i.e., more species show a positive relationship between body size and latitude, and/or a negative relationship between temperature and body size than the converse (Meiri & Dayan 2003). Although identifying the presence or absence of Bergmannian patterns is an important starting point, it is more biologically interesting and challenging to reflect on why spatial patterns in body size of any kind exist in mammal species. What selective pressures drive the evolution of body-size variation between populations?

Hypotheses proposed to explain spatial body-size patterns

Most hypotheses proposed to explain spatial body-size patterns centre around heat conservation, heat dissipation, seasonality or primary productivity (e.g., Smith *et al.*1995; Wigginton & Dobson 1999). The following five subsections document the development of each of the principle existing hypotheses. These are followed by a consideration of other explanations posed to explain body-size patterns, in addition to the idea that multiple mechanisms may act together to influence body size. Potential problems associated with evidence supporting the principle hypotheses are considered in the summary at the end.

Heat conservation

Bergmann (1847) hypothesised that heat-conservation requirements formed the basis of the spatial body-size patterns that he observed. He proposed that individuals should be larger in cooler regions because of their lower surface-area-to-volume ratios. A greater increase in size involves a more rapid increase of volume than surface area, and since heat production of an endotherm is related to its volume, and heat loss is related to its surface, larger animals will tend to produce more heat while losing relatively less heat, an advantage in cooler climates. Known as the heat-conservation hypothesis, this explanation has traditionally been applied to Bergmann's rule at both the intraspecific and interspecific level (Mayr 1956, 1963; James 1970). Support within mammals comes from two experimental studies (Barnett & Dickson 1984; Riek & Geiser 2012) and a recent non-experimental study which found that body size of female Koalas, *Phascolarctos cinereus*, is most strongly associated with minimum annual temperature (Briscoe *et al.* 2015).

However, this explanation for the rule has been questioned by Blackburn *et al.* (1999, p. 171) who point out "the fact that body size and climate change are inversely correlated of itself provides no evidence as to why that relationship should arise. Other evidence is needed in support of the importance of heat conservation as the cause of the correlation". Ashton *et al.* (2000) reanalysed data from significant or extensively sampled studies and found no support for the hypothesis that smaller mammals conform more strongly to Bergmann's rule than larger mammals (cf. Porter *et al.* 1994; Steudel *et al.* 1994), which is expected if heat conservation is the cause. Also, head length and body length of the Long-tailed Macaque, *Macaca fascicularis*, increases with increasing latitude (Schillaci *et al.* 2009). These body-size variables, however, were not correlated with temperature, but rather minimum rainfall. In another study, average body mass (obtained from published literature) of non-volant terrestrial mammal species native to the Nearctic was found to be strongly correlated with temperature in the northern Nearctic. In contrast, across the Neotropics mammals are largest in the tropical and subtropical lowlands and smaller in the Andes, generating a positive correlation with temperature (Rodríguez *et al.* 2008). This prompted the authors to suggest that the heat-conservation hypothesis might need to be reformulated to include nonlinear relationships between body size and temperature over very broad geographical scales.

Negative evidence for heat conservation as a primary driver of body size also occurs in non-mammalian taxa. Body mass (and marginally also tarsus length) in the Israeli Chukar Partridge, *Alectoris chukar*, declines significantly with decreasing latitude in accordance with Bergmann’s rule, but ambient temperature was found to explain a much smaller fraction of the variation in body mass than evapotranspiration (Yom-Tov *et al.* 2002). Others have suggested that the inferred thermoregulatory explanations for heat conservation are compromised because Bergmann’s rule also applies to many ectotherms, which normally do not actively maintain a temperature different from that of the environment (Ashton 2001; Ashton & Feldman 2003).

Heat dissipation

Viewed from the opposite thermal extreme, spatial body-size patterns might also conceivably arise from the need to dissipate heat in warmer areas; decreased body size would be favoured because it results in increased surface-area-to-volume ratios. Evidence in support of a role for heat dissipation is found within four species of the woodrat genus, *Neotoma*, from western USA, where it may be advantageous to have smaller body masses in warmer, moist climates where evaporative cooling is more difficult (Brown & Lee 1969). The heat-dissipation hypothesis was first clearly elicited by James (1970), who noted that intraspecific body-size variation for 12 North American bird species (using wing length measurements as an indicator of body size) was more strongly related to wet-bulb than dry-bulb temperature. That is, due to the greater challenge of keeping cool, inhabitants of warm, humid environments were smaller than those living in warm, dry environments. The latter were held to be able to lower their body temperature by evaporative cooling; individuals living in sultry conditions must keep cool by lowering their rate of heat production (James 1970). Since heat production scales positively with body size, individuals can reduce heat production by being small bodied.

This hypothesis has been used to explain temporal body-size changes in *Neotoma cinerea* (Smith *et al.* 1995). Measurements from faecal pellets preserved in woodrat palaeo-middens were used to estimate body-size changes over the past 25,000 years. Changes closely tracked modelled and estimated temperature fluctuations where body-size decreased during periods of climatic warming, presumably reflecting the capacity of smaller individuals to dissipate heat and, hence, survive the stress of high ambient temperatures. Brown's unpublished data from laboratory experiments conducted in the 1960s was used to demonstrate that upper lethal temperature declines with body mass in *N. cinerea* (Smith *et al.* 1995), thus demonstrating the advantage of small body mass in warmer climates. Heat dissipation has also been proposed to explain body-size differences in male *Phascolarctos cinereus* (Briscoe *et al.* 2015).

Similarly, a concept dubbed the heat-dissipation limit theory has been applied to an idea that endotherms have an upper boundary on total energy expenditure imposed by the maximal capacity to dissipate body heat and, therefore, avoid the detrimental consequences of hyperthermia (Speakman & Król 2010). It is argued that smaller individuals in warmer areas are selectively advantaged by having a higher surface area-to-volume ratio than their larger conspecifics to promote greater heat dissipation, regardless of ambient moisture. The effects of extreme high temperatures on mortality rates of the Australian Black Flying-fox, *Pteropus alecto*, which are extending their range southward on the east coast of Australia, exposing them heatwave conditions above 41°C, show that rates are higher in adult females than males (Welbergen *et al.* 2007). Although sexual dimorphism does not occur within *P. alecto*, all females sampled from one of two sites were lactating, a period in the mammalian life cycle that is energetically demanding (e.g., Miller 1975). This finding is consistent with the heat-dissipation limit theory, which also predicts that females are beset by greater selective pressure to reduce body size in warmer conditions (Speakman & Król 2010).

Primary productivity hypothesis and the resource rule

The primary productivity hypothesis is based on Rosenzweig's (1968a) proposal that body size increases with increasing photosynthetic resource availability (primary productivity), rather than with decreasing temperatures. In his study on mammalian carnivores, Rosenzweig analysed body size against variables such as primary productivity (represented by annual actual evapotranspiration), temperature, latitude, competitive pressure and size of potential prey. He found that total primary productivity was one of the better correlates: "low productivity sets a limit to the body sizes animals can achieve" (Rosenzweig 1968a, p. 310).

Primary productivity has received strong support as a key driver of spatial body-size variation in numerous mammal species. A study of five Australian mammals found that body size in four of the species correlated better with indices of biomass productivity (moisture index and precipitation) than with temperature (Yom-Tov & Nix 1986). However, since biomass productivity and ambient temperature are related to some extent, it was difficult to separate their effects. Similarly, body size in *Sorex* shrews is generally larger in environments with higher primary productivity (measured as actual evapotranspiration) (Ochocinska & Taylor 2003).

The influence of geographic variables, such as latitude, longitude and elevation, as well as biological variables, such as vegetation, number of congeneric species, temperature and precipitation, were examined on spatial and temporal body-size patterns in California Ground Squirrels, *Spermophilus beecheyi* (Blois *et al.* 2007). Body size of modern populations was found to conform to Bergmann's rule with larger individuals in northern (wetter and cooler) portions of California (Blois *et al.* 2007). Using a model-selection approach, it was determined that precipitation, rather than temperature or other variables, may best explain variation in body size across modern spatial gradients. Precipitation may thus reflect the importance of primary production and overall forage availability in structuring body size within Ground Squirrels (Blois *et al.* 2007).

Introducing the "resource rule", McNab (2010) expanded on the primary productivity hypothesis by suggesting that body-size patterns reflect the availability and characteristics of consumed resources and in some cases the necessity to share resources with competitors. Body-size changes in Scottish populations of the Red Fox, *Vulpes vulpes*, are said to be determined by prey availability (Kolb 1978). Since the length of night available for hunting could determine the probability of finding food, it has been suggested that the observed Bergmannian body-size pattern is the result of increasing dark-time hunting hours at higher latitudes during winter (Kolb 1978). Additionally, a reanalysis of body-size data of Holarctic Foxes (from Davis 1977) showed that the correlation between body size and latitude was stronger than that of temperature (Kolb 1978). Evidence of human-induced changes in food availability has also been related to body-size differences. An increase in size of the Red Fox, *Vulpes vulpes*, and Eurasian Badger, *Meles meles*, is probably due to contemporaneous changes in Danish agriculture and land use, which, in turn, resulted in changes to the fox and badger diets (Yom-Tov *et al.* 2003).

Competitive resource availability has been proposed to explain body-size differences in the Jungle Cat, *Felis chaus*, from Israel and India (Mukherjee & Groves 2007). Cranial and dental measurements were related to independent variables such as competitive species richness, latitude, longitude, temperature and precipitation. Data from a narrow band between latitudes 24.0°N and 33.9°N, where Bergmann’s rule was largely not evident, showed that the Israeli Cats (western population) were 43% heavier than the Indian Cats (eastern population), and that body-size was negatively correlated most strongly with competitive species richness. Character displacement via sympatry with competitive species has also been used to partly explain body-size variation in species of Palearctic *Sorex* (Ochocinska & Taylor 2003), and to account for smaller size of the Red Fox in the Saharo-Arabian region, where it is sympatric with Ruppell’s Fox, *V. ruppelli* (Dayan *et al.* 1989).

In summary, competition with sympatric species may affect food availability, which in turn can influence body size via character displacement, but overall, competition *per se* appears less important than environmental variables in explaining body-size gradients (Rosenzweig 1968a; Blois *et al.* 2007).

Seasonality hypothesis

The ability to survive in environments with high climatic variability, such as those at high latitudes, has also been proposed to explain spatial body-size differences (Lindsey 1966; Boyce 1978; Geist 1987). Because energy stores increase with body size and energy requirements per unit mass decrease with body size (Lindsey 1966; Calder 1984;

Lindstedt & 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, body size is expected to increase where there is increased seasonality and low predictability of environmental conditions (i.e., in more seasonal environments). This would be an advantage at high latitudes where food resources are often seasonally scarce.

Within mammals, the seasonality hypothesis has been suggested to explain evidence of Bergmann's rule in cetaceans (Brodie 1975), Muskrats, *Ondatra zibethicus* (Boyce 1978), and Anatolian Ground Squirrels, *Spermophilus xanthoprymnus* (Gür 2010). It has been suggested that, during seasonal periods of resource abundance, natural selection favours individuals with rapid growth to a large size, while concurrently enhancing survivorship through oncoming periods of resource shortage (Boyce 1978).

*e*NPP hypothesis

An alternative explanation for geographic body-size variation based on food availability posits that body size is regulated by the net primary productivity (NPP) of plants during the growing season (Huston & Wolverton 2009, 2011). Initially dubbed the '*e*NPP (ecologically and evolutionarily relevant NPP) rule', this concept specifically refers to NPP that is available to meet the energetic and nutritional requirements of animals (and plants) during that time when they are reproducing and growing. This differs from NPP, which conventionally refers to annual rate of plant growth.

The lack of latitudinal body-size patterns observed within the tropics and the decline in body size in regions above approximately 60°N, which also link with soil quality and soil-nutrient availability, have also been explained by *e*NPP (Huston &

Wolverton 2011). Despite high solar energy input and rainfall, soils are often infertile in the tropics due to rapid soil weathering and nutrient leaching processes (Uehara & Gillman 1981, Richter & Babbar 1991). In the Northern Hemisphere temperate zone, where these processes are slower and periodic glaciation may refresh mineral resources, soil fertility tends to be higher. And in the Arctic, though soils are rich, the growing season is extremely short due to limited solar energy input and extreme low temperatures (Huston & Wolverton 2011).

Equivocal support for *e*NPP arose from a study of Richardson's Ground Squirrel, *Urocitellus richardsonii*, of North America (Gür & Gür 2012). Mean growing-season (April–August) Normalized Difference Vegetation Index (NDVI), a proxy for primary productivity, was proposed as a likely driver of geographic body-size variation in this species. However, growing-season NDVI collectively represented both *e*NPP and primary productivity; the effects of annual NDVI were not investigated. Furthermore, soil variables were not considered in the analyses (Gür & Gür 2012). As yet, the *e*NPP hypothesis *per se* remains untested, and holds the potential to effectively explain general body-size patterns often observed across latitudinal gradients.

On reflection, it is important to note that ecogeographic rules (e.g., Bergmann's rule) can exist irrespective of the validity of the physiological explanations (Mayr 1956). The suggestion, therefore, that Bergmann's heat-conservation explanation for the rule is invalid does not affect the validity of the empirical pattern (Mayr 1956). This distinction is important because Bergmann's rule and his explanation for it have been merged in the past (e.g., Geist 1987; Wiggington & Dobson 1999; Ashton *et al.* 2000; Schillaci *et al.* 2009).

Other proposed mechanisms

Predation pressure has been proposed to influence body-size variation. Large size in European mustelids purportedly reduces avian predation risk and may help explain the converse Bergmannian trends of stoats and weasels (Karpimäki & Norrdahl 1989). Similarly, because smaller-bodied species of *Sorex* shrews may have easier access to burrows and cover, smaller individuals may be more likely to avoid predation than larger individuals (Yom-Tov & Yom-Tov 2005).

Life-history characteristics may also be correlated with body size. Delayed maturity, increased litter size, increased offspring size or increased adult body size may explain Bergmannian body-size clines in cooler environments or at higher latitudes (Ashton *et al.* 2000). For example, higher growth rates and longer maturation rates characterise Swedish Moose, *Alces alces,* in colder areas compared with moose in warmer areas (Sand *et al.* 1995). Also, litter size for mammals in general increases with latitude (Lord 1960) and offspring size may be larger in cooler areas, which should increase overwintering survival (Cameron & McClure 1988). Although it may be possible that Bergmann’s rule is, at least in part, a result of selection acting on life-history characteristics, selection on litter size alone cannot be a general explanation in light of the variety of mammals that follow Bergmann’s rule that do not have variable litter sizes (Ashton *et al.* 2000). The idea that selection on life-history characteristics influences body-size patterns is probably a case of ‘the tail wagging the dog’. Body size itself likely determines life-history attributes, not the reverse.

Hypoxia has been proposed as an explanation for body-size differences in the Daurian Pika, *Ochotona daurica*, which lives at high altitudes in the Tibetan Plateau (Liao *et al.* 2006). Size is negatively correlated with altitude and thus positively correlated with temperature and oxygen concentration. Smaller body size at higher altitudes is secondarily attributed to limited food availability, due primarily to a short frost-free period (Liao *et al.* 2006).

Other possible mechanisms put forward to explain body-size patterns are more applicable at the interspecific rather than intraspecific level. The habitat-availability hypothesis has been advanced to explain spatial body-size differences in birds of North and South America (Hawkins & Diniz-Filho 2006), and co-opted to account for the greater topographic habitat zonation associated with stronger mesoscale climatic gradients, which purportedly limit the occurrence of large non-volant mammals in Neotropical mountainous areas (Rodriguez *et al.* 2008). Specifically, mammals are largest in the tropical and subtropical lowlands and smaller in higher altitudes of the Andes, generating a positive correlation with temperature. A likely explanation for such gradients is that reduced habitat sizes in mountains limit the presence of larger-sized mammals (Rodriguez *et al.* 2008).

Two possible mechanisms pertaining to phylogenetics have been proposed (Blackburn & Gaston 1986a; Blackburn *et al.* 1999; Blackburn & Hawkins 2004). The random-colonisation hypothesis proposes that larger body mass at higher latitudes may result from random ancestral colonisation and subsequent diversification. The covariation-with-mass hypothesis proposes that larger body mass at higher latitudes may result from the selective advantage of traits that happen to be tied to body mass. In addition, the migration-ability or dispersal-hypothesis, also directed interspecifically (Blackburn & Gaston 1996b; Blackburn *et al.*1999; Blackburn & Hawkins 2004), suggests that small body mass is associated with low dispersal ability. That is, small-bodied species are underrepresented at high latitudes because they have failed to disperse to these latitudes as often as have large-bodied species. In a review of geographic gradients in body size (Blackburn *et al.* 1999), random colonisation and covariation with body mass is exemplified as highly unlikely because of phylogenetically controlled analyses of birds, amphipods and isopods that show evidence for Bergmann's rule (Poulin 1995; Poulin & Hamilton 1995; Blackburn & Gaston 1996a). This hypothesis is further refuted because taxa show Bergmann's rule in areas that were covered by glaciers within the last 20,000 years (Cushman *et al.* 1993; Blackburn & Gaston 1996a, Klicka & Zink 1997), far too recent for speciation to have caused Bergmannian patterns (Blackburn *et al.* 1999). The dispersal hypothesis has been considered as unlikely because even the smallest bird species can migrate long distances (e.g. ruby-throated hummingbird, *Archilochus colubris*) (Blackburn *et al.* 1999). Furthermore, results of an analysis of body size in northern North American mammals show no relationship between time since glacial retreat and body mass (Blackburn & Hawkins 2004).

Multiple mechanisms

Spatial body-size patterns within mammal species may feasibly be driven by multiple factors. For example, the heat-conservation hypothesis, heat-dissipation hypothesis and seasonality hypothesis each received support for the Bergmannian pattern exhibited by North American bobcats, *Lynx rufus*, after the association between selected environmental variables and body size, was examined (Wigginton & Dobson 1999). Nevertheless, the heat-dissipation hypothesis received the strongest support, whereas the productivity hypothesis received no support. Wigginton and Dobson (1999, p.810) summarised by stating "these mechanisms are not easy to tease apart, as many of the climatic variables are intercorrelated". Others also point out the dilemma of discriminating between the proposed hypotheses because each hypothesis pertains to changes in environmental variables that are often highly correlated (e.g., Yom-Tov & Nix 1986; Gür 2010). Correlation between the environmental variables at hand should thus be considered when investigating body-size drivers.

It seems, therefore, that the adaptive influence exerted on animal body size by these various mechanisms might better be viewed as a collective: no single explanation can adequately describe all cases of Bergmannian size clines (Mayr 1963; Lawton 1996; Yom-Tov *et al.* 2002), or indeed other spatial body-size patterns. A goal for future research, therefore, should be to resolve the relative importance of and interplay between the various factors potentially contributing to observed body-size distribution patterns.

Hypotheses summarised

The sum of evidence suggests that Bergmann's own explanation for spatial body-size patterns (Bergmann's rule), that larger animals are better adapted to cooler conditions because of a reduced surface area-to-volume ratio (i.e., heat conservation), may be invalid or only part of the explanation. Although several studies have found close concordance between morphology and climatic variables, thereby supporting one or more of the remaining principle hypotheses (see above examples), the cautionary axiom 'correlation does not imply causation' is appropriate. This is because a climatic variable is usually correlated with other climatic variables which may actually be the factor or factors of interest, e.g., total annual precipitation is positively correlated with the predictability of precipitation (Boyce 1978). Furthermore, a climatic regime may result in particular habitat conditions, or may enhance the survival of a competitor, predator or parasite.

As Blackburn *et al.* (1999, p.169) lament “there is a fundamental gap in our knowledge about the mechanism of the rule and after 150 years, we still do not know what the mechanism is, or, indeed, whether there is only one. It is evident therefore, that much more empirical work is needed to determine the contributions of these proposed mechanisms to the overall trend”.

Strength of body-size measures

Bergmann’s rule has been framed in terms of body mass rather than a looser definition in terms of body size (Blackburn *et al.* 1999). This appears more rational because changes in body mass with latitude may be accompanied by changes in body shape (i.e., Allen’s rule). For instance, body mass may increase with latitude while some linear dimensions decrease. Restricting Bergmann’s rule to mass avoids these complications and indeed mass is commonly used as a measure of body size (Blackburn *et al.* 1999). In a review on the occurrence of Bergmann’s rule in mammals (and birds), studies using different characters as surrogates for body size were found to differ in their adherence to Bergmann’s rule (Meiri & Dayan 2003). Body mass in mammals conformed more to Bergmann’s rule, while linear measurements and dental measurements showed a weaker tendency.

Body mass may be a useful measure of size when comparing species that cover a broad size range, but it is often a poor measure for fine-grained comparison within species or among very similar species because of its high variability (Ralls 1976). Mass may vary according to season, physical condition of the animal, length of time since last feeding, reproductive condition and other factors, such as fur soaked by rain. Head plus body length (total body length minus tail length) has also often been used as a measure of body size (e.g., Rosenzweig 1968; McNab 1971; Boyce 1978; Kojola & Laitala 2001; Medina *et al.* 2007). Silva's (1998) finding that correlation of head plus body length and body mass in the terrestrial mammals is very tight ($r = 0.99$) suggests that either of these measurements are in general sound for relating body size. However, this study examined body mass across taxa; within species this correlation is likely to be significantly lower. Furthermore, using head plus body length, which must be estimated from field measurements of total length and tail length, as a direct measure of body size in many instances is limiting because these measurements are not always recorded by field mammalogists (Ralls & Harvey 1985).

Boyce (1978) suggests that skeletal measurements are usually much better indicators of body size than mass or head plus body length because of the high degree of variability of mass and potential difficulty in obtaining head plus body length measurements. Skull measurements, in particular, have several advantages over other measures such as head plus body length. They can be measured precisely and may allow the largest possible sample size because many 'skull-only' specimens in museum collections can be included. Examination of skulls also allows specimens to be aged (Ralls & Harvey 1985) and can include fossils. Cranial data, however, does have its boundaries as Rosenzweig (1968, p. 300) points out in his study on mammalian carnivores "Cranial data could not be used in this work since, though such measurements are more accurate and have a smaller coefficient of variation, they are equivocal. Part of the skull is, after all, the trophic apparatus and the size and shape of the cranium could be responding independently of body size to various selective pressures". Similarly, caution is recommended when using dental measures as surrogates for body size because selection may act differentially on them, leading to low correlations between the two measures (Meiri & Dayan 2003). For example, dental characters are likely to be influenced by factors associated with feeding, such as prey size and competition from sympatric species (Dayan & Simberloff 1996).

Despite the cautionary views of Rosenzweig (1968) and Meiri and Dayan (2003), cranial-dental data often correlates highly with body mass. For example, condylobasal length (von den Driesch 1976), a measure of skull length frequently used as a substitute for body size (e.g., Hagmeier 1958; Ralls & Harvey 1985; Janis 1990; Reynolds 2002; Mukherjee & Groves 2007), has been demonstrated to correlate relatively highly with body mass (e.g., $r^2 = 0.941$[Reynolds 2002]; $r^2 = 0.957$ [Millien 2008]). Similarly, in a study on body-size estimation of extinct rodents, a strong correlation between lower tooth row length and body mass was determined in 75 species of extant rodents ($r^2 = 0.94$) (Hopkins 2008). In a study on the prediction of extinct marsupial body mass, upper molar occlusal row length was determined as the best dental predictor of body mass among 38 extant marsupials (adjusted $R^2 = 0.967$) (Myers 2001).

The 'best' measure

Deciding how to best measure body size can be influenced by numerous factors, including: level of comparison, availability of body mass and/or head plus body length measurements, availability of skeletal elements, and tightness of the correlation of elements with body mass. Caution should be exercised when using skeletal elements with previously determined r^2 values, because many tests of correlation used averaged body-mass data (either within or between species) from reference books (e.g., Freckleton *et al.* 2003). To summarise, all measurements have inherent 'errors', but some are better than others. For comparative purposes, relative measures should be acceptable as long as one compares apples with apples. For example, average width of faecal pellets from live-trapped woodrats (*Neotoma* species) housed in a laboratory correlated well with body mass ($r^2 = 0.69$, prediction error = 21%) (Smith *et al.* 1995). Thus, faecal pellets have been used an indicator of temporal body-size changes in woodrats (Smith *et al.*1995, Smith & Betancourt 1998, 2006). Ultimately, the best way is to determine the inherent “errors” for each available measurement, then choose those measurements that have lowest “errors”.

Measurement error

Measurement error can arise from a number of sources, including observer inexperience, intra- and inter-observer variability (Blackwell *et al.* 2006), inherently flexible or ill-defined metrics (Bailey & Byrnes 1990), and a greater likelihood of larger errors with smaller measurements (i.e., in small species) (Freckleton *et al.* 2003). All may obfuscate the true pattern and should, therefore, be considered when collecting, analysing and interpreting data. Observer consistency may be optimised by a) having one person do the measurements and being rigorously consistent in approach when doing so; and b) being very explicit in how measurements were taken so that future work may faithfully repeat the methods or determine the basis for any consistent differences.

Previous studies of spatial body-size variation in Australian mammals

Study of spatial body-size variation in mammals, particularly in relation to Bergmann’s rule, has been intense in North America (e.g., Kennedy 1984; Wigginton & Dobson 1999; Blois *et al.* 2007; Smith *et al.* 2009) and Eurasia (e.g., Langvatn & Albon 1986; Sand *et* *al.* 1995; Sharples *et al.* 1996; Renaud & Michaux 2007; Schillaci *et al.* 2009). This is not so in the Southern Hemisphere, including Australia, which has a unique mammalian fauna that evolved in isolation for 40 million years prior to the collision of the continent with Southeast Asia in the Miocene (Black *et al.* 2012). It is the only continent on Earth where monotreme, marsupial, and placental mammals coexist. To date, however, there have been very few studies of geographic size variation in Australian mammals, despite observations on geographic size clines as early as the late 19th century. Spencer (1893, p. 109) noted that in the Short-beaked Echidna, *Tachyglossus aculeatus*, “we see a gradation in size, the New Guinea being the smallest and Tasmanians the largest”.

Yom-Tov and Nix (1986) published the first work on the effect of latitudinal or climatic variation on Australian mammals. All five species studied (Long-beaked Echidna, *Tachyglossus aculeatus*; Common Brushtail Possum, *Trichosurus vulpecula*; Eastern Grey Kangaroo, *Macropus giganteus*; Western Grey Kangaroo, *M. fuliginosus*; Red Kangaroo, *M. rufus*) showed trends that conform to Bergmann’s rule. In four of the five species, they found that body size was often better correlated with indices of biomass productivity than temperature, but since these factors are correlated they found it difficult to separate their effects. In addition, since few specimens used in their analysis had the required minimum set of body measurements, Yom-Tov and Nix (1986) considered their study preliminary. Consistent with Bergmann’s rule, body size of *Phascolarctos cinereus* and three glider species, *Petaurus breviceps*, *P. norfolcensis* and *P. australis* has been found to decrease substantially towards the tropics (Smith 1973; Russell 1984; Quin *et al.*1996; Briscoe *et al.* 2015).

Three other published studies on native Australian mammals do not reveal clinal variation in accordance with Bergmann’s rule. Differences in body size occur among populations of the Mountain Brushtail Possum, *Trichosurus caninus*, but no likely cause could be identified (Lindenmayer *et al.* 1995). Body size in the Southern Brown Bandicoot, *Isoodon obesulus*, was not correlated with rainfall or temperature but was related to habitat structure; larger individuals were found in open forest habitats and smaller individuals among swamp reeds (Cooper 1998). It has been speculated that body mass of the Sandy Inland Mouse, *Pseudomys hermannsburgensis*, may be influenced by factors such as food availability or heterothermy and sociality rather than latitude or ambient temperature (Tomlinson & Withers 2009).

Reversed Bergmannian patterns observed in the Platypus, *Ornithorhynchus anatinus,* at small scales or within an individual river basin in south-eastern Australia might pertain to suitable platypus habitat, where relatively lower rainfall and higher temperatures are typically associated with larger-bodied individuals (Furlan *et al.* 2011).

Australia: an ideal platform for body-size studies

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 (Australian Bureau of Meteorology 2008). A substantial decline in rainfall also occurs from near the coast to the arid interior. The bulk of Australia lies between latitudes 10°41’S (Cape York, Queensland) and 43°38’S (South East Cape, Tasmania), and between longitudes 113°.09’E (Steep Point, Western Australia) and 153°38’E (Cape Byron, New South Wales). This marked latitudinal *and* longitudinal variation makes Australia ideal for examining environmental drivers of mammalian body size.

Over the last two decades there have been significant refinements in how data are collected on biological surveys and stored within museum collections, such that a broader range of variables are now recorded. Climatic and environmental data are also now more detailed and broadly available for analysis, which is particularly critical as a foundation for this thesis. This is exemplified in Chapter 2, in which I use Australia's most widespread marsupial, the Common Brushtail Possum, *Trichosurus vulpecula*, as a model species to test five proposed drivers of geographic body-size variation: heat conservation, heat dissipation, primary productivity, seasonality and *e*NPP.

PART 2: HUMAN-INDUCED BODY-SIZE EVOLUTION

Spatial and temporal body size patterns may be counteracted by anthropogenic impacts such as climate change (e.g., Huey *et al.* 2012), pastoral activities (e.g., Taylor 1985), access to human refuse (e.g., Stringham 1989) and harvesting of wild populations (Allendorf *et al.* 2008). This section provides a background overview for Chapters 3 and 4, which investigate spatial and temporal size variation in several species of *Macropus*.

Selection against desirable phenotypes

Humans have long exploited wild populations of animals for food, clothing and tools. Harvest of wild populations is often non-random; certain individuals are more likely to be chosen for harvest from a population on phenotypic attributes such as size, morphology or behaviour. If the desired phenotype has a genetic basis, the non-harvested individuals will be left to reproduce and genes promoting less-desirable phenotypes will be selected over future generations (Allendorf *et al.* 2008). Essentially, the effect is opposite to that of domestic breeding, where there is a tendency to increase the frequency of desired phenotypes and decrease the frequency of less-desired phenotypes. Selection against desirable phenotypes via human harvest has been demonstrated in wild animal populations. For example, the frequency of African Elephants, *Loxodonta africana*, without tusks increased from 10% to 38% in South Luangwa National Park, Zambia, due to the effects of poaching for ivory (Jachmann *et al.* 1995). Similarly, trophy hunting for Bighorn Sheep, *Ovis canadensis*, in Alberta, Canada, caused a decrease in horn size, because rams with larger horns had a greater probability of being hunted (Festa-Bianchet *et al.* 2004).

However, harvest need not be selective to cause genetic change; consistently increasing mortality selects for increased and/or earlier allocation of energy to reproduction and can culminate in reduced size at maturity (Law 2007). Selection for smaller body size is thus expected to be strongest for size-selective harvesting regimes that target large individuals (Fenberg & Roy 2008). Empirical evidence of human-induced dwarfing is demonstrated in commercial fish species for which harvest mortality can exceed natural mortality by as much as 400% (Mertz & Myers 1998; Jorgensen *et al.* 2007; Audzijonyte *et al.* 2013). Genetic change in response to harvesting is manifested by changes in size at sexual maturity in the Western Rock Lobster, *Panulirus cygnus*, off the west coast of Australia, which has declined substantially over the past 35 years (Melville-Smith & de Lestang 2006; Allendorf *et al.* 2008).

Contemporary harvest-induced body-size evolution

There is increasing evidence that human harvesting or culling has led to the direct extinction of numerous terrestrial mammals (Burney & Flannery 2005; Prowse *et al.*

2013), but the phenotypic (notably body-size) evolution of contemporary harvest programmes for mammals are poorly understood (Allendorf & Hard 2009). Wild populations of mammal species under current harvest practice include whales (Barstow 1990; Amundsen *et al.* 1995), primates (Chapman & Onderdonk 1998; de Thoisy *et al.* 2005), ungulates (Milner-Gulland & Clayton 2002; Coulson *et al.* 2004) and kangaroos (Grigg 2002; Pople *et al.* 2010).

Simulation modelling for populations of large mammals suggests that a 10% proportional increase in mortality rates should cause around a 20% decrease in body size and a 10% drop in age at maturity (Purvis 2001). Using a stochastic, density-dependent, individual-based model, Proaktor *et al.* (2007) suggested that mass at maturity of the Red Deer, *Cervus elaphus*, declined by up to 20% in harvested populations. A similar model suggests that size-selective harvesting of Red Kangaroos, *Macropus rufus*, may result in smaller body size of a given age (Figure 2, Tenhumberg *et al.* 2004).

However, in scenarios with dispersal between the refuge population and the harvested population, the median proportion of size alleles across loci remains virtually unchanged in both populations (Tenhumberg *et al.* 2000). Similarly, a model based on De Roos *et al.*'s (1992) escalator boxcar train concept (a numerical method used to investigate population models in which individuals differ by size or other physiological characteristics) was used to demonstrate that size-selective harvesting has the potential to reduce the average size-at-age of *Macropus* kangaroos, providing there is no dispersal from refuge populations (Hacker *et al.* 2004). It has been argued that the range size of genetic populations is much larger than the harvest localities, thus loss of gene diversity in kangaroos through selective harvesting is likely to have negligible effect on specific traits, including size (Hale 2004). Other reasons advanced for low loss of genetic diversity of harvested populations include: 1) harvest targets all males not just the largest males; 2) larger, older males may not pass significant fitness benefits to offspring; 3) fitness traits are inherited through both sexes; and 4) populations are not selectively stable because food availability varies (Hale 2004). Hale (2004, p. 75) concluded that “the likelihood of a long-term genetic impact of kangaroo harvesting as currently practiced is negligible”.

Certainly, the rate of human-induced evolutionary change is likely to be slow (Tenhumberg *et al.* 2004; Andersen & Brander 2009) and, therefore, difficult to observe with short-term ecological studies. However, fossil records and historical wildlife collections provide excellent sources of data for examining body-size changes over longer timescales.

Prehistoric hunting

The selective pressure of prehistoric hunting by humans has been proposed as a major contributor to the dwarfing in North American megafaunal species through the Pleistocene (2.6 million to 12 thousand years ago) (Edwards 1967; Martin 1984; McDonald 1984). Through the Holocene (last 12 thousand years), dwarfing has occurred in American Bison, *Bison bison* (Dalquest 1959; Schultz & Hillerud 1977), Bighorn Sheep, *Ovis canadensis* (Harris & Mundel 1974) and Jaguar, *Felis onca* (Kurtén 1965).

Selective human hunting pressure has also been proposed as an explanation for the dwarfing of some extinct megafaunal marsupial species into smaller, still-extant forms following the arrival of humans in Australia about 50,000 years ago (Marshall & Corruccini 1978; Flannery 1994; Johnson 2006). Rock art of the Arnhem Land plateau in northern Australia, which dates back at least 40,000 years, depicts a number of kangaroo species evidently utilised by Australian Aborigines (Murray & Chaloupka 1984), indicating a long history of human exploitation. To date, within-species dwarfing has only been demonstrated in the Eastern Grey Kangaroo, *Macropus giganteus*, Pleistocene representatives of which may have been nearly four times the mass of living *M. giganteus* (Helgen *et al.* 2006).

Kangaroo harvesting over the past 200 years

Following the settlement of Europeans in Australia from the late 18th century, kangaroos were harvested for food, skins and sport (Robertshaw & Harden 1989). By the late 19th century, kangaroos were considered pests and legislation was introduced to encourage their destruction through a system of bounties (Robertshaw & Harden 1989). One commercial outcome was the development of trade in kangaroo products (primarily skins), which was extended to include meat in the mid-20th century (Pople & Grigg 1999). Claims by some conservationists / preservationists / humane societies in the 1970s that kangaroo populations were threatened by harvesting led to the temporary closure of export of kangaroo products in 1973 (Pople & Grigg 1999). Subsequently, state conservation agencies have enforced strict regulations on the commercial harvest of kangaroo and wallaby species of the genus *Macropus* (Grigg 2002). Furthermore, legislation no longer considers kangaroos pests, but rather protected species for which a licence to harvest is required (Pople & Grigg 1999).

Current commercially-harvested species include the Red Kangaroo, *M. rufus*, in areas of Queensland (QLD), New South Wales (NSW), South Australia (SA) and Western Australia (WA); the Eastern Grey Kangaroo, *M. giganteus*, in areas of QLD and NSW; the Western Grey Kangaroo, *M. fuliginosus*, in areas of NSW, SA and WA; the Common Wallaroo or Euro, *M. robustus*, in areas of QLD, NSW and SA; and the Red-necked Wallaby, *M. rufogriseus*, in areas of Tasmania and its offshore islands (see 'Population, quota and harvest statistics', http://www.environment.gov.au/search/site/kangaroo%20harvest, for summary of sustainable quota and total harvest data for each species 2000–2013).

It has been implied that size-selective harvesting of native Australian macropods might be sufficient to cause an evolutionary reduction in body size (Croft 1999; Hacker *et al.* 2004; Tenhumberg *et al.* 2004), but this idea has not been tested. In Chapter 3 I test the hypothesis that progressive dwarfing occurs in populations subjected to chronic mortality stress and size-selective harvesting in the Eastern and Western Grey Kangaroos and Red-necked Wallaby. These species are widespread and have largely disjunct ranges. In Chapter 4 I test the hypothesis that human-induced body-size evolution occurs in species of *Macropus* that largely overlap in their distribution. Furthermore, in each species, environmental drivers of spatial body-size variation were examined to test the main hypotheses proposed to explain observed body-size changes.

PART 3: THE ISLAND RULE

Islands often provide classic examples of evolutionary and ecological phenomena, including changes in body size (Foster 1964; Van Valen 1973; Lomolino 1985, Sondaar 1991; Lister 1996). Differences in the body size of closely-related island and mainland populations of mammals were first quantified by Foster (1964). From a survey of the literature, Van Valen (1973) showed that smaller species often evolve larger bodies (gigantism) and larger species tend to evolve smaller bodies (dwarfism) on islands. He named this pattern of centralizing body-size evolution the island rule, concluding that "The regular evolution of mammalian body size on islands is an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals" (Van Valen 1973 p. 72). Among non-mammalian vertebrates, the island effect or body-size shifts on islands have been reported in lizards (e.g., Soulé 1966; Rand *et al.* 1975; Pregill 1986), snakes (e.g., Cliff 1954; Boback & Guyer 2003; Keogh *et al.* 2005), tortoises and turtles (e.g., Hooijer 1951; Jaffe *et al.* 2011), and birds (e.g., Parker 1984; Clegg & Owens 2002). However, the pattern is most notable in mammals. This section provides detailed background information for Chapter 5, in which I investigate island body-size patterns in two widespread Australian mammal species, *Rattus fuscipes* and *Trichosurus vulpecula*.

Dwarfism and gigantism on islands

Numerous examples of island dwarfing in large, now-extinct Quaternary mammals have been observed, including proboscideans (e.g., Sondaar 1977; Roth 1992; van den Bergh *et al.* 2007), cervids (Lister 1989, 1996), hippopotamids (Simmons 1988; Grubb 1993), bovids (Croft *et al.* 2006; Kohler & Salvador 2009), antilocaprids (van der Geer 2008), canids (Wozencraft 2005; Lyras *et al.* 2006), felids (e.g., Mazák 1981), hominins (Brown *et al.* 2004), and diprotodontid marsupials (Wells & Prideaux 2006). There are extant island dwarf canids (Wayne *et al.* 1991), suids (Endo *et al.* 2002), lagomorphs (Foster 1964), sloths (Anderson & Handley 2002), heteromyid rodents (Lawlor 1982), deer (e.g., Miller *et al.* 2002), bovids (Burton *et al.* 2005) and non-human primates (Bromham & Cardillo 2007). Island gigantism of smaller species characterises several species of extant rodents, including rats, mice and squirrels (e.g., Hall 1938; Heaney 1978; Millien & Gonzalez 2011; Lister & Hall 2014), and some fossil rodents (e.g., Freudenthal 1976; Millien & Jaeger 2001; Millien 2004).

Generality of the island rule

Several recent studies have focused on ascertaining just how broadly applicable the island rule is across the majority of vertebrate taxa. Discussion has centred on resolving whether a general graded pattern in body size (gigantism in small species to dwarfism in large species) occurs across most vertebrate taxa on islands or whether patterns are limited to relatively few clades. Using large comparative datasets, several studies have suggested that the rule holds in most vertebrate taxa (Lomolino 1985, Clegg & Owens 2002; Boback & Guyer 2003; Lomolino 2005; Lomolino *et al.* 2006; Bromham & Cardillo 2007; Welch 2009). However, other studies have argued that there is no evidence for generality of the rule (Meiri *et al.* 2004, 2006, 2008; Meiri 2007), that the pattern of the rule is relatively weak (McClain *et al.* 2012), and that the rule does not characterise clades (Meiri *et al.* 2008). As it stands, insular size shifts within mammals appear to be concentrated in a few key mammalian clades; carnivores, heteromyid rodents and artiodactyls typically dwarf on islands, whereas murid rodents usually increase in size (Meiri *et al.* 2008). A recent analysis within insular, non-heteromyid rodents showed that, at lower taxonomic levels, smaller species increase in size while larger species decrease (Durst & Roth 2012). Moreover, the magnitude of size shifts within a single species can vary among islands (e.g., Foster 1964; Anderson & Handley 2002). Thus, body-size evolution on islands appears to be a complex combination of patterns that may vary in direction and magnitude across species.

Proposed drivers of insular body-size shifts

Multiple independent processes have been proposed to explain insular body-size shifts in vertebrates. These have generally been grouped into species-level traits, biotic interactions or island attributes. Most are listed separately below, but some are likely highly correlated.

Species-level traits

Food type: Lawlor (1982) proposed that body-size shifts are dependent on the type of food available to specialists and generalists. That is, large size should be favoured among food generalists because they exploit a more homogeneous environment, while a reduction in size should be favoured in food specialists since their food supply will be distributed more heterogeneously.

Original body size: Krzanowski (1967) proposes that some cases of gigantism might be explained by a greater ability of larger individuals of an original population to cover the distance separating islands from the mainland than smaller individuals. If body size is a heritable character, genes transmitted to future generations will thus result in a larger-bodied population than the initial population.

Optimal clade mass: The effects of systematic position have been argued to influence island body-size evolution (Brown *et al.* 1993; Damuth 1993), with each clade postulated to have an optimal size range.

Tropic level and lifestyle class: Trophic level and lifestyle class (i.e., arboreal, terrestrial or volant) have also been proposed to influence island body-size evolution (Lomolino 1985; Heaney 1978; McClain *et al.* 2012).

Biotic interactions

Reduced predation pressure: Predation pressure on islands in general should be lower than on the mainland because both space and prey abundance are limited (Foster 1964;

Sondaar 1977, Heaney 1978; Lawlor 1982; Adler & Levins 1994). Sondaar (1977) suggests that reduced (often absent) predation pressure on islands allows larger species to attain smaller sizes because the advantages of large size for defending against or eluding predators are diminished or lost. Similarly, small mammals, which avoid predation by dashing to refuges, should evolve to be larger (Heaney 1978).

Reduced interspecific competition: Reduced interspecific competition of insular communities allows individuals to exploit otherwise restricted food supplies. An increase in the amount of available food on islands should select for larger individuals of smaller species (Foster 1964; Lomolino 1985; Dayan & Simberloff 1998; McNab 2010). Furthermore smaller species are more likely to undergo competitive release, and thus increase in size (Schoene 1970; McNab 1971; Lomolino 1985). In larger species, increases in insular body size through reduced interspecific competition are constrained by resource limitation (see ‘Island-specific attributes’).

Increased intraspecific competition: Selection for smaller size in large mammals on islands could be influenced by strong intraspecific competition for available resources (Heaney 1978; Lomolino 1985; Roth 1992) and thus should be highly correlated with resource limitation.

High and stable population densities (island syndrome): Adler and Levins (1994) defined an island syndrome in which high and stable population densities produce body-size increases. They propose that higher densities lead to reduced reproductive output, which then lead to larger body size.

Island-specific attributes

Island area: The magnitude of the island effect on size evolution has been held to be roughly inversely proportional to island area, i.e., small mammals increase and large animals decrease in size as island area decreases (Heaney 1978). The relationship is purportedly due largely to the availability of resources, which may be expected to vary regularly with factors such as predation, interspecific competition and food limitation (Heaney 1978).

Time and distance of isolation: The magnitude of island body-size evolution is presumed to be positively related to duration of isolation and distance from the mainland source of the island population, i.e., small mammals increase and large animals decrease in size as island isolation increases (Foster 1964, 1965; Carlquist 1974). Essentially, as isolation of an island increases, the strength of the proposed factors driving island body-size evolution also increases (Foster 1965).

Resource limitation: Resource (i.e., food) limitation in a spatially-limited system should generate selection on large mammals to decrease in size so as to reduce energy requirements (Sondaar 1977; Heaney 1978). It has also been hypothesised that resource limitation may be responsible for the island effect, due to changes in intraspecific competition related to home-range size (Marquet and Taper 1998).

Climate (temperature and rainfall): Island temperature has been proposed to have a negative relationship with body size of small mammals (Millien & Damuth 2004) as well as mammals across a broad taxonomic range (McClain *et al.* 2012), because of thermoregulatory requirements (Bergmann 1847; James 1970). Similarly, rainfall is proposed to have a negative relationship with body size across a broad taxonomic range of island mammals and is likely to reflect low productivity (food limitations) traditionally associated with island environments (McClain *et al.* 2006).

Meiri *et al.* (2008, p. 141) provides a fitting summary of the principal explanations proposed to drive insular body-size shifts: “The rule is believed to emanate from small mammals growing larger to control more resources and enhance metabolic efficiency, while large mammals evolve smaller size to reduce resource requirements and increase reproductive output”.

Evidence for and against explanations of insular body-size shifts

Body-size reduction in island heteromyid rodents has been attributed to their specialisation on limited and coarse-grained food supplies (seeds, i.e., food type) (Lawlor 1982). Yet, island rodent data show size-shift direction differs across a number of specialist species: three carnivorous rodents all increase in size, while three granivores all decrease in size (Durst & Roth 2012). A large dataset across numerous taxa shows no convincing evidence for phylogenetic affinities as a predictor of island body size within mammals in general or within clades (Meiri *et al.* 2008). By contrast, among models testing specific hypotheses proposed to explain the island rule, island body-size evolution is best explained by a species traits model, including mainland body size, trophic level and lifestyle class (McClain *et al.* 2012). Although mainland body mass has been shown to be the strongest predictor of size shift direction in rodents on islands, no significant patterning of mainland body mass occurs at higher taxonomic levels (Durst & Roth 2012). The suggestion of original body size as a possible explanation for gigantism in some island bats (Krzanowski 1967) is difficult to test and may in fact be undermined by more recent findings that bats do not show a tendency towards gigantism (Meiri *et al.*

2008). Furthermore, Krzanowski's (1967) use of wing length as a surrogate for body size may be flawed because wing length is closely related to flight behaviour and often differs between islands and mainlands (Meiri *et al.* 2005).

Evidence that the presence or absence of predators have a consistent influence on island body-size evolution across a broad range of taxa is shown to be negligible (Meiri *et al.* 2008). Similarly, predation and competition has little or no effect on body sizes of insular carnivores (Raia & Meiri 2006), nor does competition influence House Mouse, *Mus musculus*, body size on Scottish and Faroese islands (Lister & Hall 2014). By contrast, dwarfism in ungulates on Mediterranean islands is largely explained by interspecific competition and, to a lesser extent, the presence of predators (Raia & Meiri 2006). To date, the effects of intraspecific competition *per se* on dwarfism of island mammals have not been examined. Likewise, the island-syndrome hypothesis (Adler and Levins 1994) has not yet been explicitly tested for its effect on gigantism (it was not proposed for dwarfism). Further assessment of this hypothesis awaits more population-level data than are currently available (Durst & Roth 2012).

Regression tree analyses across a broad taxonomic range of mammals show that gigantism in small species is more pronounced for populations inhabiting smaller islands (Lomolino *et al.* 2012). By contrast, a positive relationship between island area and body size has been demonstrated in the House Mouse (Lister & Hall 2014). In larger mammals, island area has no detectable influence on the degree of dwarfism (Lomolino *et al.* 2014). Furthermore, regression analyses applied to a dataset of broad taxonomic range show that island area does not influence body-size changes in either large-bodied or small-bodied insular mammals (Meiri *et al.* 2006). A subsequent study found no substantial evidence that either island area or isolation influence body-size evolution on islands (Meiri *et al.*

2008). Explanations for the rule have been tested using various models; models with least support reflected those pertaining to distance from the mainland (McClain *et al.* 2012). No evidence has been produced in support of island area or distance from mainland on body-size evolution of three-toed sloths (genus *Bradypus*), but time since isolation appears to have been important (Anderson & Handley 2002).

The relative effects of isolation and climate change on the size of island populations of the Japanese rodent, *Apodemus speciosus*, in conjunction with evolutionary rates calculated since the last glacial maximum, illustrate that body-size evolution of small-island populations has been less than half as rapid as on the "mainland-type" larger islands of Japan (Millien & Damuth 2004). Effectively, this demonstrates that small-island populations responded slower in the face of selection for smaller size associated with the climate warming since the last glacial maximum. Rather than causing a net increase in size, the island effect is proposed to have been partly counteracted by the general postglacial trend of decrease in body size (i.e., body-size decreased with temperature increase) (Millien & Damuth 2004).

Resource limitation / availability

Despite the fact that several explanations for the island rule, in particular dwarfism, largely pivot on resource limitation (Kurtén 1972; Van Valen 1973; Lomolino 1985; Marquet and Taper 1998) very little research has investigated the direct effects of resource availability on island body size. This is most likely due to difficulties associated with quantifying the difference between resource availability on islands and the mainland. Indeed, studies that discuss the effects of resource limitation often use island area and competition as auxiliaries, because of their intimate association with resource availability (e.g., Heaney 1978).

Recent advances in climatic data availability now make it plausible to test the prediction of insular body-size shifts based on resource availability and to examine the effects of thermoregulatory response. Three recent studies have tested the effects of a range of factors and variables, including climatic variables, on island body-size evolution. McClain *et al.*'s (2012) study of island body size in mammal species suggests that a model pertaining to primary productivity is a near-equally strong contingent for insular size shifts (relative to their species traits model). They report that cooler, less productive islands produce shifts towards larger body sizes while warmer, more productive islands produce shifts towards smaller ones. Similarly, Durst and Roth's (2012) classification tree analysis on rodents found island variables, including precipitation, were significant in predicting direction of change (body size increased with decreased precipitation while body size decreased with increased precipitation), although their roles were context dependent. Lomolino *et al.* (2012) found support for several conventional hypotheses proposed to explain island body-size evolution, as well as more pronounced gigantism of small mammals on islands with colder and more seasonal climates.

The relationship between productivity and island body size described by McCain *et al.* (2006, 2012) and Durst and Roth (2012) appears to uphold the general opinion that islands are characterised by low resource (food) availability (McClain *et al.* 2006). However, this relationship runs counter to that predicted by productivity processes proposed to explain spatial and temporal body-size differences; i.e., a positive relationship between body size and productivity (e.g., Rosenzweig 1968; Kolb 1978; Yom-Tov & Nix 1986; Blois, *et al.* 2007; Gür & Gür 2012). By contrast, the negative relationship between temperature and body size (Millien & Damuth 2004; Lomolino *et al.* 2012; McClain *et al.* 2012) follows patterns predicted by thermoregulation-based hypotheses posed to explain spatial and temporal body-size differences. Lomolino (2005) suggested that body size *in general,* not just dwarfism, should correlate with characteristics of the island, including productivity, but he did not state the direction of the expected relationship (i.e., positive or negative).

An autecological approach to investigate the island rule

The use of broad-scale taxonomic datasets (e.g., Meiri *et al.* 2008; Durst & Roth 2012; Lomolino *et al.* 2012; McCain *et al.* 2012) confounds the potential for quantifying the strength of individual biological determinants of island body-size evolution. In Chapter 5, I use an autecological approach to examine a) the island-rule pattern, and b) processes proposed to explain island body-size evolution. Model species selected were two Australian native mammals with continental-scale distributions that include offshore islands: the Australia Bush Rat, *Rattus fuscipes,* and Common Brushtail Possum, *Trichosurus vulpecula*. Skull measurements of island and mainland specimens were used in conjunction with biotic (predation, interspecific competition) and abiotic (e.g., island area, isolation interval, temperature, rainfall) covariates to determine a) strength and direction of island body-size shifts, and b) key variables that best explain island body-size evolution.

GENERAL INTRODUCTION SUMMARISED

The influence of factors such as climate, isolation and human impact on body size is no doubt complex because such factors frequently interact with one another and are likely to be context dependent (e.g., Millien & Damuth 2004). Such interactions are further complicated by an array of often highly-correlated biotic factors that might also affect body size, e.g., population size, range size, location within a range, intra- and inter-specific competition, predation pressure, sexual dimorphism and individual traits, including life history. However, at a broader scale, such factors are less likely to affect body size than climatic factors and or human impact. Despite extensive research the strength of independent and interacting body size determinants remains uncertain. This study uses rigorous empirical data in conjunction with sophisticated analyses to tease apart primary drivers of body size in several Australian mammals, thereby contributing to the understanding of this fundamental evolutionary trait.

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CHAPTER 2

LEAN-SEASON PRIMARY PRODUCTIVITY AND HEAT DISSIPATION AS KEY DRIVERS OF GEOGRAPHIC BODY-SIZE VARIATION IN A WIDESPREAD MARSUPIAL

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CONTEXT

In this chapter I test five different hypotheses proposed to explain spatial and temporal body-size patterns in mammals: heat conservation, heat dissipation, primary productivity, seasonality and ecologically and evolutionarily relevant net primary productivity, using Australia's most widespread marsupial, the Common Brushtail Possum, *Trichosurus vulpecula*. In this chapter I also examine the island effect.

STATEMENT OF AUTHORSHIP

RAC prepared the experimental design, collected the data, performed the analyses and wrote the manuscript. TAAP contributed to experimental design, helped develop analytical methods, contributed to analyses, provided guidance and advice and commented on the draft manuscript. GJP contributed to experimental design and provided guidance and advice, and commented on the draft manuscript and contributed to the discussion.

ABSTRACT

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.

INTRODUCTION

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 (e.g., Rosenzweig 1968; Boyce 1978; Yom-Tov & Nix 1986; Dayan *et al.* 1989; Smith *et al.* 1995; Wigginton & Dobson 1999; Ashton *et al.* 2000; Ashton 2002; Meiri *et al.* 2004; Mukherjee & Groves 2007; Blois *et al.* 2007; Gür & Gür 2012; Orcutt & Hopkins 2013; Briscoe *et al.* 2015; Prowse *et al.* 2015). 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 (e.g., Smith *et al.*1995;

Wigginton & 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 & 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 (e.g., Boyce 1978). Because energy stores increase with body size faster than energy requirements (Lindstedt & 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 (see Yom-Tov & 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 (e.g., Rosenzweig 1968; Kolb 1978; Yom-Tov & Nix 1986; Blois, *et al.* 2007; Gür & Gür 2012).

An alternative explanation for geographic body-size variation based on food availability posits that body size is regulated by NPP during the growing season of plants when many animals are reproducing and growing (Huston & Wolverton 2009, 2011). This concept, termed "ecologically and evolutionarily relevant" NPP (*e*NPP), differs from NPP, which is conventionally interpreted as the *annual* rate of plant growth. The '*e*NPP rule' (Huston & 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 evolve smaller bodies (e.g., 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 varies extensively 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 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 *e*NPP hypothesis specifically by determining whether productivity over the growing season can best explain geographic body-size patterns. Discriminating between the proposed hypotheses (Table 2.1) poses a dilemma to researchers because, as Yom-Tov and Nix (1986) and others (e.g., 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 & 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 & How 2008). Extensive geographic variation in both size and pelage has led to prior separation of *T. vulpecula* into different species or subspecies (e.g., Kerle *et al.* 1991). However, genetic and taxonomically reliable morphological evidence (Taylor & Foulkes 2004) indicates that there are insufficient differences between populations to justify recognition of more than one species.

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 & Król)	Body size decreases with humidity in warm environments / with temperature	James (1970), Speakman & 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 CO2 / 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 & Wolverton (2011)	Primary productivity variables calculated over the growing seasons

Table 2.1. 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.

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. 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 (see Table S2.1, Supplementary Information). Since CBL did not differ between sexes for the subset of specimens of known sex (see Fig. S2.1, Supplementary Information), 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 2011) and functions within the R package `raster` (Hijmans & van Etten 2012).

We aligned environmental variables with the hypothesised mechanisms driving geographic body size variation as follows (summarised in Table 2.1):

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 0900 and 1500 h), calculated across years 1900–2011 (SummerWetBulbTemp, AnnualWetBulbTemp). 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 y^{-1}]) (CenW), which Roxburgh *et al.* (2004) calculated from datasets derived from ESOCLIM (1921–1995) (McMahon *et al.* 1995).

eNPP – *e*NPP 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) (e.g., Boyce 1978; Medina *et al.* 2007; Gür & 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 km^2, 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 km^2, n=12), Bathurst Island (2 600 km^2, n=7), Centre Island (84 km^2, n=2), Flinders Island (1 367 km^2, n=10), Kangaroo Island (4 400 km^2, n=27) and Magnetic Island (52 km^2, n=7) and single specimens from Croker Island (332 km^2) and Milingimbi Island (60 km^2).

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 (version 3.0.3; R Development Core Team 2014). 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 X is the matrix of explanatory variables and $\boldsymbol{\beta}$ is the vector of coefficients. The spatially dependent error term, **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), **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 `errorsarlm` within *R* package `spdep` (Bivand & Piras 2015).

We used Akaike's information criterion with a correction for finite sample sizes (AICc) (Burnham & 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 & 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*) (see Table S2.2, Supplementary Information). 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.

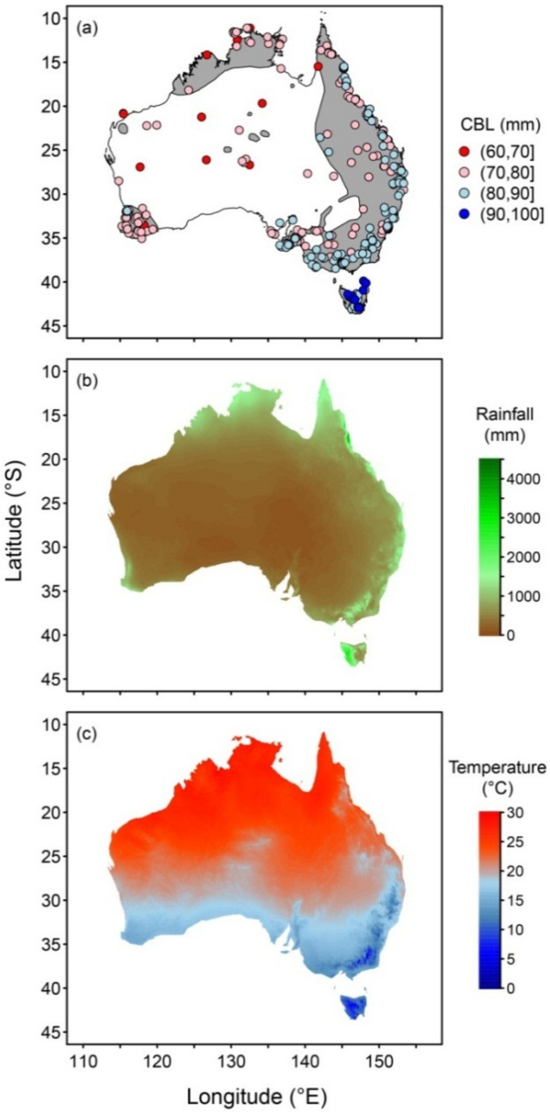

Figure 2.1. (a) Colour coded points represent spatial pattern of condylobasal length (CBL; mm) for *Trichosurus vulpecula*. Shaded area depicts current *T. vulpecula* distribution (IUCN 2013). Climatic layers are (b) annual rainfall and (c) mean annual temperature for Australia.

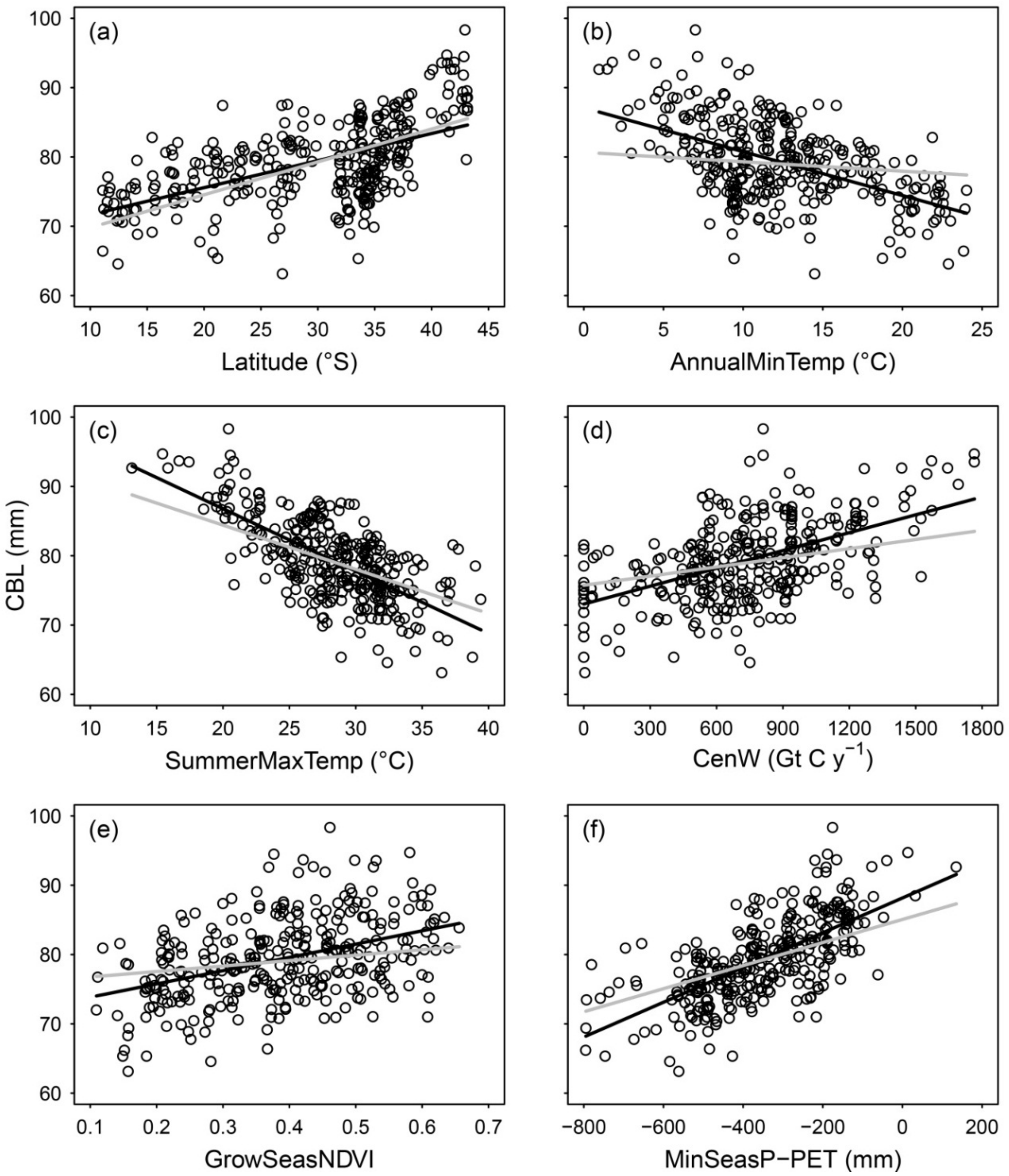

Figure 2.2. Fitted relationships between body size (condylobasal length [CBL]) and latitude (a) and also the top AICc-ranked predictor from each hypothesis for both aspatial models (black line) and spatial autoregressive models (grey line); (b) mean annual minimum temperature (AnnualMinTemp [heat conservation]), (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]).

	Aspatial models			**Spatial SAR models**			
Model	R^2	**AICc**	**δAICc**	R^2	**AICc**	**δAICc**	**λ**
Null	-	2021.0	0	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	0.275	1921.3	149.4	0.554	1792.1	48.3	0.852
SummerMaxTemp	0.453	1832.2	60.4	0.596	1752.8	8.9	0.754
CenW	0.277	1920.7	148.9	0.589	1764.2	20.3	0.833
GrowSeasNDVI	0.174	1962.5	190.7	0.570	1780.4	36.6	0.852
MinSeasP-PET*	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**

Table 2.2. 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 (δAICc) 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), 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). *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.

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. 2.1). However, *T. vulpecula* body-size variation does conform to Bergmann's Rule and increases with latitude (Fig. 2.2a). The spatial SAR model fitting this latitude effect, which received strong AICc support relative to the equivalent aspatial model (Table 2.2), estimated the stronger relationship between CBL and latitude (0.520 ± 0.214 mm $°S^{-1}$ [estimate ± 95% confidence interval] compared to 0.398 ± 0.062 mm $°S^{-1}$).

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. 2.2b-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. 2.2f). 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 2.2, Fig. 2.2). In contrast, the heat conservation and eNPP hypotheses received little support (both $R^2 < 0.30$, Table 2.2, Fig. 2.2).

Equivalent spatial SAR models were strongly supported over the mono-causal models (lower AICc and higher R^2 values) (Table 2.2). The spatial autoregression coefficient for these spatial models was always high (all $\lambda \geq 0.75$, Table 2.2) 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. 2.2) 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 2.2). Back-transformed coefficient estimates for the variables SummerMaxTemp and MinSeasP–PET were -0.637 ± 0.171 mm CBL per °C and 0.017 ± 0.005 mm CBL per mm P–PET, respectively. While those for the AnnualMinTemp, CenW and GrowSeasNDVI were -0.136 ± 0.194 mm CBL per °C, 0.004 ± 0.002 mm CBL per Gt C y^{-1} and 7.86 ± 4.14 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 2.2). For both the aspatial and spatial SAR analyses, the top AICc-ranked multi-causal model was of the form CBL = SummerMaxTemp + MinSeasP–PET + Island. However, the deviance residuals from the aspatial model of this form were spatially autocorrelated, particularly within 1000 km (Fig. 2.3), so we focus on the equivalent spatial 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. 2.4; 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. 2.4).

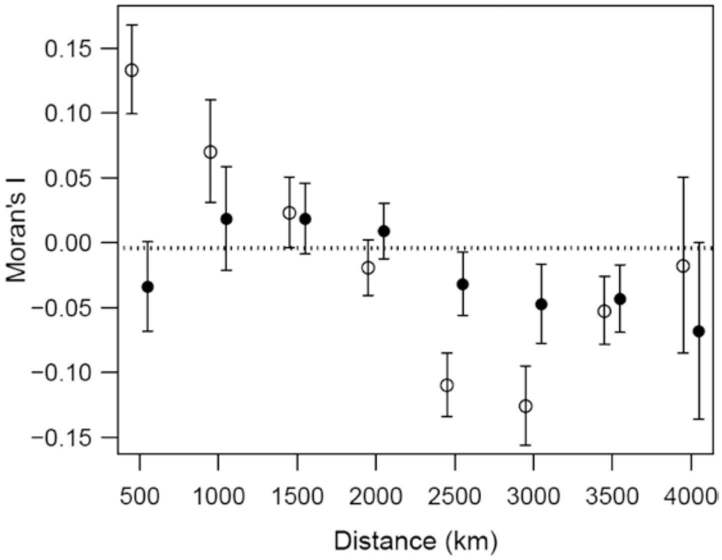

Figure 2.3. Plot of Moran's *I* values of both aspatial (open circles) and spatial SAR models (closed circles) at 500 km intervals. Values near +1.0 indicate positive spatial autocorrelation while values near –1.0 indicate negative spatial autocorrelation. Values near zero indicate a random spatial pattern.

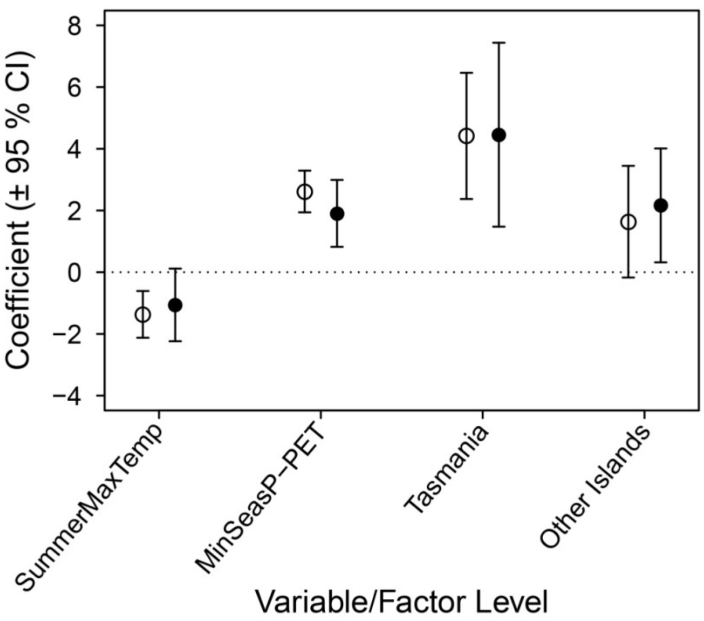

Figure 2.4. Plot of coefficients (± 95 % CI) for each variable / factor level in the selected aspatial (open circles) and spatial SAR (closed circles) multi-causal model; mean summer maximum temperature (SummerMaxTemp), minimum seasonal values for precipitation minus potential evapotranspiration (MinSeasP–PET), 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).

DISCUSSION

Our study identifies primary productivity as the most important environmental driver of *Trichosurus vulpecula* body size (Fig. 2.4), 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 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 & 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*. Growing season NDVI was positively correlated with body size, which is predicted by Huston and Wolverton's *e*NPP hypothesis, but support for this relationship was very weak (Table 2.2, Fig. 2.2). Furthermore, our support for lean season productivity is counter to the predictions of *e*NPP; 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.* 2015), in the male Koala, *Phascolarctos cinereus* (Briscoe *et al.* 2015) and within species of the North American woodrat genus *Neotoma* (Brown & 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 & Król 2010). Increased food availability and cooler temperatures therefore most likely explain increased body size of populations occurring in southeastern Australia (Fig. 2.1)

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 & Nix 1986; Kerle *et al.* 1991). *T. 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. 2.1). 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 (e.g., Hopper & 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 years ago (van Dyck & 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 (e.g., Yom-Tov 1986; Huston & 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 (see Table S2.3, Supplementary Information). 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 off shore 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 summermaxtemp 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 (e.g., Gür 2010; Yom-Tov & 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 (λ = 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 & Yom-Tov 2005), as have human impacts (e.g., Rowe-Rowe & Crafford 1992). Additionally, competition with sympatric species (e.g., Mukherjee & 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 INFORMATION

Cranial parameters	***r***	***n***
Condylobasal length (CBL)	0.842	200
Total jaw length (TJL)	0.842	203
Greatest zygomatic breadth (ZB)	0.772	185
First principal component (PC1)	0.876	184

Table S2.1. Pearson’s correlation coefficient (*r*) for different cranial parameters against body mass, for *n* specimens for which data were available. From a principal component analysis of these parameters, the correlation between PC1 and body mass is also presented. We selected CBL as our body-size representative because PC1 could only be calculated for a subset of specimens for which all cranial measurements were available.

	AnnualMinTemp	**SummerMaxTemp**	**CenW**	**GrowSeasNDVI**	**MinSeasP-PET**
AnnualMinTemp	1	0.692	−0.255	−0.188	−0.482
SummerMaxTemp	0.692	1	−0.631	−0.433	−0.726
CenW	−0.255	−0.631	1	0.673	0.757
GrowSeasNDVI	−0.188	−0.433	0.673	1	0.656
MinSeasP-PET	−0.482	−0.726	0.757	0.656	1

Table S2.2. Spearman’s rank correlation coefficient are presented for variables selected to represent each hypothesis; mean annual minimum temperature (AnnualMinTemp), mean summer maximum temperature (SummerMaxTemp), Australian Continental NPP estimate based on fluxes of carbon / nutrients and CO2 / water (CenW), growing season Normalised Difference Vegetation Index (GrowSeasNDVI), minimum seasonal precipitation minus potential evapotranspiration (MinSeasP-PET).

	Aspatial Models			Spatial SAR Models			
Soil Variable	***R*²**	**AICc**	**δAICc**	***R*²**	**AICc**	**δAICc**	**λ**
Bulk density (0–30 cm)	0.196	1954.0	182.2	0.562	1786.9	43.0	0.855
Soil nutrient availability	0.004	2021.8	250.0	0.556	1792.8	48.9	0.868
Clay content percentage (0–30 cm)	0.001	2022.9	251.1	0.560	1789.8	45.9	0.871

Table S2.3. Model selection for aspatial and spatial SAR models of *Trichosurus vulpecula* condylobasal length that used soil variables as covariates. The following is shown for each candidate soil 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 (δAICc) relative to the top-ranked model within each model type.

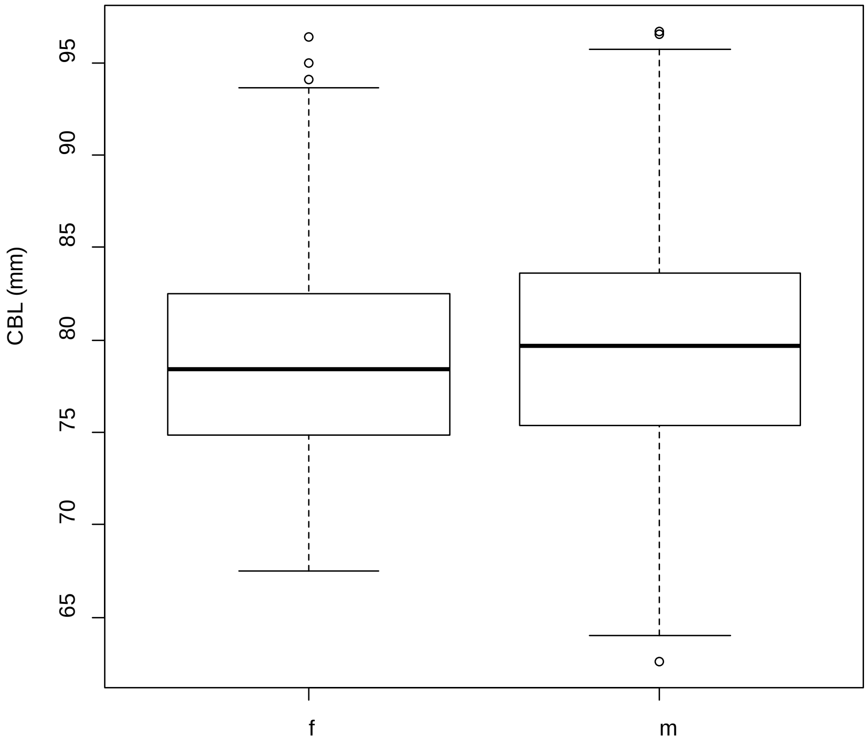

Figure S2.1. Boxplot of female (f) and male (m) condylobasal length (CBL) (mm), showing the median (lines within boxes), the interquartile range (boxes), 1.5 times the interquartile range from the box ends (whiskers), and outliers beyond the whiskers (points). Mean CBL for females (mean = 78.91, n = 237) and males (mean = 79.84, n = 261) was not significantly different (t = –1.72, df = 488, p = 0.086). Given this, and since separating the sexes would have reduced the sample size by 28%, sexes were pooled for all further analyses.

CHAPTER 3

EMPIRICAL TESTS OF HARVEST-INDUCED BODY-SIZE EVOLUTION ALONG A GEOGRAPHIC GRADIENT IN AUSTRALIAN MACROPODS

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CONTEXT

In this chapter I test the hypothesis that Australian macropods subjected to size-selective commercial harvesting progressively dwarf in body size. I also examine environmental drivers of body size as well as island effects.

STATEMENT OF AUTHORSHIP

TAAP prepared much of the experimental design, collected data, performed analyses and wrote the manuscript. RAC contributed to the experimental design, collected data and helped write the manuscript. CNJ helped conceptualise the project, assisted with analyses and contributed to the discussion. GJP helped collect data, provided guidance and advice, commented on drafts and contributed to the discussion. BWB helped conceptualise the project, assisted with analyses and contributed to the discussion.

ABSTRACT

Life-history theory predicts the progressive dwarfing of animal populations that are subjected to chronic mortality stress, but the evolutionary impact of harvesting terrestrial herbivores has seldom been tested. In Australia, marsupials of the genus *Macropus* (kangaroos and wallabies) are subjected to size-selective commercial harvesting. Mathematical modelling suggests that harvest quotas (c. 10–20% of population estimates annually) could be driving body-size evolution in these species. We tested this hypothesis for three harvested macropod species with continental-scale distributions. To do so, we measured more than 2000 macropod skulls sourced from wildlife collections spanning the last 130 years. We analysed these data using spatial Bayesian models that controlled for the age and sex of specimens as well as environmental drivers and island effects. We found no evidence for the hypothesized decline in body size for any species; rather, models that fit trend terms supported minor body size increases over time. This apparently counterintuitive result is consistent with reduced mortality due to a depauperate predator guild and increased primary productivity of grassland vegetation following European settlement in Australia. Spatial patterns in macropod body size supported the heat dissipation limit and productivity hypotheses proposed to explain geographic body-size variation (i.e. skull size increased with decreasing summer maximum temperature and increasing rainfall, respectively). There is no empirical evidence that size-selective harvesting has driven the evolution of smaller body size in

Australian macropods. Bayesian models are appropriate for investigating the long-term impact of human harvesting because they can impute missing data, fit nonlinear growth models and account for non-random spatial sampling inherent in wildlife collections.

INTRODUCTION

Life-history theory predicts that smaller body size will be favoured selectively under conditions of chronically increased mortality rates, such as those imposed by human harvesting (Jorgensen *et al.* 2007; Allendorf *et al.* 2008). High harvest-induced mortality selects for increased and/or earlier allocation of energy to reproduction and can culminate in reduced size at maturity (Audzijonyte *et al.* 2013). Selection for smaller body size is expected to be strongest for size-selective harvesting regimes that target large individuals and thus remove fast-growing individuals preferentially (Fenberg & Roy 2008). The best-known empirical examples of human-induced dwarfing are those of commercial fish species for which harvest mortality can exceed natural mortality by more than fourfold (Mertz & Myers 1998; Jorgensen *et al.* 2007; Audzijonyte *et al.* 2013).

Human harvesting or culling of terrestrial mammal populations has been sufficiently strong to drive species to extinction (Burney & Flannery 2005; Prowse *et al*. 2013); however, the evolutionary effects of contemporary harvest programmes are poorly understood (Allendorf & Hard 2009). Simulation modelling for large-mammal populations suggests that a 10% proportional increase in mortality rates should cause around a 20% decrease in body size and a 10% drop in age at maturity (Purvis 2001). However, the rate of human-induced evolutionary change is likely to be slow (Tenhumberg *et al.* 2004; Andersen & Brander 2009) and therefore difficult to observe with short-term ecological studies. In contrast, fossil records and historical wildlife collections afford the possibility of examining body-size changes over longer time scales.

In Australia, the selective pressure of prehistoric human hunting following human arrival about 50 000 years ago has been proposed as a cause of the dwarfing of some marsupial species (Marshall & Corruccini 1978; Flannery 1994; Johnson 2006). For example, the eastern grey kangaroo *Macropus giganteus* has potentially undergone a fourfold reduction in body mass since the late Pleistocene (Helgen *et al.* 2006). Following the arrival of Europeans in Australia in the late 1700s, kangaroos were considered to be pests; legislation encouraged their destruction, and a commercial trade in skins was extended to include meat in the mid-1900s (Pople & Grigg 1999). In 1973, however, the export of kangaroo products was banned due to concerns that harvesting threatened the long-term viability of kangaroo populations. Since the late 1970s and early 1980s, therefore, the commercial harvest of kangaroos and wallabies of the genus *Macropus* has been regulated by State conservation agencies (Grigg 2002; Pople *et al.* 2010). These agencies set species-specific annual harvest quotas that range up to c. 20% of the population estimate for management zones; however, harvest rates can exceed 20% for certain areas within these zones (Tenhumberg *et al.* 2004). In New South Wales, for example, 1 million kangaroos out of an estimated 83 million individuals were harvested or culled in 2003 (Commonwealth of Australia 2012). Macropod harvesting is typically size selective because operators target large animals above a threshold weight (particularly large males) (Hacker *et al.* 2004; Hale 2004). Mathematical models for kangaroos suggest that even the current, heavily regulated harvest practices should be sufficient to drive evolution towards smaller body size, providing no significant refuge populations are left unharvested (Hacker *et al.* 2004; Tenhumberg *et al.* 2004).

Environmental drivers of geographic body-size variation complicate the investigation of allometric trends over time, particularly when specimens have been collected in the ad hoc manner typical of wildlife collections. One of the best-known macroecological principles, Bergmann's rule, states that the body sizes of homeotherms are larger in cooler climates and higher latitudes (Bergmann 1847). Although originally formulated at the interspecific level (Blackburn, Gaston & Loder 1999), this pattern has also been applied to intraspecific body-size variation and holds for kangaroos (Yom-Tov & Nix 1986). The classical explanation for Bergmann's rule is that larger mammals have a smaller surface-area-to-volume ratio and therefore retain heat more efficiently in cold climates (Mayr 1963; but see Speakman & Król 2010). However, there are many exceptions to Bergmann's rule (Huston & Wolverton 2011) and so various alternative, non-mutually exclusive hypotheses have been advanced to explain geographic patterns in body size, including (i) heat dissipation (smaller animals dissipate heat more readily and are favoured in hotter climates) (Speakman & Król 2010), (ii) fasting endurance (larger animals can better endure productivity bottlenecks typical of high latitudes) (Kendeigh 1969; Arnett & Gotelli 2003), (iii) net primary productivity (NPP; food availability can limit growth) (Rosenzweig 1968) and (iv) ecologically and evolutionarily relevant net primary productivity (*e*NPP; body-size variation reflects NPP during the growing season) (Huston & Wolverton 2011). Further, an equally controversial pattern known as the Island rule (Van Valen 1973) is described for mammals as gigantism in small species and dwarfism in large species following isolation on islands (Lomolino 2005; Lomolino *et al.* 2012).

In this study, we investigated the empirical evidence for human-induced body-size evolution in three species of the genus *Macropus* from the late 1800s to the present. To do so, we accessed nine wildlife collections and measured more than 2000 skulls of three harvested species: the eastern and western grey kangaroos (*M. giganteus* and *M. fuliginosus*, respectively) and the red-necked wallaby (*M. rufogriseus*). Each species has a continental-scale distribution that includes populations that were isolated on islands following late-Pleistocene sea-level rise (Fig. 3.1). *M. giganteus* and *M. fuliginosus* are believed to have evolved in the east and the west of Australia, respectively, after the once continuous distribution of the ancestral grey kangaroo was split, probably by the Nullarbor Plain (Van Dyck & Strahan 2008; Neaves *et al.* 2009). The home ranges of these large kangaroos vary markedly between habitats and environments, ranging from tens of hectares up to several hundred hectares in size (Jaremovic & Croft 1987; Arnold *et al.* 1992), and there is evidence of long-distance dispersal events particularly in males (e.g., one *M. fuliginosus* male was recorded moving 85 km; Priddel *et al.* 1988). The smaller *M. rufogriseus* is distributed from Gladstone, Queensland, south to Tasmania, and occupies smaller home ranges of c. 5–50 ha (Johnson 1987; Wiggins *et al.* 2010). All three species are grazers and sexually dimorphic, with adult males substantially larger than adult females (*M. giganteus*: 19–85 kg cf. 17–42 kg, *M. fuliginosus*: 19–85 kg cf. 17–42 kg, *M. rufogriseus*: 15–27 kg cf. 11–16 kg; Van Dyck & Strahan 2008).

Both grey kangaroo species are currently harvested in some mainland States (*M. giganteus*: Queensland and New South Wales; *M. fuliginosus*: Western Australia, South Australia and New South Wales), whereas the harvest of *M. rufogriseus* is now restricted to Tasmania and its offshore islands. However, these species are also culled in States where they are not harvested commercially. We compiled information on the age and sex of macropod specimens to control for rapid changes in average age or sex ratios due to recent selective hunting (Tenhumberg *et al.* 2004). Using skull size as a calibrated proxy for body size, we used nonlinear Bayesian hierarchical modelling to test the hypothesis that size-selective harvesting has caused an evolutionary size reduction in contemporary macropod populations. After properly correcting for the confounding effects of age, sex and environmental drivers, we found no evidence of human-induced evolution of smaller body size in these species.

MATERIALS AND METHODS

Macropod body size

We sourced macropod skulls with known sampling locations (latitude and longitude) from museum and wildlife collections and the Palaeontology Laboratory at Flinders University. For each specimen, we recorded three skull size measurements (± 0.01 mm) using digital callipers (Mitutoyo, Aurora, IL, USA), specifically condylobasal length (CBL, or skull length), maximum skull width (SW) and lower jaw length (JL), as well as sex and weight where available. Subsequently, we focused on CBL as an index of body size because there was a strong, loglinear relationship between CBL and animal weight for all three species (see Fig. S3.1, Supplementary Information). As macropods age, their molars erupt at the posterior end of the molar row, progress forwards and are shed as they wear (Augusteyn *et al.* 2003). To control for the age of each specimen, therefore, we also estimated the molar index (MI) of each skull, which is defined as the number of maxillary molars (including fractions) that have moved past the anterior rim of the eye orbits and is closely related to age within each sex (Kirkpatrick 1965). For each species, the total sample size (n), total number of sampling sites (nSites) and the proportion of animals for which sex was known were *M. giganteus* (n = 719, nSites = 176, 85%), *M. fuliginosus* (n = 602, nSites=282, 61%) and *M. rufogriseus* (n = 856, nSites=119, 93%).

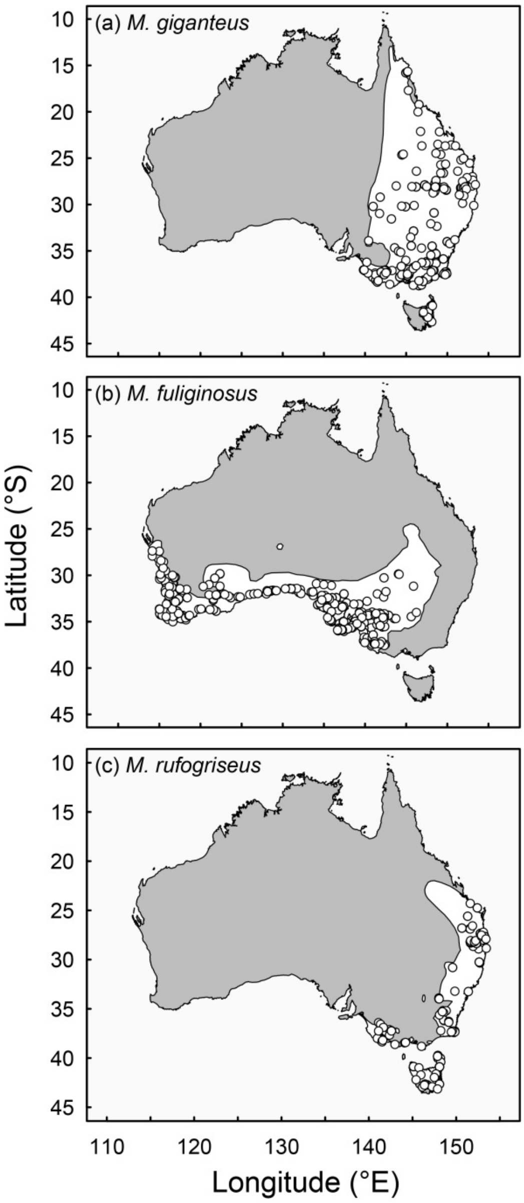

Figure 3.1. Unique sampling locations for skulls of (a) Eastern Grey Kangaroo, *Macropus giganteus* (176 sites), (b) Western Grey Kangaroo, *M. fuliginosus* (282 sites), and (c) Red-necked Wallaby, *M. rufogriseus* (119 sites). The current IUCN distributions are shown for each species (IUCN 2013).

Environmental covariates

To account for environmental drivers of macropod body size, we assumed that the locations where skulls were sampled were indicative of the environmental conditions in which these animals developed. We justify this assumption by noting that all three macropod species inhabit regions where temporal variations in climate and productivity are highly correlated over large areas, meaning that major bottlenecks are not easily escaped by movement.

We sourced the following gridded environmental covariates (all 0.05° resolution) for Australia from the Australian Bureau of Meteorology (BoM): (i) mean monthly minimum and maximum daily temperature (for all months over 1912-2009), (ii) total monthly rainfall (for all months over 1901-2009), (iii) mean monthly wet-bulb daily temperature for 0900 and 1500 h (preaveraged over 1900-1911) and (iv) mean monthly values of the Normalised Difference Vegetation Index (NDVI, for all months over 1992–2012) which is a satellite-derived index of vegetation condition ranging from -1 to +1 (Rouse *et al.* 1974). From these data sets, we identified putative environmental covariates relevant to each of the five hypotheses advanced to explain geographic variation in body size (see the Introduction), as follows:

(1) *Heat conservation*. We calculated the mean minimum daily temperature over the winter months (WinterMinTemp), averaged across all available years.

(2) *Heat dissipation*. We calculated the mean maximum daily temperature over the summer months (SummerMaxTemp), averaged across all available years. However, since an animal’s ability to dissipate heat is not solely a function of temperature, we also calculated mean wet-bulb daily temperature (an average of 0900 h and 1500 h records) for the summer months (SummerWetBulbTemp). Wet-bulb temperature, which depends primarily on air temperature and humidity, is the lowest temperature that can be reached by the evaporation of water only.

(3) *Productivity*. Primary productivity is rainfall-limited throughout much of Australia, so as an index of productivity we calculated mean annual rainfall (AnnualRain), averaged across all available years. Similarly, mean annual NDVI was used as an alternative, empirical measure of productivity (AnnualNDVI).

(4) *eNPP*. To evaluate this hypothesis, we defined the growing season for each grid cell as the set of months with a mean temperature in excess of 15 °C and averaged productivity variables over these growing seasons (GrowSeasRain and GrowSeasNDVI, respectively).

(5) *Fasting endurance*. Since the fasting endurance hypothesis is couched in terms of an animal’s ability to survive productivity bottlenecks, we averaged productivity variables over the least productive season (MinSeasRain and MinSeasNDVI, respectively).

The predicted sign of the relationship between macropod body size and these environmental covariates is shown in Table 3.1. We collated all covariates across a common 0.05° spatial grid matching that of the BoM temperature data sets. The spatial data were prepared using the R computing environment (R Development Core Team 2011) and functions within the R package raster (Hijmans & van Etten 2012).

Model		***Macropus giganteus***			***Macropus fuliginosus***			***Macropus rufogriseus***		
		δDIC	***R*2**	**CV *R*2**	**δDIC**	***R*2**	**CV *R*2**	**δDIC**	***R*2**	**CV *R*2**
(a) Aspatial models										
Null		205	0.840	0.789	60	0.902	0.791	61	0.778	0.756
Mono-causal models										
Heat conservation	WinterMinTemp (–)	203	0.840	0.790	42	0.905	0.793	62	0.778	0.756
Heat dissipation	SummerMaxTemp (–)	**9**	**0.878**	**0.828**	46	0.904	0.793	62	0.778	0.755
	SummerWetBulbTemp (–)	23	0.876	0.824	60	0.902	0.790	53	0.780	0.758
Productivity	AnnualRain (+)	148	0.851	0.803	6	0.909	0.805	**45**	**0.783**	**0.759**
	AnnualNDVI (+)	88	0.863	0.814	40	0.905	0.797	60	0.779	0.755
*e*NPP	GrowSEasRain (+)	181	0.844	0.793	25	0.907	0.804	46	0.782	0.759
	GrowSeasNDVI (+)	147	0.852	0.804	47	0.904	0.795	55	0.780	0.756
Fasting endurance	MinSeasRain (–)	76	0.867	0.819	54	0.903	0.792	62	0.778	0.755
	MinSesaNDVI (–)	138	0.854	0.805	50	0.903	0.794	60	0.779	0.755
Multi-causal models										
	SummerMaxTemp + AnnualRain	12	0.878	0.828	8	0.909	0.805	36	0.785	0.760
	SummerMaxTemp + AnnualRain + Island	**0**	**0.880**	**0.829**	**0**	**0.911**	**0.809**	**0**	**0.795**	**0.769**
(b) Spatial CAR models										
	SummerMaxTemp + AnnualRain + S	**0**	**0.919**	**0.850**	**0**	**0.930**	**0.808**	13	0.829	0.783
	SummerMaxTemp + AnnualRain + Island +S	34	0.919	0.850	1	0.929	0.810	**0**	**0.830**	**0.786**
	SummerMaxTemp + AnnualRain + Trend + S	105	0.920	0.850	26	0.930	0.807	32	0.829	0.781
	SummerMaxTemp + AnnualRain + Island + Trend + S	131	0.920	0.850	19	0.928	0.810	14	0.829	0.785

Table 3.1. Model selection results for *Macropus, M. giganteus*, *M. fuliginosus* and *M. rufogriseus*. (a) Summaries of the aspatial models that include the null, mono- and multi-causal models evaluated. For the mono-causal models, the expected sign of coefficient is shown in brackets and results are reported in grey type if this was not matched by the sign of the parameter estimate. For each species, the top DIC-ranked model within each of the mono-causal and multi-causal model subsets is shown in bold type. (b) Summaries of the spatial models that included conditional autoregressive (CAR) spatial random effects (S). For each species, the top DIC-ranked spatial model is shown in bold type, and the selected models are boxed (see main text and Fig. 3.3). The following is shown for each candidate model: (1) the change in the deviance information criterion relative to the top-ranked model for each step (δDIC; lower values indicate a better fitting model), (2) the coefficient of determination (R^2), and (3) the coefficient of determination obtained from 5-fold cross-validation (CV R^2).

Island effects

To correct for possible island effects, we classified specimens as originating from the Australian mainland, the large (c. 68,000 km^2) island of Tasmania or from smaller offshore islands, and we considered this as a 3-level factor for statistical analysis. Sample sizes for each species within each of the mainland, Tasmania and small island levels were as follows: *M. giganteus* (696/23/0), *M. fuliginosus* (504/ 0/98) and *M. rufogriseus* (589/45/222). Samples of *M. fuliginosus* and *M. rufogriseus* from small islands were derived solely from Kangaroo Island, South Australia (c. 4,400 km^2); or Flinders Island, Bass Strait (c. 1,840 km^2), respectively.

Bayesian model fitting

We used nonlinear Bayesian hierarchical models to analyse spatial variation in macropod skull size because this method of statistical analysis permitted the inclusion of an imputation model for missing sex records (Gimenez *et al.* 2009) as well as consideration of spatial autoregressive effects (Smith, Anderson & Millar 2012). The models were fit using WINBUGS version 1.4.3 (Gilks, Thomas & Spiegelhalter 1994, http://www.mrc-bsu.cam.ac.uk/bugs) called through R using the package R2WINBUGS (Sturtz, Ligges & Gelman 2005). Assuming a Gaussian error structure and uninformative priors, we modelled the expected CBL for specimen i of sex j using a negative exponential growth model that allowed for rapid growth during early development followed by a smooth deceleration to an upper asymptote.

This nonlinear model took the form

$$\mathrm{CBL}_i = L_{\infty.j} - (L_{\infty.j} - \beta)\mathrm{e}^{-(k_j \mathrm{MI}_i)} + \boldsymbol{\theta}\mathbf{X}_i$$

where β is the intercept (common to both sexes), $L_{\infty.j}$ is the sex-specific upper asymptote, k_j is the sex-specific growth rate, $\boldsymbol{\theta}$ is the vector of coefficients and $\mathbf{X}_i$ is the vector of covariates. This model assumes constant sex-specific growth rates k_j while the covariates affect both the intercept and asymptote equally (i.e. covariate effects shift the entire growth curve up or down). This can be seen by rearrangement of the nonlinear model as follows

$$\mathrm{CBL}_i = L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i - (L_{\infty.j} - \beta + \boldsymbol{\theta}\mathbf{X}_i - \boldsymbol{\theta}\mathbf{X}_i)e^{-(k_j \mathrm{MI}_i)}$$

$$\mathrm{CBL}_i = (L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i) - [(L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i) - (\beta + \boldsymbol{\theta}\mathbf{X}_i)]e^{-(k_j \mathrm{MI}_i)}$$

Comparing this reformulation to the initial model we can see that, after accounting for the covariates, $(L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i)$ is the effective asymptote and $(\beta + \boldsymbol{\theta}\mathbf{X}_i)$ is the effective intercept. In Bayesian statistics, missing covariate values can be treated as unknown quantities for which a posterior distribution can be estimated. When one covariate has missing values but all other covariates are fully observed, an appropriate option is to specify a regression model to impute the missing covariate values as a function of other covariates, thereby accounting for between-covariate correlation structure (Lunn *et al.* 2012). Therefore, we implemented a logistic imputation model for missing sex records of the form:

$$\mathrm{logit}(j) = a + b\mathrm{MI}_i + \boldsymbol{\delta}\mathbf{X}_i$$

which allowed the uncertainty arising through imputation to propagate throughout the model and influence the estimation of $\boldsymbol{\theta}$ (Gimenez *et al.* 2009).

In addition to fitting aspatial models, we tested spatial models that assumed a Gaussian conditional autoregressive (CAR) spatial process such that

$$S_p \mid \boldsymbol{S}_{-p} \sim N\left(\mu + \phi \sum_{q \in N_p} w_{pq} S_p, \frac{1}{w_{pq}\tau^2}\right)$$

where $\boldsymbol{S}_{-p}$ is the vector of spatial random effects excluding that for the site p, ø controls the overall spatial correlation, N_p is the set of neighbouring sites and τ is the precision (i.e.

inverse of the variance). For these spatial models, the intercept parameter β from the exponential growth model above was removed to prevent over-parameterisation.

The nonlinear model therefore became

$$\mathrm{CBL}_i = L_{\infty.j} - L_{\infty.j}\mathrm{e}^{-(k_j \mathrm{MI}_i)} + \boldsymbol{\theta}\mathbf{X}_i + S_p \mid \boldsymbol{S}_{-p}$$

This spatial model can be reformulated as

$$\mathrm{CBL}_i = (L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i + S_p \mid \boldsymbol{S}_{-p})$$
$$- [(L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i + S_p \mid \boldsymbol{S}_{-p}) - (\boldsymbol{\theta}\mathbf{X}_i + S_p \mid \boldsymbol{S}_{-p})]\mathrm{e}^{-(k_j \mathrm{MI}_i)}$$

from which we can see that the combined effect of the covariates and spatial CAR process is to shift the growth curve up or down, with $(L_{\infty.j} + \boldsymbol{\theta}\mathbf{X}_i + S_p \mid \boldsymbol{S}_{-p})$ now the effective asymptote and $(\boldsymbol{\theta}\mathbf{X}_i + S_p \mid \boldsymbol{S}_{-p})$ the effective intercept. We adopted a row-standardized weighting scheme for spatial random effects that assignedequal weights to all neighbouring sites (i.e. $w_{pq} = 1/n_p$) (Carroll *et al.* 2010) and defined the neighbourhood extent using a radius of 250 km (the minimum distance ensuring all specimens had at least one neighbour).

For each model, we ran three Markov chains for 60,000 iterations, with a burn-in of 10,000 and a thinning rate of 50 iterations to reduce autocorrelation between samples generated by the Metropolis-Hastings algorithm. We used uninformative prior distributions on all parameters, specifically flattened normal distributions ($\mu = 0$, $\sigma = 1{,}000$) for all coefficients and uniform distributions on the interval [0,10] for the standard deviation of the CAR process and the Gaussian error terms. We assessed convergence by visually inspecting the chains and with the Gelman- Rubin statistic (Gelman & Hill 2007). To check the suitability of the nonlinear model structure we: (i) assessed the assumption of Gaussian errors with histograms and quantile–quantile plots of standardized residuals, (ii) assessed the assumption of homogeneous errors with plots of standardized residuals again fitted values and (iii) performed posterior predictive checks that compared the fit of the observed data to that of replicate data generated from the fitted model (Gelman *et al.* 1996). To investigate the possibility of spatial autocorrelation in the residuals of aspatial and spatial models, we used Moran’s I spatial autocorrelation coefficient, calculated at a range of distance lags.

Examples of the WINBUGS code for aspatial and spatial CAR models are given in Appendix 1.

Model selection

We compared candidate models using the deviance information criterion (DIC), a Bayesian parsimony-oriented metric of trade-off between precision and bias, in which lower values indicate better model performance (a reduction of 10 DIC points or more is usually taken as evidence in favour of a given model) (Gelman *et al.* 1996; Carroll & Johnson 2008; Carroll *et al.* 2010). To ensure the DIC was calculated appropriately for these hierarchical models, we calculated explicitly the partially marginalized deviance (Millar 2009; Smith *et al.* 2012). We also compared the fitted and true values of CBL using the coefficient of determination, both from the full model (R^2) and from 5-fold cross-validation fits (CV R^2). Using these metrics, we then evaluated a candidate model set using a two-step procedure:

(1) Within each hypothesis advanced to explain body-size variation, we ranked candidate models by DIC and sought to identify the one best environmental predictor of body size.

(2) Using aspatial and spatial CAR models, we explored multicausal spatial drivers, island effects and trends in macropod body size over the post-European period.

To test the sensitivity of the model selection process to specification of prior distributions, we also ran all models using inverse-gamma priors ($1/\Gamma(0.01, 0.01)$) for the variances and uniform priors on the interval $[-1000, 1000]$ for the spatial covariates.

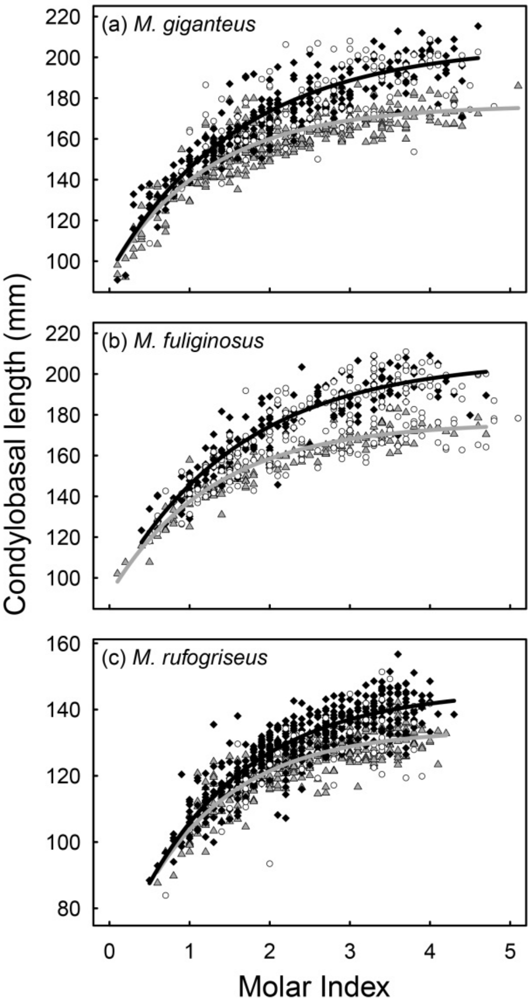

Figure 3.2. Sex-specific, negative exponential growth curves from the null, aspatial models fitted for (a) *Macropus giganteus*, (b) *M. fuliginosus* and (c) *M. rufogriseus*. Data and fitted relationships are represented as follows: males (back diamonds, black lines), females (grey triangles, grey lines) and specimens for which sex was imputed using the Bayesian imputation model (open circles).

RESULTS

Mono-causal spatial drivers of body size

Bayesian nonlinear models supported heat dissipation and primary productivity as the primary environmental drivers of macropod body size. Although null, aspatial models (i.e. those that fit the negative exponential growth curve only) accounted for a large proportion of the skull size variation for each species (all R^2 between 0.78 and 0.90; Table 3.1, Fig. 3.2), mono-causal models that included one environmental covariate had improved DIC rankings. For *Macropus giganteus*, the heat-dissipation hypothesis received strong DIC support (Table 3.1) and a negative relationship (posterior mean [95% credible interval]) between skull size and summer maximum temperature was estimated (−1.01 [−1.15, −0.88] mm°C^{-1}). For both *M. fuliginosus* and *M. rufogriseus*, the top DIC-ranked mono-causal models supported the productivity hypothesis (Table 3.1) and estimated a positive relationship between skull size and annual rainfall (0.0099 [0.0070, 0.0127] and 0.0035 [0.0018, 0.0051] mm.mm rainfall^{-1}, respectively).

The heat conservation and fasting endurance hypotheses propose inverse body-size relationships with temperature and the severity of the least productive season, respectively. We found no evidence to support these hypotheses; in fact, the estimated relationships with skull size were positive (i.e. the wrong sign) for minimum winter temperature (two out of three species) and minimum seasonal productivity (all three species). Further, we found no evidence that productivity during the growing season (*e*NPP) was a better predictor of skull size than productivity variables calculated on an annual basis. On these grounds, we excluded *e*NPP predictors from subsequent evaluation in the multi-causal models.

Multi-causal models including island effects and trends

Once again, multi-causal models supported the heat dissipation and primary productivity hypotheses. However, the residuals of the top-ranked aspatial models were spatially autocorrelated, particularly within 300 km (see residual spatial correlograms for the aspatial models in Fig. S3.2, Supplementary Information). We therefore focus on spatial CAR models here because they accounted explicitly for this residual spatial autocorrelation and also improved model fit (lower deviance and higher R^2 and CV R^2, Table 3.1).

For all three species, spatial multi-causal models supported the heat dissipation and productivity hypotheses and Island effects were additionally supported for *M. rufogriseus* (Table 3.1). For these top DIC-ranked multi-causal models, we evaluated the posterior support for each parameter estimate. For *M. giganteus* and *M. rufogriseus*, we found strong support for negative relationships between skull size and summer maximum temperature (Fig. 3.3a,c), with a negative coefficient estimated in 89% and 96% of posterior draws, respectively. There were positive relationships between skull size and annual rainfall for all three species (Fig. 3.3), for which posterior support ranged from 65% (*M. giganteus*) to 100% (*M. fuliginosus*). For *M. rufogriseus*, there were negative effects on skull size due to isolation on small offshore islands (–4.60 mm [–8.54, –0.78]) as well as on the large island of Tasmania (–5.11 mm [–8.41, –1.83]).

There was no support for a declining trend in body size over time for any of the three macropod species (Table 3.1). Inclusion of a trend term in the spatial models was not supported by DIC ranking and, importantly, reduced the CV R^2 obtained. In fact, the top DIC-ranked spatial models that included trend terms actually estimated an increase in body size over time for all three species (0.042 mm year $^{-1}$ [0.021, 0.054] for *M. giganteus*; 0.018 mm year $^{-1}$ [0.011, 0.026] for *M. fuliginosus*; and 0.025 mm year $^{-1}$ [0.008, 0.036] for *M. rufogriseus*) (Fig. 3.4).

Residual diagnostics and posterior predictive checks demonstrated that the nonlinear model structure was appropriate for modelling body-size data from all three species (see Fig. S3.3, Supplementary Information). When alternative prior distributions were tested, model selection rankings were identical except that an Island effect for *M. fuliginosus* received greater support (see Table S3.1, Supplementary Information). Using these alternative priors, positive changes in body size over time were still estimated for all three species.

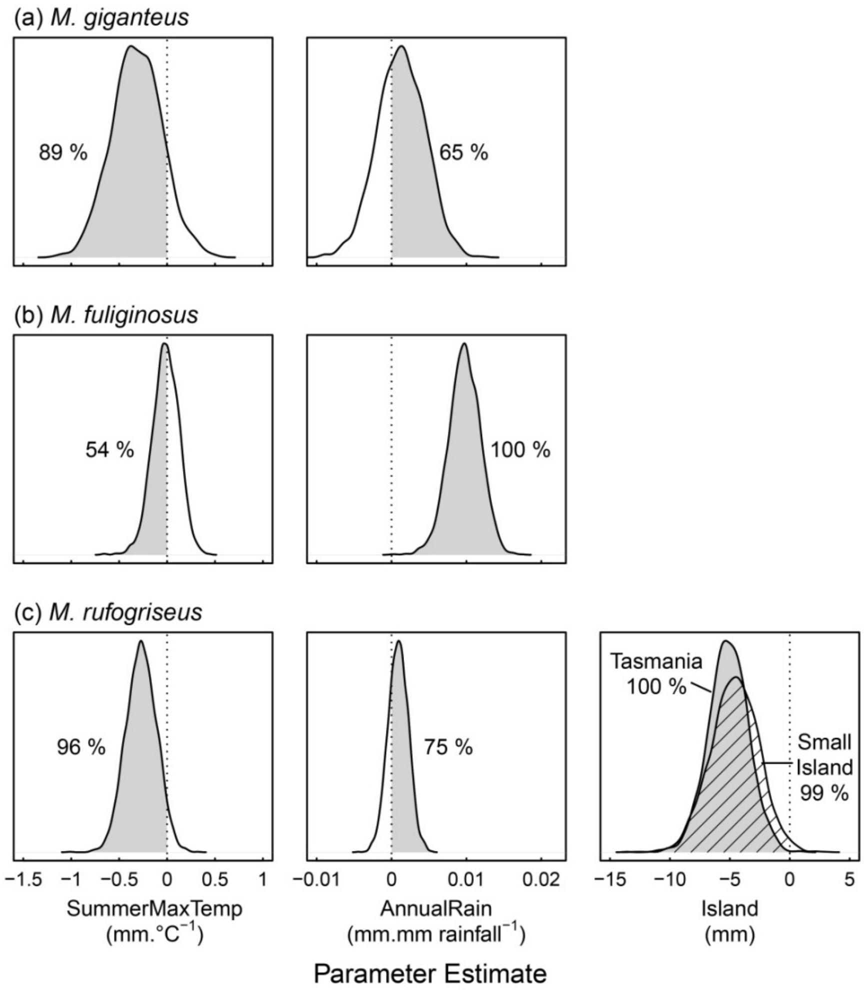

Figure 3.3. Environmental drivers of macropod body size for (a) *Macropus giganteus*, (b) *M. fuliginosus* and (c) *M. rufogriseus*. Plots show posterior distributions for parameters estimated using the selected spatial model for condylobasal length: SummerMaxTemp + AnnualRain (*M. giganteus*, *M. fuliginosus*) or SummerMaxTemp + AnnualRain + Island (*M. rufogriseus*). The posterior support for the sign of the mean parameter estimate is illustrated by shaded regions, and the percentage of posterior samples producing estimates of that sign is stated. Across all three species, skull size decreased with increasing summer maximum temperature (SummerMaxTemp) and increased with higher annual rainfall (AnnualRain), although the former relationship was weak for *M. fuliginosus*. For *M. rufogriseus*, negative island effects on body size also received strong support, both on Tasmania and on smaller offshore islands.

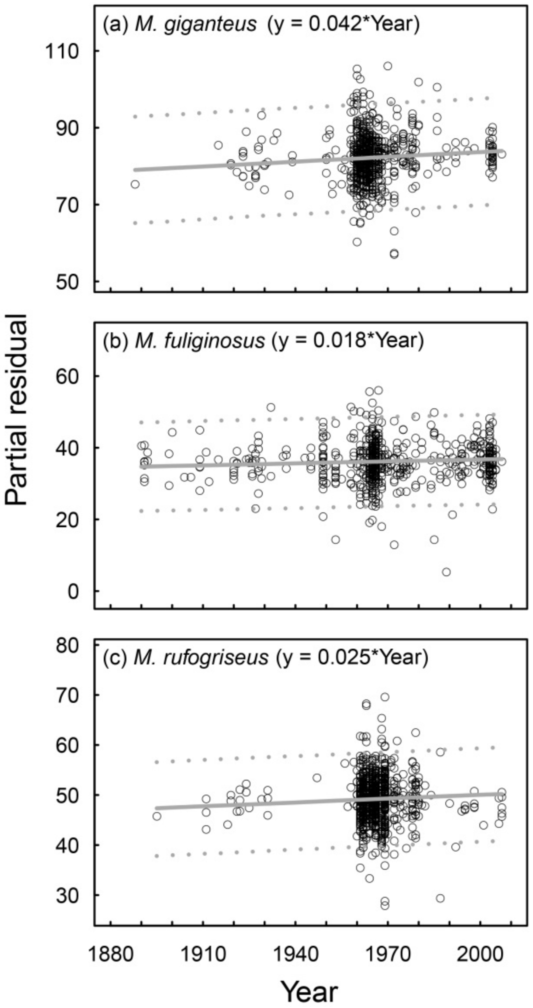

Figure 3.4. Trends in macropod body size, after correcting for environmental drivers, for (a) *Macropus giganteus*, (b) *M. fuliginosus* and (c) *M. rufogriseus*. Plots show partial residuals and the fitted trend in units of mm yr^{-1} (± 95 % prediction intervals) from the top DIC-ranked spatial CAR model of those including a trend term.

DISCUSSION

It has been asserted, but never demonstrated, that the size-selective harvesting of native Australian macropods might be sufficient to cause an evolutionary reduction in body size (Hacker *et al.* 2004; Tenhumberg *et al.* 2004). Here, we have shown, using robust statistical modelling of wildlife skeletal collections spanning the last 130 years, that there is no evidence for such a decline in three macropod species. Historical harvest practices might therefore have been insufficient to cause a change in allele frequencies due to immigration from inaccessible refuge populations that remain unharvested (Tenhumberg *et al.* 2004). Alternatively, uncertainty in the species-specific population size estimates used to set annual harvest quotas (Pople 2008), the failure of commercial hunters to meet quotas, or spatial variation in the intensity of harvesting/ culling programmes might have rendered harvest rates insufficient to select for smaller body size, at least over the timescale of our study. We note, however, that commercial records probably underestimate the true macropod harvest because there is ongoing illegal culling of macropods for the purposes of sport or vegetation protection, although this is impossible to quantify (RSPCA Australia 2002).

Interestingly, after correcting for environmental drivers and the age and sex of macropod specimens, we found evidence of small, positive trends in skull size (Fig. 3.4, although note the statistical inclusion of trend terms was not supported by DIC or cross-validation). The overall results are consistent with a release from predation pressure, not increased mortality due to human harvesting. Prior to European arrival in the late 1700s, c. 50,000 thousand years of hunting by indigenous Australians had left a depauperate ecological system bereft of large terrestrial vertebrates, within which humans and dingoes (and thylacines in Tasmania) were the last remaining predators capable of hunting macropods efficiently (Johnson 2006; Prowse *et al.* 2014a). Europeans persecuted dingoes because they preyed on livestock and, during the 1880s, 5,614 km of ‘dingo fence’ was constructed to protect south-eastern Australia’s grazing rangelands from dingo incursions. The fence is maintained to this day, and dingoes are poisoned and shot both inside and outside this barrier. We think it probable, therefore, that the release of macropods from dingo predation was not offset by a subsequent increase in European harvesting pressure. Supporting this hypothesis, today kangaroos and emus are more abundant inside the dingo fence where dingo populations are more tightly controlled (Caughley *et al.* 1980; Pople *et al.* 2000; Letnic & Koch 2010).

Selection for increased macropod body size might also have been favoured by European pastoral activities, such as the provision of water in arid and semi-arid landscapes (Blaney *et al.* 2000), the clearing of forest and woodland habitats, and/or the improvement of native pastures with fertilisers and exotic grasses (Taylor 1985). A further intriguing hypothesis is that a temporal increase in macropod body size could have been driven by an increase in the frequency and intensity of extreme heat events as a consequence of human-induced climate change (McKechnie & Wolf 2010; Huey *et al.* 2012). In theory, larger endotherms are expected to have a higher thermal inertia and greater energy reserves and therefore should experience lower mortality rates during extreme heat waves (Huey *et al.* 2012). Unfortunately, we were unable to test this hypothesis because temporal, gridded data sets relating to the occurrence of extreme heat events are not freely available for Australia.

The relative importance of thermoregulatory requirements versus primary productivity in driving geographic variation in the body size of endotherms has been a controversial topic in evolutionary ecology (Huston & Wolverton 2011). Our results for the three *Macropus* species support both the heat dissipation and productivity hypotheses (Fig. 3.3). Strong, negative relationships between skull size and average summer maximum temperature for *M. giganteus* and *M. rufogriseus* support the ‘heat dissipation limit’ theory. That is, smaller individuals in the hotter, lower latitudes have a high surface-area-to volume ratio which is expected to promote heat dissipation and improve reproductive fitness (Speakman & Król 2010). Admittedly, our models are correlative and this statistical relationship might overlook the importance of extreme heat events in selecting for larger body size. However, we found no evidence to suggest that macropod body size increased in the arid interior of Australia where the most extreme heat events occur away from the moderating effects of the ocean (see Fig. S3.4, Supplementary Information). Macropod skull size was also positively related to annual rainfall, a useful proxy of primary productivity in Australia's water-limited environments, which is consistent with population modelling that found NDVI is no better than rainfall at predicting changes in kangaroo density (Pople *et al.* 2010).

M. rufogriseus skulls were smaller on the large island of Tasmania (c. 65 000 km2) and Flinders Island (c. 1840 km2) than expected from fitted relationships with summer maximum temperature and annual rainfall, even after spatial autoregressive processes were modelled explicitly (Fig. 3.3c). Island effects (when fitted) were negative but not clearly supported for *M. giganteus* or *M. fuliginosus*; however, the Tasmanian sample size for *M. giganteus* was small (n = 23 only) and DIC-based support for reduced *M. fuliginosus* size on Kangaroo Island was sensitive to specification of the prior distributions used. The traditional explanation for a reduction in body size on islands is the 'resource-limitation' hypothesis (Van Valen 1973), which states that the limited area and total productivity of small islands, together with the unusually high densities attained by many insular populations, should select for smaller body size. Although resource limitation is feasible for *M. rufogriseus* on Flinders Island, such a mechanism seems unlikely to apply on Tasmania. Further, Lomolino *et al.* (2012) reviewed island effects comprehensively and found that for large mammals (> c. 3 kg) there is no relationship between insular body size and island area. Rather, they found that large mammals isolated on islands were likely to exhibit size reduction if they relied solely on terrestrial food sources or were isolated along with competitor species. These criteria hold true for island populations of the macropods we considered. However, a thorough investigation of island effects on Australian mammals would require data for species with multiple island populations that are separated geographically (e.g., *Rattus fuscipes*; Hinten *et al.* 2003).

As body size increases, total energy demands increase more slowly than the rate at which fat is stored (Calder 1984). When external food is limiting, therefore, the fasting endurance of larger animals should be greater due to their increased capacity for energy storage per unit of body mass (Speakman & Król 2010). However, we found no support for the fasting endurance hypothesis; rather, we found positive relationships between minimum seasonal rainfall (or minimum seasonal NDVI) and body size (Table 3.1). These results are consistent with the productivity hypothesis because they suggest that body size is limited by productivity bottlenecks. Similarly, we found no evidence to support the recently proposed '*e*NPP hypothesis' (Huston & Wolverton 2011); *e*NPP, calculated as either total rainfall or mean NDVI over the growing season, was no better at predicting macropod body size than the same productivity variables calculated on an annual basis. Admittedly, we defined the growing season as the set of months with a mean temperature in excess of 15 °C, whereas the growing season may not depend solely on temperature but also rainfall. However, we also investigated the ability of maximum seasonal values of total rainfall or mean NDVI to account for macropod body-size variation, but these variables were not supported over productivity variables calculated on an annual basis (data not shown).

Wildlife collections afford the possibility of investigating spatial drivers and temporal changes in animal body size, particularly given the increased availability of high quality climatic and other spatial environmental data over the last decade. However, historical collections also pose some unique challenges – data on specimens (such as gender or geographic location) are frequently incomplete, and the pattern of spatial sampling is likely to be biased by site accessibility and the personal preferences of scientists and collectors. In the past, researchers have often chosen to discard large numbers of specimens from their analyses because, for example, the age or stage of specimens was unknown (Yom-Tov & Nix 1986). We have shown here how Bayesian models are appropriate for such analyses because they can impute missing data (thereby making full use of the historical information), fit nonlinear growth models and account for non-random spatial sampling patterns.

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DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository: http://doi.org/10. 5061/dryad.c3tc6 (Prowse *et al.* 2014b). Data files: Macropod specimen details and extracted spatial covariate values.

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SUPPLEMENTARY INFORMATION

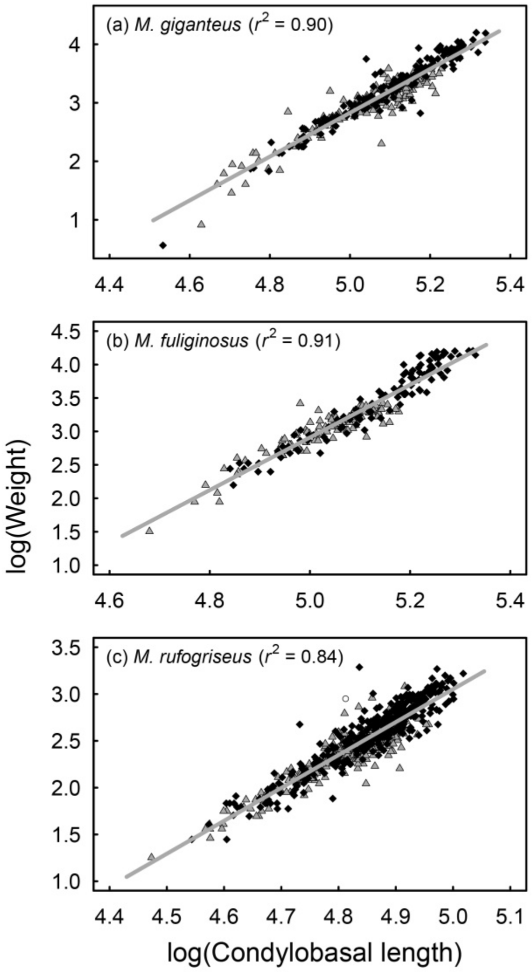

Figure S3.1. Log-log plots showing the relationship between live body weight and condylobasal length (i.e., skull length) for three macropod species: (a) *Macropus giganteus*, (b) *M. fuliginosus*, and (c) *M. rufogriseus*. Linear regression lines and corresponding r^2 values are shown for each species. Data are represented as follows: males (back diamonds, black lines); females (grey triangles, grey lines); specimens with unknown sex (open circles).

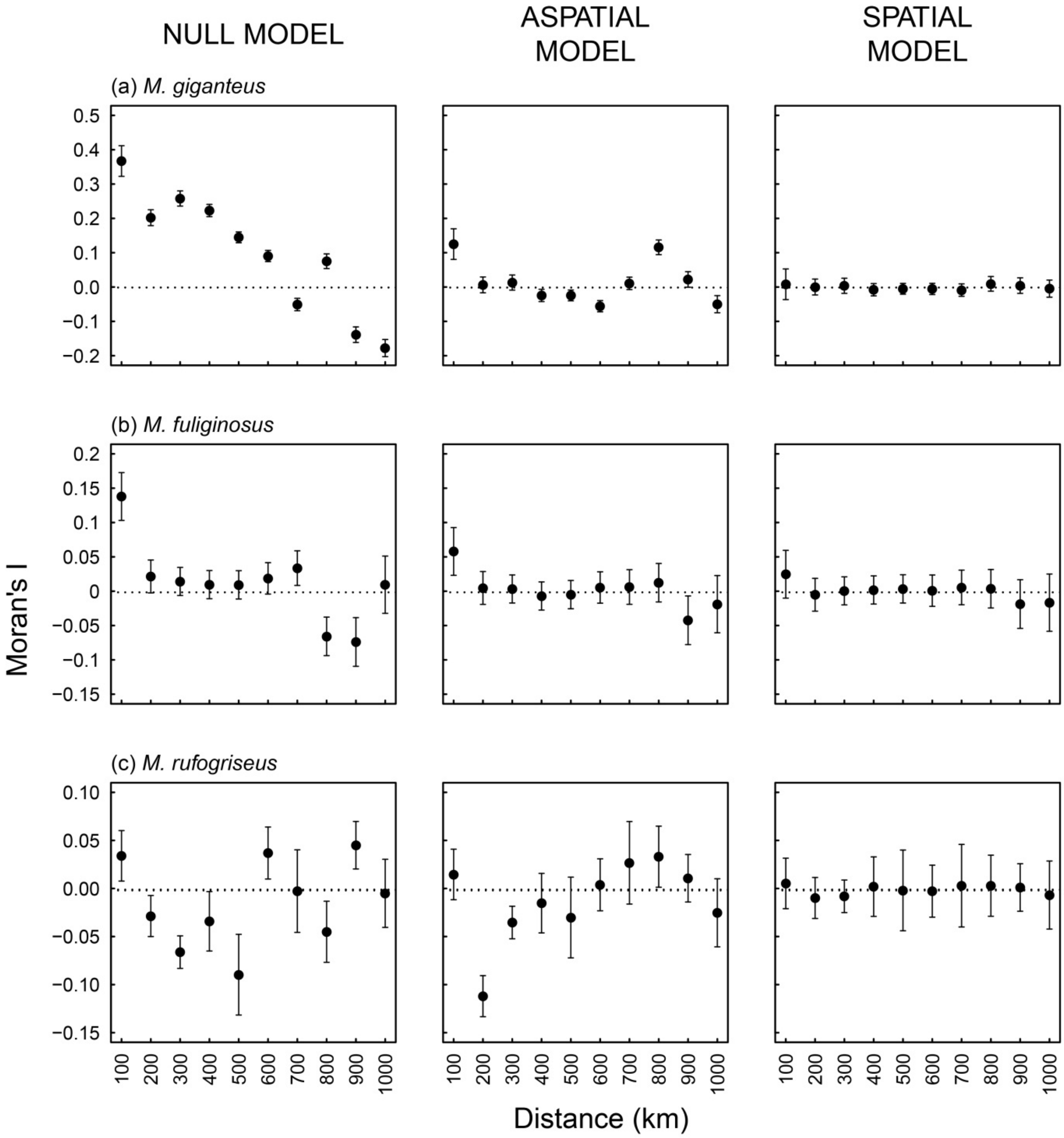

Figure S3.2. Spatial correlograms for the residuals of non-linear Bayesian models for condylobasal length of: (a) *Macropus giganteus*, (b) *M. fuliginosus*, and (c) *M. rufogriseus*. Points plot Moran's I statistic (± the square root of its variance) for the null, aspatial model and the top DIC-ranked aspatial and spatial CAR models for each species (see Table 3.1 of the main text for model specifications). The dotted, horizontal guidelines indicate the Moran's I statistic expected under the null hypothesis of no spatial autocorrelation. Note that only spatial CAR models could account for spatial autocorrelation within 300 km.

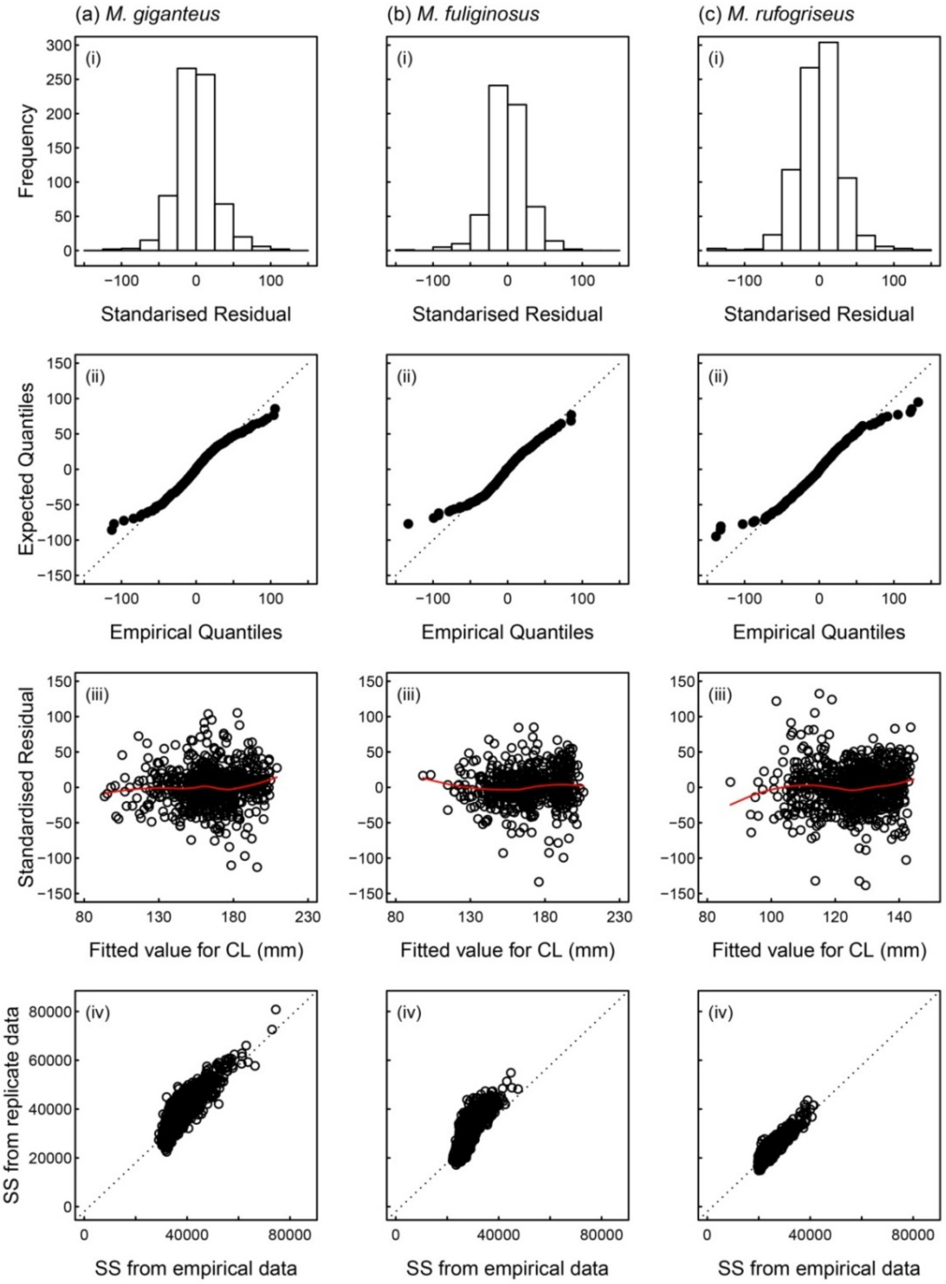

Figure S3.3. Residual diagnostics for the spatial model selected for: (a) *Macropus giganteus*, (b) *M. fuliginosus*, and (c) *M. rufogriseus*. The following is shown for each species: (i) a histogram of standardised residuals (i.e., residuals divided by their estimated standard errors derived from the MCMC output), (ii) a quantile-quantile plot that compares the empirical residual quantiles to those expected assuming a Gaussian error distribution, (iii) a plot of standardised residuals again fitted values of condylobasal length (CBL), and (iv) a posterior predictive check that contrasts the fit (residual sums of square [SS]) of replicated data generated from the posterior distribution to that of the observed data.

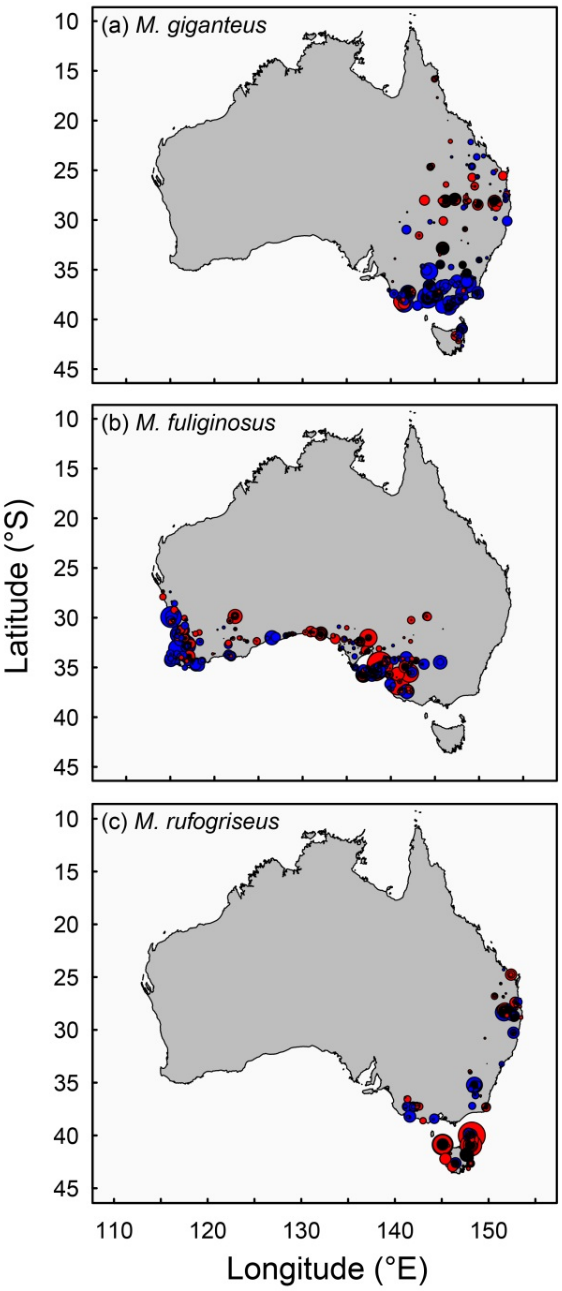

Figure S3.4. Spatial pattern of residuals in condylobasal length (mm) from the null, aspatial model fits (i.e., models accounting for age and sex only) for (a) *Macropus giganteus*, (b) *M. fuliginosus* and (c) *M. rufogriseus*. Negative and positive residuals are shown as red and blue points, respectively, and the size of each point is directly proportional to the absolute value of the residual.

MODEL		*Macropus giganteus*			*Macropus fuliginosus*			*Macropus rufogriseus*		
		δDIC	R^2	CV R^2	δDIC	R^2	CV R^2	δDIC	R^2	CV R^2
(a) Aspatial Models										
Null		205	0.840	0.789	58	0.902	0.790	62	0.778	0.756
Mono-causal models										
Heat Conservation	WinterMinTemp (–)	202	0.840	0.790	43	0.905	0.793	62	0.778	0.756
Heat Dissipation	SummerMaxTemp (–)	**10**	**0.878**	**0.828**	46	0.904	0.794	62	0.778	0.755
	SummerWetBulbTemp (–)	22	0.876	0.824	61	0.902	0.790	53	0.780	0.758
Productivity	AnnualRain (+)	149	0.851	0.803	**5**	**0.909**	**0.805**	**44**	**0.783**	**0.759**
	AnnualNVDI (+)	87	0.863	0.814	40	0.905	0.796	60	0.779	0.755
eNPP	GrowSeasRain (+)	181	0.844	0.793	25	0.907	0.804	46	0.782	0.759
	GrowSeasNVDI (+)	145	0.852	0.804	46	0.904	0.795	54	0.780	0.756
Fasting endurance	MinSeasRain (–)	76	0.867	0.819	54	0.903	0.792	62	0.778	0.755
	MinSeasNDVI (–)	139	0.854	0.805	49	0.903	0.794	60	0.779	0.755
Multi-causal models										
SummerMaxTemp + AnnualRain		11	0.878	0.827	9	0.909	0.805	36	0.785	0.760
SummerMaxTemp + AnnualRain + Island		**0**	**0.880**	**0.829**	**0**	**0.911**	**0.809**	**0**	**0.795**	**0.769**
(b) Spatial CAR Models										
SummerMaxTemp + AnnualRain + S		**0**	**0.920**	**0.850**	10	0.929	0.808	27	0.829	0.783
SummerMaxTemp + AnnualRain + Island + S		37	0.920	0.850	**0**	**0.928**	**0.810**	**0**	**0.830**	**0.787**
SummerMaxTemp + AnnualRain + Trend + S		89	0.920	0.851	23	0.930	0.808	63	0.829	0.781
SummerMaxTemp + AnnualRain + Island + Trend + S		152	0.920	0.850	20	0.928	0.809	61	0.829	0.785

Table S3.1. Model selection results for the three *Macropus* species using different prior specifications for (a) aspatial models and (b) spatial models that included conditional autoregressive (CAR) spatial random effects. In comparison to the prior distributions used for models presented in Table 3.1 of the main text, these models used uniform distributions on the interval [–1000,1000] for all coefficients and inverse-gamma distributions (1/Γ(0.01,0.01)) for the variances. Note that changing the priors had little effect on the model selection process, with the exception that a negative Island effect was supported for *M. fuliginosus* on Kangaroo Island (red box). All other details are as for Table 3.1 in the main text.

CHAPTER 4

ENVIRONMENTAL AND HUMAN-INDUCED BODY-SIZE EVOLUTION IN TWO WIDESPREAD KANGAROOS WITH LARGELY OVERLAPPING DISTRIBUTIONS

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CONTEXT

In this chapter I test prevailing hypotheses proposed to explain spatial and environmental body-size patterns in mammals using datasets for Australia's two most widely-distributed kangaroos, *Macropus robustus* and *M. rufus*. I also test the hypothesis that larger *Macropus* body size might be favoured by increased resource availability due to European pastoral activities and examines the island effect.

STATEMENT OF AUTHORSHIP

RAC prepared much of the experimental design, collected data, performed analyses and wrote the manuscript. TAAP contributed to the experimental design, helped develop the analytical methods, assisted with data collection, provided guidance and advice, and commented on the draft manuscript. GJP helped collect data, provided guidance and advice, commented on drafts and contributed to the discussion.

ABSTRACT

Spatial and environmental patterns of body-size variation have been documented within many species of mammals. Here we test five different hypotheses hitherto proposed to explain such patterns in mammals: heat conservation, heat dissipation, primary productivity, seasonality and ecologically and evolutionarily relevant net primary productivity, using datasets for Australia's two most widely-distributed kangaroos, *Macropus robustus* and *M. rufus*. Spatial autoregressive models controlling for age, sex and island effects were used to identify environmental predictors that optimised model performance within each hypothesis and to evaluate multi-causal explanations for spatial body-size patterns. We also tested the hypothesis that body size has increased over time due to increased primary productivity of grassland vegetation and water availability following European settlement in Australia. Productivity emerged as the key explanation driving larger body size in both species. Additionally, we found support for heat conservation as a key explanation driving larger body size in *M. robustus*. Body size increased over time in *M. robustus*, which supports the idea of increased resource availability, but we found little evidence for temporal body-size trend in *M. rufus*.

INTRODUCTION

Optimal body size of animal species maximizes the potential for growth and reproduction and changes with varying climatic conditions (Porter *et al.* 2000). Mammalian body-size studies often focus on: (a) empirical spatial and environmental patterns of variation which often pertain to Bergmann's rule (i.e., an increase in body size with increasing latitude and or decreasing ambient temperature) (Bergmann 1847; see also Rensch 1938, 1959; Mayr 1956; Blackburn *et al.* 1999; Meiri 2011); and (b) testing prevailing hypotheses proposed to explain such patterns, including heat conservation, heat dissipation, primary productivity and seasonality. Heat conservation was originally proposed by Bergmann (1847) as a key mechanism driving observed geographic patterns in body size. Other prevailing explanations for spatial patterns are heat dissipation (James 1970, Speakman & Król 2010), seasonality (Lindsey 1966) and primary productivity which is based on the availability of food resources (Rosenzweig 1968; Wigginton & Dobson 1999; McNab 2010). Similarly, ecologically and evolutionarily relevant Net Primary Productivity (*e*NPP) (Huston & Wolverton 2009), which is based on food availability that is regulated by the NPP of plants during the growing season, has most recently been proposed as an explanation (Huston & Wolverton 2011). Of these hypotheses, primary productivity has received most support as the primary predictor of spatial body-size variation in numerous species of mammals (Rosenzweig 1968; Kolb 1978; Yom-Tov & Nix 1986; Yom-Tov & Geffen 2006; Blois *et al*. 2007; Gür 2010; Gür & Gür 2012; Prowse *et al.* 2015; Correll *et al.* 2015).

Recently, we identified productivity and heat dissipation as the primary drivers of spatial body-size variation in the Eastern Grey Kangaroo (*Macropus giganteus*), Western Grey Kangaroo (*M. fuliginosus*) and Red-necked Wallaby (*M. rufogriseus*) (Prowse *et al.* 2015). To explore determinants of body-size within *Macropus* further, we examined body-size variation in *M. robustus* (Common Wallaroo) and *M. rufus* (Red Kangaroo), which have distributions that span most of the continent, including much of arid Australia. Previous work on *M. rufus* suggests that body size correlates most with productivity (Yom-Tov & Nix 1986), but dataset limitations restricted interpretations. We test the idea that productivity and heat dissipation, rather than heat conservation, seasonality or *e*NPP, are the primary explanations for spatial body size variation body in *M. robustus* and *M. rufus*. For *M. robustus*, we also examine whether Barrow Island populations are smaller than might be predicted were those areas contiguous with the mainland, i.e., impacted by the island effect (e.g., Foster 1964; Lomolino 2005).

Investigations of environmental drivers of geographic body-size variation are further complicated by body-size trends over time. An increase in body size of *M. giganteus*, *M. fuliginosus* and *M. rufogriseus* over the last 130 years (Prowse *et al.* 2015), may be due to release from predation pressure following the persecution and incursions of dingoes in Australia by Europeans since the late 1880s (Johnson 2006; Prowse *et al*. 2015). However, the release of macropods from dingo predation and, to a large degree, hunting by aboriginal Australians may have been offset by a subsequent increase in European harvesting pressure (Pople & Grigg 1999; Grigg 2002; Pople *et al.* 2010). Selection for increased macropod body size might instead have been favoured by increased food and water availability due to European pastoral activities. Such activities include, the provision of water in arid and semi-arid landscapes (Blaney *et al.* 2000), the clearing of forest and woodland habitats, and/or the improvement of native pastures with fertilisers and exotic grasses (Taylor 1985). After correcting for the confounding effects of age, sex, environmental drivers and island effect we examine human-induced evolution of larger body size in *M. robustus* and *M. rufus*.

MATERIALS AND METHODS

Study species

Macropus robustus and *M. rufus* are members of the subgenus *Osphranter* within *Macropus* (Dawson 1995). *Macropus robustus* consists of four subspecies and is the most widely distributed species of *Macropus* (Dawson 1995). *M. r. robustus* occurs in eastern Australia on the eastern and western slopes of the Great Dividing Range; *M. r. woodwardi* extends from north-western Australia to Arnhem Land in the Northern Territory; *M. r. isabellinus* is restricted to Barrow Island in Western Australia and *M. r. erubescens* covers most of the remaining range (Dawson 1995). *M. rufus* is the largest extant marsupial and second only to *M. robustus* among macropodids in the extent of its distribution, which spans the Australian interior.

Both species occur in environments of high climatic variability and low climatic predictability with periods of extreme temperatures and aridity. Water and energy loss (through thermoregulation) is minimized due to advanced physiological and behavioural adaptations. Both species need to drink little free water and pant to induce evaporative cooling (Dawson 1995). *M. robustus* is largely sedentary and seeks shelter in natural refuges during periods of extreme temperature (Clancy & Croft 2008). Diet primarily consists of grasses although selected grass species may vary between subspecies (Taylor 1983). They can survive on nutrient-poor food thereby eliminating the need to travel vast distances or to move at high speeds to forage for nutrient-rich plants (Dawson 1995). *M. rufus* has the ability to travel widely in response to adverse environmental conditions (Croft 1981), providing occasion to follow nutrient-rich forage and avoid forage paucities. Diet primarily consists of grasses and, during wet seasons, forbs but may include shrubs (Dawson & Ellis 1994) and some chenopods in drier seasons (Bailey *et al.* 1971; Barker 1987). Both species are sexually dimorphic, with adult males substantially larger than adult females (*M. robustus*: 28–42 kg cf. 18–24 kg, *M. rufus*: 55–85 kg cf. 18–40 kg [Dawson 1995]).

Cranial parameters

Three cranial dimensions (± 0.01 mm), condylobasal length (CBL) (von den Driesch 1976), total jaw length (TJL) (Myers 2001) and greatest zygomatic breadth (ZB), were recorded from specimens with known geographic coordinates using Mitutoyo digital calipers. Specimens were sourced from Australian museums and wildlife collections. Weight and sex of specimens were recorded where available. As macropods age, their molars erupt at the posterior end of the molar row, progress forwards and are shed as they wear (Augusteyn *et al.* 2003). To account for age we measured the molar index (MI) of each specimen (Inns 1982), which is defined as the number of molars anterior to a reference line on the rims of the eye orbits (Kirkpatrick 1964). For both species the total sample number (n), number of samples for which sex was known and total number of sites (nSites) were: *M. robustus* (n = 961; m = 282; f = 287; nSites = 499 ranging from 13.05–35.0°S and 113.8–153.0°E); *M. rufus* (n = 529; m = 111; f = 219; nSites = 312 ranging from 14.8–35.3°S and 113.8°E to 150°E). Because CBL was most highly correlated with body weight for both species, this parameter was used as our body size representative (see Table S4.1, Supplementary Information).

Environmental variables

We sourced gridded environmental covariates for Australia from datasets obtained from the Australian Bureau of Meteorology (BoM), the British Atmospheric Data Centre (BADC) and an Australian continental Net Primary Productivity (NPP) estimate, AussieGrass, based on fluxes of carbon / nutrients and CO2 / water (see Roxburgh *et al.* 2004). Spatial data was prepared using the R computing environment (R Development Core Team 2011) and functions within the R package `raster` (Hijmans & van Etten 2012). Covariates were collated across a common 0.05° spatial grid to match that of the BoM datasets. Raster data sets were up-scaled (or down-scaled) by firstly aggregating (or disaggregating) layers to a 0.05° grid then rescaling datasets to a common extent using bilinear interpolation. Spatial data from BoM and BADC were summarised on a seasonal and annual basis. In order to test the *e*NPP hypothesis, we defined the growing season for each grid cell as the set of months with a mean temperature > 15 °C (www.bom.gov.au). Environmental variables used to test the hypotheses are presented in Table 4.1, as are the proposed mechanism and predicted pattern of the hypotheses. For explanations of how the predictors relate to the hypotheses see Correll *et al.* (2015). Since NPP (and *e*NPP) is largely dependent on soil quality and soil nutrient availability (Wolverton *et al.* 2009) we also considered 0-30cm soil clay content percent (Clay30) (Australian Soil Resource Information System) in model selection.

Island effects and temporal trends

To account for possible island effects in *M. robustus*, specimens were classified as originating from the Australian mainland, or from Barrow Island (ca. 202 km^2), and we considered this as a 2-level factor for statistical analysis. Sample sizes were 482/17, respectively. We examined trends in macropod body size over time post-European arrival in Australia from the late 19th Century to 2009.

Model fitting

We used spatial autoregressive (SAR) models (Bivand *et al.* 2008) to examine the ability of each environmental variable, and combinations of these variables, to explain body-size differences in both species of *Macropus*. 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 X is the matrix of explanatory variables and $\boldsymbol{\beta}$ is the vector of coefficients. The spatially dependent error term, **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 or -1 indicate strong positive or negative spatial autocorrelation, respectively), **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.

Akaike information criteria with a correction for finite sample sizes (AICc) (Burnham & Anderson 2002) was used as a means to: (a) select the best predictor within each hypothesis and b) select the best multi-causal model to predict body-size, island effects and trends in macropod body size over the post-European period. Prior to running multi-causal models, we determined the degree of correlation between the environmental variables identified for each hypothesis by calculating Spearman's rank correlation coefficient (*R*). Variables that were highly correlated ($R \geq 0.80$) were excluded from model combinations (see Table S4.2, Supplementary Information). Given a set of models, AICc balances the number of parameters and fit to the log likelihood and chooses the candidate model that minimizes the information loss, i.e., lowest AICc value indicates best performing model (Burnham & Anderson 2002, p. 70). We selected top-ranking mono-causal models and multi-causal models on the basis of lowest AICc values. Sex (m, f) and island effect (Barrow Island) were considered as factors in the models. A regression with cubic polynomial terms $MI + MI^2 + MI^3$ allowed us to fit a growth curve with reasonable flexibility.

Hypothesis	**Mechanism**	**Predicted pattern**		**Environmental variables used to test Hypotheses**
Heat conservation	Reduced surface to volume ratios of larger individuals increases heat conservation in colder environments	Body size decreases with temperature	Bergmann (1987)	Mean winter minimum temperature (*WinterMinTemp*) (C°), averaged across 1912–2009.
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 & Król (2010)	Mean summer maximum temperature (*SummerMaxTemp*) (C°), averaged across 1912–2009.
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)	Coefficient of variation (CV) of seasonal environmental variables (e.g., *SeasMinTempCV* [C°]).
Productivity	Body size depends on availability of food resources (primary productivity)	Body size increases with productivity	Rosenzweig (1968), Wigginton & Dobson (1999), McNab (2010)	Annual calculations of: (1) precipitation (mm) averaged across 1911–2009, (2) precipitation minus potential evapotranspiration (P-PET) (mm) averaged across 1911–2009, (3) areal actual evapotranspiration (mm) based on the period 1961– 1990, (4) the Normalised Difference Vegetation Index mean averaged across January 2008 – March 2012; Australian continental Net Primary Productivity (NPP) estimate, *Aussiegrass* (Gt C y^{-1}) (see Roxburgh *et al.* 2004).
*Ecologically and evolutionarily relevant net primary productivity (*e*NPP)*	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 & Wolverton (2011)	Primary productivity variables calculated over the growing seasons (e.g., *GrowSeasP-PET* [mm]).

Table 4.1. Proposed mechanism, predicted pattern and variables used to test hypotheses proposed to explain patterns of spatial and temporal body size variation (adapted from Correll *et al.* 2015).

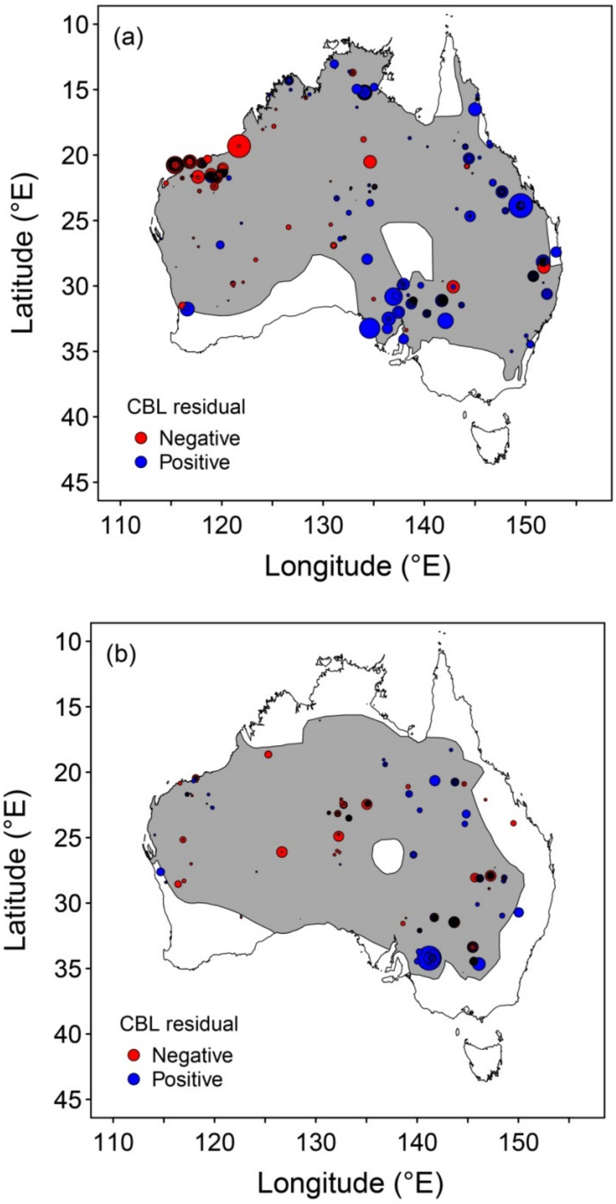

Figure 4.1. Spatial pattern of residuals in condylobasal length (mm) from an aspatial model (i.e., models accounting for age and sex only) fitted for (a) *Macropus robustus* and (b) *M. rufus*. Negative and positive residuals are shown as red and blue points, respectively, and the size of each point is directly proportional to the absolute value of the residual. Shaded areas depict current distribution (IUCN 2013).

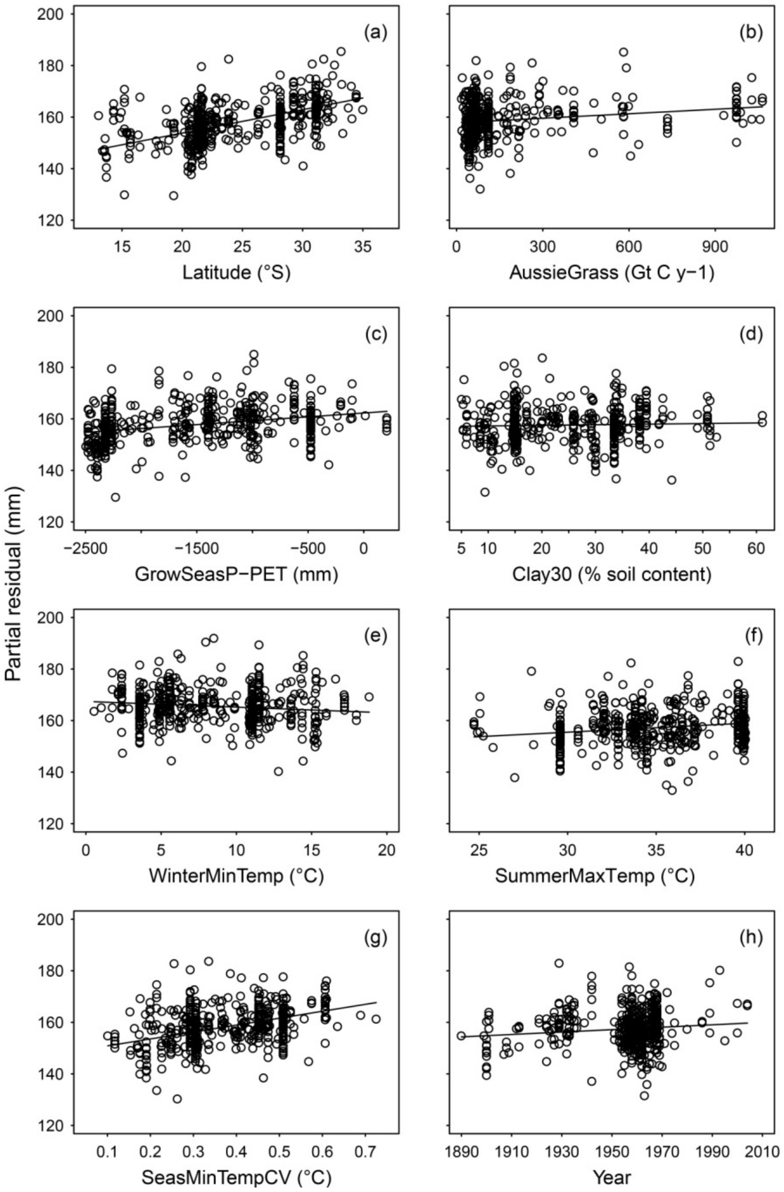

Figure 4.2. For *Macropus robustus*, fitted relationships for spatial autoregressive models between partial residuals (mm) and latitude (a) and also the top AICc-ranked predictor from each hypothesis (inclusive is soil quality); (b) net primary productivity estimate (AussieGrass [productivity]), (c) growing season precipitation minus potential evapotranspiration (GrowSeasP-PET [*e*NPP]), (d) 0-30cm percent soil clay content (Clay30 [soil quality]), (e) mean winter minimum temperature (WinterMinTemp [heat conservation]), (f) mean summer maximum temperature (SummerMaxTemp [heat dissipation]), (g) coefficient of variation of seasonal minimum temperature (SeasMinTempCV [seasonality]). And also (h) year.

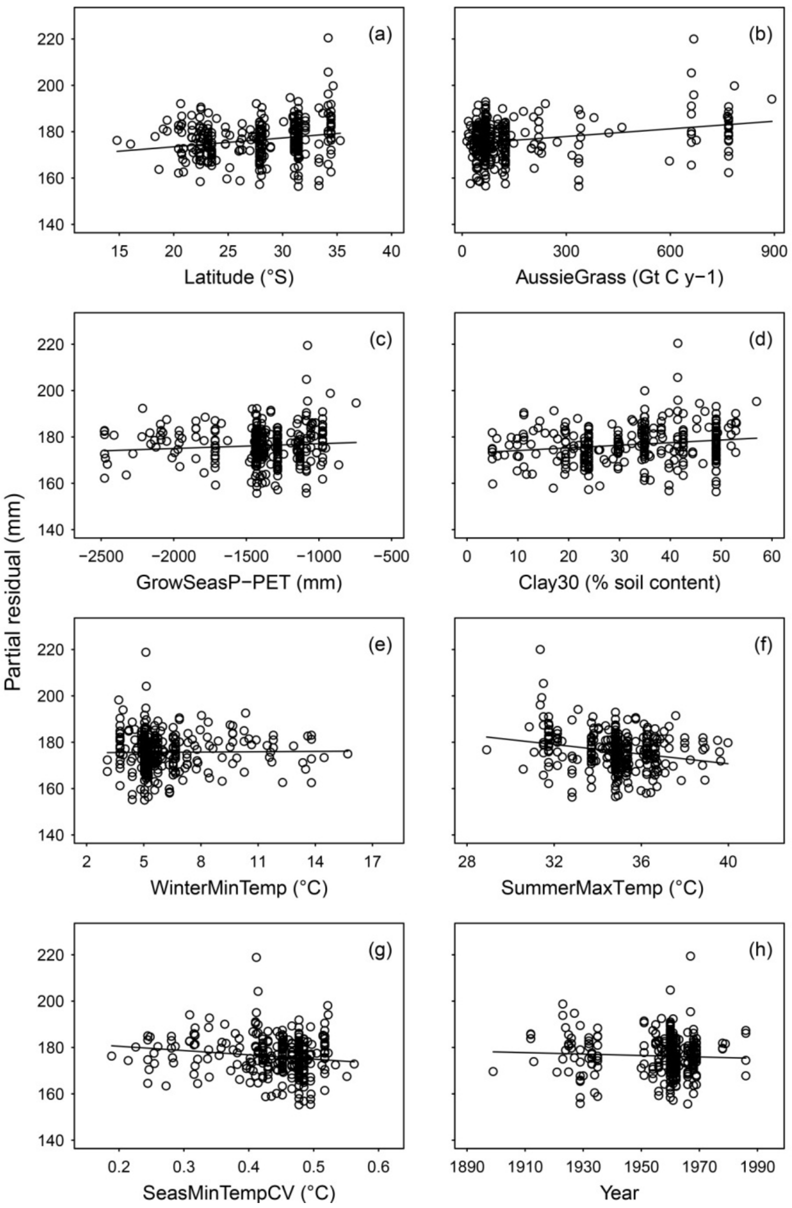

Figure 4.3. For *Macropus rufus*, fitted relationships for spatial autoregressive models between partial residuals (mm) and latitude (a) and also the top AICc-ranked predictor from each hypothesis (inclusive is soil quality); (b) net primary productivity estimate (AussieGrass [productivity]), (c) growing season precipitation minus potential evapotranspiration (GrowSeasP-PET [*e*NPP]), (d) 0-30cm percent soil clay content (Clay30 [soil quality]), (e) mean winter minimum temperature (WinterMinTemp [heat conservation]), (f) mean summer maximum temperature (SummerMaxTemp [heat dissipation]), (g) coefficient of variation of seasonal minimum temperature (SeasMinTempCV [seasonality]). And also (h) year.

RESULTS

Geographic body-size variation

Specimens of both species are, in general larger, in south eastern Australia than in the remainder of the continent (Fig. 4.1). Body size of both species increases with latitude and conforms to Bergmann's rule (Fig. 4.2a, 4.3a), although spatial SAR modelling estimated a stronger relationship between CBL and latitude in *M. robustus* than in *M. rufus*. (–0.908 ± 0.438 mm CBL per °S [estimate ± 95% confidence interval] cf. –0.382 ± 0.328 mm CBL per °S). After accounting for age and sex, there is more unexplained variation for *M. rufus* than for *M. robustus* (Fig. 4.1).

Mono-causal environmental drivers of body size

AICc values of mono-causal SAR models supported net primary productivity (AussieGrass) as the key determinate of body size in both *Macropus* species (Table 4.2). The parameter estimate between AussieGrass and body size was positive for both *M. robustus* (0.006 ± 0.002 mm CBL per Gt C yr, Fig. 4.2b) and *M. rufus* (0.011 ± 0.004 mm CBL per Gt C yr, Fig. 4.3b), which follows the pattern predicted by the productivity hypothesis. Similarly, the *e*NPP hypothesis posits a positive relationship between body size and productivity during the growing season (GrowSeas). A positive relationship was projected between GrowSeasP-PET and body size in both species (*M. robustus,* 0.003 ± 0.002 mm CBL per mm P-PET, Fig. 4.2c; *M. rufus* 0.002 ± 0.004 mm CBL per mm P-PET, Fig 4.3c) but, on the basis of AICc ranking, support for this hypothesis was weak. Body size was positively related to soil clay content (Clay30) (*M. robustus,* 0.023 ± 0.074 mm CBL per clay content, Fig. 4.2d; *M. rufus,* 0.113 ± 0.076 mm CBL per clay content, Fig. 4.3d), which follows the pattern predicted by both productivity and *e*NPP, but support for soil clay content was also weak.

Both thermoregulatory hypotheses predict negative relationships between temperature and body size, where body size decreases with temperature. This trend was projected between winter minimum temperature and *M. robustus* (–0.22 ± 0.096 mm CBL per °C, Fig. 4.2e) and was also projected between mean summer maximum temperature and *M. rufus* (–1.039 ± 0.631 mm CBL per °C^{-1}, Fig. 4.3f). However, the trend between mean summer maximum temperature and *M. robustus* (0.347 ± 0.344 mm CBL per °C) and mean winter minimum temperature and *M. rufus* (0.048 ± 0.259 mm CBL per °C; Fig. 4.3e) was positive. Thus, we excluded these variables, for the relevant species, from subsequent evaluation in multi-causal model analyses. Furthermore, we were unable to support either the heat conservation or dissipation hypothesis based on weak AICc rankings. The seasonality hypothesis proposes a positive relationship between body size and seasonal variability. Although a positive relationship was projected between the coefficient of variation (CV) of seasonal minimum temperature and *M. robustus* body size (26.879 ± 12.083 mm CBL per °C, Fig. 4.2g), AICc ranking provided no support for this hypothesis. Furthermore, a negative relationship between CV seasonal minimum temperature and *M. rufus* body size (–18.501 ± 18.195 mm CBL per °C) (Fig. 4.3g), rather than the predicted positive relationship, prompted our exclusion of this variable from subsequent evaluation in multi-causal models for this species. The spatial autoregression coefficients for the models for *M. robustus* were, in each case, high (all $\lambda \geq 0.70$, Table 4.2) demonstrating strong positive spatial autocorrelation in body size that could not be explained by predictor variables. For *M. rufus* however, λ values of the models ranged from low (0.226) to moderate (0.553), exhibiting weak to modest positive spatial autocorrelation with body size.

Model		*Macropus robustus*				*Macropus rufus*			
		R^2	**AICc**	**δAICc**	**λ**	R^2	**AICc**	**δAICc**	**λ**
Null		0.826	3373.6	45.4	0.796	0.835	2203.9	28.1	0.493
Mono-causal models									
	Latitude	0.832	3359.4	31.2	0.794	0.838	2200.8	25.1	0.505
	Year	0.829	3368.5	40.2	0.800	0.836	2205.0	29.3	0.489
Heat Conservation	WinterMinTemp	0.833	3355.6	27.4	0.788	0.837	2206.0	30.1	0.489
Heat Dissipation	SummerMaxTemp	0.830	3372.8	44.5	0.838	0.841	2195.8	20.1	0.537
Productivity	AussieGrass	0.835	3350.7	22.5	0.814	0.848	2179.9	4.1	0.484
*e*NPP	GrowSeasP-PET	0.826	3370.5	42.3	0.7	0.836	2205.0	29.2	0.553
Seasonality	SeasMinTempCV	0.833	3357.0	28.8	0.803	0.837	2202.0	26.3	0.510
Soil quality	Clay30	0.826	3375.3	47.1	0.791	0.837	2200.7	24.9	0.226
Multi-causal models									
	AussieGrass + WinterMinTemp	0.840	3334.9	6.7	0.780	–	–	–	–
	AussieGrass + SummerMaxTemp	–	–	–	–	0.848	2182.0	6.2	0.484
	AussieGrass + Year	0.837	3347.1	18.8	0.815	0.848	2182.0	6.2	0.481
	AussieGrass + GrowSeasP-PET	0.835	3349.2	21.0	0.742	0.85	2176.9	1.1	0.355
	AussieGrass + Clay 30	0.835	3352.8	24.5	0.811	**0.851**	**2175.7**	**0.0**	**0.43**
	AussieGrass + SeasMinTempCV	0.837	3345.6	17.3	0.792	–	–	–	–
	AussieGrass + WinterMinTemp + Barrow Island	**0.843**	**3328.2**	**0.0**	**0.779**	–	–	–	–
	AussieGrass + WinterMinTemp + Barrow Island + Year	0.843	3329.0	0.8	0.781	–	–	–	–
	AussieGrass + Clay30 + Year	–	–	–	–	0.851	2177.8	2.1	0.424
	AussieGrass + *GrowSeasP-PET+ Year	–	–	–	–	0.85	2178.9	3.2	0.35

Table 4.2. Hypotheses and model selection for spatial SAR models of *Marcopus robustus* (*n* = 499) and *M. rufus* (*n* = 312) condylobasal length (CBL) + molar index (MI) + sex. 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), 3) the change in AICc (δAICc) relative to the top-ranked model within each model type, and 4) the spatial autoregression coefficient (λ). To test the heat-conservation and heat-dissipation hypotheses we used mean minimum winter temperature (WinterMinTemp) and mean summer maximum temperature (SummerMaxTemp), respectively. In the case of the seasonality, productivity and *e*NPP hypotheses, for each of the single-causal models, multiple putatively relevant covariates were tested but only the top-ranked model is shown. For both species, these included coefficient of variation of seasonal minimum temperature (SeasMinTempCV), NPP estimate based on fluxes of carbon / nutrients and CO2 / water (AussieGrass), precipitation minus potential precipitation calculated over the growing seasons (GrowSeasP-Pet). The top multi-causal models selected for *M. robustus* and *M. rufus* were of the form CBL+ MI + sex ~ AussieGrass + WinterMinTemp + Barrow Island and CBL+ MI + sex ~ AussieGrass + Clay30, respectively (bold type). *Parameter estimate for GrowSeasP-PET was negative which is opposite to that predicted by the *e*NPP hypothesis.

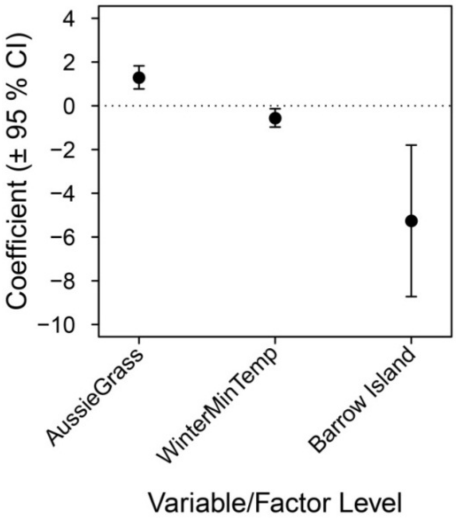

Figure 4.4. Plot of parameter estimates for *Macropus robustus* (coefficients [±95% CI]) for each variable/factor level in the selected spatial SAR multi-causal model; net primary productivity estimate (AussieGrass), mean winter minimum temperature (WinterMinTemp) and Barrow Island. Note that the coefficients 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).

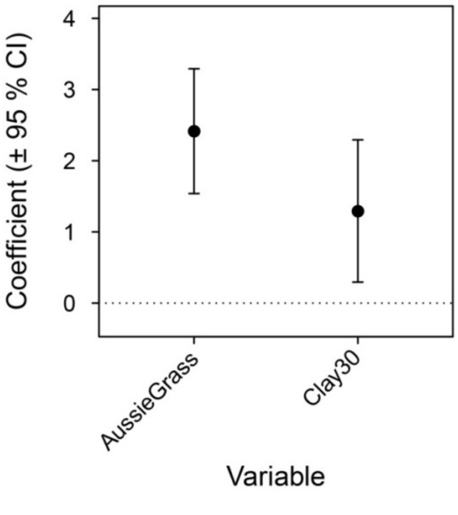

Figure 4.5. Plot of parameter estimates for *Macropus rufus* (coefficients [±95% CI]) for each variable in the selected spatial SAR multi-causal model; net primary productivity estimate (AussieGrass) and percent soil clay content (Clay30). Note that the coefficients presented for the environmental covariates 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).

Multi-causal drivers of body size including island effect

Our multi-causal models supported the primary productivity and heat conservation hypotheses (Table 4.2). We found a positive effect between AussieGrass and body size in both *Macropus* species (*M. robustus,* 0.005 ± 0.002 mm CBL per Gt C yr; *M. rufus*, 0.011 ± 0.004 mm CBL per Gt C yr) and a positive effect between soil clay content and *M. rufus* body size (0.101 ± 0.078 mm CBL per clay content) (Figs 4.4 & 4.5). For *M. robustus*, winter minimum temperature presented a moderate negative effect on body size (–0.136 ± 0.103 mm CBL per °C) and a strong negative effect is apparent in the isolated population of Barrow Island (–5.262 ± 3.462 mm CBL) (Fig 4.4).

Temporal trends

We found an increasing *M. robustus* body-size trend over time (0.047 ± 0.034 mm CBL per year, Fig. 4.2h). No inclining trend in body size over time was projected by the model for *M. rufus*. Although the model that included trend terms for *M. rufus* estimated a decrease in body size over time (-0.031 ± 0.064 mm CBL per year, Fig. 4.3h), confidence intervals for this trend term overlap zero; thus no temporal trend is evident in this species.

DISCUSSION

Macropus robustus and *M. rufus* both exhibit Bergmannian trends where condylobasal length (our body size proxy) increases with latitude and decreases with temperature (Figs 4.2 and 4.3 [a,e,f,]). Our spatial autoregressive (SAR) models supported the primary productivity hypothesis as a key explanation for geographic body-size variation in *Macropus robustus* and *M. rufus*. These results are consistent with observations of primary productivity (i.e., annual rainfall / moister index of wettest quarter) as a key positive driver of spatial body-size variation in the Western Grey Kangaroo (*M. fuliginosus*), Eastern Grey Kangaroo (*M. giganteus*), Red-necked

Wallaby (*M. rufogriseus*) and Red Kangaroo, *M. rufus* (Yom-Tov & Nix 1986; Prowse *et al.* 2015). Net primary productivity is very sensitive to variation in environmental conditions that affect plant growth, particularly the availability of mineral nutrients and water in the soil (Wolverton *et al.* 2009). The top AICc-ranked multi-causal model for *M. rufus* (AussieGrass + Clay30) projected a positive relationship between body size and soil clay content. Clay soils generally have a large water-holding capacity and are better able to supply nutrients to plants than other soil types (Gupta & Larson 1979). Productivity has received most support as a key driver of spatial body-size variation in marsupials (Yom-Tov & Nix 1986; Correll *et al.* 2015; Prowse *et al.* 2015) and numerous species of placental mammals (e.g., Rosenzweig 1968; Kolb 1978; Yom-Tov & Nix 1986; Blois *et al.* 2007; Gür 2010; Gür & Gür 2012).

After examining the top AICc-ranked multi-causal model for *M. robustus* (AussieGrass + WinterMinTemp + Barrow Island), we also found support for the heat conservation hypothesis as a key explanation for geographic body-size variation, i.e., body size increased with decreased winter minimum temperature, thus conforming to Bergmann’s rule. By contrast, we find no support for heat conservation as a driver of body-size variation in *M. rufus*.

Within warmer regions, individuals living in dry environments are predicted by the heat dissipation hypothesis (James 1970) to lower their body temperature more easily 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. Likewise, smaller individuals in hotter, lower latitudes have a high surface-area-to-volume ratio which is predicted to promote heat dissipation and improve reproductive fitness (Speakman & Król 2010). Previously, we propose heat dissipation to explain body-size differences within *Macropus giganteus, M. fuliginosus* and *M. rufogriseus* (Prowse *et al*. 2015). However, the current study provides less support for this hypothesis in *M. rufus* or *M. robustus.*

In environments with high seasonality and low climatic predictability, the seasonality hypothesis predicts that larger individuals are more likely to survive food shortages because of their greater capacity for fat storage (Lindsey 1966). Periods of food shortage occur with greater frequency at higher latitudes, where environments are more seasonal, and thus more seasonal regions should have larger individuals. We found no support for this hypothesis in *M. rufus* and *M. robustus*. In fact, the relationship between the coefficient of variation of seasonal minimum temperature and *M. rufus* body size was negative, which is opposite to that predicted by seasonality. This is consistent with prior observations of a negative relationship between *M. rufus* body size and annual temperature range (Yom-Tov & Nix 1986). A positive correlation between increasing *stability* of seasonal minimum temperature and *M. rufus* body size might relate to plant growth where relative constancy of minimum temperatures maintains more readily available food. Alternatively, it may be a thermoregulatory response or it may relate to some other unknown factor.

Macropus robustus is a predominantly sedentary species (Dawson 1995), and increased body-size variation compared with *M. rufus* may be predicted to enhance survival rates in environments of high variability / low predictability. *M. rufus* is highly mobile by comparison and individuals occupy large ranges (Dawson 1995) which implies an increased ability to disperse to more suitable locations, thus reducing the selective pressure for greater body-size response.

Spatial autoregression coefficients (λ) for the top-ranked SAR models for *M. robustus* were always high (all $\lambda \geq 0.70$, Table 2) signifying that environmental drivers included in this study could only account for some of the spatial pattern in the data. For *M. rufus*, λ values of the top SAR models were considerably lower (0.226−0.553), indicating that environmental drivers accounted for more of the spatial pattern in the data than unaccounted variables.

The temporal body-size trend for *M. robustus* showed a marginal increase post-European arrival (late 19th Century through 2009). This is consistent with the suggestion that human-induced factors, such as the provision of water in arid and semi-arid landscapes (Blaney *et al.* 2000), the clearing of forest and woodland habitats, and/or the improvement of native pastures with fertilisers and exotic grasses (Taylor 1985), have selected for increased body size in species of *Macropus* (Prowse *et al*. 2015). However, we found little evidence for a temporal trend in *M. rufus*. For this species, it is possible that the predicted temporal body-size increase due to increased food and water availability may have been overridden by human-induced factors favouring decreased body size. Since European settlement in Australian during the late 18th Century, kangaroos have been hunted for a commercial trade in skins which was extended to include meat in the mid-20th Century (Pople & Grigg 1999). Currently, both *M. rufus* and *M. robustus* are commercially harvested throughout New South Wales, Queensland, South Australia and Western Australia (Pople & Grigg 1999). High harvest-induced mortality selects for increased and/or earlier allocation of energy to reproduction which can result in reduced size at maturity (Audzijonyte *et al.* 2013). Moreover, selection for smaller body size is expected to be stronger when larger individuals are targeted (such is the case with harvesting), thus preferentially removing fast-growing individuals (Fenberg & Roy 2008). Although the proportion of commercially harvested *M. rufus* is larger than that of *M. robustus* (36% of the four mainland species harvested cf. 10% [www.environment.gov.au/resource/commercial-kangaroo-harvesting-fact-sheet]), the number of individuals harvested as a percentage of their sustainable quota is slightly lower for *M. rufus* than *M. robustus* (54% cf. 56%). However, these harvest numbers are based on recent years (averaged across 2000–2012) and may not reflect earlier harvesting practices. Nonetheless, absence of a temporal body-size trend for *M. rufus* suggests that this species might not tolerate commercial hunting pressure to the same extent as its congenerics. Future clarification of post-European human-induced changes in body size would benefit from the analysis of late Holocene fossil samples.

CONCLUSION

We used spatial simultaneous autoregressive models to examine spatial and human-induced temporal (post-late 19th Century) body-size patterns in Australia's two most widely distributed kangaroo species, *Macropus robustus* and *M. rufus*. Our results support productivity as a key explanation for geographic body-size variation in both species, but also support the heat conservation hypothesis in *M. robustus*. Hypotheses explaining body-size variation should thus not be viewed as mutually exclusive. Auxiliary roles for other factors, including those associated with alternative hypotheses, may also influence body size simultaneously. We demonstrate a marginal increase in *M. robustus* body size over the last 150 years and suggest that this trend occurs because of increased water availability and primary productivity of grassland vegetation following European settlement in Australia and is not due to a depauperate predator guild. Little evidence of temporal body-size trend was detected in *M. rufus*. Although wildlife collections provide scope to investigate spatial drivers and temporal changes in animal body size, sampling is likely to be biased by factors such as by availability, selected cull periods and preferences of collectors. Rigorous investigation of late Holocene fossil samples may provide clarification of post-European human-induced changes in body size.

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SUPPLEMENTARY INFORMATION

	Macropus robustus		*Macropus rufus*	
Cranial parameters	***r***	**Bm-*n***	***r***	**Bm-*n***
Condylobasal length (CBL)	0.907	166	0.758	148
Total jaw length (TJL)	0.889	160	0.766	105
Zygomatic breadth (ZB)	0.866	166	0.691	147
Principle Component 1 (PC1)	0.903	160	0.758	104

Table S4.1. Pearson's coefficient correlation (*r*) of cranial parameters against body mass. From a principal component analysis of the cranial parameters, correlation between our selected component (PC1) and body mass is also presented. Total samples with known body mass (Bm-*n*). Missing values for some of the measurements from the *Macropus rufus* overall dataset reduced the number of TJL samples (TJL *n* = 429, PC1 *n* = 398, ZB *n* = 526) and so CBL (*n* = 500) was used as our body-size representative for both species (*M. robustus*; CBL *n* = 935, TJL *n* = 817, PC1 *n* = 794, ZB *n* = 951).

Macropus robustus	WinterMinTemp	SummerMaxTemp	AussieGrass	Clay30	GrowSeasP-PET	SeasMinTempCV
WinterMinTemp	1	0.637	–0.267	–0.469	–0.662	–0.981
SummerMaxTemp	0.637	1	–0.483	–0.484	–0.919	–0.608
AussieGrass	–0.267	–0.483	1	0.239	0.530	0.315
Clay 30	–0.469	–0.484	0.239	1	0.498	0.438
GrowSeasP-PET	–0.662	–0.919	0.530	0.498	1	0.629
SeasMinTempCV	–0.981	–0.608	0.315	0.438	0.629	1
Macropus rufus						
SummerMaxTemp	1	–0.597	–0.763	–0.2		
AussieGrass	–0.597	1	0.457	0.155		
GrowSeasP-PET	–0.763	0.457	1	0.021		
Clay30	–0.2	0.155	0.021	1		

Table S4.2. Spearman's rank correlation coefficient of top environmental variables selected represent each hypothesis for *Macropus robustus* and *M. rufus*; mean winter minimum temperature (WinterMinTemp), mean summer maximum temperature (SummerMaxTemp), Australian Continental NPP estimate based on fluxes of carbon / nutrients and CO_2 / water (AussieGrass), 0–30-cm soil clay content percent (Clay30), growing season precipitation minus potential evapotranspiration (GrowSeasP-PET), coefficient of variation of seasonal minimum temperature (SeasMinTempCV).

CHAPTER 5

IS THERE REALLY AN ISLAND RULE? AN AUTECOLOGICAL APPROACH REVEALS THAT DETERMINANTS OF MAINLAND BODY SIZE ALSO RULE ON ISLANDS

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CONTEXT

In this chapter I test prevailing explanations proposed to describe island body-size patterns in mammals using datasets for two widely-distributed Australian mammals, the Australian Bush Rat, *Rattus fuscipes*, and Common Brushtail Possum, *Trichosurus vulpecula*. I also test the hypothesis that explanations for more general (i.e., spatial and temporal) body-size patterns, such as productivity and or temperature, might also apply on islands.

STATEMENT OF AUTHORSHIP

RAC prepared much of the experimental design, collected data, contributed to the analyses and wrote the manuscript. TAAP performed analyses and commented on a draft manuscript. MGG commented on a draft manuscript. GJP helped collect the data, provided guidance and advice, commented on drafts and helped refine the discussion.

ABSTRACT

The island rule is a recognised pattern of body-size evolution, most often noted in mammals, where larger species are held to become smaller bodied and smaller species larger on islands. Proposed explanations for body-size patterns have largely centred on species-level traits, biotic interactions and island-specific traits but, in general, fail to consider explanations for more general (i.e., spatial and temporal) body-size patterns, such as productivity and or temperature. Furthermore, broad-scale taxonomic datasets commonly used to investigate explanations for the island rule restrict quantifying the strength of individual biotic and abiotic determinants. Here we apply an autecological approach using skull measurements from island and mainland representatives of the Australian Bush Rat, *Rattus fuscipes*, and Common Brushtail Possum, *Trichosurus vulpecula*. We explicitly test how different biotic and abiotic covariates (including temperature and rainfall) influence island body-size patterns. We refute two fundamental features of the rule by showing that 1) size shifts within a species are not unidirectional; and 2) that species with a larger initial (mainland) body mass can actually increase in size instead of decreasing in size, as predicted under the island rule. Moreover, the absence of any detectable overall island effect shows that the island rule is upheld in neither species. Island area, distance from mainland, interval of isolation, and numbers of competitors or predators exert no influence on island body-size patterns in these species. Rather, temperature is the best predictor of *T. vulpecula* island body size followed by productivity. However, we were unable to demonstrate the presence of any predictors of *R. fuscipes* body size. Our findings provide empirical support for primary drivers of body-size variation among island populations of these species, refuting the general validity of the island rule, and demonstrate that productivity and temperature might account for many island body-size patterns in mammals.

INTRODUCTION

When mainland animals colonize islands or are separated on land-bridge islands the newly isolated populations may undergo significant evolutionary changes in body size. Larger species have been observed to become smaller (dwarfism) and smaller species larger (gigantism) (e.g., Foster 1964; Lomolino 2005). While also recorded in reptiles and birds (e.g., Soulé 1966; Rand *et al.* 1975; Parker 1984; Pregill 1986; Clegg & Owens 2002; Boback & Guyer 2003; Keogh *et al.* 2005; Jaffe *et al*. 2011) body-size shifts on islands, or the island effect, has been most commonly documented in mammals. Classic examples include Pleistocene dwarfing of elephants and deer (e.g., Sondaar 1977; Lister 1989, 1996), but it has also been reported in modern carnivores (Wayne *et al.* 1991), artiodactyls (Endo *et al.* 2002; Miller & Harley 2001), sloths (Anderson & Handley 2002), heteromyid rodents (Lawlor 1982), and primates (Bromham & Cardillo 2007). Similarly, gigantism of small species on islands has been noted in rodents, including several extant murids and squirrels (e.g., Hall 1938; Heaney 1978; Adler 1996; Millien & Gonzalez 2011; Lister & Hall 2014), and some fossil taxa (e.g., Freudenthal 1976; Millien & Jaeger 2001; Millien 2004). This pattern of centralizing body-size evolution is known as the 'island rule' (Van Valen 1973). One quantification of the rule argued that species smaller than 282 g tend to increase in size on islands, while species larger than approximately 2.7 kg become smaller (Lomolino *et al*. 2012).

A range of studies have tested and confirmed the generality of the island rule across vertebrates using large comparative datasets (Clegg & Owens 2002; Boback & Guyer 2003; Lomolino 2005; Lomolino *et al.* 2006; Bromhan & Cardillo 2007; Welch 2009). By contrast, other recent research has suggested that the island rule may not hold in most mammal groups and brings its broader applicability into question. These studies argue that: a) there is no evidence for generality of the rule (Meiri *et al.* 2004, 2006; Meiri 2007); b) the pattern of the rule is relatively weak (McClain *et al.* 2012); and c) the rule lacks consistency within clades purported to adhere to it (Meiri *et al.* 2008). As it stands, insular size shifts within mammals appear to be concentrated in a few key clades: carnivores, heteromyid rodents and artiodactyls typically dwarf on islands, whereas murid rodents usually become larger (Meiri *et al.* 2008). Furthermore, the magnitude of size shifts within species can vary among islands (e.g., Anderson & Handley 2002).

Multiple independent factors have been proposed to explain insular body-size shifts in vertebrates. These fall into three categories:

(1) Species-level traits e.g., original body size (Foster 1964; Lomolino 1985, 2005) and the type of food available to specialists/generalists (Lawlor 1982);

(2) Biotic variables, e.g., reduced predators and interspecific competitors (Foster 1964; Sondaar 1977; Lomolino 1985; Adler & Levins 1994; Dayan & Simberloff 1998; McNab 2010), increased intraspecific competition (Heaney 1978; Lomolino 1985; Roth 1992);

(3) Island-specific traits, such as island area (Heaney 1978), isolation (time/distance) (Foster 1964, 1965; Carlquist 1974), climate (Millien & Damuth 2004), and resource limitation (Sondaar 1977; Heaney 1978; Marquet &Taper 1998).

Predictions of these processes are summarised in Table 5.1.

Many studies investigating more broad-scale body-size patterns (i.e., across continents or long-term time periods) in mammals advocate productivity and or temperature as the most important drivers of body size (e.g., Kolb 1978; Yom-Tov & Nix 1986; Smith *et al*. 1995; Blois *et al.* 2007; Gür & Gür 2012; Prowse *et al*. 2014; Briscoe *et al.* 2015; Correll *et al.* 2015). Body-size is predominantly maintained by energy (food) input; based on the availability of food resources, the productivity hypothesis thus predicts that body-size increases with productivity (Rosenzweig 1968; McNab 2010). Conversely, thermoregulatory based hypotheses predict a decrease in body size with temperature. The heat conservation hypothesis proposes that individuals living in cooler regions minimise heat loss because of their lower surface-area-to-volume ratio (Bergmann 1847). Similarly, the heat dissipation hypothesis proposes that higher

Process	**Prediction**	**Reference**
Phylogenetic affinities	Smaller bodied species increase in size / larger bodied species decrease in size	Foster (1964), Lomolino (1985, 2005)
Food type	Decreased available food type = decreased body size of smaller specialist species Increased available food type = increased body size of smaller generalist species	Lawlor (1982)
Reduced predation pressure	Body size of larger species decreases with reduced predation pressure	Foster (1964), Sondaar (1977) Lomolino (1985), Adler & Levins 1994
Reduced interspecific competition	Body size of smaller species increases with reduced interspecific competition	Foster (1964), Lomolino (1985) Dayan & Simberloff (1998), McNab (2010)
Increased intraspecific competition	Body size of larger species decreases with increased intraspecific competition	Heaney (1978) Lomolino (1985), Roth (1992)
Island area	Small mammals increase and large animals decrease in size as island area decreases	Heaney (1978), Millien & Damuth (2004)
Isolation (time/distance)	Small mammals increase and large animals decrease in size as island isolation increases	Foster (1964, 1965), Carlquist (1975),
Temperature	body size decreases with temperature increase	
Resource limitation	Small mammals increase and large animals decrease in size with decreasing resource availability	Sondaar (1977), Heaney (1978) Marquet & Taper (1998)

Table 5.1. Processes proposed to explain body-size evolution on islands and their predictions.

surface-area-to-volume of smaller individuals in warmer regions facilitates heat loss (James 1970; Speakman & Król 2010). It seems reasonable therefore that those mechanisms that apply across space and time should also apply on islands, yet the direct effects of productivity and temperature on island body sizes have received little attention (Durst & Roth 2012; Lomolino *et al.* 2012; McClain *et al.* 2012). Furthermore, several explanations for island body-size patterns may ultimately depend on resource availability (Kurtén 1972; Van Valen 1973; Lomolino 1985; Marquet & Taper 1998). Such deficiencies have likely been due to the difficulty of quantifying resource availability (primary productivity) and temperature prior to the recent increased availability of large climatic datasets.

Contrary to the pattern predicted by the productivity hypothesis, the negative relationship between productivity and island body size demonstrated in rodents (Durst & Roth 2012) and in a broad-scale mammalian dataset (McClain *et al.* 2012), appears to uphold the general opinion that islands are characterised by low food (resource) availability (e.g., Heaney 1978; Marquet & Taper 1998). However, this opinion is inferred from the assumption that there is a positive relationship between resource availability and island area (e.g., Marquet & Taper 1998). A negative relationship between temperature and island body size has been demonstrated in small mammals (Lomolino *et al*. 2012) and in both large and small mammals (McClain *et al.* 2012) which provides support for thermoregulatory response. The importance of productivity as a driver of spatial and temporal body-size changes in rodents is well illustrated in several studies (Blois *et al.* 2007; Medina *et al.* 2007; Pergams & Lawler 2009; Gür 2010; Gür & Gür 2012). Likewise, temperature has been proposed to explain spatial and or temporal rodent body-size differences (Smith *et al*.1995; Millien & Damuth 2004).

Critically, macroecological studies that use broad taxonomic data-sets confound the ability to quantify the strength of individual environmental and climatic determinants of island body-size shifts. Our study applies a more useful approach by taking into account the unique autecological conditions encountered by different island populations of two widespread native Australian mammals, the Bush Rat, *Rattus fuscipes*, and Common Brushtail Possum, *Trichosurus vulpecula*. By comparing body sizes of island and mainland populations we investigate the influence on island body-size patterns of different covariates, biotic (predation, interspecific competition) and abiotic (e.g., island area, isolation interval, temperature, rainfall).

We suggest that mechanisms that drive more general body size patterns also play an important role in determining island body size and those determinants traditionally proposed to explain island body size shifts have little or no effect on body size. Thus, the Island rule might not be upheld. We test the hypothesis that primary productivity and temperature are more important in determining island body-size evolution in *R. fuscipes* and *T. vulpecula* than more traditional explanations.

MATERIALS AND METHODS

Study species

Rattus fuscipes and *Trichosurus vulpecula* are common, nocturnal mammals broadly distributed across mainland Australia. Populations also occur on numerous land-bridge islands isolated by late-Pleistocene sea-level rise (Lambeck & Chappell 2001). Therefore, they provide excellent model species for empirically addressing factors influencing body size in isolated populations. *Rattus fuscipes* is an omnivorous murid rodent with an adult weight range of 40–225 g (Lunney 2008). It is sexually dimorphic, with adult males weighing up to 27% more than females. *R. fuscipes* occurs mostly in heathland regions spanning approximately one-third of the Australian coast and/or hinterland (Lunney 2008). *T. vulpecula* is a primarily folivorous, arboreal phalangerid marsupial with an adult weight range in Australia of 2.6–4.2 kg, with males considerably larger than females on average (Kerle & How 2008). *T. vulpecula* is more widespread and occupies a more diverse array of habitats than any other Australian marsupial (Kerle & How 2008). Despite extensive variation in size and pelage, current genetic and morphological evidence supports both *R. fuscipes* and *T. vulpecula* as single species (Taylor & Horner 1973; Robins *et al*. 2014; Taylor & Foulkes 2004).

Cranial parameters

We sourced island and mainland skulls with known geo-reference (latitude and longitude) data from Australian museum and wildlife collections. For *Rattus fuscipes*, two cranial parameters, condylobasal length (CBL) and total jaw length (TJL), were measured (± 0.01 mm) using Mitutoyo digital calipers from 779 adults (m = 395, f = 384). Adults were recognised as specimens with fully erupted third molars and/or fused skull sutures (Lidicker 1966). After evaluating the correlation between the two cranial parameters and known body weight, we chose CBL as the best body-size representative (see Table S5.1, Supplementary Information). Likewise, for *T. vulpecula* we used CBL (n = 489; m = 255, f = 234), which shows a strong, log-linear relationship with body mass (Correll *et al.* 2015; Supplementary material Appendix 1), as a proxy for body size.

Biotic and abiotic variables

Covariates applicable to mainland and island samples

Gridded total monthly rainfall for all months from 1901 to 2009, and mean monthly minimum and maximum daily temperature for all months from 1912 to 2009 (both 0.05° resolution) were sourced from the Australian Bureau of Meteorology (BoM). Spatial data were prepared using the R computing environment (R Development Core Team 2011) and functions within the R package `raster` (Hijmans & van Etten 2012). As an index of productivity we calculated mean annual rainfall (Rain), averaged across all available years. To evaluate the role of temperature, we calculated the mean daily temperature averaged across all available years (Temp).

We extracted temperature and rainfall values for each sample from the 0.05°-resolution temperature and rainfall layers. *R. fuscipes* specimens originated from 672 distinct grid cells ranging from latitude 16.05°S to 39.08°S and longitude 113.7°E to 153.5°E; while *T. vulpecula* 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. We centred and standardised variables by their standard deviations to facilitate comparison of statistical models involving variables with different units and to provide a better fit for JAGS models.

Island-specific covariates

Number of potential interspecific competitors and predators on each island was determined for both species from the Atlas of Living Australia (www.ala.org.au). Island area (km^2) was obtained from local government sources. Distance from mainland (km) was measured using Google Earth's tool to calculate the straight-line distance to the nearest mainland area. Bathymetric depth data was obtained from Geoscience Australia (www.ga.gov.au/scientific-topics/marine/bathymetry). Time since isolation (kyr) was estimated using these data and published sea-level curves (Lambeck & Chappell 2001; Belperio *et al.* 2002; Lewis *et al.* 2013). Sampled islands and their respective biotic and island specific covariates are presented in Table 5.2.

	Island name	***n* specimens**	***n* competitors**	***n* predators**	**State**	**Island area (km^2)**	**Distance from mainland (km)**	**Time since isolation (kyr)**
Rattus fuscipes	Dog	10	0	1	SA	0.4	31.2	9.0*
	East Wallabi	13	0	0	WA	3.2	56	10.4^
	Eyre	18	0	2	SA	10	1.6	6.2*
	Fraser	13	5	18	QLD	1840	2.4	7.5^
	French	1	2	14	VIC	111	1.8	7.7^
	Goat	10	0	4	SA	3.3	12	6.7*
	Great Glennie	21	0	0	VIC	1.4	6.8	11.2^
	Greenly	17	0	0	SA	1.7	29	13.3^
	Hopkins	4	0	1	SA	1.6	4.5	7.7*
	Kangaroo	23	2	17	SA	4400	13.5	8.9*
	Liguanea	4	0	1	SA	1.8	3.7	9.3*
	Mondrain	7	0	1	WA	8.1	11	12.2^
	North Gambier	7	0	5	SA	0.8	34.5	9.1*
	Pearson	15	1	1	SA	2.1	62	9.3*
	Perforated	2	0	1	SA	0.7	15	9.0*
	Waldegrave	11	0	5	SA	2.9	2.5	7.0*
	Williams	10	0	1	SA	1.4	1.9	9.2*
	Woody	1	2	1	WA	2.4	7.5	10.4^
Trichosurus vulpecula	Kangaroo	30	2	1	SA	4400	13.5	8.9*
	Tasmania	92	2	1	TAS	64519	199	14§
	Flinders	12	1	1	TAS	1367	140	14§
	Magnetic	7	3	2	QLD	52	4.4	7.5^
	Barrow	14	NA	NA	WA	202	53.5	8.8^
	Bathurst	7	2	2	NT	2600	62.4	9.7^
	Centre	2	NA	NA	NT	84	7.8	7^
	Croker	1	1	2	NT	332	2.7	7^
	Milingimbi	1	NA	2	NT	60	0.5	7^
	Erith	4	NA	NA	TAS	3.2	81	14§
	Deal	15	NA	NA	TAS	15.8	85	14§
	North Keppel	9	NA	1	QLD	6.3	11.7	7.5^
	Thistle	2	NA	1	SA	40	7.5	7.7*

Table 5.2. Islands from which *Rattus fuscipes* and *Trichosurus vulpecula* specimens were obtained and their respective biotic and island-specific covariates including sea-level curve reference: *Belperio *et al.* (2002), ^Lewis *et al.* (2013), §Lambeck & Chappell (2001).

Model fitting

We used Bayesian hierarchical models to analyse spatial variation in *R. fuscipes* and *T. vulpecula* condylobasal length (CBL) because this method allowed us to include random effect structures, while: (1) incorporating covariates applicable to all specimens (e.g., rainfall) and those only applicable to specimens from islands (e.g., island area); and (2) performing Gibbs variable selection (Tenan *et al.* 2014). The models were fit using *JAGS* version 3.4 called through *R* using the package r2jags version 3.14 (Plummer 2011). For each model, we ran three Markov chains for 60 000 iterations, with a burn-in of 10 000 and a thinning rate of 50 iterations to reduce autocorrelation between samples. We assessed convergence by visually inspecting the chains and with the Gelman-Rubin statistic (Gelman & Hill 2007). To investigate the possibility of spatial autocorrelation in the residuals of the different models fitted, we used Moran's I spatial autocorrelation coefficient, calculated at a range of distance lags.

MODEL 1 (Null model)

To investigate the effects of island isolation on the body size of these species, we initially fitted a simple model that only accounted for the sex of individuals and whether they sampled from the Australian mainland or islands isolated by late-Pleistocene sea-level rise. Assuming a Gaussian error structure, we modelled the expected CBL for a specimen from island j as:

$$\mathrm{CBL} = \boldsymbol{\alpha} + \boldsymbol{\beta_0}\mathrm{Sex} + \boldsymbol{\beta_1}\mathrm{Island}_j$$

where Sex is an indicator variable equal to 1 if the specimen is male and Island_j is the effect of being from the jth island. To account for correlations between specimens from the same islands, we treated the island terms as random effects that were assumed to come from a gaussian distribution with a prior mean of zero and prior standard deviation of $U(0,10)$. Hence the 'global' island effect (i.e., the mean effect of island isolation for each species) is simply the posterior mean of this distribution.

MODEL 2

We then fitted a model that accounted for the effect of a number of potentially relevant environmental covariates, and used Gibbs variable selection to account for uncertainty in whether all these covariates should be included. Assuming k potential covariates have been identified, Gibbs variable selection employs an auxiliary, indicator variable γ_k such that $\gamma_k = 1$ indicates the presence and $\gamma_k = 0$ indicates the absence of covariate j in the model, such that $\boldsymbol{\theta}_j = \gamma_k\boldsymbol{\delta}_k$, where $\boldsymbol{\theta}$ is parameter vector used after multiplying the parameter vector $\boldsymbol{\delta}_k$ by the indicator variable γ_k. We specified uninformative priors such that when $\gamma_\mathrm{k} = 1$ the prior for covariate k was $N(0, 1000)$ but when $\gamma_\mathrm{k} = 0$ a less diffuse 'pseudoprior' of $N(0, 100)$ was used. Using such a pseudoprior helps to improve the mixing of the MCMC sample and reduces the probability that the variable selection procedure will become fixed on a single variable set (Tenan *et al.* 2014). The model formulation was therefore:

$$\mathrm{CBL} = \boldsymbol{\alpha} + \boldsymbol{\beta_0}\mathrm{Sex} + \boldsymbol{\beta_1}\mathrm{Island}_j + \Sigma\gamma_k\boldsymbol{\delta}_k\boldsymbol{X}_k$$

For covariate vectors $\boldsymbol{\delta_k}$ that were only relevant to island specimens, these only contributed to the likelihood calculation for specimens sampled from islands.

MODEL 3

For both species, residual analysis for Models 1 and 2 revealed evidence of spatial autocorrelation, indicating that these models could not account for some of the geographic variation in body size. In particular, specimens from eastern Australia were larger than expected based on the fitted models. We therefore fitted a final model which extended Model 2 by allowing the MCMC algorithm to split the data from each species into two distinct groups (west and east) and fitted an additional effect of being in the east group. The division lines for splitting into these two regions (optimised by the model) are shown in Figure 5.1.

Examples of the WinBUGS code for all models are provided in Appendix 2.

RESULTS

Island body-size patterns

Null model

The null model shows that, for *Rattus fuscipes*, the overall global effect of specimens is for them to be smaller than those from the mainland (Fig.5. 2a). Specimens from Fraser and Great Glennie Islands are larger than those from the mainland (Fig. 5.2a). Conversely, specimens from all other islands are smaller than those from the mainland. However, confidence intervals for Greenly, Liguanea, Perforated and Woody Islands each overlap zero.

For *Trichosurus vulpecula,* the null model shows that the overall global effect is centred on zero (Fig. 5.3a), which indicates that, overall, *T. vulpecula* island samples are not statistically distinguishable in size to those of adjacent mainland populations. Specimens from Flinders Island and Tasmania are larger than those from the mainland, whereas samples from Barrow and Crocker Islands are smaller than those from the mainland. Confidence intervals for all other islands overlap zero.

Covariate effects on body size

After accounting for all additional covariates, the global effect is centred on zero (Fig. 5.2b), which indicates that *R. fuscipes* island samples are not statistically distinguishable in size to those of adjacent mainland populations (relative east / west regions). *R. fuscipes* samples from Fraser and Great Glennie Islands exhibited larger body sizes than their eastern mainland counterparts (confidence intervals did not overlap zero). Samples from East Wallabi and Greenly Islands are smaller and larger, respectively, than those on the adjacent western mainland.

Confidence intervals for samples from all other islands overlap zero; thus the negative effects on islands in the west region disappear.

When all covariates were accounted for, the overall global effect for *T. vulpecula* remains on zero (Fig. 5.3b). Possum specimens from Flinders Island remain larger than those from the eastern mainland. Confidence intervals for samples from all other islands overlap zero, indicating no island effect from any of these islands. Thus, samples from Barrow and Croker Islands are no longer significantly negative and those from Tasmania are no longer significantly positive.

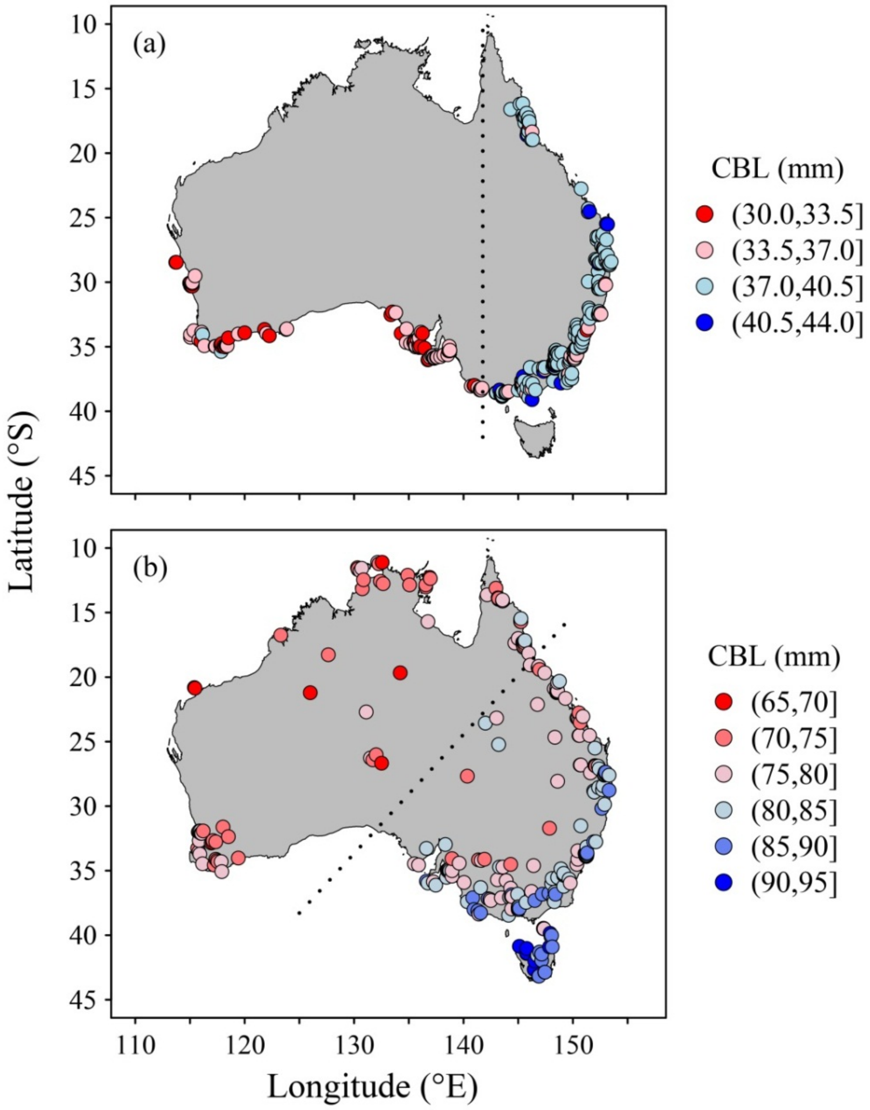

Figure 5.1. Division lines between east–west regions for (a) *Rattus fuscipes* and (b) *Trichosurus vulpecula*.

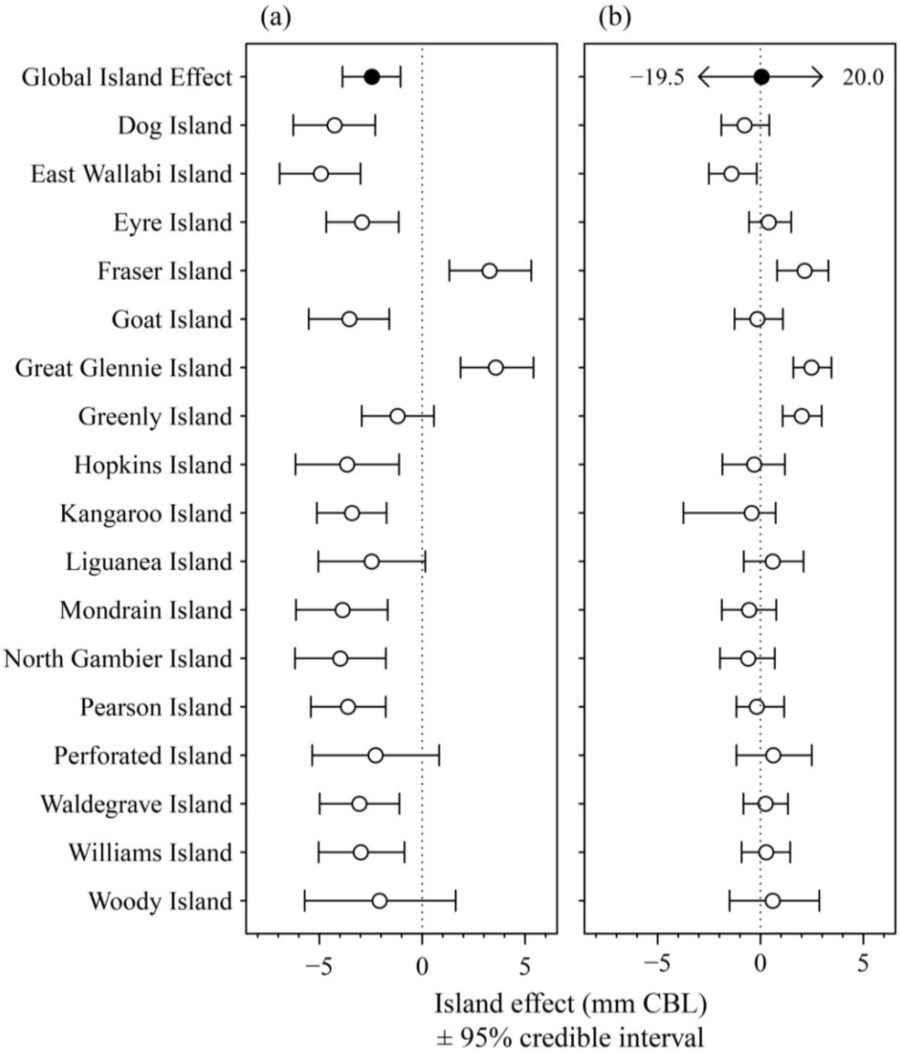

Figure 5.2. Island effects and global island effect for *Rattus fuscipes* CBL relative to mainland. Null model fitted with the covariate sex (a) and model fitted with all covariates (b).

Sex (male) and region (east) both have a positive effect on *R. fuscipes* island body size (Fig. 5.4a). The remaining covariates centre on zero, thus, they have no detectable effect on island body-size evolution in this species. For *T. vulpecula*, covariates sex (male), region (east) and rainfall each have a strong positive effect on island body size in (Fig. 5.4b), whereas temperature has a negative effect. These results are consistent with the productivity and the heat conservation hypotheses. Since all other covariates centre on zero, and or have very large confidence intervals, they have no detectable effect on body size of island *T. vulpecula* specimens.

Temperature and rainfall effects on CBL for each island as well as island location are presented in the Supplementary Information (Figs S5.2–S5.3).

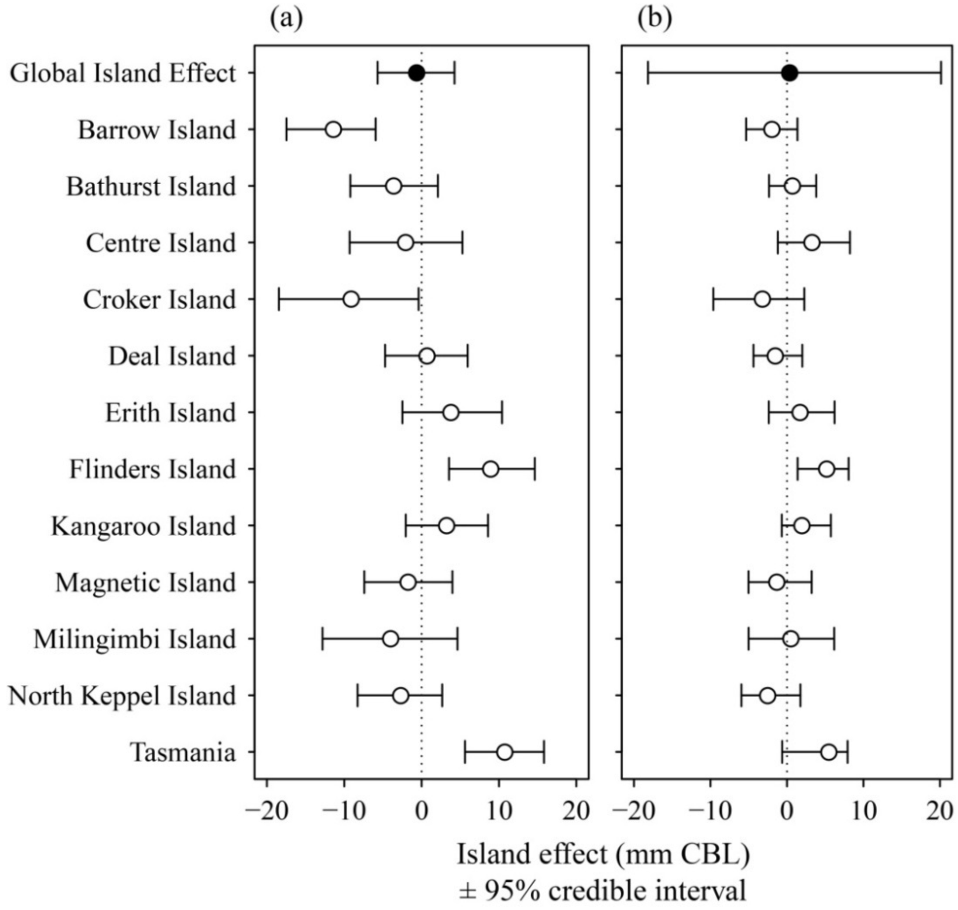

Figure 5.3. Island effects and global island effect for *Trichosurus vulpecula* CBL relative to mainland. Null model fitted with the covariate sex (a) and model fitted with all covariates (b).

Spatial autocorrelation of residuals

For both species, deviance residuals from the null model as well as the covariate model were spatially autocorrelated (i.e., most Moran's I values were significantly different from zero) (see Fig. S5.1, Supplementary Information).Whereas the covariate model that included region, showed reduce spatial autocorrelation (Moran's I values were all near zero); thus we focus on this model and the comparative null model.

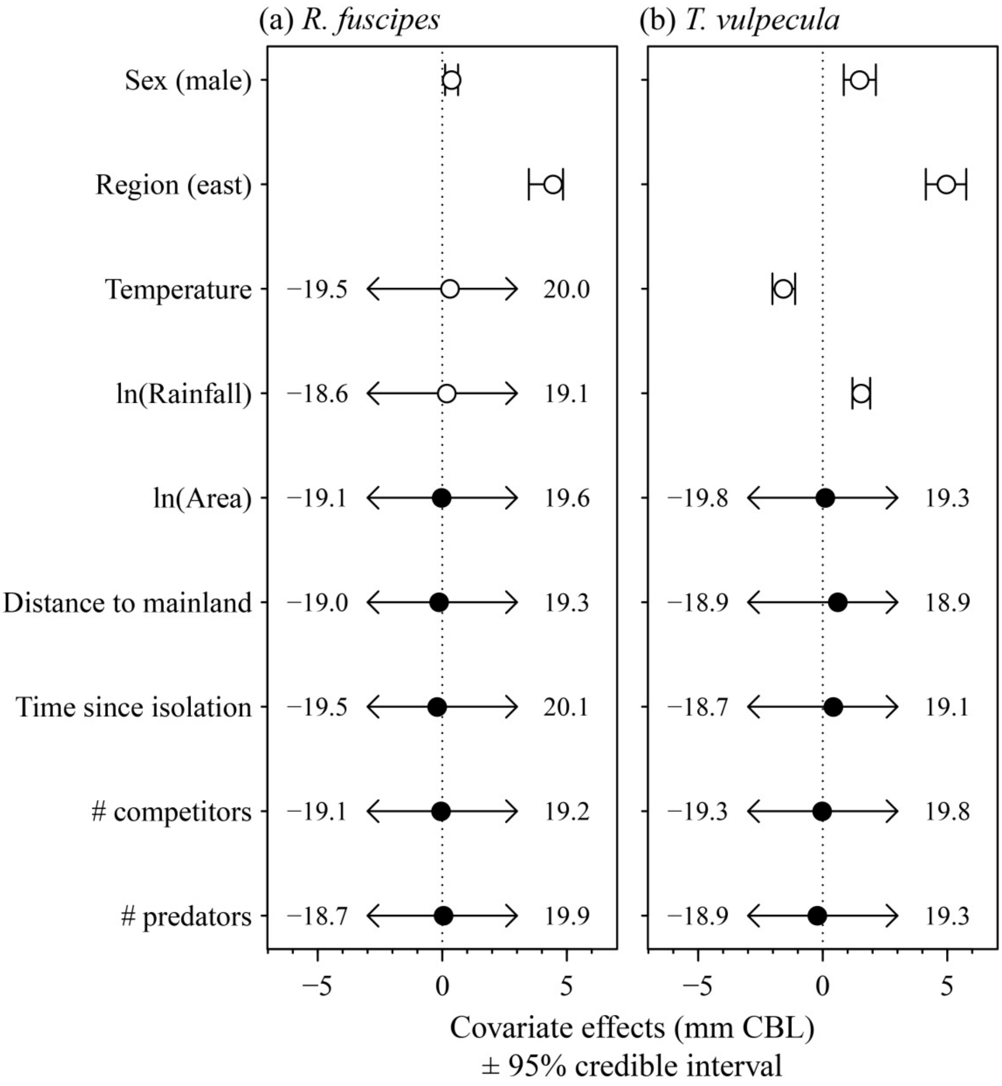

Figure 5.4. Covariate effects for island CBL samples.

DISCUSSION

Island body-size shifts

After accounting for covariates including region, global island effects for both *Rattus fuscipes* and *Trichosurus vulpecula* show that, on average, body size on islands does not differ to that of the adjacent mainland. Our study identified island body-size shifts in both species that are not consistent with the island rule (Foster 1964; Lomolino 1985). According to the rule, *R. fuscipes* should get larger on islands and *T. vulpecula* should get smaller. We found that *T. vulpecula* samples from Flinders Island are larger than their eastern mainland counterparts, which runs counter to the prediction that species greater than 2.7 kg should decrease in size on islands (Lomolino *et al.* 2012). Furthermore, the global island effects from the null model show that *R. fuscipes* CBL is on average c. 2 mm smaller on islands than mainland samples while that of *T. vulpecula* shows no difference.

Rattus fuscipes samples from East Wallabi and Greenly Islands are smaller and larger, respectively, than those on the adjacent western mainland. This marked within region island body-size variation may be due to higher temperatures experienced by East Wallabi Island than those experienced by Greenly Island (Fig. S3a). Populations from Fraser and Great Glennie Islands are larger in body size than their eastern mainland counterparts. The non-unidirectionality of size shifts on islands in *R. fuscipes* violates a core prediction of the island rule. We suggest that the body-size response of mammalian species isolated on islands might not be predetermined by the starting body size. A similar situation has been observed in the two Australian tiger snakes (*Notechis*), which are smaller on some islands and larger on others (Keogh *et al.* 2005). Smaller snake size evolves when island prey items are smaller than on the adjacent mainland, while larger island snakes evolve when prey items are larger than on the mainland. Food attributes were not included in our covariates, but both species are herbivorous, and the dominant food items (i.e., leaves, fruit, seeds) occupy the same general size range in all areas. For both species, populations from all other islands do not differ from their mainland counterparts.

When all covariates were considered, island body-size shifts occur in only four of 17 island populations of *R. fuscipes* and just one of 12 island populations for *T. vulpecula*. More significantly, we found no evidence for global island effect in either species. Thus, the island effect is likely to be much less fixed than has been proposed (Lomolino *et al.* 2012 etc.).

Key drivers of island body size

Previously proposed explanations for island body-size patterns have largely centred on species-level traits, biotic interactions and island-specific traits, and have been the topic of much debate (Dayan & Simberloff 1998; Michaux *et al.* 2002; Meiri *et al.* 2005; Lomolino 2005; Meiri 2007; White & Searle 2007). We found no evidence that island area, isolation (distance and time), number of competitors and number of predators influence patterns of island body size in either *R. fuscipes* or *T. vulpecula*. Rather, temperature and productivity are the most important determinants for *T. vulpecula*. Our results support the hypothesis that primary productivity and temperature are more important than more traditional explanations in determining island body-size evolution in *T. vulpecula*. This is consistent with previous findings that productivity and thermoregulation (heat dissipation) are the most important drivers of spatial *T. vulpecula* body-size patterns across its entire range (Correll *et al.* 2015). Furthermore, the negative relationship between temperature and *T. vulpecula* body size from islands follows the pattern highlighted by McClain *et al.* (2012) and Lomolino *et al.* (2012). We suggest that prevailing explanations (i.e., productivity and temperature) for spatial and temporal body-size patterns in mammals also apply on islands.

We found no evidence for temperature or productivity as drivers of body size in *R. fuscipes*, but the strong body size increase that occurs in the eastern region of Australia (Fig 1a) may be due (at least in part) to rainfall. Indeed, when regional effect was not considered, rainfall has a strong positive effect on *R. fuscipes* (results not shown). However, since our samples were biased in space (e.g., we had no samples from arid areas in the interior), we were unable to confirm the relationship of rainfall to body size. The apparently insignificant role that temperature plays in driving *R. fuscipes* island body size deviates from the form of more pronounced gigantism in small mammals on colder islands (Lomolino *et al.* 2012). This may reflect an insufficient temperature range from where we sampled or may reflect other physiological or behavioural adaptations to temperature such as fur properties (e.g., Briscoe *et al.* 2015) or cathemeral activities (e.g., Jacobs 2008).

Body size in *T. vulpecula* populations from northern (tropical) islands is likely to be more limited by thermoregulatory responses to high annual temperatures, while productivity increases in importance as a size determinant on southern (temperate) islands. This is matched by the greater productivity that is likely, in part, responsible for larger *R. fuscipes* body sizes in eastern island populations.

McClain *et al.* (2006) propose that the island rule is a result of selection on body size in a resource-constrained environment. Our positive relationship between island productivity and body size in *T. vulpecula* (and possibly *R. fuscipes*) runs counter to that found by Durst and Roth (2012) and McClain *et al.* (2012) in other mammals and may suggest that the general characterisation of islands as environments of limited resources does not uphold.

Unidentified determinants of island body-size evolution

After accounting for all covariates, the island body-size shifts that we observe (Figs. 2b, 3b) suggest that additional, unidentified factors contribute to these changes. A study of genetic diversity in *R. fuscipes* on 13 islands off the South Australian coast identified island area as the primary factor maintaining genetic variation (Hinten *et al.* 2003). If low genetic diversity, due to small populations and an initial founder effect, is driving body-size shifts in *R. fuscipes* and *T. vulpecula*, then one might expect to see correlation between body size and island area, which we did not. Similarly, genetic diversity is predicted to decrease with isolation (Frankham 1997) but we found little evidence for isolation (distance or time) as a predictor of island body-size evolution in either species. However our study did not examine genetic diversity so any conclusions here are premature.

CONCLUSIONS

Our study produced three important results. First, body size changes didn’t follow the island rule. We found insular body size changes occurred in both directions within *Rattus fuscipes* disputing a fundamental feature of the island rule; single direction of body size shifts. Island *Trichosurus vulpecula* samples that are larger than expected compared to their mainland counterparts disputes the prediction that species greater than 2.7 kg should decrease in size on islands. More importantly, we found no overall global island effect in either *R. fuscipes* and *T. vulpecula* which indicates that body size of island populations do not differ in size to those of adjacent mainland populations. Second, we found temperature and rainfall were the most important determinants of island body size evolution in *T. vulpecula*. Although we were unable to effectively demonstrate temperature or rainfall as drivers of island body size in *R. fuscipes*, the strong size increase that occurs in the eastern region of Australia is likely due (or partly due) to rainfall. We found no evidence for more conventional explanations for island body-size changes such as island area, isolation (distance and time), number of competitors and number of predators. Rather, prevailing explanations (i.e., productivity and temperature) for spatial and temporal body-size patterns in mammals might also apply on islands. Additional unaccounted abiotic or biotic factors contribute to the observed island body-size changes in both species, but such factors are unlikely to include genetic diversity. Third, we show that using a null model in conjunction with models that consider relevant covariates can reveal potential biases towards island effects. Furthermore, covariate models can effectively demonstrate the strength of the covariates at hand that cause island body size shifts.

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SUPPLEMENTARY INFORMATION

Cranial parameters	***r***	**n**
Condylobasal length (CBL)	0.794	334
Total jaw length (TJL)	0.742	327

Table S5.1. Pearson's correlation coefficient (*r*) for cranial parameters against body mass. CBL was more highly correlated and so was used as our body-size representative (*n* = 854, m = 396, f = 386, sex unknown = 72).

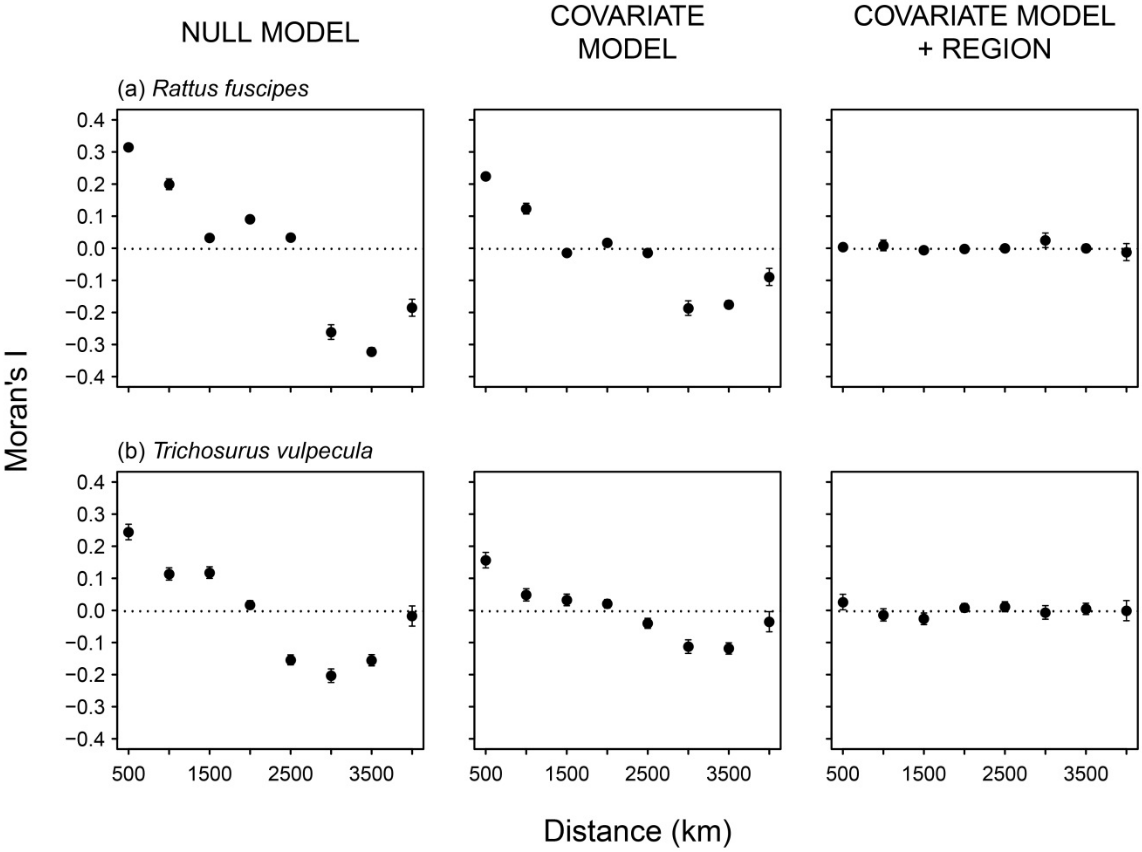

Figure S5.1. Spatial correlograms for the residuals of null, covariate and covariate + region models at 500 km intervals. Moran's I values near + 1.0 indicate positive spatial autocorrelation while values near –1.0 indicate negative spatial autocorrelation. Values near zero indicate a random spatial pattern.

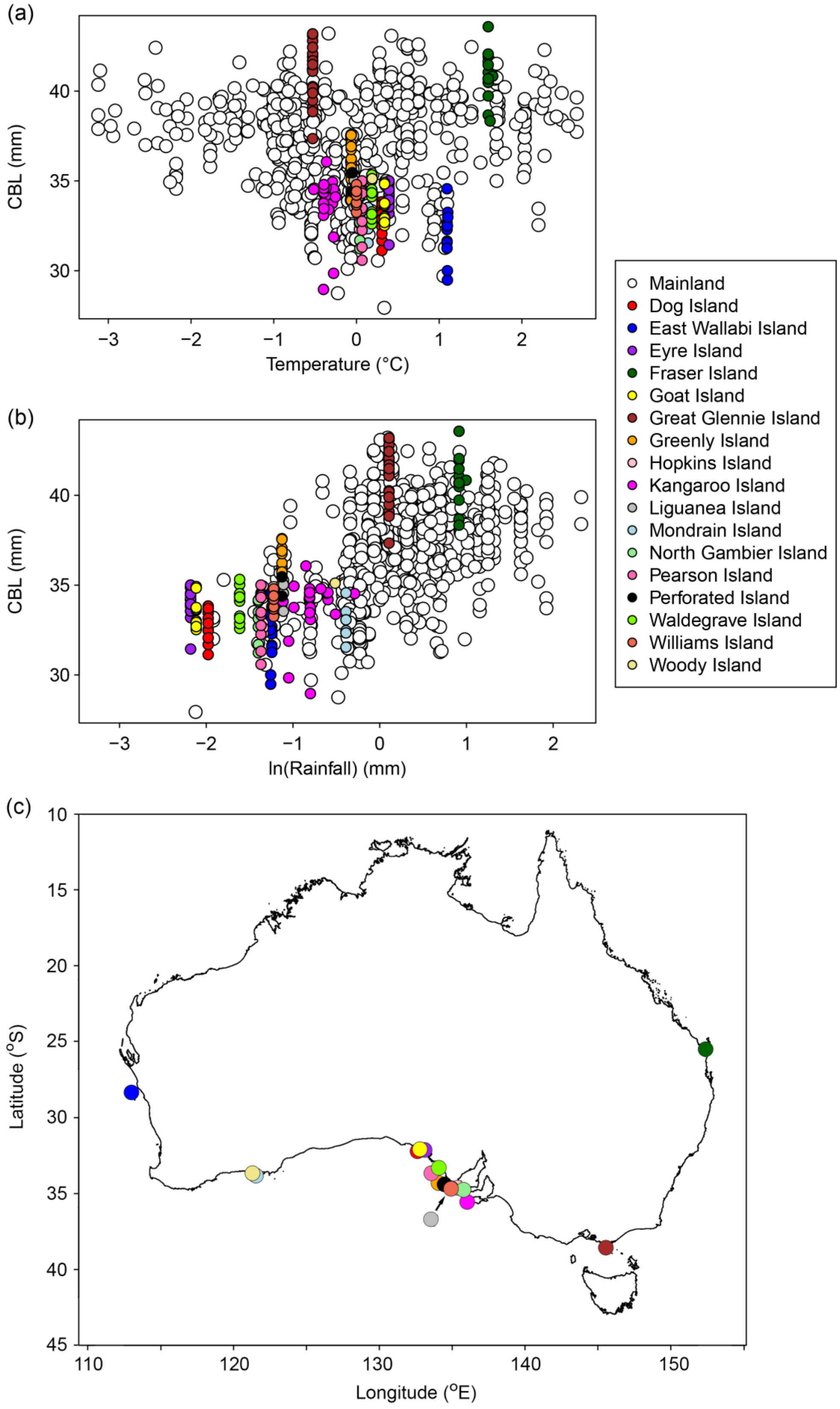

Figure S5.2. Effects of temperature (a) and rainfall (b) on *Rattus fuscipes* CBL for each island and island location (c).

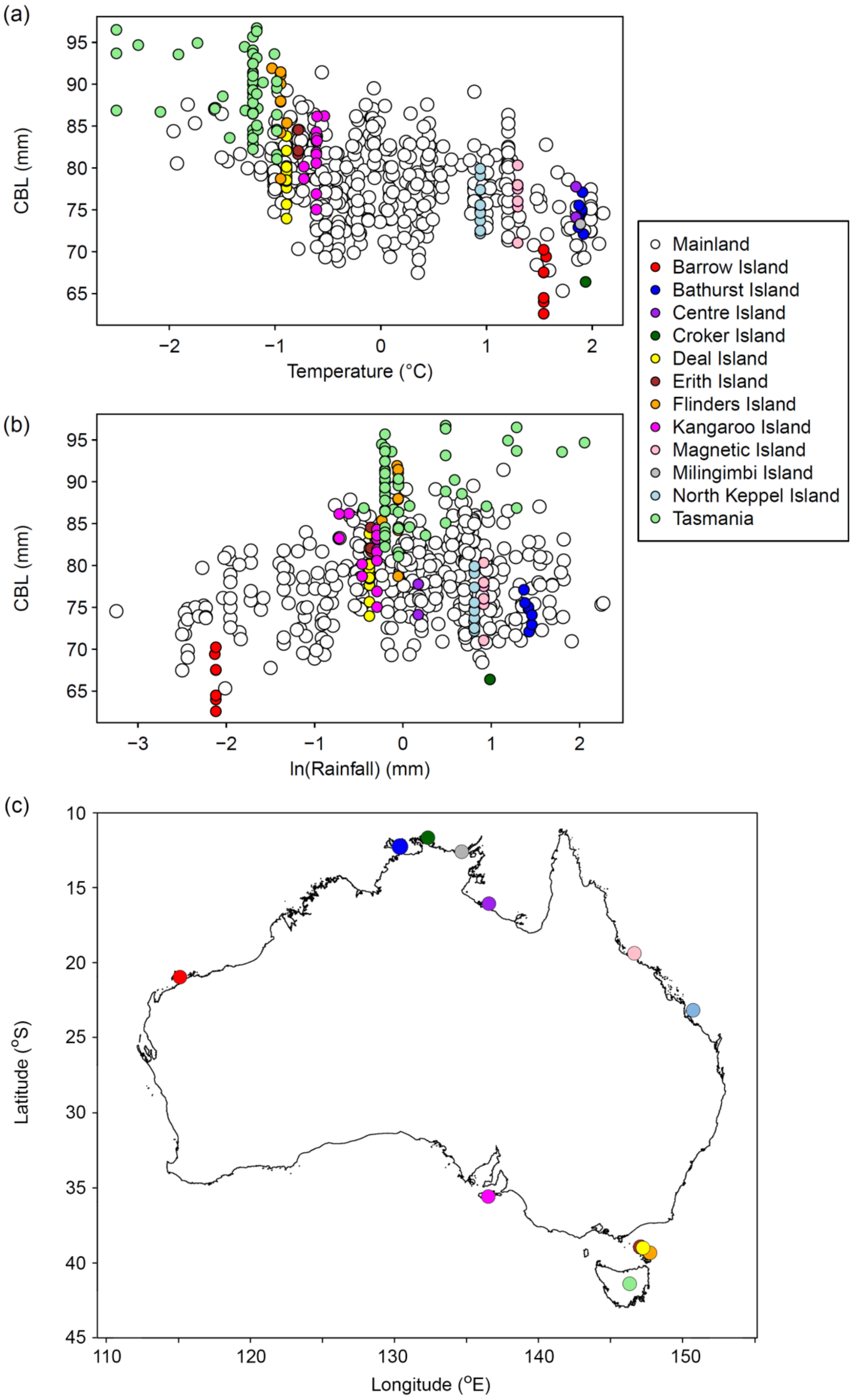

Figure S5.3. Effects of temperature (a) and rainfall (b) on *Trichosurus vulpecula* CBL for each island and island location (c).

CHAPTER 6

GENERAL DISCUSSION

This discussion synthesises the main findings of this study including key concepts or questions variably addressed by the data chapters and considers areas for future attention. Part 1 reviews spatial body-size patterns, particularly in relation to Bergmann's rule, and environmental determinants within the study species. Part 2 presents temporal body-size trends observed in species of *Macropus* and possible drivers. Part 3 examines island body-size shifts in the relevant study species, explains why apparent island body-size shifts should be viewed with caution, and proposes key drivers responsible for body-size evolution on islands. Part 4 considers the analytical challenges encountered by this study. Part 5 considers the potential effects of anthropological warming on body size, discusses problems associated with interpreting contemporary body-size shifts in response to climate change, and highlights the value of wildlife collections and the fossil record for interpreting climatic changes. It also reflects on the potential roles of ontogeny and selection in size shifts and on the means by which these might be tested, and also suggests other areas for future research on body-size determinants. Please note that some repetition of the content of chapter discussions was unavoidable here because chapters are formatted as individual publications, which did not allow for a fuller discussion of results and placement in the broader context.

PART 1: SPATIAL BODY-SIZE VARIATION

Spatial body-size patterns

Trichosurus vulpecula, *Macropus giganteus*, *M. fuliginosus*, *M. rufogriseus*, *M. robustus* and *M. rufus* each exhibit a Bergmannian trend where body size increases with latitude and/or decreases with temperature (Fig. 2.2a–c; Table 3.1; Figs 4.2a, e, f & 4.3a, e, f) conforming with findings of earlier studies (Yom-Tov & Nix 1986; Kerle *et al.* 1991). No relationship was detected between temperature and *Rattus fuscipes* body size (Fig. 5.4a), but latitudinal body-size trends were not examined in this species.

A persistent debate within past studies relates to which species and which taxonomic level Bergmann's rule should apply (Blackburn *et al.* 1999; Watt *et al*. 2010; Meiri 2011). This study demonstrates that, at a broad continental scale, Bergmann's rule occurs in *T. vulpecula* and species of *Macropus*. Bergmannian patterns have also been demonstrated in other marsupials, including *Phascolarctos cinereus* (Briscoe *et al.* 2015) and three species of *Petaurus* (Smith 1973; Russell 1984; Quin *et al.*1996). By contrast, a spatial body-size pattern that is not consistent with Bergmann's rule has been observed in *T. caninus* (Lindenmayer *et al.* 1995, 2002). However, the magnitude of morphological and genetic differences between the larger northern form and smaller southern form of *T. caninus* suggest two distinct species (Lindenmayer *et al.* 2002). A non-Bergmannian pattern has also been observed in *Isoodon obesulus* (Cooper 1998). Samples of *Isoodon obesulus* were restricted to southwest Western Australia, which may have placed limitations on spatial and/or climatic effects. Overall, as a generalised pattern, Bergmann's rule appears to characterise Australian marsupials that occupy a broad latitudinal / temperature range.

Is Bergmann’s rule scale-dependent?

An argument has been made that Bergmann’s rule might be an artefact of non-random sampling (Meiri *et al.* 2004). Studies of spatial body-size variation generally select species on the bases of broad geographic distributions and abundance, in which case patterns of spatial size variation are likely to be a priori. However, Bergmann defined the rule by stating that “animals of a ‘similar organisation’ should be of larger body size if they inhabit higher latitudes” (Bergmann 1847), which advocates that the rule should apply to species that are widespread. Therefore, it could be argued that the exclusion of geographically-restricted species does not form a valid basis for refuting Bergmann’s rule *per se* (cf. Meiri *et al.* 2004). Certainly, the geographic or temperature scale over which a species is sampled most likely contributes significantly to whether Bergmann’s rule is recognised or not and may explain some cases of non-Bergmannian patterns. For example, findings that the Tiger, *Panthera tigris*, does not follow the rule (Meiri *et al.* 2004) conflicts with common knowledge (e.g., Nowak 1999), but might reflect the fact that specimens of the northern, larger subspecies, *P. tigris altaica*, were not sampled (Meiri *et al.* 2004). Another example comes from the only species of *Dipodomys* that conforms to Bergmann’s rule, Ord’s Kangaroo Rat, *Dipodomys ordii*, which has by far the largest geographic range of any species in the genus (Wilson & Ruff 1999).

Geographic and/or temperature scale is likely to be a significant factor in determining spatial body-size patterns and, thus, should be considered when testing for Bergmann’s rule. While latitude is on its own is convenient for a broad-scale comparison that tests for the existence of the pattern – it is not the covariate with which determinants for the pattern can be explored (Hawkins & Diniz-Filho 2004). However, it should be noted that temperature, or other covariates, might also only represent a proxy for an unknown factor rather than the primary driver itself.

Spatial body-size determinants

For *Trichosurus vulpecula* and all five species of *Macropus* investigated here, evidence provided strong support for the productivity hypothesis. Primary productivity may also be driving body-size differences in *Rattus fuscipes* and has been shown to be an important environmental driver of spatial body-size variation in numerous species of mammals (e.g., Rosenzweig 1968; Kolb 1978; Yom-Tov & Nix 1986; Blois et al. 2007; Gür & Gür 2012). For the kangaroos, mean annual productivity is the primary factor controlling adult body size (Table 3.1; Table 4.2), whereas productivity during the leanest season primarily controls body size in *T. vulpecula* (Table 2.2). Furthermore, soil clay content, which is likely to play a significant role in primary productivity, was determined as a strong driver of *M. rufus* body size (Table 4.2).

Body size in five of the six species is also strongly determined by thermoregulatory requirements (Table 2.2; Table 3.1; Table 4.2). No evidence for thermoregulatory response was detected in *Macropus rufus* or *Rattus fuscipes* (Table 4.2; Fig. 5.4a). For *T. vulpecula*, *M. giganteus*, *M. fuliginosus* and *M. rufogriseus*, negative relationships between body size and average summer maximum temperature support the heat-dissipation hypothesis (James 1970; Speakman & Król 2010). This hypothesis has been proposed to explain body-size differences in male *Phascolarctos cinereus*, (Briscoe *et al.* 2015) and within species of the North American woodrat *Neotoma* (Brown & Lee 1969; Smith *et al.* 1995).

The strong negative relationship between winter minimum temperature and *M. robustus* body size suggests heat conservation is a key driver of body-size differences in this species. Bergmann's original heat conservation hypothesis has been proposed as an explanation of spatial body-size differences in female koalas (Briscoe *et al.* 2015). The difference between the relative importance of heat dissipation and heat conservation in male and female koalas might be due to sexual size dimorphism (males are larger than females) or reflect sex-specific differences in ecology and physiology (Briscoe *et al.* 2015). Although sexual size dimorphism occurs within *T. vulpecula* and species of *Macropus*, it is unknown whether the importance of thermoregulatory response differs between sexes within these species; sexes were not differentiated for those analyses.

Strong support was not detected for either the seasonality or the *e*NPP hypotheses in *T. vulpecula* and species of *Macropus* (Table 2.2; Table 3.1; Table 4.2). Although a positive relationship was found between growing season variables and body size of *T. vulpecula* and species of *Macropus*, which is predicted by the *e*NPP hypothesis (Huston & Wolverton 2011), in each case, support for these relationships was very weak. Furthermore, support for lean-season productivity in *T. vulpecula* is counter to the predictions of *e*NPP, where body size is expected to increase with productivity of the most-productive season, not the leanest season.

Lack of evidence for temperature effects on spatial body size differences in *R. fuscipes* and *M. rufus*, may reflect other adaptations to temperature change, either physiological (e.g., Allen’s rule) or behavioural (e.g., dispersal to more suitable locations; Holt 1990; Visser 2008).

Overall, food availability and temperature appear to be the most likely explanation for spatial body-size differences in *T. vulpecula* and species of *Macropus*. This suggests that primary productivity and thermoregulatory requirements may combine to drive body-size evolution. Indeed, in a review of key predictors of geographical and temporal changes in body size, Yom-Tov and Geffen (2011, p. 531) observe that “frequently, the principal predictors of body size are food availability during the period of growth and ambient temperature…”.

Local and global effects of productivity and thermoregulatory requirements

The importance of productivity and thermoregulatory requirements may vary considerably between regions and may be scale-dependent. For example, in the tropics, where one 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. Similarly, body-size samples that are of broad geographic scale, such as those that traverse the Australian continent, might highlight a global importance of primary productivity while those of a fine scale, e.g., Australia's far north, might feature a local importance of thermoregulatory requirements. Geographic scale and regional effects should thus be considered when examining the importance of productivity and thermoregulatory requirements.

PART 2: HUMAN-INDUCED BODY-SIZE EVOLUTION

Temporal body-size trends

Skull measurements from extensive wildlife collections spanning the last 150 years, along with robust statistical modelling, were used to show that that there is no evidence for a temporal body-size decline in four of five kangaroo species (Fig. 3.4; Fig. 4.2h). Historical harvest practices of *Macropus giganteus*, *M. fuliginosus*, *M. rufogriseus* and *M. robustus* post-European settlement (late 19th Century through 2009) might therefore have been insufficient to cause a change in body size because of a) immigration of individuals from inaccessible refuge populations that remain unharvested (Tenhumberg *et al.* 2004), b) the range size of genetic populations is much larger than the harvest localities (Hale 2004), and/or c) harvest rates were deficient to select for smaller body size (over the timescale of the current studies).

Possible drivers of temporal body-size increases in *Macropus*

Contrary to expectation, this study revealed evidence of a small increase in *Macropus giganteus*, *M. fuliginosus*, *M. rufogriseus* and *M. robustus* body size over this time period, which is more consistent with a release from predation pressure of humans and dingos (and thylacines in

Tasmania) (Johnson 2006). However, a more likely explanation for selection of increased macropod body size is increased food and water availability due to European pastoral activities (Taylor 1985; Blaney *et al.* 2000). Indeed, here primary productivity is shown to be a key determinant of spatial body size differences within these species. Another possible explanation for the observed temporal size increase is an increase in the frequency and intensity of extreme heat events as a consequence of human-induced climate change (Huey *et al*. 2012) (see 'Contemporary body-size shifts' in Part 5 for further discussion). This hypothesis was unable to be tested because temporal, gridded datasets relating to the occurrence of extreme heat events are not readily available for Australia.

Temporal body-size trends in *Macropus rufus*

Little evidence of temporal body-size change was detected in *Macropus rufus* over the study period. For this species, it is possible that the predicted temporal body-size increase due to increased food and water availability may have been overridden by human-induced factors favouring decreased body size such as commercial harvesting practices or thermoregulatory response to overall increasing temperature (e.g., Millien & Damuth 2004; Huey *et al.* 2012). Rapid decline in body size of two Alaskan horses in the late Pleistocene has been attributed to a coincident climatic/vegetational shift rather that human hunting (Guthrie 2003), but no evidence for changes in *Macropus* body size as a response to increasing temperature was found over the study time period (results not shown).

Wildlife sampling is likely to be biased by factors such as availability, selected cull periods and preferences of collectors, therefore, body-size data from harvested kangaroo samples, and or late Holocene fossil samples, would provide a more rigorous investigation of temporal body-size trends.

PART 3: THE ISLAND RULE

"There is much confusion and contradiction in the literature concerning the size of insular mammals" (Hesse *et al.* 1962)

Island body-size shifts

Island body-size shifts identified in *Rattus fuscipes* and *Trichosurus vulpecula* are not consistent with the island rule (Figs 5.2, 5.3) (Foster 1964; Lomolino 1985). After accounting for all covariates, populations of *R. fuscipes* were shown to be both smaller and larger than those on the adjacent western mainland, depending on the island. This indicates that body-size response of mammalian species isolated on islands need not be unidirectional, nor is it predetermined by the initial body size. *T. vulpecula* samples from Flinders Island are larger than their eastern mainland counterparts, which runs counter to the prediction that species greater than 2.7 kg should decrease in size on islands (Lomolino *et al.* 2012). Furthermore, when all covariates were considered, no evidence for an overall global island effect was found in either species. Manifestation of the island effect is likely to be less common than has been proposed (e.g., Lomolino *et al.* 2012).

This study revealed a reduction in skull size for island populations of *M. rufogriseus*, both on the large island of Tasmania and on Flinders Island (Fig. 3.3c). Similarly, *M. robustus* specimens from Barrow Island were smaller than their mainland counterparts (Table 4.2). Body-size shifts in either of these species were not explained by environmental drivers were these regions contiguous with the mainland. Thus, body-size shifts in species of *Macropus* may concur with the island rule. However, since covariates were not included in the analyses for the kangaroos, interpretation of this apparent pattern should be viewed with caution. Such biases are demonstrated in Chapter 2, where the results clearly show that *T. vulpecula* is larger on Tasmania and other islands than would be predicted by minimum precipitation minus potential evapotranspiration and summer maximum temperature were they contiguous with the mainland (Fig. 2.4). This may indeed be the case, but after all covariates are considered, the island effect is clearly demonstrated only in the *T. vulpecula* population from Flinders Island.

Key drivers of island body size

Proposed explanations for island body-size patterns have largely centred on species-level traits, biotic interactions and island-specific traits, and have been the topic of much debate (Dayan & Simberloff 1998; Michaux *et al.* 2002; Meiri *et al.* 2005; Lomolino 2005; Meiri 2007; White & Searle 2007). The current study found no evidence that island area, isolation (distance and time), number of competitors and number of predators exert influence over island body-size evolution in either *R. fuscipes* or *T. vulpecula*. Heaney (1978) argued that the only manner in which he could envision isolation *per se* affecting body size is through inbreeding, loss of genetic variability, and subsequent loss of overall fitness. He further argued that such an explanation is tenuous, because it suggests no mechanism and leaves unexplained the phenomenon of large and small mammals responding oppositely in body size changes on small islands “the correlation between “isolation”, as measured by distance, with body size is spurious…” (Heaney 1978, p. 37).

Nonetheless, it is difficult to gauge what index best reflects isolation in the form of distance, e.g., distance to nearest mainland, nearest larger island, nearest more species-rich island (Meiri *et al.* 2008). Similarly, the effects of predators and competitors on different mammalian species are likely to be complex: predation pressure and interspecific competition is probably more related to their abundance and the actual species present rather than their richness (Meiri *et al.* 2008).

For *T. vulpecula*, temperature and rainfall (productivity) were found to be the most important predictors of island body size. However, an effect of temperature or rainfall on *R. fuscipes* could not be demonstrated. Because these are the same primary drivers of body-size variation between mainland populations of these species, this provides support for the idea that the island rule lacks validity. More importantly, as is the case with more general (i.e., spatial and temporal) body-size patterns in mammals, productivity and temperature might account for many island body-size patterns.

As with spatial and temporal body-size patterns and determinants, those that are particular to islands are likely to be scale dependent. For example, a subsection of islands that experience similar climatic conditions might show a body-size shift / key determining factor (e.g., island area) that differs to that from islands of various climatic conditions. Thus, where possible, sampling from islands that encompass a broad geographic scale should also be considered when examining island body-size patterns and determinants in mammals.

PART 4: ANALYTICAL CHALLENGES

It has been lamented that differentiating between hypotheses proposed to explain body-size differences is problematic because environmental variables that pertain to the hypotheses are often highly correlated (e.g., Yom-Tov & Nix 1986; Wigginton & Dobson 1999; Gür 2010). This problem was addressed, in part, by a) comparing ‘aspatial’ regression models as well as either simultaneous autoregressive (SAR) (*T. vulpecula*, *M. robustus* and *M. rufus*) models or Gaussian conditional autoregressive (CAR) models (*M. giganteus, M. fuliginosus* and *M. rufogriseus*) that accommodate both single-cause and multi-causal explanations for spatial body-size variation within a species, b) using model selection procedure based on information criteria (AIC/DIC) to tease apart the best-supported body-size drivers and c) excluding environmental variables that were highly correlated from the same fitted model. Moran's *I* spatial autocorrelation coefficient was used to examine the possibility of spatial autocorrelation in the deviance residuals of aspatial and spatial (SAR or CAR) models. In each case, the spatial models were less spatially autocorrelated than the aspatial models (Fig. 2.3, Fig. S3.2). That is, the pattern expressed by the spatial models was more random than that of the aspatial models which was either more clustered or dispersed. The spatial models were also better fit (higher R^2 values) than the aspatial ones (Tables 2.2, 3.1).

Furthermore, spatial autoregression coefficients can be used to demonstrate the presence and strength of unaccounted abiotic or biotic factors (e.g., predation, competition, population genetics and human impacts) that might contribute to spatial body-size patterns. For example, the top-ranked spatial SAR models for *T. vulpecula* and *M. robustus* estimated strong spatial autoregression coefficients ($\lambda = 0.627$ and 0.770, respectively, relative to the null SAR models ($\lambda = 0.869$ and 0.796, respectively) indicating that environmental drivers included in those studies could only account for some of the spatial pattern in the data for each of these species (i.e., explaining 28 and 3% of the spatial autocorrelation in skull size within a 500 km-neighbourhood radius, respectively). Such analytical methods can help separate the effects of correlated environmental variables, as well as highlight the importance of such variables, thus shedding more light on the primary body-size drivers at hand.

To account for missing sex data, Bayesian models were applied in the analyses for *M. giganteus M. fuliginosus* and *M. rufogriseus*. Such models can impute missing data (thereby making full use of the historical information), fit non-linear growth models and accounted for non-random spatial sampling patterns.

PART 5: EXPLORING BODY SIZE FURTHER

Contemporary body-size shifts

Body-size shifts in response to temperature change can occur over contemporary and geological timescales, and can apply to species as well as to populations and communities (Millien *et al.* 2006). It has been predicted that the direction of selection on endotherm body size will swing depending on the nature of temperature change (Gardner *et al.* 2011). A gradual increase in mean temperature should exert sustained selective pressure for small size if water budgets are limiting. Since larger endotherms are expected to have a higher thermal inertia and greater energy reserves, occasional exposures to sufficiently high daily temperatures will periodically reverse the direction of selection on size (Gardner *et al.* 2011). Larger individuals should therefore experience lower mortality rate during extreme heat waves (Huey *et al.* 2012). For example, it has been suggested that smaller-bodied desert birds are more vulnerable to dehydration and overheating under short-term exposure to extreme high temperatures (McKechnie & Wolf 2010). The effects of human-induced climate change on body-size changes should thus consider both the occurrence of extreme heat events as well as overall temperature increase if such data is readily available.

In some hot, arid regions, temperature may negatively affect food availability due to the negative relationship between ambient temperature and precipitation (Yom-Tov & Geffen 2011). Thus, in such regions, increases in temperature might decrease productivity, thereby reducing body size. The effects of a gradual increase in temperature on body size may be the opposite in cold climates, where it may result in increased length of the growing season and, therefore, elevated primary production. This would consequently increase food availability, allowing individuals to utilize the extra energy available for growth and to increase in body size (Millien *et al.* 2006). For example, recent increases in body size of the American Marten, *Martes* *americana*, in Alaska (Yom-Tov *et al.* 2008) and both stoat, *Mustela ereminea*, and male Weasels, *Mustela nivalis*, in Sweden (Yom-Tov *et al.* 2009) were attributed indirectly to global warming where elevated winter temperatures increased food availability. Furthermore, elevated temperature, especially during the winter, may also enable animals to divert energy from maintenance to growth and in turn increase in body size (Millien *et al.* 2006).

Evidence of climate change from the fossil record

The fossil record provides valuable background information for exploring the potential effects of anthropogenic warming (e.g., Blois *et al.* 2013). In particular, the Pleistocene was a period of repeated climatic fluctuations. For example, Greenland ice-core records suggest at least 20 abrupt warming events during the last glacial period (Dansgaard *et al.* 1993). Body-size changes in *Neotoma cinerea* in response to temperature change are evident over the Holocene, with individuals becoming smaller during the warmer, interglacial conditions of the mid-late Holocene and larger during the cooler, glacial conditions of the late Pleistocene (Smith *et al.* 1995; Smith & Betancourt 1998, 2003). Size changes documented in Quaternary and Mio-Pleistocene mammal species have been attributed the climate change (e.g., Alberdi *et al.* 1995; Renaud *et al.* 1999; Guthrie 2003; Blois & Hadly 2009; Blois *et al.* 2013).

Despite complexities associated with drawing parallels between changes in species morphology (i.e., body size) and the pattern of climate change over long periods of time, some correlations can be drawn between changes in species morphology and anthropogenic climate change. Such correlations highlight the value of wildlife collections and fossil specimens, and the continued need for documenting biological diversity, as a means of interpreting the effects of contemporary climate change.

Ontogeny versus selection

The degree to which ontogeny (phenotypic plasticity) and selection (genetic coding) influence body-size patterns remains unclear. It has been suggested that many studies that examine the mechanisms responsible for body-size clines use phenotypic data, and confound genetic and phenotypic plasticity sources of variation (Stillwell 2010). Possible experiments to explore the question of ontogeny versus selection 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). Yet another way in which the potential role of genetics might be investigated would be to determine occurrence of body-size correlates with genetic information. Recent temporal changes in avian body size have been demonstrated as clearly non-genetic. Analyses of breeding values in Red-billed Gulls, *Larus novaehollandiae scopulinus,* from New Zealand, showed no evidence of any genetic change over 45 years (Teplitsky *et al.* 2008) despite concurrent decreased body size. However, some researchers (Garant *et al.* 2005; Salewski *et al.* 2010) claim that changes in body size within passerine species may not merely be the result of phenotypic plasticity but may also hint at genetically-based adaptations.

Future research

This thesis improves our understanding of body-size determinants in several Australian mammals, but raises further questions that could be addressed in future studies. For example, examining body size and environmental variables from different scales (i.e., global effect versus local effect) and different regions (e.g., tropical versus temperate) may be used to determine whether the importance of environmental determinants differ between scale and region. Furthermore, studies on species that exhibit sexual size dimorphism might test for sexual differences in spatial body-size patterns (e.g., Rensch's rule) and determinants. Body-size data from harvested samples of species of *Macropus* could be used as a more direct means of investigating the potential effects of body size on contemporary kangaroo harvesting practices. In addition, temporal body-size trends in *Macropus* through the Pleistocene can be investigated to seek evidence of pre-European hunting practices or relate to changes in climate. Investigations of body-size patterns in other island mammals could also be explored further and should include productivity and temperature among the determinants examined. This might be predicted to reveal that island body-size determinants are ultimately the same as those posed to explain spatial and temporal patterns on continents. Finally, although not covered in this thesis, more research is required to understand the genetic determinants of body-size patterns to appreciate the relative roles of ontogeny (phenotypically plastic possibly due to epigenetics) and selection (genetically coded). Genome-wide association studies may potentially be used to understand genetic variants associated with a morphological trait (i.e., body size).

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CONCLUSIONS

Bergmann's rule, as a generalised pattern, is apparent within Australian marsupials that occupy a broad latitudinal / temperature range. Resolution of geographic and/or temperature scale is likely to be a significant factor in determining spatial body-size patterns and thus, should be considered when testing for Bergmannian patterns. Food availability and temperature are the most likely explanation for spatial body-size differences in *Trichosurus vulpecula* and species of *Macropus*; primary productivity and thermoregulatory requirements are evidently key counterparts in driving body-size evolution. However, the importance of productivity and thermoregulatory requirements may vary considerably between regions and may be scale dependent. This thesis highlights the importance of multi-causal variables responsible for spatial body-size variation; i.e., body size is not driven by a single mechanism. Thus, hypotheses explaining body-size variation in endotherms should not be viewed as mutually exclusive. Highly-correlated environmental variables used in body-size studies can be partially dealt with by a) applying 'aspatial' regression models as well as simultaneous autoregressive (SAR) models that accommodate both single-cause and multi-causal explanations for spatial body-size variation, b) using model selection procedure based on information criteria to tease apart the best-supported body-size drivers and c) excluding highly correlated environmental variables from the same fitted model. Similarly, spatial autoregression coefficients estimated by top-ranked spatial SAR models be can be used to demonstrate the presence and strength of unaccounted abiotic or biotic factors. Furthermore, Bayesian models are appropriate for investigating long-term studies such as the impact of human harvesting because they can impute missing data, fit non-linear growth models and account for non-random spatial sampling inherent in wildlife collections.

The results of this study demonstrate a slight increase in body size in *Macropus giganteus*, *M. fuliginosus*, *M. rufogriseus* and *M. robustus*, post-European arrival, which may be in response to increased food and water availability due to European pastoral activities. However, little evidence of body-size change was detected in *M. rufus* over this time period.

Finally, the island effect is shown to occur in only four of 17 island populations of *Rattus fuscipes* and just one of 12 island populations for *T. vulpecula*. Moreover, no evidence for overall global island effect was found in either species. Thus, the island rule is likely to be much less fixed than has been proposed. No evidence was found that island area, isolation (distance and time), number of competitors and number of predators exert influence over island body-size evolution in either *R. fuscipes* or *T. vulpecula*. Rather, temperature is the best predictor of *T. vulpecula* island body size followed by productivity. However, this study was unable to effectively demonstrate an effect of temperature or rainfall on *R. fuscipes*. Because these are the same primary drivers of body-size variation between mainland populations of these species, this provides support for the idea that the island rule lacks validity. Inclusion of the covariates in question in model analyses, as well as sampling from islands of various climatic conditions is imperative when examining island body-size patterns and determinants.

The ability to define body size determinants (albeit environmental, human-induced and or island specific) provides a useful means for understanding the most important mechanism or mechanisms, responsible for driving body size evolution. Mechanisms driving spatial (including island) and temporal body-size patterns in mammals appear, in general, to be “one and the same”. That is, productivity and thermoregulatory responses may well be driving body-size evolution generally.

APPENDICES

APPENDIX 1

WinBUGS code examples for (a) aspatial and (b) spatial CAR models. The following code is for non-linear Bayesian models of condylobasal length (CBL) for *Macropus giganteus*. Both example models are of the form CBL ~ SummerMaxTemp + WinterMinTemp + Island. Note that for the spatial model in (b), the overall mean of the spatial random effects (mu) replaces the intercept, so the intercept parameter (beta) from the exponential growth model is no longer required.

(a) Aspatial model

```
model {

    ##############
    ## PRIORS
    ##############

    ## Growth curve parameters
    Linf ~ dnorm(0, 0.001)
    beta ~ dnorm(0, 0.001)
    k ~ dnorm(0, 0.001)
    Linf.m.eff ~ dnorm(0, 0.001) ## male effect on asymptote (Linf)
    k.m.eff ~ dnorm(0, 0.001) ## male effect on growth rate (k)

    ## Environmental parameters
    pSummerMaxTemp ~ dnorm(0, 0.001)
    pWinterMinTemp ~ dnorm(0, 0.001)
    pTassie ~ dnorm(0, 0.001) ## Island effect of Tasmania

    ## Imputation model parameters
    alpha.sex ~ dnorm(0, 0.001)
    p2CL ~ dnorm(0, 0.001)
    p2MI ~ dnorm(0, 0.001)
    p2SummerMaxTemp ~ dnorm(0, 0.001)
    p2WinterMinTemp ~ dnorm(0, 0.001)
    p2Tassie ~ dnorm(0, 0.001)

    ## Gaussian error structure
    norm.sd ~ dunif(0, 10)
    norm.var <- norm.sd*norm.sd
    norm.tau <- 1/norm.var

    #############
    ## LIKELIHOOD
    #############

    pi <- 3.14159

    for(i in 1:n) {
```

```
        ## normal likelihood
        CL[i] ~ dnorm(eta[i], norm.tau)

        ## negative log-likelihood
        ll[i] <- (-0.5*log(2*pi)) + (-0.5*log(norm.var)) - (pow((CL[i]-eta[i]),2)/(2*norm.var))
        nll[i] <- -ll[i]

        ## non-linear model
        eta[i] <- (Linf+Linf.m.eff*Sex_male[i]) - ((Linf+Linf.m.eff*Sex_male[i])-beta)*exp(-
(k+k.m.eff*Sex_male[i])*MI[i]) + pSummerMaxTemp*SummerMaxTemp[i] +
pWinterMinTemp*WinterMinTemp[i] + pTassie*Tassie[i]
     }

     #############
     ## IMPUTATION MODEL FOR SEX
     #############

     for(i in 1:n) {
        Sex_male[i] ~ dbern(p.sex[i])
        logit(p.sex[i]) <- alpha.sex + p2CL*CL[i] + p2MI*MI[i] + p2SummerMaxTemp*SummerMaxTemp[i]
+ p2WinterMinTemp*WinterMinTemp[i] + p2Tassie*Tassie[i]
     }

     #############
     ## ASSESS MODEL FIT WITH POSTERIOR PREDICTIVE CHECK
     #############

     for(i in 1:n) {
        sq.res[i] <- pow(CL[i]-eta[i], 2)  ## squared residuals for observed data
        CL.new[i] ~ dnorm(eta[i], norm.tau)  ## replicate data, one new dataset for each MCMC
sample
        sq.res.new[i] <- pow(CL.new[i]-eta[i], 2)  ## squared residuals for replicate data
     }
     fit <- sum(sq.res[])
     fit.new <- sum(sq.res.new[])

     ############################
     ## SEMI-MARGINALISED DEVIANCE RESIDUALS
     ############################

     for(i in 1:n) {
        dev.res[i] <- step(CL[i]-eta[i])*sqrt(nll[i]) - step(eta[i]-CL[i])*sqrt(nll[i])
        squared_dev.res[i] <- pow(dev.res[i],2)
     }
     sum_dev.res <- 2*(sum(squared_dev.res[1:n])) ## semi-marginalised deviance
}
```

(b) Spatial CAR model

```
model {

     ##############
     ## PRIORS
     ##############

     ## CAR model
     m[1:nCells] ~ car.proper(mu[], C[], adj[], num[], M[], tau.S, gamma.S)
     for (site in 1:nCells) {
        mu[site] <- mu.S
     }
     mu.S ~ dnorm(0, 0.001)
     sd.S ~ dunif(0, 100)
     tau.S <- 1/(sd.S*sd.S)
     gamma.min <- min.bound(C[], adj[], num[], M[])
     gamma.max <- max.bound(C[], adj[], num[], M[])
     gamma.S ~ dunif(gamma.min, gamma.max)

     ## Growth curve parameters
     Linf ~ dnorm(0, 0.001)
     k ~ dnorm(0, 0.001)
     Linf.m.eff ~ dnorm(0, 0.001) ## male effect on asymptote (Linf)
     k.m.eff ~ dnorm(0, 0.001) ## male effect on growth rate (k)
```

```
    ## Environmental parameters
    pSummerMaxTemp ~ dnorm(0, 0.001)
    pWinterMinTemp ~ dnorm(0, 0.001)
    pTassie ~ dnorm(0, 0.001) ## Island effect of Tasmania

    ## Imputation model parameters
    alpha.sex ~ dnorm(0, 0.001)
    p2CL ~ dnorm(0, 0.001)
    p2MI ~ dnorm(0, 0.001)
    p2SummerMaxTemp ~ dnorm(0, 0.001)
    p2WinterMinTemp ~ dnorm(0, 0.001)
    p2Tassie ~ dnorm(0, 0.001)

    ## Gaussian error structure
    norm.sd ~ dunif(0, 10)
    norm.var <- norm.sd*norm.sd
    norm.tau <- 1/norm.var

    #############
    ## LIKELIHOOD
    #############

    pi <- 3.14159

    for(i in 1:n) {

       ## normal likelihood
       CL[i] ~ dnorm(eta[i], norm.tau)

       ## negative log-likelihood
       ll[i] <- (-0.5*log(2*pi)) + (-0.5*log(norm.var)) - (pow((CL[i]-eta[i]),2)/(2*norm.var))

       nll[i] <- -ll[i]

       ## non-linear model
       eta[i] <- (Linf+Linf.m.eff*Sex_male[i]) - (Linf+Linf.m.eff*Sex_male[i])*exp(-
(k+k.m.eff*Sex_male[i])*MI[i]) + pSummerMaxTemp*SummerMaxTemp[i] +
pWinterMinTemp*WinterMinTemp[i] + pTassie*Tassie[i] + m[cell[i]]
    }

    #############
    ## IMPUTATION MODEL FOR SEX
    #############

    for(i in 1:n) {
       Sex_male[i] ~ dbern(p.sex[i])
       logit(p.sex[i]) <- alpha.sex + p2CL*CL[i] + p2MI*MI[i] + p2SummerMaxTemp*SummerMaxTemp[i]
+ p2WinterMinTemp*WinterMinTemp[i] + p2Tassie*Tassie[i]
    }

    #############
    ## ASSESS MODEL FIT WITH POSTERIOR PREDICTIVE CHECK
    #############

    for(i in 1:n) {
       sq.res[i] <- pow(CL[i]-eta[i], 2)  ## squared residuals for observed data
       CL.new[i] ~ dnorm(eta[i], norm.tau)  ## replicate data, one new dataset for each MCMC
sample
       sq.res.new[i] <- pow(CL.new[i]-eta[i], 2)  ## squared residuals for replicate data
    }
    fit <- sum(sq.res[])
    fit.new <- sum(sq.res.new[])

    ##############################
    ## SEMI-MARGINALISED DEVIANCE RESIDUALS
    ##############################

    for(i in 1:n) {
       dev.res[i] <- step(CL[i]-eta[i])*sqrt(nll[i]) - step(eta[i]-CL[i])*sqrt(nll[i])
       squared_dev.res[i] <- pow(dev.res[i],2)
    }
    sum_dev.res <- 2*(sum(squared_dev.res[1:n])) ## semi-marginalised deviance
}
```

APPENDIX 2

WinBUGS code examples for models 1, 2 and 3.

Model 1: sex and island effects only

```
model{

  ##################
  ## Priors
  ##################

  ## Prior for intercept
  alpha ~ dnorm(0,0.001)

  ## Prior for intercept and covariate effects applicable to all specimens
  pSexMale ~ dnorm(0,0.001)

  ## Priors for island-level effects
  pIslandYes ~ dnorm(0,0.001)

  ## Random island effects
  tau.is <- pow(sigma.is,-2)
  sigma.is ~ dunif(0,100)
  is.random[1] <- 0
  for (j in 2:nIsland) {
    is.random[j] ~ dnorm(0,tau.is)
  }

  ## Normal error distribution
  tau.error <- pow(sigma.error,-2)
  norm.var <- pow(sigma.error,2)
  sigma.error ~ dunif(0,100)

  ##################
  ## Likelihood
  ##################

  pi <- 3.14159

  for (i in 1:n) {
    CL[i] ~ dnorm(eta[i],tau.error)

    ## model component applicable to all specimens
    eta1[i] <- alpha + pSexMale*SexMale[i]

    ## additional model component applicable to island specimens
    eta2[i] <- IslandYes[i]*pIslandYes + is.random[INum[i]]

    ## complete model
    eta[i] <- eta1[i] + eta2[i]

    ## negative log-likelihood
    ll[i] <- (-0.5*log(2*pi)) + (-0.5*log(norm.var)) - (pow((CL[i]-eta[i]),2)/(2*norm.var))
    nll[i] <- -ll[i]
  }

  #############################
  ## SEMI-MARGINALISED DEVIANCE RESIDUALS
  #############################

  for(i in 1:n) {
```

```
  dev.res[i] <- step(CL[i]-eta[i])*sqrt(nll[i]) - step(eta[i]-CL[i])*sqrt(nll[i])
  squared_dev.res[i] <- pow(dev.res[i],2)
  }
  sum_dev.res <- 2*(sum(squared_dev.res[1:n])) ## semi-marginalised deviance

}
```

Model 2: sex, covariate, and island effects

```
model{

  ##################
  ## Priors
  ##################

  ## Priors for variable indicators
  for (k in 1:nVars) {
    g[k] ~ dbern(0.5)
  }

  ## GVS priors for coefficients
  ## first column is beta.mean.prior, second column is beta.tau.prior
  for (k in 1:nVars) {
      beta.priors[k,1] <- (1-g[k])*mu.beta.ps
      beta.priors[k,2] <- (1-g[k])*tau.beta.ps + g[k]*0.001
  }

  ## Prior for intercept
  alpha ~ dnorm(0,0.001)

  ## Prior for intercept and covariate effects applicable to all specimens
  pSexMale ~ dnorm(0,0.001)
  pTemp ~ dnorm(beta.priors[1,1],beta.priors[1,2])
  pLogRain ~ dnorm(beta.priors[2,1],beta.priors[2,2])

  ## Priors for island-level effects
  pIslandYes ~ dnorm(beta.priors[3,1],beta.priors[3,2])
  pLogArea ~ dnorm(beta.priors[4,1],beta.priors[4,2])
  pDist2ml ~ dnorm(beta.priors[5,1],beta.priors[5,2])
  pTSI ~ dnorm(beta.priors[6,1],beta.priors[6,2])
  pNComp ~ dnorm(beta.priors[7,1],beta.priors[7,2])
  pNPred ~ dnorm(beta.priors[8,1],beta.priors[8,2])

  ## Random island effects
  tau.is <- pow(sigma.is,-2)
  sigma.is ~ dunif(0,100)
  is.random[1] <- 0
  for (j in 2:nIsland) {
    is.random[j] ~ dnorm(0,tau.is)
  }

  ## Normal error distribution
  tau.error <- pow(sigma.error,-2)
  norm.var <- pow(sigma.error,2)
  sigma.error ~ dunif(0,100)

  ##################
  ## Likelihood
  ##################

  pi <- 3.14159

  for (i in 1:n) {
    CL[i] ~ dnorm(eta[i],tau.error)

    ## model component applicable to all specimens
    eta1[i] <- alpha + pSexMale*SexMale[i] + g[1]*pTemp*Temp[i] + g[2]*pLogRain*LogRain[i]

    ## additional model component applicable to island specimens
    eta2[i] <- IslandYes[i]*(g[3]*pIslandYes + g[4]*pLogArea*LogArea[i] +
```

```
                             g[5]*pDist2ml*Dist2ml[i] + g[6]*pTSI*TSI[i] +
                             g[7]*pNComp*NComp[i] + g[8]*pNPred*NPred[i]) +
                             is.random[INum[i]]

    ## complete model
    eta[i] <- eta1[i] + eta2[i]

    ## negative log-likelihood
    ll[i] <- (-0.5*log(2*pi)) + (-0.5*log(norm.var)) - (pow((CL[i]-eta[i]),2)/(2*norm.var))
    nll[i] <- -ll[i]
  }

  #############################
  ## SEMI-MARGINALISED DEVIANCE RESIDUALS
  #############################

  for(i in 1:n) {
  dev.res[i] <- step(CL[i]-eta[i])*sqrt(nll[i]) - step(eta[i]-CL[i])*sqrt(nll[i])
  squared_dev.res[i] <- pow(dev.res[i],2)
  }
  sum_dev.res <- 2*(sum(squared_dev.res[1:n])) ## semi-marginalised deviance

}
```

Model 3: sex, covariate, region and island effects

```
model{

  ##################
  ## Priors
  ##################

  ## Priors for variable indicators
  for (k in 1:nVars) {
    g[k] ~ dbern(0.5)
  }

  ## GVS priors for coefficients
  ## first column is beta.mean.prior, second column is beta.tau.prior
  for (k in 1:nVars) {
      beta.priors[k,1] <- (1-g[k])*mu.beta.ps
      beta.priors[k,2] <- (1-g[k])*tau.beta.ps + g[k]*0.001
  }

  ## Prior for intercept
  alpha ~ dnorm(0,0.001)

  ## Prior for intercept and covariate effects applicable to all specimens
  pSexMale ~ dnorm(0,0.001)
  pTemp ~ dnorm(beta.priors[1,1],beta.priors[1,2])
  pLogRain ~ dnorm(beta.priors[2,1],beta.priors[2,2])

  ## Priors for island-level effects
  pIslandYes ~ dnorm(beta.priors[3,1],beta.priors[3,2])
  pLogArea ~ dnorm(beta.priors[4,1],beta.priors[4,2])
  pDist2ml ~ dnorm(beta.priors[5,1],beta.priors[5,2])
  pTSI ~ dnorm(beta.priors[6,1],beta.priors[6,2])
  pNComp ~ dnorm(beta.priors[7,1],beta.priors[7,2])
  pNPred ~ dnorm(beta.priors[8,1],beta.priors[8,2])

  ## Priors for longitude division
  longBreak ~ dunif(113,154)
  pEast ~ dnorm(beta.priors[9,1],beta.priors[9,2])

  ## Random island effects
  tau.is <- pow(sigma.is,-2)
  sigma.is ~ dunif(0,100)
  is.random[1] <- 0
  for (j in 2:nIsland) {
    is.random[j] ~ dnorm(0,tau.is)
  }

  ## Normal error distribution
  tau.error <- pow(sigma.error,-2)
  norm.var <- pow(sigma.error,2)
  sigma.error ~ dunif(0,100)

  ##################
  ## Likelihood
  ##################

  pi <- 3.14159

  for (i in 1:n) {
    CL[i] ~ dnorm(eta[i],tau.error)

    ## model component applicable to all specimens
```

```
    eta1[i] <- alpha + pSexMale*SexMale[i] + g[1]*pTemp*Temp[i] +
                       g[2]*pLogRain*LogRain[i] + g[9]*pEast*step(gridLong[i]-longBreak)

    ## additional model component applicable to island specimens
    eta2[i] <- IslandYes[i]*(g[3]*pIslandYes + g[4]*pLogArea*LogArea[i] +
                             g[5]*pDist2ml*Dist2ml[i] + g[6]*pTSI*TSI[i] +
                             g[7]*pNComp*NComp[i] + g[8]*pNPred*NPred[i]) +
                             is.random[INum[i]]

    ## complete model
    eta[i] <- eta1[i] + eta2[i]

    ## negative log-likelihood
    ll[i] <- (-0.5*log(2*pi)) + (-0.5*log(norm.var)) - (pow((CL[i]-eta[i]),2)/(2*norm.var))
    nll[i] <- -ll[i]
  }

  #############################
  ## SEMI-MARGINALISED DEVIANCE RESIDUALS
  #############################

  for(i in 1:n) {
  dev.res[i] <- step(CL[i]-eta[i])*sqrt(nll[i]) - step(eta[i]-CL[i])*sqrt(nll[i])
  squared_dev.res[i] <- pow(dev.res[i],2)
  }
  sum_dev.res <- 2*(sum(squared_dev.res[1:n])) ## semi-marginalised deviance

}
```

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