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Arguments about the extinction of Australia's megafauna have largely rested on anthropogenic factors consequent upon the arrival of humans there, and have lacked any appreciation of the possibilities of climate/environmental changes taking place during the late Quaternary. Moreover, the status of the megafauna at the extinction and in the period leading up to it has largely been ignored. This article assesses the species that existed during the late Quaternary, their continental dispersal, the likely impact of negative climate change during that time and the effect this had on their demography and variety. These factors are discussed together with a synthesis of present data regarding Australia's mega 2004: fauna demography and which species may have reached the extinction threshold. One interpretation of the data suggests a mid-late Quaternary process of demographic fragmentation, disjunction and fluctuation, a restricted continental distribution among a diminishing group and a limited and reducing species variety due to climate and environmental change. It is argued that increasing continental aridity during the mid-late Quaternary was a forcing mechanism behind species distribution, changes to that distribution and population reduction through episodic but widespread drought and vegetation change. This resulted in alteration of the biogeographic status of the megafauna, with increasing stress on and reduction of the population as a whole. In particular, it changed population composition and reduced species variety and overall population size by the beginning of the last glaciation, such that at the time of human entry the population had reached a precarious stage vulnerable to any level of subsequent anthropogenic activity with the arrival of humans in Australia.

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Arguments continue regarding the cause of world megafaunal extinctions during the last glacial cycle and the part that humans may have played in them (Whitney-Smith 1996; MacPhee 1999; Meltzer 2004). The exact timing and reasons for Australian extinctions continue to initiate research and debate. In Australia, the balance of opinion has anthropogenic factors, particularly hunting and firing with consequent landscape change, as direct causes of extinction of up to 55 megafauna species between 30 and 50 kyr ago (Horton & Wright 1981; Murray 1984, 1991; Rich *et al.* 1985; Wright 1986; Flannery 1990a, b, 1994; Choquenot & Bowman 1998; Webb 1998; Miller *et al.* 1999; Mulvaney & Kamminga 1999; Field & Fullager 2001; Roberts *et al.* 2001; Brook & Bowman 2002; Johnson 2002, 2006; Barnosky *et al.* 2004; Johnson & Prideaux 2004; Wroe *et al.* 2004; Trueman *et al.* 2005). The Australian extinctions included the loss of 85% of terrestrial animal species with average weights in excess of 44 kg (Flannery 1990a; Murray 1991; Roberts *et al.* 2001). This 'sudden' demise has been termed 'blitzkrieg', reflecting perceived rapidity of the event eliminating a continent-wide population through hunting. The underlying assumption behind the use of this emotive term is a total demise of all these species in a very short time and that they lived everywhere.

The argument is poorly served by the evidence, however. The difficulty solving the megafaunal extinction issue is that we have little understanding of the extinc-

tion timing of individual species, their prior continental distribution, biogeography or of the number still existing at the proposed time of extinction. Moreover, we cannot be sure that the most recent date for any given species represents the last animal. Another problem is that a large part of the continent is yet to be properly surveyed to establish where megafauna lived, and museum collections and field assemblages remain largely undated. The spatial and temporal distribution of megafauna is therefore largely unknown, although vital if we are to understand the reasons for the extent and timing of this event. It is argued here that disposition of the megafauna population at extinction was such that 'blitzkrieg' is a totally unsuitable concept. A growing number of researchers, however, are positing environmental change during the late Quaternary, change that could have been a forcing mechanism reducing the number of megafauna species reaching the accepted extinction threshold (Webb 2006; Wroe & Field 2006). Although an environmental cause was posited some time ago (Horton 1984), albeit that, in the absence of present data, this was focused on the Last Glacial Maximum (LGM).

While extinction is a natural function of evolution, it can be argued that an anthropogenic role in it is not. Beyond this is the argument that the presence of people is the only factor different from those of previous glaciations which the megafauna survived: but how well did they survive? In Australia, the claim has been made

Table 1. Extinct megafauna ≥ 50 kg ($n = 32$) over 230 sites.

Extinct megafauna species	Age (kyr) after Wroe & Field (2006)	Weight (kg) after Johnson (2006)	%	SE		LEB	SW	NE ³	NW ³
				ESE	WSE				
JF <i>Ramsaya magna</i> 1	–	100	0.4	✓					
JF <i>Macropus pearsoni</i> 2	–	150	0.9	SEQ					
JF <i>Phascologomys medius</i> 3	–	50	1.3	✓					
J 'Simosthenurus' <i>baileyi</i> 3	164	55	1.3		✓				
WM <i>Wonambi naracoortensis</i> 3	55	80	1.3		✓				
JMF <i>Macropus ferragus</i> 3	52	150	1.3	✓	✓				
J 'Procoptodon' <i>williamsi</i> 3	MIS5	150	1.3	✓	✓				
MF <i>Simosthenurus orientalis</i> 5	–	250	2.2	✓	✓	✓			
J <i>Sthenurus stirlingi</i> 6	75	170	2.6		✓	✓			
JF <i>Procoptodon pusio</i> 7	–	75	3.0	✓		✓			
JMF 'Procoptodon' <i>oreas</i> 8	–	100	3.5	✓		✓			
JMF <i>Protemnodon roechus</i> 9	47	170	3.9	✓	✓		✓		
JMF <i>Sthenurus atlas</i> 12	52	150	5.2	✓	✓	✓	✓		
JMF <i>Sthenurus andersoni</i> 13	52	72	5.7	✓	✓	✓	✓		
JMF 'Simosthenurus' <i>pales</i> 15	164	150	6.5	✓		✓			
JMF <i>Simosthenurus maddocki</i> 15	164	80	6.5		✓		✓		
JMF 'Procoptodon' <i>gilli</i> 16	164	54	7.0	✓	✓	✓			
JMF <i>Procoptodon rapha</i> 16	–	150	7.0	✓	✓	✓			
JMF <i>Palorchestes azeal</i> 16	164	500	7.0	✓	✓	✓	✓	✓	
JMF <i>Phascolonius gigas</i> 16	47	200	7.0	✓	✓	✓	✓	✓	✓
JMF 'Procoptodon' <i>browneorum</i> 22	46	50	7.6	✓	✓	✓	✓	✓	✓
JMF <i>Sthenurus tindalei</i> 18	52	130	7.8	✓	✓	✓	✓		
WM <i>Megalania prisca</i> 18	–	700	7.8	✓	✓	✓		✓	
J <i>Metasthenurus newtonae</i> 22	164	55	9.6	✓	✓	✓			
JMF <i>Protemnodon anak</i> 25	52	130	10.9	✓	✓	✓	✓	✓	
JMF <i>Protemnodon brehus</i> 26	52	110	11.3	✓	✓	✓	✓	✓	
JMF <i>Zygomaturus trilobus</i> 30	55	500	13.0	✓	✓	✓	✓	✓	✓
JMF <i>Procoptodon goliah</i> 32	47	230	13.9	✓	✓	✓	✓		
JMF <i>Simosthenurus occidentalis</i> 41	46	120	17.8	✓	✓	✓			
JMF <i>Thylacoleo carnifex</i> 45	47	110	19.6	✓	✓	✓	✓	✓	
W <i>Genyornis newtoni</i> 69	50	200 ²	30.0	✓	✓	✓	✓	✓	✓
JMF <i>Diprotodon optatum</i> 93	47	2700 ¹	40.4	✓	✓	✓	✓	✓	✓
Quadrant total				25	26	20	13	9	4

J = Johnson (2006); M = Murray (1996); F = Flannery (1990); W = Webb, this study.

SEQ = Found only in Southeast Queensland,

¹ Average weight (male).

² Maximum weight.

³ North of latitude 24°.

% = Percentage of a species in 230 sites. Italic numbers = number of sites containing this species.

that the megafauna disappeared around 45 kyr ago (Roberts *et al.* 2001) because that is close to the accepted date for the arrival of humans. The latter is not yet an accepted fact, however (Webb 2006); others suggest that the final extinction was much later (Trueman *et al.* 2005), indicating that a large overlap existed between humans and megafauna. If the ~45 kyr date is correct, then two possibilities emerge: either humans were there some time before the final extinction, thus imposing stresses on these animals over a long period and reducing the population over time, or they arrived 45–50 kyr and rapidly eliminated them. Certainly, if people were a direct cause, the timing of that event is even more important as a signpost of human presence on the continent not necessarily tied to standard archaeological evidence.

Understanding megafaunal population biology and, in particular, its temporal and spatial disposition over

the last four glacial cycles is central to understanding the processes leading to the final extinction as well as to assessing how many species were involved. There is also a need to understand whether there were climatic or environmental trends unrelated to glacial cycles, but exacerbated by them, that disadvantaged these animals. Another approach is to try to assess the disposition of megafauna populations before and after humans arrived. The list of species involved fluctuates between 19 and 60, depending on the author (Flannery 1990b; Murray 1991; Barnosky *et al.* 2004; Wroe *et al.* 2004; Johnson 2006; Wroe & Field 2006). Thirty-two species have been chosen here distributed across 230 fossil sites in Australia and Tasmania (Table 1), but excluding Papua New Guinea, which was part of the Greater Australian continent (Sahul). The lack of understanding of the range of species, their distribution and structure makes it difficult to include PNG in this article.

The Australian megafauna list excludes animals weighing <50 kg and those that dwarfed across the Pleistocene–Holocene boundary, including *Wallabia indra-bicolor*, *Phascolarctos stirtoni-cinereus*, *Macropus titan-giganteus*, *Macropus siva-agilis* and *Macropus cooperi-bicolor* (Murray 1991). Animals whose taxonomy is in doubt have also been excluded. Weights have been defined using Johnson's (2006) table 2.1 (pp. 18–20) and Murray's (1991) fig. 35 (p. 1126), and the weight definition of megafauna is a little heavier (50 kg) than Martin's (1984) >44 kg standard. Further consideration for species inclusion is dependent on the timing of extinction; at present, the timing for only one (*Genyornis newtoni*) is anywhere near certain (Miller *et al.* 1999), although *Diprotodon* may be close to that same threshold (Roberts *et al.* 2001). Seven species regularly included in the extinction group are now suspected of becoming extinct prior to the late Pleistocene event (Long *et al.* 2002; Wroe & Field 2006) (Table 1), but have been included together with others for whom extinction timing is lacking. This leaves only seven species that almost certainly reached the 45–50 kyr extinction event. It could therefore be argued that the extinction of only seven species over 5000 years does not in itself constitute a 'blitzkrieg', or even an unusual event beyond a natural process of species extinction.

Animal families experiencing creeping extinction trends during the Pliocene and early Pleistocene included Diprotodontids, wombats and koalas, trends which resulted in a comparatively limited variety of these groups by the late Quaternary (Long *et al.* 2002). In contrast, macropods thrived during the Quaternary with more than 60 species in the Holocene. A number of species, some often included in the extinction event, became extinct before the penultimate glacial maximum (Wroe & Field 2006; Prideaux *et al.* 2007b). These included two Palorchestids, '*Simosthenurus*' *baileyi*, '*Simosthenurus*' *pales*, '*Simosthenurus*' *maddocki*, '*Procoptodon*' *gill*, '*Procoptodon*' *williamsi*, *Metasthenurus newtonae*, *Bohra paulae*, *Baringa* spp. and the Diprotodontids *Nototherium mitchelli*, *Euowenia grata* and *Euryzygoma dunense*. Besides not knowing exactly how many species existed when humans arrived, arguments are constrained by poorly understood temporal and spatial distribution of the species. Future research will focus on these two issues, particularly the dating of individual species. Almost all species lack accurate minimum dates, but every effort has been made to ensure that those included in this study lived in the late Quaternary (Roberts *et al.* 2001; Johnson 2006; Wroe & Field 2006).

Megafauna distribution

Late Quaternary site distribution shows megafauna inhabited an area from Cape York (15° south) to southwestern Australia and into the southern Lake Eyre Basin (LEB) (Fig. 1). In eastern Australia, they lived

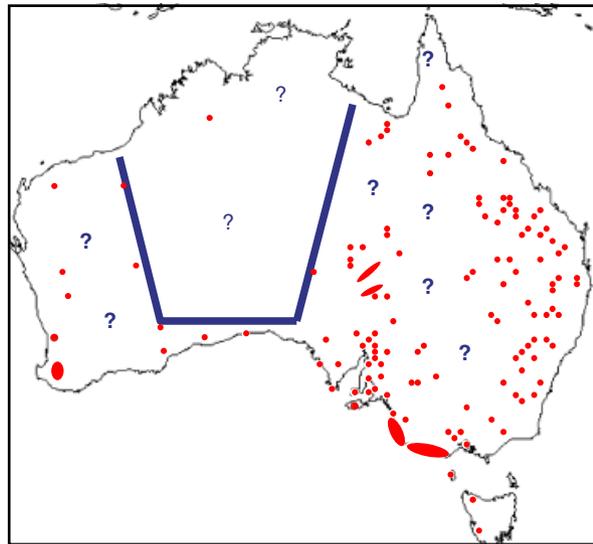


Fig. 1. Distribution of late Quaternary Australian megafauna sites.

either side of the Great Divide from the coast to inland plains. During low sea level, animals spread to Tasmania, as far as the Florentine Valley (42° south), on to King Island, as part of the exposed Bassian Bridge, and to Kangaroo Island (Williams 1980; Horton 1984; Murray 1991; Prideaux *et al.* 2004; Wells *et al.* 2006). Presumably, they also moved on to the continental shelf during glacial maxima. Fossil site distribution in eastern Australia is extensive but patchy in north, central and western Queensland and north and central New South Wales. The largest 'empty' region, however, encompasses a large part of western and central Australia. With the exception of three examples in outback Western Australia, each containing only a single species (*Diprotodon optatum*), there is a total lack of megafauna sites in the Western Deserts and Northern Territory, which covers an area of more than 2×10^6 km². Western Australian megafauna foci are the southwest corner east to the Nullarbor Plain with three single animals found along the central western coast. With these exceptions, almost the entire western half of the continent is devoid of sites. This area, however, may indicate merely an absence of evidence because of its remoteness and lack of survey. Taphonomy often dictates visibility, composition and preservation of fossil assemblages. Fossils may be present but unexposed; interment conditions do not preserve or bone is destroyed on exposure. Moreover, differential rates of preservation, survey bias, environmental conditions as well as a variety of other factors, such as the presence or absence of suitable age sediments and domestic livestock, can all skew the picture and the perceived presence of species. Nevertheless, our present understanding of megafauna distribution requires that until proven otherwise the 'empty' areas represent places uninhabited or, at best, very sparsely populated by these animals. Personal surveys of Quaternary

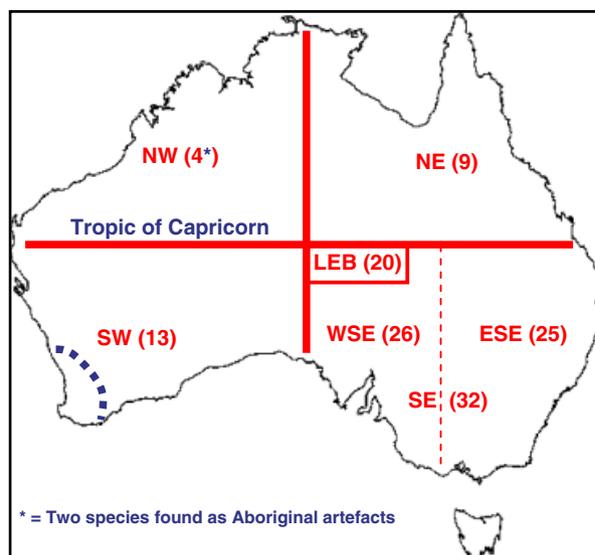


Fig. 2. Distribution of 32 megafauna species across four Australian quadrants.

exposures around 13 lakes in the Great Victoria, Tanami and Gibson Deserts have yielded no fossil megafauna remains or *Genyornis* eggshell.

To quantify megafauna distribution using present evidence, Australia has been divided into four quadrants using the Tropic of Capricorn (lat. 24°) and longitude 134°. Placing 230 late Quaternary megafauna sites within these quadrants indicates that the southeast has all 32 species in this study, making it the best stocked corner of the continent (Fig. 2; Table 1). Dividing this southeast (SE) quadrant into eastern (ESE) and western (WSE) sub-regions shows an almost equal distribution, i.e. 25 and 26 species, respectively. Seven are missing from the ESE and 6 from the WSE; 13 others are endemic to both sub-regions. This distribution suggests that most megafauna species favoured the more reliable fodder and water resources of temperate and semi-tropical climates over arid and semi-arid conditions requiring biological and behavioural adaptive specializations. The former could support mosaic vegetation consisting of grasslands, wet and dry sclerophyll forest, savannah woodland, rainforest thickets and shrub lands offering a wide range of browsing and grazing habitats. Permanent water in lakes, streams and back swamps of southeastern Australia probably underpinned the variety of megafauna found there. Range extension northeast and southwest would have been dictated by the permanence of food and water resources in those areas. It is logical, therefore, that because megafauna required good water and fodder, southeast Australia would offer the most stable environment and would therefore be an area that could serve as a species feeder to other regions. Southeastern Australia also contains the biggest late Quaternary sites, including Lancefield, Reddestone and Cuddies Springs and fossil

lake systems of the Darling and Willandra and Lakes Victoria and Callabonna. Other highly productive areas include the eastern Darling Downs, the Lake Eyre palaeoriver systems, cave systems such as Russenden, Wellington, Naracoorte and Mount Gambier as well as many other open sites across the southeast. The good preservation environments of caves, particularly vertical sink holes, have acted as natural traps and pitfalls, greatly enhancing our understanding of megafauna morphology and species variety and distribution (Wells *et al.* 1984; Prideaux *et al.* 2000, 2007a, b).

The next largest quadrant is the southwest (SW), with 13 species, all of which are also found in the WSE. Without cave assemblages in southwestern Australia, such as Mammoth, Devil's Lair, Strong's, Tight Entrance, Skull, Moondyne and many others, Western Australia would be almost devoid of megafauna (Prideaux *et al.* 2000, 2004). The Nullarbor is similar; without its cave assemblages it too would appear to be megafauna empty (Prideaux *et al.* 2007b). The northeast (NE) quadrant, above the Tropic of Capricorn, is the next smallest, with nine species. Finally, the northwest (NW) quadrant is the smallest, with only four species. The last-mentioned includes *Phascolonus gigas*, *Diprotodon optatum*, *Zygomaturus trilobus* and '*Procoptodon*' *browneorum*, the latter two found as Aboriginal artefacts (Akerman 1973). These four species are the most ubiquitous of all megafauna and are found throughout the continent. Quanbun in the Kimberley has yielded *Protemnodon brehus* and *anak* and *Phascolonus gigas*, but this site is believed to be Pliocene, although it requires formal dating (Long *et al.* 2002).

The southern LEB forms a sub-region that is attached to central Australia in its northwest and in the WSE sub-region to the south. Twenty species have been identified from sites around Lake Eyre (Tirari Desert), Coopers Creek, the Diamantina/Warburton River north as far as Birdsville and Kallakoopah Creek. All these are found in the WSE sub-region, thus positioning the LEB as a northerly extension of this area with the distinct possibility of species moving between the two. Ten of the SW quadrant and eight of the NW species are found in the LEB as well as the four found in the northwest. The four NW species are widely distributed megafauna, but so too are *Protemnodon anak*, *Protemnodon brehus*, *Palorchestes azeal* and *Thylacoleo carnifex*. *Genyornis* is also found widely across southern Australia and into the centre as far as Lake Lewis, Northern Territory, with 42 eggshell sites and 69 fossil bone sites (G. Miller, pers. comm. 2005). The lack of *Genyornis* eggshell further west around Lake Mackay leaves Lake Lewis as the eastern limit of distribution of this bird in central Australia and the only late Quaternary megafauna species represented there.

Differential spacing of fauna usually reflects suitability of habitat and ecological adaptation, but even at

its most environmentally benevolent the Quaternary Australian continent probably posed challenges to long-term species distribution. Even in optimum times the size of Australia's mid-late Quaternary animal populations was probably not commensurate with the size of the continent because species were sparsely distributed outside the southeast. Modern marsupial distribution shows that 112 of 145 species live in eastern Australia, with 69 in the west (Strahan 2000). Using the above quadrant system shows most species concentrated in the southeast (131) with 67 in the northeast, 45 in the southwest, 39 in the northwest, 22 in the LEB and 30 in central desert regions, a distribution broadly reflecting that of the megafauna.

The Diprotodontids were the most ubiquitous animals, with *Diprotodon optatum* and *Zygomaturus trilobus* living from Cape York to King (40°) and Kangaroo Islands and into the LEB (Tedford & Wells 1990; Tedford *et al.* 1992; Webb 2006; Wells *et al.* 2006). *Diprotodon* appears in sites encircling the central Australian deserts and semi-arid regions (Fig. 3). *Zygomaturus* also enjoyed a wide distribution from the Kimberley to southwest Tasmania, from the LEB to Western Australia's Murchison and southwest (Wyrwoll & Dortch 1978). Unfortunately, most of these examples are undated, so while they occur in environments that are today arid, their presence may indicate wetter times and this could be the case with the remote *Diprotodon* sites of Lake Darlot and Karonie in the Western Australian Goldfields. Animals inhabiting isolated patches can begin to display morphometric variation from larger populations. *Diprotodon* distribution suggests that it may have had a behavioural and physiological capability enabling it to withstand at least semi-arid habitats. It may also have had physiological adaptations to semi-arid conditions, such as urine

concentration and a low metabolic rate similar to wombats. This could explain the widespread distribution of the giant wombat *Phascolonus gigas*, which was possibly adapted to semi-arid conditions like its smaller modern cousin the hairy-nosed wombat (*Lasiorchinus* sp.). *Diprotodon* distribution exemplifies broad adaptation to many environments and collagen isotope study of their dental enamel indicates an opportunistic browser and grazer of C₃ and C₄ plants (Gröcke 1997). Clearly, any climatic or environmental change switching between these plant groups would not have disadvantaged this animal. Other dietary evidence associated with their remains from Lake Callabonna indicates a diet of chenopods, sclerophyll shrubs, grasses and daisies (Stirling 1900; Johnson 2006). It may also have been semi-aquatic, as has been suggested for its smaller cousin *Zygomaturus trilobus*, living much of the time in or very close to rivers and lakes like a marsupial hippo (*ibid.* 2006). Its presence in the LEB, with its many late Quaternary palaeoriverine environments and the Murchison and Oakover River finds, might be explained that way. However, while Diprotodontid remains in the LEB are overwhelmingly found close to or associated with lacustrine and riverine environments, it is hard to differentiate whether they kept close to water for all the usual reasons, i.e. whether they actually needed to wallow in it or that such environments re-deposited assemblages. However, while crocodiles and hippos avoid each other, deep crocodile tooth marks of *Pallimnarchus pollens* on Diprotodontid long bones in the LEB suggest that the two shared a riverine environment and that they did not enjoy a similar arrangement.

Canonical distribution indicates that within a biological community there is a pattern which includes some very rare species, many species that are fairly abundant and just a few that are very abundant (Preston 1962). That is almost the case with the frequencies of the 32 species examined here (Table 1). The exception is the category 'very abundant', which is something that is not apparent for any species listed, although *Diprotodon* is by far the commonest, occurring in over 40% of the 230 sites examined. At the other end of the abundance scale there are 12 species (38.4%) that are found in less than 5% of sites with only 5 reaching the 40–55 kyr window.

Megafaunal population fluctuation

Interglacial maxima brought highstand sea levels and a wetter continental interior from a strong monsoon with a deep southerly incursion. In Australia, glacials were marked by oceanic transgression to a maximum low-stand of around –145 m a.s.l. coupled with extensive aridity, expanding desert and blowing dust in central Australia (Hesse 1994). Fluctuating sea levels during

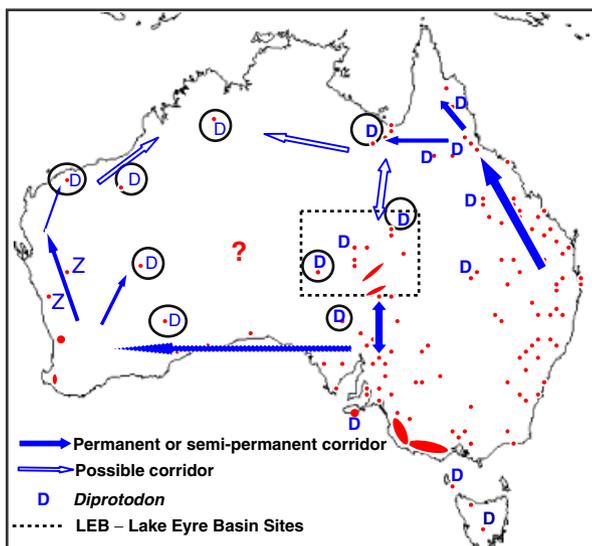


Fig. 3. Megafauna dispersal, migration corridors and *Diprotodon* encirclement of the arid centre.

the last 200 000 years exposed the continental shelf to some extent for almost 95% of that time. Antarctic ice cores indicate that the last three glacial cycles were longer with wider swings (EPICA 2004; McManus 2004). One interpretation of these findings for Australia is increasing Ice Age length, severity and continental aridity. The penultimate glaciation may also have been particularly arid and somewhat longer than the previous one. Build-up to the Last Glacial Maximum was marked by trending down but fluctuating sea levels and few pluvial episodes with increasing aridity encouraged by a weakening monsoon that moved north (English *et al.* 2001; Kershaw *et al.* 2003a, b; Pack *et al.* 2003; DeVogel *et al.* 2004). Glacials signalled extensive drying in Central Australia and megafauna depopulation for periods of variable length with the possibility of local extinctions through tethering and isolation. Intermittent amelioration of conditions might have occurred from time to time, allowing reoccupation for limited periods, but each downturn subjected animals to cumulative population reduction.

Megafauna biogeography therefore differed between glacial and non-glacial phases. It responded in different ways and to different degrees at various times in different parts of the continent, i.e. both species and parts of the continent were affected to a greater extent than others. This would have led to regional biogeographic differentials affecting some species more than others. Cumulative effects of such differentials probably forced the repositioning of animals, i.e. sorting species composition and initiating migration and redistributing and eliminating species, thus changing the wider regional population. An example would be any expansion of the western deserts during glaciations. This would have engulfed much of the west Australian coast and the Nullarbor, largely isolating the southwest and effectively separating the continent east from west for most of its width and north from south except for the east coast strip. The result would have been habitat fragmentation and contraction, niche shrinkage, demographic disjunction, restricted migration opportunities and isolation. All these were regulated by distance effects between refuges and smaller niches as well as refuges disappearing together with any resident megafauna. In some cases, critical colony size would be reached, reducing animal populations to non-viable levels with differential extinction rates and changes to species distribution and breeding patterns, thus reducing the overall continental population. Moreover, small isolated populations would suffer genetic drift and founder effect leading to expression of harmful alleles over the medium to long term.

Each arid phase would effectively move populations from inland to the coasts and onto the almost 2.5×10^6 km² of emerging continental shelf, 70% of it in the north, while almost twice that area of central Australia became arid. Animals living adjacent to this shelf would

have gradually moved onto it without really noticing the transition. On present evidence, however, few species lived in the north, although the presence of *Diprotodon* on southern offshore islands suggests these species probably took the opportunity to move onto any emergent landform. Other émigrés to the northern shelf would have been those known to have lived in the north, including *Zygomaturus*, '*Procoptodon*' *brownneorum*, *Phascolonius gigas*, *Protemnodon anak*, *Protemnodon brehus*, *Megalania prisca* and *Thylacoleo carnifex*. Other possibilities include those depicted in Aboriginal rock art. An image in Deaf Adder Gorge, Arnhem Land, depicts a quadruped with muscular hind quarters, long tongue, prominent claws and a coarse coat. It has been suggested that this is *Palorchestes* sp.: perhaps another Diprotodontid that could have lived on the shelf (Chaloupka 1993: p. 100). Chaloupka records an Arnhem Land image representing *Thylacoleo* and the short faced *Sthenurus*, but these are cautious interpretations (Murray & Chaloupka 1984). A possible artistic depiction of *Thylacoleo* has also been recorded from the north Kimberley (Akerman 1998). A large emu-like bird painted in a cave on Cape York has been interpreted as *Genyornis newtoni*; if true, this is the only evidence of this bird in the tropics (Tresize 1971). If these artistic drawings do record megafauna, however, and if the extinction threshold is 45 kyr, it suggests people were in Australia and widespread some time before that, and that the drawings have to be the oldest true art in the world. Moreover, if Palorchestids became extinct before the penultimate glaciation, as their present dating indicates, the Deaf Adder Gorge art, on its present interpretation and assuming humans were responsible for its demise, takes on a completely new significance for the arrival of humans in Australia.

Megafauna migration

The subject of megafauna palaeomigration is a difficult one. Long-distance migration is not part of extant marsupial behaviour, so there is no model with which to compare this behaviour in extinct megafauna. It is possible that Diprotodontids were herd species, and like their placental cousins could be assumed to have migratory habits. Nevertheless, animals moving from central Australia to the northern continental shelf embark on a long journey. Species distribution suggests that the vast majority were adapted to one kind of niche or another similar to modern animals. The sparse occupation of Western Australia suggests that long-distance migration was not the norm; that few were natural migrators or the environment was not conducive to long-term habitation or migratory flow. Alternatively, kangaroos must have been capable of rapid deployment in response to climatic change or environmental downturn. Knowing so little about the

behaviour of extinct species, however, hinders prediction of response and avoidance techniques of any particular species. Since long-term drought and glacial climate change are comparatively slow processes, it can be assumed that animal responses were also slow and that their response was limited until a particular food or water threshold had been reached. The only concept that is worth pursuing seems to be that of an end result. In other words, when environmental change took place, whether short-term or long-term, the result would have been displacement of animals from the affected region to a region that could sustain them. The consequence is one group of animals moving in on others, either displacing them or equilibrating to about the same number of animals dictated by the carrying capacity of the particular area and resulting in a net loss of individuals.

Desert was the most common migration barrier, with the vast western and Northern Territory deserts the biggest barriers to east–west or north–south animal movement. Sea level fluctuation and arid expansions were further factors in effect turning the Australian continent into a circular archipelago of ‘islands’ separated by large uninhabited regions that in better times would have had, or served as, migration corridors. Animal demographics would have reflected this pattern as the population fragmented with various groups sheltering in refugia that varied in size from small outliers to very large regions such as the southeast. Closure of interconnecting corridors could have caused broad demographic disjunction separating groups for long periods and producing a series of ‘metapopulations’ or small groups separated from one another in ‘patches’ (Gilpin 1987).

Corridors, patches and feeders

The concept of corridors and patches is applicable in the case of the issues raised here. Migration success depends on area and distance effects, particularly population and patch size, with different species requiring different minimum areas to support a viable population. An orderly relationship exists between patch and population size with different sized populations following a species–area relationship, where dividing an area by 10 divides the fauna by 2 (MacArthur & Wilson 1967). The arrangement and morphology of patches is also important. Increasing distance between patches reduces the chance of successful migration, and the smaller the patch the harder gene transfer is between regions which makes the group less viable. Small patch populations, therefore, are always in danger of becoming inbred, although a cluster of patches may contain more genetic variance than a single large population of the same size. Generally, however, patches have a homogeneous structure with low genetic variety be-

cause of their limited gene pools. Long-term isolation prevents natural rates of turnover, thus compounding these problems and increasing their predisposition to extinction. Small patches also have less species diversity; they host fewer animals, they have more extinctions, they are more vulnerable even to small environmental disturbances or change and they receive animals – they do not export them. Large patches cope better with environmental disturbance, resulting in more stable populations. In combination, these principles are used below together with the MacArthur and Wilson equilibrium model (1967: p. 22, fig. 8) to interpret how glacial cycles could have affected megafauna populations across the continent. Instead of oceanic isolation, as described by MacArthur and Wilson, the model is applied here to fragmented megafauna populations across Australia as spreading aridity during glaciations closed corridors and reduced and eliminated habitats in the same way that oceanic waters isolate islands.

Corridor types include short-broad, long-broad, short-narrow and long-narrow. The distribution of Australia’s megafauna suggests patches linked by such corridors that opened and closed at different times and for different lengths of time. Once opened, they provided animal transfer between patches, depending on the size of the patch at either end, and on the length and width of the linking corridor. Larger patches have more animals and wider corridors have more habitable area available for interchange, thus enhancing passage success. Short-broad corridors allow constant movement between patches under almost any environmental circumstance (Gilpin 1987). This type of corridor connects large patches usually with large feeder populations because environments that have them also support large animal populations. South-eastern Australia was probably the prime example of this form and can be envisaged as a closely knit cluster or series of large and intermediate patches joined by short, very broad, corridors extending along the coast and some distance inland from South Australia to southern Queensland.

Conversely, narrow corridors close more easily and have a more limited habitat area than wider ones, thus making transfers more difficult and less successful. These are exemplified by inland river and stream channels that draw animals along them, but are easily closed during drought and low catchment precipitation. Remote and small patches have fewer species and thus smaller populations. They are also less likely to have large animals and yield fewer migrations, suffer more extinctions, do not offer long-term safety and are not good refuges. So ‘... the probability of extinction is inversely related to the area of the patch ...’ (ibid. 1987: p. 136). Area and distance effects are directly relevant to Australian megafauna demography in the late Quaternary, where the likelihood of the population fragmenting into variably sized patches and experiencing

long-term isolation during glacial cycles may have been a direct factor in their eventual demise.

Corridor distance is important because the probability of migration along a corridor falls exponentially with distance: the longer the corridor the greater the risk and less the likelihood of successful traverse. Longer corridors close more readily than shorter ones; fewer animals successfully pass from one end to the other; gene flow becomes tenuous; and the opportunity of closure at some point along it is always greater than is the case with short corridors. However, the chances of gene exchange increase if a large feeder patch with greater numbers of animals lies at one end, in which case the traverse will be generally unidirectional from the larger to the small patch. Similarly, the narrower the corridor the more readily it closes with deteriorating conditions. Short-narrow corridors are more successful than long-narrow varieties because traverse time is less, increasing transfer success as long as corridor stability prevails. The principle of this can be seen in Fig. 4, where the abscissa or animal transfer numbers increase as patches become larger and corridors shorter and wider. Short-narrow corridors can be envisaged between populations in south and north Queensland and WSE and the LEB. They were probably longer but narrow between northeastern Queensland and the Gulf region.

Two corridor variables, width and length, combine to produce the degree of passage along them. Long narrow corridors are the most unstable because they

increase traverse time and confine lateral movement even during optimum conditions and they close more readily. Examples include the Nullarbor Plain, joining the WSE sector and the southwest, the southwest-northwest corridor, joining the SW with the NW, the Kimberley-Northern Territory link, the long north-south palaeochannels of the LEB and from Lake Eyre northwest into central Australia. The presence of *Genyornis* at Lake Lewis may demonstrate this principle possibly being at the end of the long increasingly narrowing corridor from Lake Eyre to the south (Fig. 3).

The available data suggest that dominant continental megafauna movement was east to west and south to north. Gene flow radiated largely from the well-stocked southeast. The SW and NW received these only when optimal corridor conditions prevailed, thus accounting for the same species on both sides of the Nullarbor and along the east coast. The SW was also a large enough patch to be self-sufficient during times when corridors were closed. It is likely that the primary demographic dichotomy among Australia's megafauna was the division between the southwest and southeast, each regularly functioning as independent entities for extended periods of time during glacials. The southwest group was always self-supporting because of the temperate environment and a population large enough to provide genetic rigour. The scatter of fossil sites across the Nullarbor, and the sharing of species there between the southwest and WSE, underscores the function of the Nullarbor corridor. Megafauna species in Thylacoleo

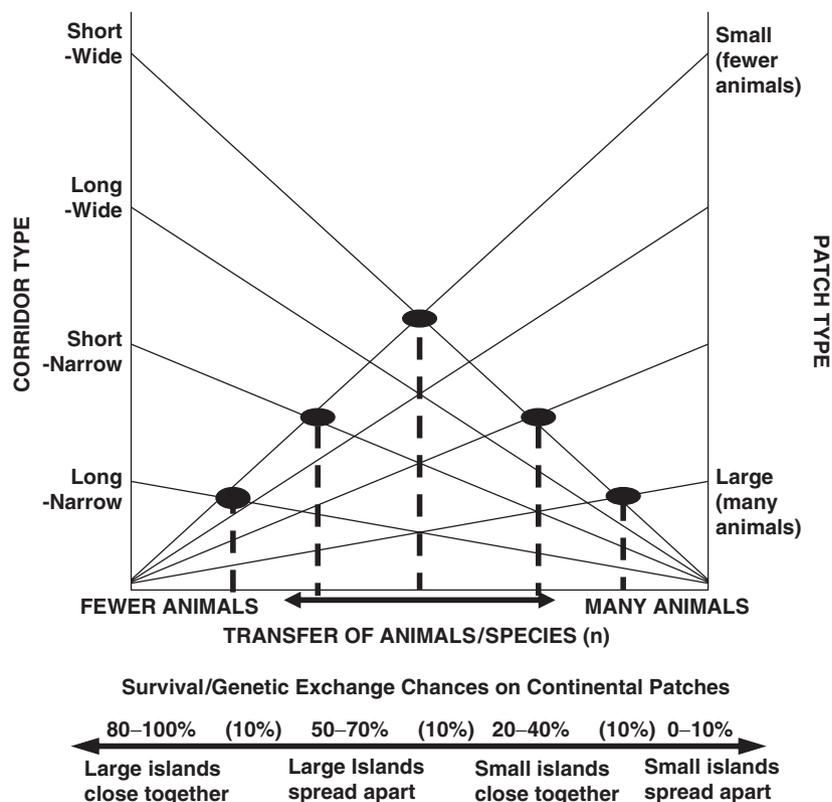


Fig. 4. Animal transfer between different size corridor and patch types showing species-area relationship (extensively changed after MacArthur & Wilson 1967).

Cave on the central Nullarbor can be found in all quadrants, *Thylacoleo* in three, including the LEB, and the rest in the WSE or both WSE and SW (Prideaux *et al.* 2007a). This strongly suggests that a corridor existed across this rather difficult landscape, perhaps opening and shutting at various times depending on environmental conditions. It also suggests that the very large WSE was a well-stocked feeder of animals moving from east to west, because no true megafauna species is unique to the southwest, as well as providing animals to the LEB to the north (see below). Moreover, it seems to support the principle that large patches (WSE) export animals (genes) and that smaller patches (SW) receive them.

The fact that the four NW species lived in all quadrants not only suggests they were adaptable but that it was difficult for other species to migrate there. There must have been a corridor at one time or another, but this connected the NW with either the Gulf or the SW. Support for the latter may come from the presence of Diprotodontids in the Murchison, Pilbara and inland Western Australia. Northward migrations could have used the Greenough, Murchison, Gascoyne, Ashburton and DeGrey Rivers as stopovers along the SW–NW corridor (Fig. 3). To go further required crossing the edge of the Great Sandy, which was devoid of such waterways, although there may have been freshwater soaks along the beaches of the region. Pollen records gathered from deep sea cores taken on the adjacent Exmouth Plateau suggest that the northwest experienced high summer rainfall (450–300 mm) at 100 kyr with marked wet periods at 100, 80 and 70 kyr and ‘... open grass-rich Eucalyptus woodland ...’ (van der Kaars & De Dekker 2002, 2003; van der Kaars *et al.* 2006: p. 888). This pattern roughly corresponds to the LEB, where the reducing megalake stages of Lake Eyre occurred at 125, 80 and 75 kyr, with 332, 216 and 74 km³ fills, respectively (Magee 1997; DeVogel *et al.* 2004). It is likely that a southerly monsoon incursion opened the SW–NW corridor to migration, although the Great Sandy region was probably always a difficult area to traverse, experiencing frequent and long-term closures, open only during interglacials. During glacial maxima, aridity probably expanded further south, presenting an even more extensive barrier for animals moving north.

Rivers were natural corridors facilitating megafauna movement, and the Cooper and Warburton/Diamantina systems of the LEB and the Willandra–Darling systems would have served this function perfectly. The long narrow LEB corridors were reliable only during regular catchment flow and local precipitation events during southerly monsoon incursions. Animals may have moved into the LEB from the north, but the similarity of species in both the WSE and LEB and the limited species association between the LEB and the NE suggests that the main feeder was probably from

the south. LEB channel flow and lake fillings probably lured animals into the LEB, but there had to be a corridor. They were then confined by surrounding semi-arid country only to become stranded and tethered to dwindling water holes when the systems dried, thus precipitating episodes of local extinction. This is an important difference between the SW and LEB populations. It is likely that the latter population periodically disappeared during arid phases only to repopulate the region with the relief of aridity made possible through the close proximity of better environments and a well-stocked WSE that could provide the animals. The Willandra–Darling river systems were extensions of much more productive areas in the Riverina, and retreat there was a comparatively short journey. Conversely, even though experiencing megalake fillings, Lake Mackay with its limited catchment is likely not to have had a corridor leading to it, thus megafauna did not reach or live there. Extensive survey of late Quaternary sediments around this lake has yielded no evidence of megafauna.

The southeast supplied species not only to the west but also to the northeast, with an extension to the Gulf region, although there were fewer animals because of increasing source or feeder distance and the possibility of increasingly smaller intervening patch populations. Megafauna variety is less than might be expected in the lush tropical environments of the NE and far less than that of the SE, which reflects the pattern of the SW in relation to the NW. It is likely, however, that the corridor linking the SE to the NE was more reliable than the SW–NW corridor. Reduced numbers of megafauna species in northern parts of the continent may, however, reflect a fauna with limited adaptation to rain-forest and tropical/sub-equatorial environments. This may also explain the general paucity of megafauna species in Papua New Guinea compared to southern regions of Sahul.

Unimpeded genetic mixing in the southeast maintained genetic vigour, enabling it to better maintain its populations and produce migrant animals, whereas in many other areas around the continent fitness must have suffered to varying degrees in accordance with environmental downturns, changes in species composition and overall numbers in small populations and extensive periods of isolation through corridor closure. However, it is possible that the entire megafauna population was under increasing stress from slow continental drying and the Quaternary glacials.

Increasing aridity in the late Quaternary

Habitat restoration following glacial aridity was essential for populations if they were to recover to pre-arid levels. To accomplish this meant a complete restoration to

preglacial environmental conditions. A growing body of evidence now suggests that such recovery could have been progressively difficult during the mid-late Quaternary due to increasing continental aridity (Callen & Nanson 1992; Nanson *et al.* 1992, 1993, 1998; Chen *et al.* 1993; Magee *et al.* 1995; Magee 1997; Magee & Miller 1998; Bowler *et al.* 1998; Jablonski & Whitfort 1999; Johnson *et al.* 1999; Wang *et al.* 1999; Kershaw & Whitlock 2000; Moss & Kershaw 2000; Bowler *et al.* 2001; English *et al.* 2001; Kershaw *et al.* 2003a, b; Pack *et al.* 2003; DeVogel 2004). This trend is summed up by Kershaw and co-workers '... all Australian records ... show some trend towards drier climatic conditions superimposed on glacial cyclicality through the late Quaternary' (p. 1277). They suggest that 'superimposed on this ... is a trend towards drier and/or more variable climates within the last 350 000 years' (p. 1271). Other research has concluded there is a series of '... Australian records that indicate increased continental aridity in the Late Quaternary' (Pack *et al.* 2003: p. 629). That evidence is a change from C₃ woodland to C₄ grassland in northwestern Australia indicating reduction in total rainfall and increased seasonal precipitation suggesting a drying climatic regime. Lake Lewis lies much further to the southeast, yet within the southern limit of monsoon incursion work there has shown widespread dune formation after the last interglacial stage (English *et al.* 2001). This reflects an earlier proposition that dune building in the Simpson Desert increased during the late Quaternary beginning around 300 kyr (Wasson 1989). Other evidence reduced catchment precipitation and channel flow to the LEB during the last interglacial leading to increasingly reduced lake fillings and fluvial activity (DeVogel *et al.* 2004: table 1). Work at Lakes Amadeus and Woods in Central Australia underwent a reducing late Quaternary rainfall pattern, particularly within the monsoonal catchment (Chen *et al.* 1993; Bowler *et al.* 2001). Evidence of decreasing monsoonal activity in the late Quaternary comes from Magela Creek in the Northern Territory, where increasing sediment deposition suggests a drying climate more than a wetter one which would have precipitated flushing (Nanson *et al.* 1993). The aeolian dust record underpins the picture of increasing aridity across eastern Australia with sustained increases in particle levels from a drier environment beginning around 350 kyr (Hesse 1994).

In the northeast, vegetation changes included reduced rainforest species and increased open woodland, eucalypt and grass species (Kershaw *et al.* 2003a). Long periods of aridity during Marine Isotope Stage 6 with changes to fodder regimes could have put non-arid adapted species under increasing stress even on the east coast. Palaeontological evidence from work in central eastern Queensland shows replacement of rainforest adapted by arid-adapted animal species around 180 kyr (Hocknull 2005; Hocknull *et al.* 2007). Palaeoenvironmental changes, including retraction of vine thicket and increasing grasses not associated with anthropogenic activity, have

been observed in southeastern Queensland accompanied by reduction in megafauna species variety (Price & Sobbe 2005; Price 2006; Price & Webb 2006). Twenty-two (82%) of the 27 herbivorous extinct megafauna species chosen here were browsers, although 6 (27%) probably became extinct prior to the penultimate glacial maximum (Table 1). The impact of such climatic change, albeit probably gradual and variable in many regions, must have taken a toll on browsers in the long term.

Different species required different minimum areas for support depending on their size, behavioural patterns and adaptive qualities. Large browsers living in small patches, for example, would not be supported in the medium term. Patch fragmentation could then follow with vertical and lateral niche shrinkage and reduction in niche variety. This would compound problems of population maintenance, particularly among small populations; larger areas were less susceptible to this than smaller ones. One effect of fragmentation is that while animal populations can exist, the resulting fragments do not necessarily represent places where future population recovery can take place when conditions change. Indeed, they are more likely to be traps leading to localized extinction, particularly during extreme, long-term climatic events. Smaller animals were less vulnerable to such change and would survive longer than larger animals in a given patch size and their faster reproduction rates aided them in maintaining population numbers. Broadly adapted, generalist animals had the best chance of survival during these times, but larger, specialist animals with longer life spans were less likely to cope.

One argument against environmental stress as a cause of megafaunal extinctions is the persistence of these animals through previous glacial events, but not all species did persist (see above). With mounting evidence for increased environmental stress during the last three glacial episodes, the possibility exists in some parts of the continent for cumulative stressing of animals, perhaps affecting some species more than others. This process is likely to have led to species withdrawal from some areas which, from the point of view of an isolated assemblage, could look like local extinction. Moreover, while a particular species may have survived, its demography possibly changed as its overall population size and distribution dwindled and became confined.

Megafaunal population depression

Late Quaternary palaeoenvironmental change cannot be ignored in any future discussion of megafaunal extinction. The data suggest that late Quaternary megafaunal biogeography is likely to have been detrimentally changed with each glaciation, increasing biogeographic stresses among various species living in different regions of the continent. Increasing aridity would also mean large-scale shrinkage of benign environments and

replacement with harsher ones demanding greater adaptive qualities. Habitable areas increasingly shifted towards Australia's periphery, particularly to the south and east coasts, as well as to the exposed continental shelf when exposed. In the case of small refuge areas, animals faced the difficulty of 'turnover'. Originally conceived as an explanation for balancing oceanic island populations, 'turnover' is just as useful for describing isolated continental patch populations suffering habitat contraction (MacArthur & Wilson 1967). It occurs where a given carrying capacity can support only a certain number of animals and resident groups suffer or become reduced when migrating animals move in. A natural balance occurs when the burgeoning effects of population increase are circumvented by population reduction through extinction until species equilibrium is achieved maintaining the original population size in any given area. So, while animals retreating from deteriorating conditions looked for refuges, however fast that occurred, refuges would have supported only a given number of animals, and glacial episodes would naturally have reduced these further in marginal regions. Any negative climatic fluctuation changed refuge environments so that some always teetered on the edge of oblivion. In turn, the balance is determined by the marginality of the particular area: those with plenty of fodder/water supported more animals than those with less, but the refuge area could not increase its capacity even by 10% until more favourable environmental shifts occurred at glacial termination when habitat expansion was possible. Therefore, there was a very small limit on the number of animals and species that could be 'saved' by migration.

Spreading aridity closed corridors, long-narrow ones first then short-narrow types. This would have fragmented habitats and trapped and isolated many groups. Long-wide corridors shrank to long-narrow ones, thus reducing the ability of animals to move along them. Conscious movement is not considered here, but instead an extremely slow shift of groups within the retreating hem of comparative abundance. Inland populations would move towards the edge, occupying continental shelf and crossing to now-bridged offshore islands. New habitats opened as those of central Australia closed. The possibility for population replacement over time only occurred in places where it was large enough to allow recovery and where habitat supported the process. One consequence of being a small isolated population is viability, with different species requiring different minimum numbers and areas to maintain themselves (Shaffer 1981, 1987, 1990; Shaffer & Samson 1985). Minimum viable populations differ between species, but all are subject to uncertainty through human-induced systemic pressures and/or stochastic events which include demographic, environmental, natural catastrophes and genetic stochasticity, such as the accumulation of harmful alleles or 'genetic

load' (Gilpin 1987). The first three may have occurred with the onset of glacial conditions, but the latter is an additional factor of importance. The genetic load of a large population is spread thinly and expressed rarely, but in small or reducing populations it can lead to inbreeding, depression and infant mortality through limited breeding pairs. Over time, a range of dysfunctional developments or adverse biological or morphological traits emerges as rare or harmful recessive alleles become homozygous. Founder effect compounds the consequences of isolation, with small populations having a reduced expression of the parent gene pool. Isolation causes genetic drift such that an unrepresentative gene pool moves even farther from the original stock. Small populations are also subject to a critical reproductive rate dictated by reduced numbers of reproductive females. The loss of females compounds the problem; eventually a level of reproduction is reached that is below minimum replacement numbers and the group is no longer viable. This process is underpinned when reproduction rates are long, as for the largest megafauna. Rapid population recovery in short-term amelioration events was difficult for long-lived, large species that produced only one offspring and had a long gestation period (Holliday 2005). Therefore, megafaunal population recovery is likely to have been a long-term process dictated by enough habitat restoration following glacial events to support that recovery. Population collapse is prevented only by animals of that particular species, but isolation would have prevented that from taking place. The lack of new arrivals reduces species turnover to zero and net losses are greater than replacements, resulting in non-equilibrium (Brown 1971, 1978). Australia's megafaunal species might have been bigger given the size of the continent, but the above scenario may have imposed limits on range and species variety. On the wider continent, the relationship between the number of species and the area they occupied must have been significantly affected during glacial times when many regions were devoid of suitable habitats for most species. Under these circumstances it has to be assumed that species-area ratios increased, with a reduction in food and water supplies across most of the continent resulting in fewer animals and a greatly reduced continental population. The broader environment would also have confined larger species to particular areas, suggesting that populations were never large and had limited distribution. Facing a world of increasing and rapid environmental/climatic change during late Quaternary would have brought all the above factors into play, impacting large species first.

A palaeoecological factor

The Wallaroo (*Macropus robustus*) and red kangaroo (*Macropus rufus*) are the only extant, large and widely

distributed marsupials in Australia. Smaller species, such as the Bilby (*Macrotis lagotis*), common Brushtail Possum (*Trichosurus vulpecular*) and Western Quoll (*Dasyurus geoffroii*), were widespread, but have severely contracted since European colonization. Five others, the Western Barred Bandicoot (*Perameles bougainville*), Rufous Hare-wallaby (*Lagorchestes hirsutus*), Burrowing Bettong (*Bettongia lesueur*), Greater Stick-nest Rat (*Leporillus conditor*) and Shark Bay Mouse (*Pseudomys fieldi*), now live only as relic populations on small islands off the western Australian coast. All had extensive ranges throughout inland and central Australia at European arrival (Strahan 2000). Reasons for the drastic contractions as well as the total extinction of another 17 species since 1788 include the introduction of cats, foxes, rats, rabbits, domestic livestock and the cessation of Aboriginal mosaic burning, among other possibilities (Strahan 2000; Flannery & Schouten 2001) (Table 2). None can be posited as an absolute or solitary extinction cause for any species, few are substantiated to any degree and none apply to all disappearances. At least half the species were already rare, had extremely limited ranges or were delicately balanced. Many were animals whose demographic circumstances made them vulnerable to any change in their habitat and are unlikely to have survived even minor change in their life patterns (Shaffer 1987). Furthermore, it cannot be confirmed, or be rejected, that any of these species is likely to have become extinct with or without colonization by non-Aboriginal people and their domestic animals.

Modern examples cannot be unique. Certain megafauna species must have been similarly placed with restricted or confined habitats and some species/populations precariously poised. Such conditions are part of the natural pattern among animal populations. Like our modern fauna, some megafauna were rare, some were common and they must have had a complex relationship with the environment, including species

composition in any given population. Any environmental change either favoured or disfavoured them to a greater or lesser degree and affected some species more than others. The part this cycle played in the maintenance of some ecotones and vice versa, overlaid with the background of changing climate and the possibility of increasing aridity, made for a tapestry of contrasting and complex factors the detail of which is now lost. Nevertheless, basic relationships drawn from extant species and standard biogeographic and ecological principles are needed if the extinction problem is to be understood.

The long evolutionary history of the megafauna must have been intimately tied to their symbiotic relationship with plant communities and the maintenance of favourable niches. Seed dispersal through frugivorous browsing on medium-sized shrubs must have been one of these. Dromonorthids, the larger kangaroos (Sthenurines, Simosthenurines, Protomnodons and Procoptodonts) and the Diprotodontids were among those that probably helped maintain certain ecosystems, such as vine thickets, which included numerous other plant species bearing edible fruits, berries and seeds (Murray & Vickers-Rich 2004). If Australia experienced increased aridity during the last 300 000–400 000 years it could have become a step-wise forcing process, together with an elevated fire frequency, for change to Australia's plant regimes favouring fire-adapted plants and grasses at the expense of fire-sensitive communities that withdrew to remnant patches and fire-shadows. Such changes would have had a particularly negative impact on browsers. Their populations would have contracted to isolated pockets of plant communities that they were reliant upon. Numbers would slowly be reduced to unsustainable proportions and the part they once played in seed dispersal would be reduced, forming a negative feedback and further reducing the spread of already contracting plant species. Over thousands of years, such processes must have affected megafauna

Table 2 Marsupial extinctions on the Australian mainland since 1788.

Common name (n = 17)	Scientific name	Extinction time	Location	Range
Darling Downs Hopping-mouse	<i>Notomys mordax</i>	1840's	SE inland Qld	Extremely limited
Big-eared Hopping Mouse	<i>Notomys macrotis</i>	1843	SW Aust	Extremely limited
Great Hopping-mouse	<i>Notomys</i> sp.	?1900	Flinders SA	Extremely limited
Basalt Plains Mouse	<i>Pseudomys</i> sp.	?1900	SE Vic	Extremely limited
Toolache Wallaby	<i>Macropus greyi</i>	1939	SE SA & SW, Vic.	Extremely limited
Desert Rat-kangaroo	<i>Caloprymnus campestris</i>	1935	CA	Very limited
Broad-faced Potoroo	<i>Potorous platyops</i>	1875	SW Aust	Three limited patches
Lesser Bilby	<i>Macrotis leucura</i>	1950's	CA	Two broad patches
White-footed Rabbit Rat	<i>Conilurus albipes</i>	1845	SE Aust (Q to SA)	Broad
Gould's Mouse	<i>Pseudomys gouldii</i>	1857	Inland Aust	Broad
Eastern Hare-wallaby	<i>Lagorchestes leporoides</i>	1889	SE Inland Aust	Broad
Short-tailed Hopping-mouse	<i>Notomys amplus</i>	1896	CA	Extensive
Pig-footed Bandicoot	<i>Chaeropus ecaudatus</i>	1901	Inland Aust	Extensive
Long-tailed Hopping-mouse	<i>Notomys longicaudatus</i>	1901	Inland Aust	Extensive
Lesser Stick-nest Rat	<i>Leporillus apicalis</i>	1933	Inland Aust	Extensive

population composition and dispersal across the continent, resulting in contraction of species and population reduction while grazing macropods flourished. Modern Australian floral distributions have prompted some to suggest that eucalypt domination fragmented these communities, indicating a driver of increased aridity (Murray & Vickers-Rich 2004: pp. 300–301). Moreover, the loss of habitat and reduction in species numbers and variety could have led to a certain ‘ecological naïveté’ (Quammen 1997: p. 206; Wroe & Field 2006). This term has been applied to island species that, being isolated, have adapted to ecological circumstances in which predation and competition are minimal. With the staggered loss of competitive groups of megafauna over time, some niches may have been left with animals habituated to the lack of competition and even with the general lack of predation by Australia’s few carnivore species. The size of carnivore guilds must also have been tied to any downturn in herbivore population size. Such trends would have left pockets of animals unable to respond when eventually confronted by the arrival of humans.

Megafauna at the extinction event

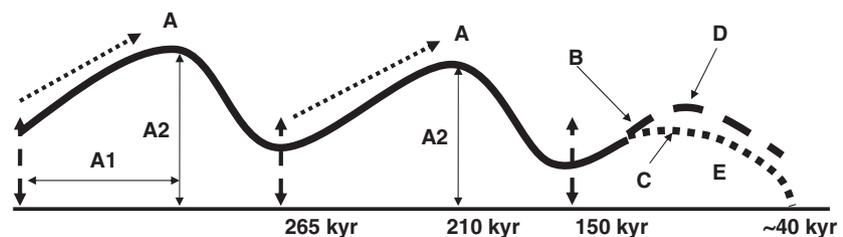
The question of extinction timing is not an essential part of this article, although the above comments suggest that the event was staggered. It is vital to extinction arguments, however, that accurate terminal ages for all extinct species are determined. A series of previously published dates has been used to show that only 16 of the 32 species in this study reached an extinction window of 55–40 kyr, although this number is reduced to 7 if the 50–45 kyr window is used (Roberts *et al.* 2001; Wroe & Field 2006). Some of these dates are also subject to errors putting them before or beyond that

window. There are eight other species without minimum dates. Three species seem to have become extinct during the last interglacial and early in the last glacial, while seven disappeared before the penultimate glacial maximum. Overall, however, it is suggested that the cumulative effect of gradual climatic change over several hundred thousand years had a variable impact on the 32 species included here, resulting in their gradual reduction and the demise of some species prior to the main extinction event (Fig. 5). It is therefore suggested that the final extinction consisted of, at most, the 16 species noted above over 15 000–20 000 years living in restricted areas of the continent. The animals reaching the window are generally the largest of the megafauna and those most widespread, and, therefore, probably those possessing the broadest adaptive qualities. With one species becoming extinct every thousand years, these results point to a less than ‘blitzkrieg’ event.

A human factor

Archaeological evidence for the arrival of humans in Australia is poised between 50 and 60 kyr (Roberts *et al.* 1990, 1994, 1998). Using more tenuous evidence, it has been suggested that people could have arrived during the penultimate glaciation around 150 kyr (Webb 2006). The main criticism of this claim is that no ‘solid’ supporting evidence of a human presence (skeletal or implement) has been found, although many parts of the continent have yet to be thoroughly surveyed archaeologically. I now use the above argument about the lack of evidence to suggest that megafauna did not live in these places.

Megafauna distribution during the late Quaternary seems to have been poised precariously. Present evidence shows that the bulk of this fauna did not live on the front line of human landings in the north and



A = Megafauna population peaks and troughs during the mid-late Quaternary glacial cycles showing increasingly slow recovery (dotted arrow and A1 distance), and inability to reach previous peaks (thin vertical arrow A2) and steady decrease in species variety and overall population size at glacial peaks (hatched arrows).

B = Attempted population recovery after penultimate glaciation.

C = Population ceases normal recovery trajectory.

D = Time at which population would normally begin to decrease at onset of last glaciation.

E = Extinction spiral caused by:

- glacial conditions and increasing aridity shrinking rangelands;
- minor anthropogenic hunting and burning combine to impact on relict fragmented and dispersed populations;
- low reproduction rates among large species prevent replacement frequency required to support ongoing population.

Fig. 5. Mid-late Quaternary megafauna population trend.

northwest, but was tucked away at the farthest point from them. Nevertheless, any anthropogenic interference with a population that was delicately poised in most parts of the continent must have had its consequences, particularly for a group whose most successful species (the very large varieties) were vulnerable in terms of their likely slow reproductive capabilities. The arrival of humans on a continent of increasing aridity and the development of landscape firing techniques would have compounded climatic trends and their environmental consequences, such as boosting the continued spread of grasses at the expense of browsing vegetation favoured by most megafauna species.

It is also worth considering that humans probably developed mosaic burning in Australia. It has been pointed out elsewhere that the use of this technique in islands in southeast Asia would not have been particularly beneficial; moreover, it would have damaged tropical rainforest habitats (Webb 2006). Although humans lived in Indonesia for almost two million years there is no evidence of them using fire on the landscape. Such change is not instantaneous, however, so human entry into Australia, particularly if it began during the last interglacial, may have been environmentally silent in terms of landscape alteration until after the development of widespread and repetitive anthropogenic burning at a greater frequency than naturally ignitions, which due to a drier climate may have been increasing in the late Quaternary. The impact from initial human/megafauna contact would therefore have been from minimal hunting, which, given the small size of the first migrations, must have been negligible with the slow trickle of arrivals. It is also worth remembering that in southeast Asia, as the jump-off point for people coming to Australia, there is no evidence of a human impact on larger animals there. Any impact in Australia would have taken place first among the sparse animal populations of the north. The low frequency and restricted dispersal of many species suggested by this study then made them vulnerable through the taking of single animals, particularly females. Even restricted burning of particular landscapes when it began may have been severe on delicately balanced niches, the species occupying them, and those with restricted dispersal. Any impact varied depending on glacial or interglacial conditions affecting patch size and corridor presence, as described above. Given the demographic patterns for megafauna suggested here, even very minimal impact occurring over 50–120 kyr, combined with a developing firing regime, could have provided the final mechanism for extinction of the few remaining and naturally dwindling megafauna species.

Discussion

Present data suggest that late Quaternary Australian megafauna species were limited to 32. They were spar-

sely distributed over two-thirds of the continent, largely concentrated in the southeast, and most species had a limited range. A large section of central and western Australia had few, if any, animals. Species common to the LEB, southwestern Australia, the Nullarbor and the northwest strongly suggest that a few animals were more widespread than others. They were probably migratory and semi-arid adapted, while the majority of others were confined to more temperate and well-watered environments. The former were the best survivors, primarily the Diprotodontids. Their common occurrence in almost all parts of the continent, together with a couple of other species, is unlikely to be coincidence, but rather a demonstration of this adaptive strength. Their size, however, meant a reproductive strategy not conducive to maintaining the population once it began to dwindle or became fragmented.

The southwestern population was confined to a comparatively small region and one isolated during glacial maxima, although animals must have moved across a Nullarbor corridor during less arid times. The few species in the northwest poses a conundrum. Another is the apparent lack of any megafauna in central Australia with *Diprotodon* and *Genyornis* living only at the periphery. It is hard to accept that only four species lived in the northwest, but, besides taphonomic reasons, the lack of evidence might suggest that many were not adapted to, or unable to populate, this region for one reason or another. Alternatively, a suitable migratory corridor into this area may not have existed for most of the time. Moreover, if central Australia totally lacked megafauna, their ability to move to the northwest was governed either by migration up the west coast, which entailed crossing the Great Sandy Desert or moving across the north covering long distances from small feeder patches.

There is enough evidence of a drying trend in mid–late Quaternary Australia to prompt further research to refine our understanding of the strength of this phenomenon and the part it may have played in the slow demise of the megafauna in the late Quaternary. It has been suggested here that the possibility of cumulative changes in climate leading to increased aridity and expansion of arid environments, probably occurring over several glacial events, imposed environmental pressures which reduced the megafauna population over the long term. It is also proposed that this initiated migration and removal of megafauna from small patches in central parts of the continent to isolated patches on peripheral coasts and the exposed continental shelves. Moreover, the impact on trophic levels, vegetational changes and species variety brought about local extinctions, regional species withdrawal or population reduction in many parts of the continent. The lack of evidence for megafauna in the west and centre of the continent shows the magnified impact of these processes in arid and semi-arid regions, although some

areas may never have supported these animals during the last half of the Quaternary.

Conclusions

The late Quaternary saw an increased reduction in overall population size and variety of the Australian megafauna. Evidence is mounting that this was due to a commensurate increase in aridity and an expansion of arid environments due to climate change. Species variety varied across the continent, with limited numbers in most areas; only the southeast had the representative 32 species included here. Species variety was extremely limited in the northwest of the continent and it is possible that areas of central Australia were never occupied in the later Quaternary. Climatic/environmental downturn probably leading into and taking place during the late Quaternary predisposed the megafauna to a slow but irrevocable demise as aridity increased in various regions. This left a few species, some delicately balanced, in marginal areas on the continental periphery at the time of the first human arrivals. The less-populated areas were the first to succumb to this process. The slow colonization of the continent and development of firing techniques then brought about anthropogenic changes that finally saw the demise of the last remaining species in tropical and subtropical areas that had always had comparatively few species. The remaining fauna then underwent a staggered extinction process that took place in a number of isolates in areas of southeastern Australia where the population and species variety had always been greatest. Without an extensive dating programme of individual megafauna species in collections and field assemblages, however, many of the above arguments will remain as propositions only.

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