

On the rarity of big fierce carnivores and primacy of isolation and area: tracking large mammalian carnivore diversity on two isolated continents

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The hypothesis that low productivity has uniquely constrained Australia's large mammalian carnivore diversity, and by inference the biota in general, has become an influential backdrop to interpretations of ecology on the island continent. Whether low productivity has been primary impacts broadly on our understanding of mammalian biogeography, but investigation is complicated by two uniquely Australian features: isolation and the dominance of marsupials. However, until the great American biotic interchange (GABI), South America was also isolated and dominated by pouched carnivores. Here, we examine the low-productivity hypothesis empirically, by comparing large mammalian carnivore diversities in Australia and South America over the past 25 Myr. We find that pre-GABI diversity in Australia was generally comparable to or higher than diversity in South America. Post-GABI, South American diversity rose dramatically, pointing to isolation and phylogenetic constraint as primary influences. Landmass area is another important factor. Comparisons of diversity among the world's seven largest inhabited landmasses show that large mammalian hypercarnivore diversity in Australia approached levels predicted on the basis of landmass area in Late Pleistocene–Recent times, but large omnivore diversity was low. Large marsupial omnivores also appear to have been rare in South America. Isolation and competition with large terrestrial birds and cryptic omnivore taxa may have been more significant constraints in this respect. Relatively high diversity has been achieved in Late Quaternary America, possibly as a result of 'artificially' high immigration or origination rates, whereas that in contemporaneous Africa has been surprisingly poor. We conclude that isolation and landmass area, rather than productivity, are the primary constraints on large mammalian carnivore diversity. Our results quantify the rarity of large hypercarnivorous mammals world-wide.

Keywords: productivity; biogeography; marsupial carnivores; Carnivora

1. INTRODUCTION

The diversity of large mammalian carnivores in modern-day Australia is low, a fact historically attributed to low productivity (Lee & Cockburn 1985). This theme has been transferred to the fossil record, with soil nutrient deficiency stressed as a uniquely powerful constraint in Australia since the Early Miocene (Flannery 1994). These studies posited that low productivity had limited the species richness (SR) and body mass of mammalian herbivores and hence the diversity of their mammalian predators. By inference, low productivity had measurably constrained the Australian biota over geological time.

The efficacy of the low-productivity hypothesis is difficult to examine directly because it is difficult to separate soil nutrient levels from other factors, notably isolation and phylogenetic constraint (Wroe *et al.* 2004a). Direct comparison with arbitrarily defined regions within larger landmasses is problematic, because it does not account for island effects (Rosenzweig 1992; Wroe *et al.* 2004a). However, although Australia now stands alone among inhabited continents in being isolated and dominated by marsupial carnivores, until the placental invasions of the great American biotic interchange (GABI) *ca.* 3 Myr ago,

this was also true of South America (Van Valkenburgh 1999). Consequently, meaningful comparisons can be drawn between the palaeofaunas of these two isolated landmasses (Flannery 1994; Wroe 2002). Qualitative assessment of the fossil record led Flannery (1994) to conclude that the diversity of large marsupial carnivores was much higher in pre-GABI South America, but mounting evidence undermines this conclusion. Mammalian carnivore diversities in Australia's fossil faunas have been underestimated (Wroe 2002, 2003, 2004), as have the maximal body masses of key Australian taxa (Wroe *et al.* 2003, 2004b). Others have concluded that, pre-GABI, mammalian carnivore diversity was low throughout the Neogene in both continents (Marshall 1978; Van Valkenburgh 1999), as were mammalian predator–prey ratios in local faunas immediately prior to the GABI (Croft 2001, 2002).

Overall, nutrient levels in South American palaeosols are unlikely to have been comparable with those of Australia. The major influence on soil nutrient levels is geographical relief (Julien 1995). A lack of geological activity throughout the Cenozoic rendered Australia the world's flattest continent, largely explaining the general nutrient deficiency of the continent's soils (Brown *et al.* 1968), but, geologically, South America has been more dynamic. Initial formation of the Andes was complete by the Early Oligocene; however, additional uplift occurred at varying

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places, times and rates through the Late Oligocene–Pliocene (Gregory-Wodzicki 2000). While much of the Andes had reached no more than half their present elevation in the Early–Middle Miocene, this still greatly exceeds Australian relief at any time (Brown *et al.* 1968; Gregory-Wodzicki 2000).

The investigations of Croft (2001, 2002) implicate isolation and phylogenetic constraint as explanations for the observed low SR in South America and Australia, but did not consider body mass and do not directly address the low-productivity theory, which is rooted in an observed paucity of large mammalian carnivores. ‘Large’ as defined by Flannery (1994) includes species with mean body masses of 2.5 kg or more, a defensible distinction because no hypercarnivorous extant marsupials (*sensu* Van Valkenburgh 1989) are smaller than this (Jones 2003).

In this study we examine the low-productivity hypothesis quantitatively by comparing diversities over the past 25 Myr in Australia and South America and investigating the relationship between landmass area and diversity for large mammalian carnivores.

2. MATERIAL AND METHODS

(a) *Body-mass prediction*

Thirty Australian and 25 South American marsupial carnivores of 2.5 kg or more are known to have existed since Oligocene times and a further 44 large placental carnivores have also been recorded for South America (Appendix A). Including 13 fossil taxa, 129 terrestrial mammalian carnivores of 2.5 kg or more have existed on the seven largest inhabited landmasses over the past 65 000 years (electronic Appendix B). Empirically derived body-mass estimates were used for all fossil taxa (see Appendix A and electronic Appendix B).

(b) *Comparisons*

Australian and South American species were allocated to one of five time intervals (1, 24–17 Myr ago; 2, 17–10 Myr ago; 3, 10–5 Myr ago; 4, 5–3 Myr ago; 5, 3 Myr ago to the present) and plotted against three descriptors of diversity: SR, mean of all mean body masses (MMBM) and mean maximal body mass (BMM_{max}: i.e. mean body mass of the largest species). Data were \log_{10} transformed.

It is extremely unlikely that we have included all large mammalian carnivore taxa that have existed on either continent. The likelihood that the fossil record is complete is largely a function of the number of specimens and localities sampled, as well as their geographical and temporal spreads. Compilation of a complete list of localities is currently impractical and we have not attempted to account for sampling bias in this study. Temporal spread is now reasonably complete for both continents, geographical spread is less so. However, if bias is present then it probably favours South America. Out of nine Miocene South American Land Mammal Ages, the best represented has more localities than are known for the entire Australian Miocene. Thus, the Santacrucian Formation (16.5–17.5 Myr ago) contains at least 29 localities compared with 19 for Miocene Australia (Savage & Russell 1983).

Australia is 43% of the area of South America. To correct for this we generated six predictive equations through regression of SR, mean body mass and MMBM against landmass area using the Late Pleistocene–Recent dataset. Smaller landmasses were not included, either because they have had no large mammalian

hypercarnivores, or because, as parts of archipelagos, they should be treated as single landmasses (Flessa 1975). We used a cut-off of 65 000 years ago following the rationale of Burness *et al.* 2001.

Three equations were derived from the sample of all large ‘carnivores’. Feeding behaviour of each species was taken from the literature (electronic Appendices B, C and D). Of Late Pleistocene–Recent Carnivora of 2.5 kg or more, the proportion of hypercarnivores was 32%. Because most marsupials included in our analyses were probably hypercarnivorous (Wroe 2002; Johnson & Wroe 2003), we derived another three equations for meat and meat–bone specialists.

With these equations we generated predicted values for diversity on the basis of landmass area for the seven landmasses. The percentage of observed relative to predicted diversity was calculated for each (table 1). For Australian and South American taxa, the percentage of observed relative to predicted diversity was then plotted over the five time intervals.

3. RESULTS

(a) *Direct comparisons*

Between 25 Myr ago and 3 Myr ago, the overall SR of large mammalian carnivores differed little between Australia (23 species) and South America (24 species). Post-GABI, SR remained constant in Australia, but rose from four to 42 in South America (figure 1a).

MMBM showed a generally upward trend from the Early Miocene onwards on both landmasses (figure 1b). Pre-GABI, MMBM was 4.7% higher overall in South America (26.3 kg versus 25.1 kg) and slightly higher for each interval except the Late Miocene. Post-GABI this rose to 41.2%.

Regarding BMM_{max}, pre-GABI the two largest mammalian carnivores on either continent were Australian marsupial lions. In the Early–Middle Miocene and Early Pliocene, BMM_{max} was between 18.2% and 32.2% lower in Australia than in South America. In the Late Miocene, BMM_{max} was 60% lower in South America than in Australia. Post-GABI, BMM_{max} rose 38.3% in Australia, but 658% in South America (figure 1c).

(b) *Comparisons with worldwide Late Pleistocene–Recent large mammalian carnivore diversity*

(i) *All Late Pleistocene–Recent large mammalian carnivores*

The relationship between SR and landmass area for the sample inclusive of all Late Pleistocene–Recent mammalian carnivores of 2.5 kg or more was: $\log(\text{SR}) = 0.8386 \times \log(\text{area}) - 4.7634$, $r^2 = 0.93$ (figure 4a in electronic Appendices C and D). Among continents, the percentage of observed relative to predicted SR was lowest for Australia and highest for South America (table 1), but, over time, the percentage of observed relative to predicted SR for Australia was consistently higher than for South America pre-GABI. Up to this point both isolated continents showed relatively low diversity, excepting Middle Miocene Australia (figure 2a).

Predicted MMBM was 30.68 kg for Australia and 40.51 kg for South America ($\log(\text{MMBM}) = 0.3303 \times \log(\text{area}) - 0.7874$, $r^2 = 0.50$ (figure 4b in electronic Appendices C and D)). Observed MMBM was higher than predicted in Late Pleistocene–Recent Australia, North America and South America, and lower than

Table 1. Percentages of observed relative to predicted diversity for Late Pleistocene–Recent mammalian carnivores of 2.5 kg or more for seven landmasses. All, total dataset; M/M-B, hypercarnivores only; BMMax, mean maximal body mass.

	SR (all)	MMBM (all)	BMMax (all)	SR (M/M-B)	MMBM (M/M-B)	BMMax (M/M-B)
Madagascar	98.01	45.20	73.26	109.89	72.48	80.56
New Guinea	39.06	198.90	120.08	88.50	126.47	126.47
Australia	47.66	113.79	83.27	92.08	75.45	93.08
South America	140.23	137.09	165.59	122.96	198.48	180.71
North America	108.01	187.61	209.48	116.67	161.62	161.62
Africa	90.20	50.77	51.73	85.71	63.37	80.56
Eurasia	102.75	75.20	72.41	95.24	119.24	85.25

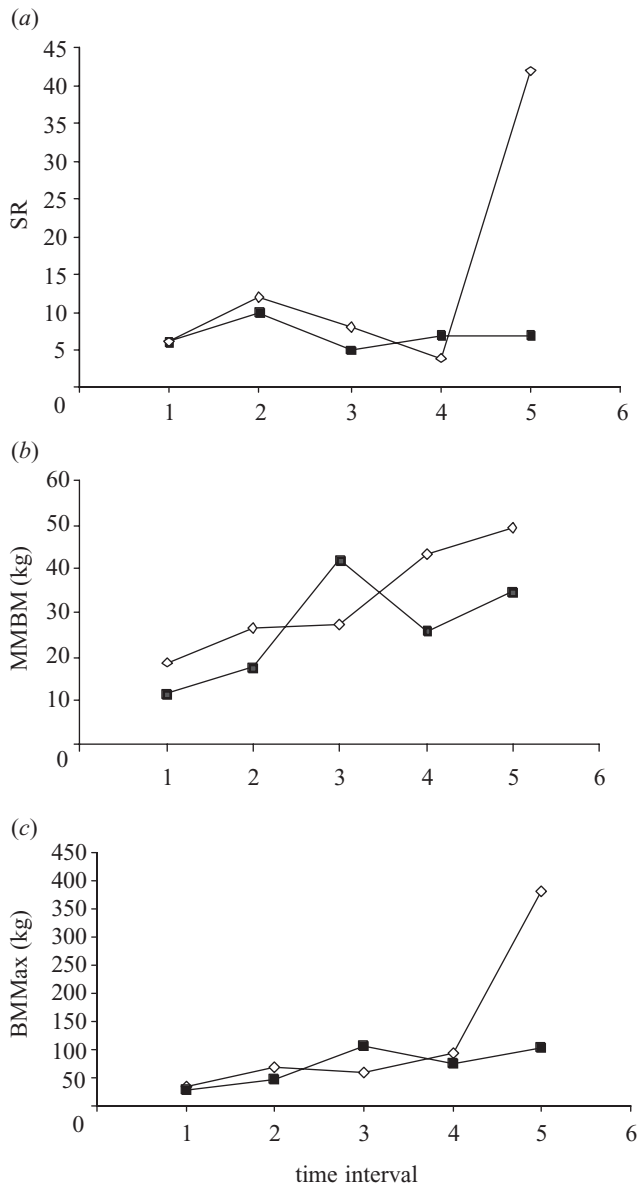


Figure 1. Direct comparisons of large (2.5 kg or more) mammalian carnivore diversity between Australia (squares) and South America (diamonds) over the past 25 Myr: (a) SR, (b) mean body mass (kg) and (c) BMMax (kg).

predicted in Eurasia and Africa in particular (table 1). The pre-GABI percentage of observed relative to predicted MMBM was slightly lower in Australia than South America until the Late Miocene, when it became much higher (figure 2b).

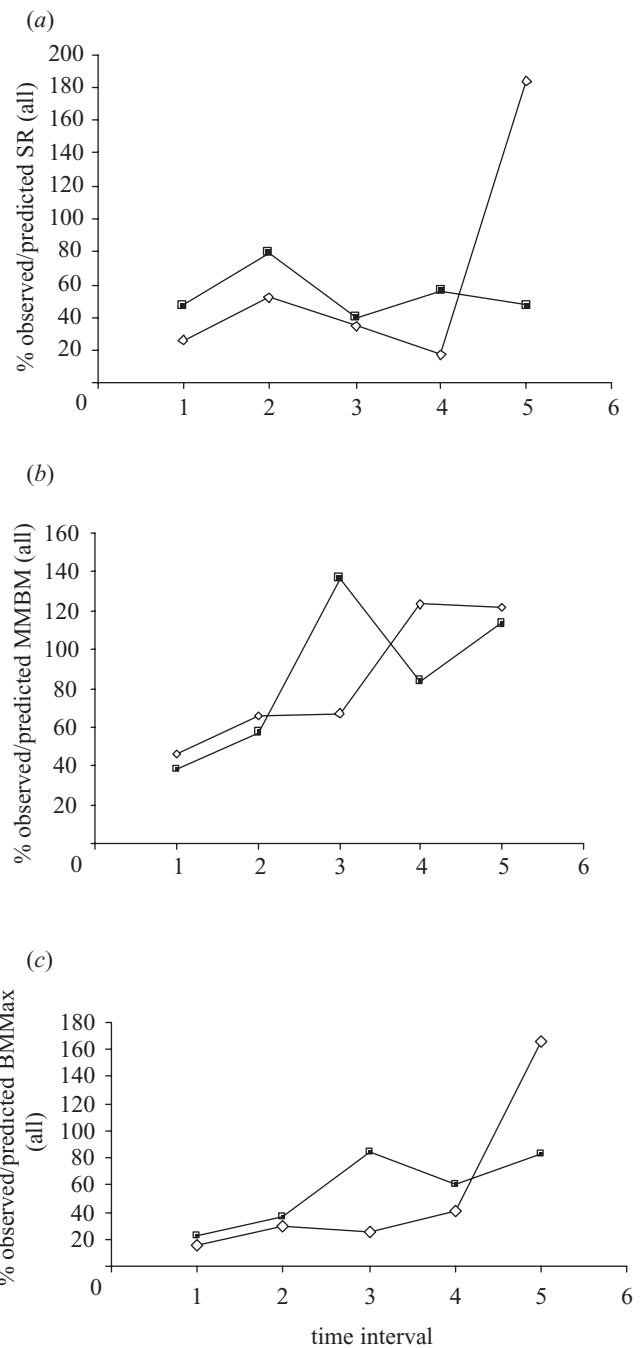


Figure 2. Observed (a) SR, (b) MMBM and (c) BMMax, as percentages of predicted for all large Australian (squares) and South American (diamonds) mammalian carnivores over the past 25 Myr.

Regression of BMMax against area was expressed as $\log(\text{BMMax}) = 0.7298 \times \log(\text{area}) + 0.0714$, $r^2 = 0.88$ (figure 4c in electronic Appendices C and D). BMMax was low in Late Pleistocene–Recent Eurasia, Australia and especially Africa, but high in North and South America. The predicted BMMax for Australia was 124.86 kg and that for South America was 230.69 kg. The percentage of observed relative to predicted BMMax was consistently higher in Australia than South America pre-GABI, but again relatively low on both continents (less than 37%) until the Late Miocene in Australia (figure 2c). Post-GABI, this remained relatively constant in Australia, but rose dramatically in South America (from 25% to 166%).

(ii) *Late Pleistocene–Recent large mammalian hypercarnivores*

Regressing SR and landmass area for Late Pleistocene–Recent mammalian hypercarnivores of 2.5 kg or more produced the following equation: $\log(\text{SR}) = 0.6964 \times \log(\text{area}) - 4.0601$, $r^2 = 0.99$ (figure 5a in electronic Appendix D). Observed SR was lower than predicted on all continents except North and South America: 92% for Australia, 123% for South America and, at 86%, lowest in Africa (table 1). Until the GABI, the percentage of observed relative to predicted SR followed a similar trend for the two island continents (figure 3a), but values were consistently higher and generally more than 100% for Australia. In pre-GABI South America the percentage of observed relative to predicted SR was less than 62% throughout, except during the Middle Miocene. Post-GABI, SR rose to 205% of the predicted value in South America, but dropped in Australia (from 130% to 92%).

The predicted MMBM for Australia was 42.41 kg and that for South America was 53.87 kg ($\log(\text{MMBM}) = 0.2842 \times \log(\text{area}) + 2.6706$, $r^2 = 0.55$ (figure 5b in electronic Appendix D)). Again, the observed MMBM was less than predicted on all continents, except North and South America and Eurasia and lowest in Africa (table 1). In Australia and South America, the percentage of observed relative to predicted MMBM was less than 50% in the Early–Middle Miocene. In the Late Miocene this rose to 99% in Australia, before falling to 61% in time interval 4 and rising to 83% in interval 5. In South America values remained consistently low until after the GABI, when they rose to 141% (figure 3b).

The predicted BMMax was 117.30 kg for Australia and 211.40 kg for South America ($\log(\text{BMMax}) = 0.7033 \times \log(\text{area}) + 0.2256$, $r^2 = 0.91$ (figure 5c in electronic Appendix D)). The percentage of observed relative to predicted BMMax was again consistently higher in Australia than South America pre-GABI, but relatively low on both continents (less than 41%) until the Late Miocene in Australia (figure 3c). Post-GABI, this remained relatively constant in Australia, but reached 179% in South America (from 32%).

4. DISCUSSION

Our direct comparisons show that, between 25 Myr ago and 3 Myr ago, SRs and BMMaxes of large Australian and South American mammalian carnivores were generally comparable (figure 1). Overall, mean body mass was ca. 5% higher in South America prior to the GABI. Post-

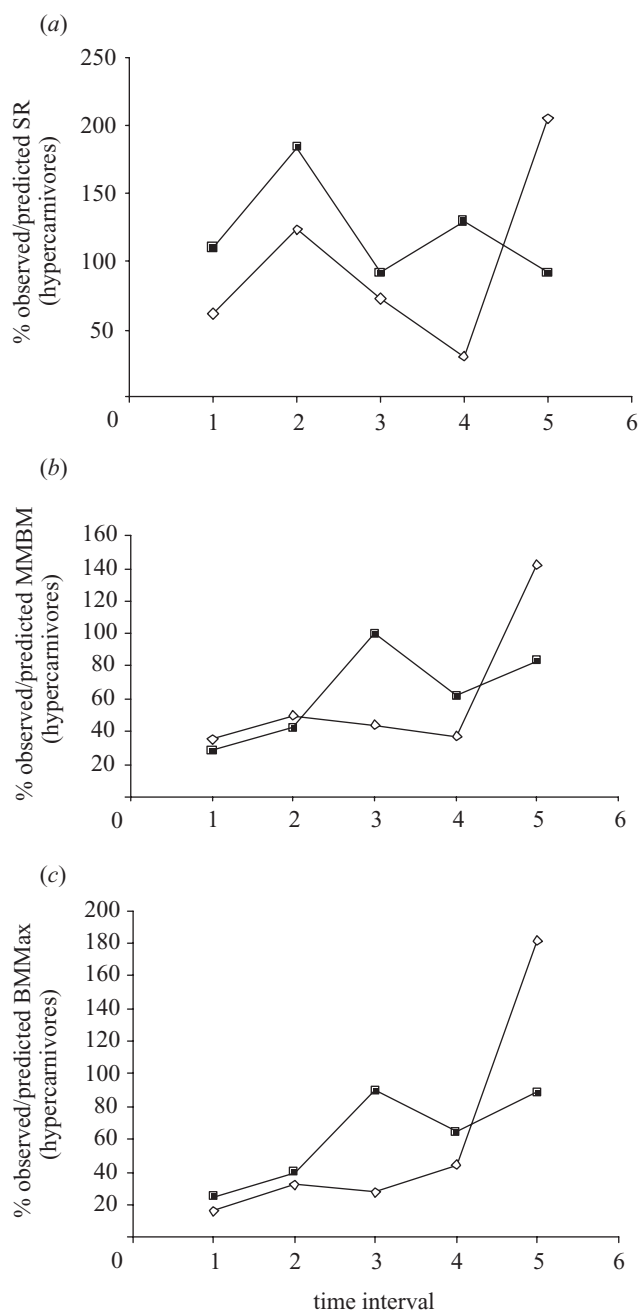


Figure 3. Observed (a) SR, (b) MMBM and (c) BMMax, as percentages of predicted for all large Australian (squares) and South American (diamonds) mammalian hypercarnivores over the past 25 Myr.

GABI, both SR and BMMax rose dramatically in South America compared with Australia. Mean body mass rose at comparable rates post-GABI on both continents. However, the largest South American species from the interval immediately prior to the GABI was a large immigrant procyonid, *Chapadmalania altaefrontis* (93.5 kg). If this species is removed from the analysis, then the same trend is apparent in South America for mean body mass as for the other descriptors.

After allowance for area, diversity in pre-GABI Australia was typically higher than in South America, whether or not we treated marsupial ‘carnivores’ as hypercarnivores (figures 2 and 3), but diversity rose dramatically post-GABI in South America. The sixfold increase in

BMMax and eightfold increase in SR between Early Pliocene and Late Pleistocene–Recent South America is difficult to rationalize as a function of soil nutrient levels. Relative to area, for Late Pleistocene–Recent hypercarnivores, SR, MMBM and BMMax were the world's highest in South America. The onset of an accelerated round of orological activity between 10 Myr ago and 7 Myr ago (Gregory-Wodzicki 2000) coincided with a decline in diversity that was not reversed until the GABI.

Arguments explaining mammalian carnivore diversity as a function of productivity assume a simple and positive relationship, but it is more often complex (Wroe 2002). Large body size can be a response to poor-quality food (Alexander 2003). For example, relative abundance of megaherbivores in African savannahs is highest in areas characterized by low soil nutrient levels (Bell 1982). Recent empirical evidence shows that, contra earlier expectations, mammalian diversity typically declines with increasing productivity (Rosenzweig 1992, 1995; Barnosky *et al.* 2001). Moreover, our results demonstrate that correlations depend on which descriptors are considered. In present-day Australia, the relationship between BMMax and SR among marsupials is inverse (Ava 2001). This is consistent with our findings. SR in Australia is highest in the Middle Miocene, a time of high rainfall and productivity (Kashiwagi & Shikazono 2003), but mean (same as MMBM, here) and BMMax are low.

There is some correspondence between the shapes of the lines that track diversity for pre-GABI Australia and South America. In both, SR peaks in the Middle Miocene and is lowest in the Late Miocene, whereas mean body mass increases from the Early to Late Miocene (figure 1a,c), suggesting that factors operating at a global scale were responsible.

Interpretations of feeding behaviours also impact strongly on this debate. The argument that large mammalian carnivore diversity reflects productivity is predicated on their position as high-order consumers. The placental taxon, Carnivora, includes many species that are dietary generalists. Consequently, unqualified comparisons between marsupial carnivore families and Carnivora may demonstrate the greater success of carnivorans as omnivores, but not necessarily as strict meat-eaters. The feeding habits of fossil carnivorans have been widely studied (Van Valkenburgh 1988, 1989; Werdelin 1997). For fossil marsupial carnivores more quantitative analyses are needed. However, it is probable that most fossil marsupial 'carnivores' were hypercarnivores (Wroe 2002; Johnson & Wroe 2003). Accepting that the propleopine kangaroo *Propleopus oscillans* was a generalist, the observed SR of hypercarnivores in Late Pleistocene–Recent Australia approached that predicted on the basis of landmass area (i.e. 5 versus 5.43).

Varying rates of consumption between taxa are also relevant, as are the ecologies of other taxa. Marsupials consume ca. 20% less than same-sized placentals, and reptiles consume far less still (Burness *et al.* 2001). In pre-GABI South America and Australia terrestrial birds and reptiles may have occupied a number of niches taken by mammals elsewhere (Marshall 1978). Large terrestrial phorusrhacoid birds, present in South America through most of the Cenozoic, were indisputably carnivorous, although

Croft (2001) argues that they were unlikely to compete with mammals¹. Fariña (1996) and Vizcaino & De Iuliis (2003) posit that some ground sloths and armadillos filled omnivore–carnivore roles. Ziphodont crocodiles were present on both continents (Marshall 1978). Whether they were terrestrial is debatable, but it is probable that they, together with more generalized crocodylians and other large reptiles, commonly took terrestrial prey (Wroe 2002). In Australia, some large terrestrial birds are omnivores, and the still-larger extinct dromornithids may also have been omnivorous–carnivorous (Wroe 1999, 2002).

Why have non-mammalian taxa in South America and Australia apparently encroached on niches occupied by mammals elsewhere? The possibility that tooth-replacement pattern has set inherent limits on the ability of the major marsupial carnivores (Dasyuromorphia and Borhyaenoidea) to diversify (Werdelin 1987a) cannot fully explain the phenomenon because, in Australia, thylacoleonid (Werdelin 1988) and propleopine (Wroe *et al.* 1998) marsupials have circumvented this constraint. In South America, omnivorous paucituberculatan marsupials have similar dentitions, and are able to kill small prey (Kirsch & Waller 1979), but do not grow to a large size. Interestingly, although our results do not support the contention that the diversity of large hypercarnivorous marsupials has been constrained by productivity in Australia, they do suggest that large marsupial omnivores have been relatively unsuccessful. Regression of SR and landmass area for large Late Pleistocene–Recent 'carnivores' of all feeding types, indicates that observed Australian SR is less than half that predicted (6 versus 12.59). Among the marsupial taxa considered here, omnivorous roles have been suggested only for propleopine kangaroos in Australia and some prothylacynines in South America. This is a maximum of 20% and 28%, respectively, of large marsupial 'carnivore' species, as opposed to 60% for omnivores among Late Pleistocene–Recent Carnivora. The most pressing question then is how to explain the paucity of large mammalian omnivores on these isolated continents?

Other questions highlighted by our analyses are why are there so many large mammalian carnivores in Late Quaternary America, and so few in contemporaneous Africa? High rates of immigration and/or origination may explain the extraordinary diversity of the former (Wroe *et al.* 2004a). Not only is it probable that immigration directly elevated carnivore diversity in Plio–Pleistocene America, but also immigrant lineages themselves may have undergone explosive radiation into 'empty' niche spaces. The extraordinary diversification of canids in post-GABI South America may exemplify the latter (Van Valkenburgh 1991). Our direct comparisons of pre- and post-GABI Australia and South America strongly reinforce the contention that immigration and extinction rates are greatly affected by isolation, although both the nature of the connections and the extent of geographical and temporal separation are critical (Rosenzweig 1995; Barnosky *et al.* 2001; Wroe *et al.* 2004a). Thus, we consider it probable that the slopes of our diversity–area regressions are 'artificially' high, because all the continental landmasses we included, except for Australia, have been variably connected throughout the Neogene. Consequently, our predictive equations for diversity based on area are likely to

produce overestimates in landmasses for which connections have been relatively poor (Africa) or non-existent (Australia).

Any temporal cut-off in diversity–area analyses, such as the one that we have applied here, is arbitrary. Increasing or decreasing the temporal range of the sample will affect diversity–area relationships. At present, it is impossible to account for both isolation and area accurately in a single predictive equation. However, given its extreme isolation relative to all other continents, it is perhaps surprising that the observed diversity of large mammalian hypercarnivores in Late Quaternary Australia is only slightly less than predicted.

In summary, our results suggest that, although large mammalian carnivore diversity in Late Pleistocene–Recent Australia is lower than that found in arbitrarily delineated areas of similar size in larger continents, for truly carnivorous taxa the overarching constraint appears to have been landmass area and, to a lesser degree, isolation. Isolation evidently had a more extreme effect in South America, with only four large mammalian ‘carnivores’ present in the 2 Myr preceding the GABI, despite its much larger landmass area. Marsupials appear to have been relatively unsuccessful as large generalists in both Australia and South America. The combined and probably related influences of isolation, phylogenetic constraint and/or competition with avian and reptilian taxa, as well as with

mammalian taxa not generally considered as ‘carnivores’, may explain these differences, but more research is needed to address this problem.

Last, our results quantify the rarity of large hypercarnivorous mammals worldwide. Only around 45 have existed over the past 65 000 years. Despite amounting to less than 6% of landmass area, Australia was home to around 10% of these.

Note added in proof. A recently published revision of the phorusrhacoid bird radiation suggests that 11 species have existed in South America since the Oligocene (Alvarenga & Hofling 2003). Two Early Miocene species were gigantic, exceeding 100 kg, and the remainder were between *ca.* 5 and 70 kg (Alvarenga & Hofling 2003). Phorusrhacoids may not have competed with mammals (Croft 2001). However, preliminary analyses in which we treat these carnivorous endotherms as ‘pseudo-mammals’ do not greatly affect our comparisons, except that BMMax and MMBM rise considerably in the Early Miocene of South America.

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APPENDIX A

All South American and Australian taxa used in the analyses.

(For extant taxa average body masses are from the literature. For marsupials, predictions were taken from the literature or calculated using published methods (Myers 2001; Wroe 2002; Wroe *et al.* 2004b). Where appropriate material was known, we used the predictive equation of Anderson *et al.* (1985), based on minimum femoral circumference (C_f). For three marsupial lions not represented by complete crania, predictions were based on geometric similitude with the closest species known from complete cranial or postcranial material. Where means were not available the medians were used. For most extinct taxa quantitatively based body-mass estimates were not available. In these instances predictive equations and their source are given respectively (equation and data). BM, body mass; Bo, Borhyaeninae; Can, Canidae; Das, Dasyuridae; Fel, Felidae; Ha, Hathylacinidae; Hyp, Hypsiprymnodontidae; Th, Thylacosmilidae; Pr, Prothylacyninae; Proc, Procyonidae; Must, Mustelidae; Tha, Thylacinidae; Thc, Thylacoleonidae; Urs, Ursidae.)

species	family	age (time interval)	body mass (kg)	equation and data	literature
South America					
<i>Cladosictis centralis</i>	Ha	1	4.4	LMRL; Myers (2001), Marshall (1981)	
<i>Anatherium herrerae</i>	Ha	1	9.7	LMRL; Myers (2001), Marshall (1981)	
<i>Pseudothylacinus rectus</i>	Pr	1	14.1	LMRL; Myers (2001), Marshall (1979)	
<i>Acrocyon riggsi</i>	Bo	1	26.3	UMRL; Myers (2001), Marshall (1978)	
<i>Arctodictis sinclairi</i>	Bo	1	23.3	3LML; Myers (2001), Marshall (1978)	
<i>Borhyaena macrodonta</i>	Bo	1	34.7	LMRL; Myers (2001), Marshall (1981)	
<i>Perathereutes pungens</i>	Ha	2	2.5	LMRL; Myers (2001), Marshall (1981)	
<i>Cladosictis patagonica</i>	Ha	2	4.0	C_f ; Anderson <i>et al.</i> (1985), Argot (2003)	
<i>Anatherium defossus</i>	Ha	2	8.0	LMRL; Myers (2001), Marshall (1981)	
<i>Prothylacinus patagonicus</i>	Pr	2	26.8	C_f ; Anderson <i>et al.</i> (1985), Argot (2003)	
<i>Lycopsis torresi</i>	Pr	2	19.4	UMRL; Myers (2001), Marshall (1979)	
<i>Arctodictis munizi</i>	Bo	2	51.6	LMRL; Myers (2001), Marshall (1978)	
<i>Borhyaena tuberculata</i>	Bo	2	21.4	C_f ; Anderson <i>et al.</i> (1985), Marshall (1978)	
<i>Acrocyon sectorius</i>	Bo	2	28.7	1UMRL; Myers (2001), Marshall (1978)	
<i>Lycopsis longirostris</i>	Pr	2	12.8	C_f ; Anderson <i>et al.</i> (1985), Marshall (1979)	
<i>Dukecynus magnus</i>	Pr	2	68.4	2LML; Myers (2001), Goin (1997)	
? <i>Arctodictis</i> sp.	Bo	2	51.6 ^a	Marshall (1978)	
<i>Anachlysictis gracilis</i>	Th	2	18.0	LMRL; Myers (2001), Goin (1997)	

<i>Chasicostylus castroi</i>	Ha	3	9.8	1UML; Myers (2001), Marshall (1981)	
<i>Pseudolycopsis cabrerai</i>	Pr	3	24.0	1UML; Myers (2001), Marshall (1979)	
<i>Stylocinus paranensis</i>	Pr	3	35.3	LMRL; Myers (2001), Marshall (1979)	
<i>Eutemnodon</i> spp.	Bo	3	16.8	3LML; Myers (2001), Marshall (1978)	
<i>Thylacosmilus atrox</i>	Th	3,4	58.0	C ₆ ; Anderson <i>et al.</i> (1985), Argot (2004)	
<i>Notocynus hermosicus</i>	Ha	3,4	3.2	1LML; Myers (2001), Marshall (1981)	
<i>Parahyaenodon argentinus</i> ^b	Bo	3,4	19.5	Marshall (1978)	
<i>Cyonasua argentina</i>	Proc	3	23.7	SKL, Carnivora; (Van Valkenburgh 1990)	R. Farina, personal communication
<i>Chapadmalania altaefrontis</i>	Proc	4	93.1	SKL, Carnivora; (Van Valkenburgh 1990)	R. Farina, personal communication
<i>Conepatus</i> sp.	Must	5	5.0		Nowak & Paradiso (1983)
<i>Arctodus</i> sp.	Urs	5	308.0		Fariña (1998)
<i>Tremarctos ornatus</i>	Urs	5	100.0		Nowak & Paradiso (1983)
<i>Smilodon fatalis</i>	Fel	5	351.0	C ₆ ; Anyonge (1993)	
<i>Smilodon populator</i>	Fel	5	375.0	C ₆ ; Anyonge (1993), Fariña (1998)	
<i>Panthera atrox</i>	Fel	5	382.0	C ₆ ; Anyonge (1993)	
<i>Panthera onca</i>	Fel	5	85.6		Gittleman (1986)
<i>Felis concolor</i>	Fel	5	51.9		Nowak & Paradiso (1983)
<i>Felis colocolo</i>	Fel	5	4.5		Nowak & Paradiso (1983)
<i>Felis jacobita</i>	Fel	5	4.0		Nowak & Paradiso (1983)
<i>Herpailurus yagouaroundi</i>	Fel	5	6.0		Nowak & Paradiso (1983)
<i>Leopardus pardalis</i>	Fel	5	9.5		Nowak & Paradiso (1983)
<i>Felis wiedii</i>	Fel	5	3.3		Nowak & Paradiso (1983)
<i>Felis geoffroyi</i>	Fel	5	4.0		Nowak & Paradiso (1983)
<i>Dusicyon avus</i>	Can	5	13.0		Van Valkenburgh (1991)
<i>Protocyon scagliarum</i>	Can	5	11.0		Van Valkenburgh (1991)
<i>Protocyon troglodytes</i>	Can	5	16.0		Van Valkenburgh (1991)
<i>Protocyon orcesi</i>	Can	5	25.0		Van Valkenburgh (1991)
<i>Chrysocyon brachyurus</i>	Can	5	22.5		Nowak & Paradiso (1983)
<i>Lycalopex vetulus</i>	Can	5	4.0		Nowak & Paradiso (1983)
<i>Pseudalopex sechurae</i>	Can	5	8.5		Nowak & Paradiso (1983)
<i>Pseudalopex griseus</i>	Can	5	8.5		Nowak & Paradiso (1983)
<i>Pseudalopex gymnocercus</i>	Can	5	8.5		Nowak & Paradiso (1983)
<i>Pseudalopex culpaeus</i>	Can	5	8.5		Nowak & Paradiso (1983)
<i>Cerdocyon thous</i>	Can	5	6.5		Nowak & Paradiso (1983)
<i>Atelocynus microtis</i>	Can	5	9.5		Nowak & Paradiso (1983)
<i>Speothos venaticus</i>	Can	5	6.0		Nowak & Paradiso (1983)
<i>Canis gezi</i>	Can	5	30.0		Van Valkenburgh (1991)
<i>Canis nehringi</i>	Can	5	30.0		Van Valkenburgh (1991)
<i>Canis dirus</i>	Can	5	50.0		Van Valkenburgh (1991)
<i>Theriodictis platensis</i>	Can	5	37.0		Prevosti & Palmqvist (2001)
<i>Theriodictis tarijensis</i> ^c	Can	5	37.0		Prevosti & Palmqvist (2001)
<i>Eira barbara</i>	Must	5	4.5		Nowak & Paradiso (1983)
<i>Conepatus semistriatus</i>	Must	5	3.5		Nowak & Paradiso (1983)
<i>Conepatus chinga</i>	Must	5	3.5		Nowak & Paradiso (1983)
<i>Conepatus humboldti</i>	Must	5	3.5		Nowak & Paradiso (1983)
<i>Procyon cancrivorus</i>	Proc	5	7.0		Nowak & Paradiso (1983)
<i>Nasua nasua</i>	Proc	5	4.5		Nowak & Paradiso (1983)
<i>Nasuella olivacea</i>	Proc	5	4.5		Nowak & Paradiso (1983)
<i>Potos flavus</i>	Proc	5	3.0		Nowak & Paradiso (1983)
<i>Lontra longicaudis</i>	Must	5	9.0		Nowak & Paradiso (1983)
<i>Lontra provocax</i>	Must	5	9.0		Nowak & Paradiso (1983)
Australia					
<i>Wabulacinus ridei</i>	Thc	1	5.3		Wroe (2002)
<i>Thylacinus macknessi</i>	Tha	1,2	9.2		Wroe (2002)
<i>Ngamalacinus timmulvaneyi</i>	Tha	1	5.7		Wroe (2002)
<i>Nimbacinus dicksoni</i>	Tha	1,2	5.0		Wroe (2002)
<i>Wakaleo oldfieldi</i>	Thc	1,2	28.4	TJL Myers (2001), Clemens & Plane (1974)	

<i>Ekaltadeta ima</i>	Hyp	1,2	17.4	TSL Myers (2001)	
<i>Nimbacinus richi</i>	Tha	2	4.9		Wroe (2002)
<i>Maximucinus muirheadae</i>	Tha	2	18.4		Wroe (2002)
<i>Priscileo roskellyae</i>	Thc	2	2.9	TSL; Myers (2001), Queensland Museum Fossil 23453	
<i>Wakaleo vanderleurei</i>	Thc	2	41.4	TSL; Myers (2001), Murray <i>et al.</i> (1987)	
<i>Ekaltadeta jamiemulvaneyi</i> ^a	Hyp	2	46.4	Wroe (1996)	
<i>Ganbulanyi djadjinguli</i>	Das	2,3	3.6		Wroe (2002)
<i>Thylacinus megiriani</i>	Tha	3	57.3		Wroe (2002)
<i>Thylacinus potens</i>	Tha	3	38.7		Wroe (2002)
<i>Tjarrpecinus rothi</i>	Tha	3	5.4		Wroe (2002)
<i>Wakaleo alcootaensis</i> ^c	Thc	3	105.0	Clemens & Plane (1974)	
<i>Thylacoleo hilli</i> ^f	Thc	4	11.2	Pledge (1977)	
<i>Thylacoleo crassidentatus</i> ^f	Thc	4	75.2	Archer & Dawson (1982)	
<i>Jackmahoneyi toxoniensis</i>	Hyp	4	23.2	PJL (Myers 2001), Australian Museum Fossil 51885	
<i>Propleopus chillagoensis</i>	Hyp	4	36.4	2UMA (Myers 2001), Wroe (1996)	
<i>Thylacinus sp.</i>	Tha	4	18.8	3LML (Myers 2001), Mackness <i>et al.</i> (2003)	
<i>Glaucodon ballaratensis</i>	Das	4	7.5		Wroe (2002)
<i>Sarcophilus moornaensis</i>	Das	4	9.1		Wroe (2002)
<i>Propleopus oscillans</i>	Hyp	5	47.1	LMRL (Myers 2001), Queensland Museum Fossil 3302	
<i>Propleopus wellingtonensis</i>	Hyp	5	35.5	LMRL (Myers 2001), University of California Museum of Paleontology 45171	
<i>Thylacoleo carnifex</i>	Thc	5	104.0		Wroe <i>et al.</i> (2003)
<i>Sarcophilus laniarius</i>	Das	5	19.4	LMRL (Myers 2001), Werdelin (1987b)	
<i>Sarcophilus harrisi</i>	Das	5	7.0		Wroe (2002)
<i>Dasyurus maculatus</i>	Das	5	2.5		Wroe (2002)
<i>Thylacinus cynocephalus</i>	Tha	5	29.5		Paddle (2000)

^a Assumes geometric similitude with *A. munizi*.

^b Assumes geometric similitude with *A. riggsi*.

^c For *T. tarijensis* we have been unable to find either an estimate or necessary data, but Prevosti & Palmqvist (2001) describe this species as slightly smaller than *T. platensis* and we have used a figure of 37 kg for both.

^d Assumes geometric similitude with *E. ima*.

^e Assumes geometric similitude with *W. vanderleurei*.

^f Assumes geometric similitude with *T. carnifex*.

REFERENCES

- Aava, B. 2001 Primary productivity can affect mammalian body size frequency. *Oikos* **93**, 205–212.
- Alexander, R. M. 2003 A rodent as big as a buffalo. *Nature* **301**, 1678–1679.
- Alvarenga, H. M. F. & Hofling, E. 2003 Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papéis Avulsos de Zoologia* (São Paulo) **43**, 55–91.
- Anderson, J. F., Hall-Martin, A. & Russell, D. A. 1985 Long-bone circumference and weight in mammals, birds, and dinosaurs. *J. Zool. Lond.* **207**, 53–61.
- Anyonge, W. 1993 Body mass in large extant and extinct carnivores. *J. Zool. Lond.* **231**, 339–350.
- Archer, M. & Dawson, L. 1982 Revision of marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and thylacoleonid evolution in the late Cainozoic. In *Carnivorous marsupials*, vol. 1 (ed. M. Archer), pp. 477–494. Sydney: Royal Zoological Society of New South Wales.
- Argot, C. 2003 Postcranial functional adaptations in the South American Miocene borhyaenoids (Mammalia, Metatheria), *Pseudonotictis*, *Sipalocyon* and *Gladosictis*. *Alcheringa* **27**, 303–356.
- Argot, C. 2004 Functional adaptive features of the postcranial skeleton of a sabertooth borhyaenoid, *Thylacosmilus atrox* (Metatheria), and palaeobiologic implications. *Alcheringa* (In the press.)
- Barnosky, A. D., Hadley, A. H., Maurer, B. A. & Christie, M. I. 2001 Temperate terrestrial vertebrate faunas in North and South America: interplay of ecology evolution and geography with biodiversity. *Conserv. Biol.* **15**, 658–674.
- Bell, R. V. H. 1982 The effect of soil nutrient availability on community structure in African ecosystems. In *Ecology of tropical savannas* (ed. B. J. Huntley & B. H. Walker), pp. 193–216. New York: Springer.
- Brown, D. A., Campell, K. & Crook, K. 1968 *The geological evolution of Australia and New Zealand*. Oxford: Pergamon.
- Burness, G. P., Diamond, J. & Flannery, T. F. 2001 Dinosaurs dragons and dwarfs: the evolution of maximal body size. *Proc. Natl Acad. Sci. USA* **98**, 14 518–14 523.
- Clemens, W. A. & Plane, M. 1974 Mid-Tertiary Thylacoleonidae (Marsupialia: Mammalia). *J. Palaeontol.* **48**, 652–660.
- Croft, D. A. 2001 Cenozoic environmental change in South America as indicated by mammalian body size distributions. *Diversity Distributions* **7**, 271–287.
- Croft, D. A. 2002 Mammalian predator–prey diversity patterns: what do they tell us about island continents? *J. Vert. Paleontol.* **22**(Suppl. to no. 3), 47A.
- Fariña, R. A. 1996 Trophic relationships among Lujanian mammals. *Evol. Theory* **11**, 125–134.

- Flannery, T. F. 1994 *The future eaters*. Sydney: New Holland.
- Flessa, K. W. 1975 Area, continental drift, and mammalian diversity. *Paleobiology* **1**, 189–194.
- Gittleman, J. L. 1986 Carnivore brain size, behavioural ecology, and phylogeny. *J. Mamm.* **67**, 23–36.
- Goin, F. J. 1997 New clues for understanding Neogene marsupial radiations. In *A history of the neotropical fauna. Vertebrate paleobiology of the Miocene in Columbia* (ed. R. F. Kay, R. H. Maden, R. L. Cifelli & J. Flynn), pp. 185–204. Washington DC: Smithsonian Institution Press.
- Gregory-Wodzicki, K. M. 2000 Uplift history of the central and Northern Andes: a review. *Geol. Soc. Am. Bull.* **112**, 1091–1105.
- Johnson, C. & Wroe, S. 2003 Causes of extinctions of vertebrates during the Holocene of mainland Australia: arrival of the dingo or human impact? *The Holocene* **13**, 1009–1016.
- Jones, M. E. 2003 Convergence in ecomorphology and guild structure among marsupial and placental carnivores. In *Predators with pouches: the biology of carnivorous marsupials* (ed. M. Jones, C. Dickman & M. Archer), pp. 285–296. Collingwood, Victoria: CSIRO.
- Julien, P. Y. 1995 *Erosion and sedimentation*. Cambridge University Press.
- Kashiwagi, H. & Shikazono, N. 2003 Climate change during Cenozoic inferred from global carbon cycle model. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **199**, 167–185.
- Kirsch, J. A. W. & Waller, P. F. 1979 Notes on the trapping and behavior of the Caenolestidae (Marsupialia). *J. Mamm.* **60**, 390–395.
- Lee, A. K. & Cockburn, A. 1985 *Evolutionary ecology of marsupials*. Cambridge University Press.
- Mackness, B. S., Wroe, S., Wilkinson, C. & Wilkinson, D. 2003 Confirmation of *Thylacinus* from the Pliocene Chinchilla local fauna. *Aust. Mammal.* **24**, 237–241.
- Marshall, L. G. 1978 *Evolution of the Borhyaenidae, extinct South American predaceous marsupials*. Berkeley: University of California Press.
- Marshall, L. G. 1979 Review of the Prothylacininae, an extinct subfamily of South American ‘dog-like’ marsupials. *Fieldiana (Geol.)* **3**, 1–50.
- Marshall, L. G. 1981 Review of the Hathyliacyninae, an extinct subfamily of South American ‘dog-like’ marsupials. *Fieldiana (Geol.)* **7**, 1–120.
- Murray, P., Wells, R. & Plane, M. 1987 The cranium of the Miocene thylacoleonid, *Wakaleo vanderleuri*: click go the shears: a fresh bite at thylacoleonid systematics. In *Possums and opossums: studies in evolution* (ed. M. Archer), pp. 433–466. Sydney: Surrey Beatty and Sons.
- Myers, T. J. 2001 Marsupial body mass prediction. *Aust. J. Zool.* **49**, 99–118.
- Nowak, R. M. & Paradiso, J. N. 1983 *Walker’s mammals of the world*, vol. II, 4th edn. Baltimore, MD: Johns Hopkins University Press.
- Paddle, R. 2000 *The last Tasmanian tiger: the history and extinction of the Thylacine*. Cambridge University Press.
- Pledge, N. S. 1977 A new species of *Thylacoleo* (Marsupialia: Thylacoleonidae) with notes on the occurrences and distribution of Thylacoleonidae in South Australia. *Rec. Sth Aust. Mus.* **17**, 277–283.
- Prevosti, F. J. & Palmqvist, P. 2001 Ecomorphological analysis of the hypercarnivore canid *Theriodictis platensis* Mercerat (Mammalia, Carnivora), based on new material from the Pleistocene of Argentina. *Ameghiniana* **38**, 375–384.
- Rosenzweig, M. L. 1992 Species diversity gradients: we know more and less than we thought. *J. Mamm.* **73**, 715–730.
- Rosenzweig, M. L. 1995 *Species diversity in space and time*. Cambridge University Press.
- Savage, D. E. & Russell, D. E. 1983 *Mammalian paleofaunas of the world*. Reading, MA: Addison-Wesley.
- Van Valkenburgh, B. 1988 Trophic diversity in past and present guilds of large predatory mammals. *Palaeobiology* **14**, 155–173.
- Van Valkenburgh, B. 1989 Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In *Carnivore behaviour, ecology and evolution* (ed. J. Gittleman), pp. 410–433. New York: Cornell University Press.
- Van Valkenburgh, B. 1990 Skeletal and dental predictors of body mass in carnivores. In *Body size in mammalian paleobiology* (ed. J. Damuth & B. J. MacFadden), pp. 181–205. Cambridge University Press.
- Van Valkenburgh, B. 1991 Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. *Palaeobiology* **17**, 340–362.
- Van Valkenburgh, B. 1999 Major patterns in the history of carnivorous mammals. *A. Rev. Earth Planet Sci.* **27**, 463–493.
- Vizcaino, S. F. & De Iuliis, G. 2003 Evidence for advanced carnivory in fossil armadillos (Mammalia: Xenarthra: Dasypodidae). *Palaeobiology* **29**, 123–138.
- Werdelin, L. 1987a Jaw geometry and molar morphology in marsupial carnivores: analysis of a constraint and its macroevolutionary consequences. *Palaeobiology* **13**, 342–350.
- Werdelin, L. 1987b Some observations on *Sarcophilus lanarius* and the evolution of *Sarcophilus*. *Rec. Queen Victoria Mus.* **90**, 1–27.
- Werdelin, L. 1988 Circumventing a constraint: the case of *Thylacoleo carnifex* (Marsupialia: Thylacoleonidae). *Aust. J. Zool.* **36**, 565–571.
- Werdelin, L. 1997 Carnivoran ecomorphology: a phylogenetic perspective. In *Carnivore behaviour, ecology and evolution*, vol. 2 (ed. J. L. Gittleman), pp. 582–624. London: Cornell University Press.
- Wroe, S. 1996 An investigation of phylogeny in the giant rat kangaroo *Ekaltadeta* (Propleopinae, Potoroidae, Marsupialia). *J. Palaeontol.* **70**, 677–686.
- Wroe, S. 1999 The bird from hell. *Nat. Aust.* **26**, 56–63.
- Wroe, S. 2002 A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas and factors influencing their diversity: the myth of reptilian domination and its broader ramifications. *Aust. J. Zool.* **50**, 1–24.
- Wroe, S. 2003 Australian marsupial carnivores: recent advances in palaeontology. In *Predators with pouches: the biology of carnivorous marsupials* (ed. M. Jones, C. Dickman & M. Archer), pp. 102–123. Collingwood, Victoria: CSIRO Publishing.
- Wroe, S. 2004 Killer kangaroos and other murderous marsupials. *Scient. Am* **14**(Special Issue), 48–55.
- Wroe, S., Brammall, J. & Cooke, B. N. 1998 The skull of *Ekaltadeta ima* (Marsupialia: Hypsiprymnodontidae?): an analysis of some cranial features among marsupials and a re-investigation of propleopine phylogeny, with notes on the inference of carnivory in mammals. *J. Palaeontol.* **72**, 738–751.
- Wroe, S., Myers, T., Seebacher, F., Kear, B., Gillespie, A., Crowther, M. & Salisbury, S. 2003 An alternative method for predicting body-mass: the case of the marsupial lion. *Palaeobiology* **29**, 404–412.
- Wroe, S., Field, J., Fullagar, R. & Jeremiin, L. 2004a Megafaunal extinction in the Late Quaternary and the global overkill hypothesis. *Alcheringa* **28**, 291–331.
- Wroe, S., Crowther, M., Dortch, J. & Chong, J. 2004b The size of the largest marsupial and why it matters. *Proc. R. Soc. Lond. B* **271**(Suppl. 3), S34–S36. (DOI 10.1098/rsbl.2003.0095.)

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