

# Megafaunal extinction in the late Quaternary and the global overkill hypothesis

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The global blitzkrieg hypothesis explains differential rates of megafaunal extinction between the world's landmasses in the late Quaternary based on a proposed leap in predation efficiency enjoyed by colonising societies. It is characterised by appealing simplicity. Selective over hunting, facilitated by naiveté to human predation, produced rapid mass extinctions of large animals wherever subsistence societies colonised new landmasses. Taken at face value the circumstantial case for blitzkrieg is compelling and despite a paucity of direct evidence it has gained considerable support. Our review of the model suggests that it overlooks much contradictory data and rests on simplistic interpretations of complex biogeographical and anthropological phenomena. These interpretations and assumptions do not account for major differences between the biotas, ecologies and human cultures of the landmasses involved. The assertion that responses of remote island species to human predation provide realistic models for those of continental taxa is poorly founded, exaggerating the likely predation efficiency of humans colonising continents. An absence of terrestrial predators over evolutionarily significant periods, together with restricted ranges and small populations, renders island faunas uniquely vulnerable to invaders. The argument, that climate cannot explain these phenomena because previous Glacial Maxima did not cause comparable extinctions, presupposes that their local effects were at least as severe as those of the Last Glacial Maximum. This has yet to be demonstrated and at most it would indirectly support a role for anthropogenic influence, not overkill *per se*. Overlooked or underplayed are the influences of translocated and other invading species. Similarly, differences in the origins, technologies and traditions of colonising human societies are rarely considered. These factors strongly impact on the predation efficiency, density and range of human populations, critically affecting the outcomes of predator-prey modelling. When a fuller constellation of influences and constraints is considered it is reasonable to posit that rapid mass extinction through selective human predation may largely describe megafaunal extinctions on remote islands, but the argument is not convincing for continents. This is especially so regarding Australia. Because even the largest Australian species were prey to endemic carnivores, their responses to human predation would not have been comparable to those of oceanic island species. No kill-sites or specialized big-game hunting/butchering tools are known and, on the basis of ethnographic and archaeological data, it is probable that predation efficiency, population density and range of the first Australians were insufficient to effect rapid mass extinction. Chronologies of human arrival and the disappearance of megafauna remain poor, but the most recent estimates for human-megafaunal coexistence in Australia range from 10,000 to 43,000 years. Although human predation may have been a contributing factor in megafaunal extinctions, rapid overkill is unlikely to describe the actual mechanism in most instances. The role of human predation and its significance relative to competing factors, human and otherwise, varied considerably between landmasses, as did the speeds with which extinctions occurred. Blitzkrieg and other mono-factorial models are heuristically valuable devices, but a growing body of evidence suggests that extinction can rarely, if ever, be attributed to a single cause.

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THE PLEISTOCENE world was dominated by conspicuous, mostly mammalian giants, collectively referred to as megafauna. Over the last 100,000 years or so, waves of extinction have squeezed much of this spectacular fauna into oblivion. Shedding light on the causes of these extinctions has occupied scientists since the early nineteenth century. Two agents have figured prominently; humans and climate. A third alternative, disease, has also gained some support (Edwards 1967, MacPhee & Marx 1997). However, the case for none has gained clear ascendancy (Grayson 1984), until now. In recent years a succession of technical and popular articles has strongly implicated humans as the driving force behind the disappearance of the megafauna (Miller *et al.* 1999, Holdaway & Jacomb 2000, Alroy 2001, Roberts *et al.* 2001). Various models of human causation have been forwarded. These include indirect means, such as habitat disturbance, the translocation of other exotic species and human-induced trophic cascades. However, one model has gained particularly widespread and public attention, 'blitzkrieg'.

First advanced under the name of 'overkill' 30 years ago, blitzkrieg has become a hypothesis aspiring to global reach (Martin 1963, 1984; Mosimann & Martin 1975). It is characterised by appealing simplicity and a compelling circumstantial case has been erected around five central observations:

- (i) rates of megafaunal extinction have been much higher on landmasses only colonised by hunter-gatherers in the last 60,000 years or so, than in Africa, where *Homo* evolved;
- (ii) remote island species, not previously exposed to humans, are pathetically vulnerable to human predation;
- (iii) ethnographic data and theoretical modelling suggest that hunter-gatherers preferentially select large prey;

(iv) late Quaternary extinctions took a significantly higher toll on large animals than on small; and

(v) climate fluctuated widely throughout the late Quaternary without producing comparable mass extinctions of megafauna - hence climate change can be eliminated from the short-list of alternative causes.

The resultant model explains the global pattern of late Quaternary extinction as follows - because they were unable to incrementally develop human-specific anti-predator responses, as African taxa presumably had, megafauna elsewhere were rapidly and selectively hunted to extinction wherever colonising hunter-gatherers made footfall. It has been applied to North America, South America, Australia, Madagascar, New Zealand and many smaller islands. At face value the overkill hypothesis appears consistent with the evidence as presented and some treat it as fact (e.g. Alroy 1999). The thesis revolves around a proposed leap in predation efficiency enjoyed by colonising humans. This increased efficiency was not strictly the product of technological advancement, but a function of naiveté to human predation among new prey species.

The issues here are important. Interpretations of megafaunal extinction have been manipulated by politicians and special-interest groups. It has been argued that because it is now 'known' that Australian Aborigines rapidly wiped out the megafauna, pastoralists are simply applying replacement therapy by stocking hard-hoofed cattle. Others have used this 'fact' to discredit Aborigines as environmental custodians (Barnett 1998). At another level, the 're-introduction' of exotic Komodo dragons to Australia (Flannery 1994) and elephants to North America (Martin 2000) has been advocated. Moreover, a sound understanding of extinctions, past and ongoing, is of obvious importance with respect to the construction and

implementation of conservation policies and while the blitzkrieg hypothesis has certainly been a useful heuristic tool, it continues to generate spirited debate (Graham & Lundelius 1984, Guthrie 1984, Diamond 1992; but see Diamond 1989, 2001; Meltzer 1995, Beck 1996, Flannery 2001, Grayson 2001, Grayson & Meltzer 2003, Wroe & Field 2001a, Brook & Bowman 2002, Johnson 2002, Wroe *et al.* 2002).

Among skeptics one obstacle in particular has fuelled reservation: a near complete absence of direct evidence. On only one of the three continents allegedly subject to blitzkrieg, North America, is there undisputed evidence of megafaunal kill-sites (as opposed to butchery-sites that might only indicate scavenging). In North America such evidence includes only two species - the woolly mammoth, *Mammuthus columbi* and the American mastodon, *Mammot americanum* (Grayson & Meltzer 2002, 2003). In response it has been argued that because blitzkrieg was quick, few kill-sites would be preserved in the fossil record (Martin 1984). This reasoning is logical, but whether it can account for the observed paucity of evidence remains debatable (Grayson & Meltzer 2003). Certainly it fails to predict differential preservation of taxa in kill contexts. In North America, the most abundant late Pleistocene fossil taxon is *Equus*, yet it is not represented in a single confirmed kill-site, whereas *Mammuthus* is represented in thirteen (Grayson 2001). Notwithstanding the possibility that one locality may be a horse kill-site (Kooyman *et al.* 2001), this differential is difficult to explain if we are to accept over-hunting as the sole cause of both extinctions. Either way, a lack of kill-sites is not evidence for rapid overkill. Consequently, blitzkrieg is commonly presented as a negative argument. Having established that humans were often at the scene, the argument rests on demonstrating that no other mechanisms can explain differences in megafaunal extinction rates between Africa and elsewhere.

In this paper we investigate the validity of conclusions and assumptions used to support the global blitzkrieg hypothesis, as well as the role of other influences that might explain the observed pattern of extinctions. Specific questions we will address include:

- (i) whether the behaviour of remote oceanic island species in response to human colonisation provides a reasonable basis for inferring the anti-predator responses of extinct continental taxa;
- (ii) to what extent might area-dependent variables explain the observed differences in extinction rates;
- (iii) were the impacts of past global climatic phenomena uniformly distributed and can we assume that for each landmass, the Last Glacial Maximum (LGM) was not the most extreme;
- (iv) what were the impacts of other exotic species; and
- (v) to what degree are differences in origins, tradition, technology and the availability of other foods, likely to have influenced the impact of colonising hunter-gatherers?

The case for global blitzkrieg is weakest with respect to Australia (Martin 1984) and we conclude with a review of the Australian evidence, but first we examine what is meant by the terms 'megafauna' and 'blitzkrieg'.

As historically applied in this debate, megafaunal species are those with an average body-mass that exceeds 44 kg (Martin 1984). However, this is an arbitrary figure and distinctions can strongly influence results and perceptions. In Australia, many species less than 44 kg are commonly treated as megafauna. In New Zealand the majority were smaller still, although all taxa exceeding around 10 kg went extinct (Anderson 1997). Alternatively, if we use a more exclusive definition of >1000 kg, great differences between constituent continents of the Old World are evident with the distinction between Africa and Europe as great as that between Africa and the New World or Australia. All inhabited landmasses other than Africa and Asia lost all taxa >1000 kg. Considering only species of 10-100 kg, South America stands together with Eurasia and Africa in suffering relatively minor late Pleistocene extinctions (<15% of species). North America and Australia document extinctions in this range

exceeding 50% (Owen-Smith 1999). Using the 'standard' definition typical of the megafauna extinction debate, severity can be shown in different ways. In Australia, one genus containing megafauna has survived, but in North America 12 remain (Martin 1984). On many islands all megafauna, by any of these criteria, were lost. Although there is clearly correlation, it is also significant that gestation period or reproductive rate, not body mass, were the critical factors determining the likelihood of extinction among late Pleistocene mammals (Kiltie 1984, Johnson 2002).

The term 'blitzkrieg' has been widely misinterpreted and misrepresented. As defined by its original author the overkill hypothesis describes a process whereby megafauna that have not previously encountered humans, are rapidly and selectively hunted to extinction immediately following first contact (Martin 1963, 1984). Extinction incorporating other human-related mechanisms, no matter how rapid, such as habitat disturbance, or translocations, is not blitzkrieg. Nor is extinction solely through human predation over long periods. In fact, other anthropogenic influences, as well as climate are explicitly excluded from the blitzkrieg model. Thus, Tim Flannery, the concept's principal advocate in Australia, treats habitat modification as a necessary consequence of blitzkrieg, not a contributing factor, i.e. following the extinction of megafauna the ensuing riotous overgrowth of vegetation had to be controlled by fire-stick farming (Flannery 1994). Similarly, evidence of increased charcoal levels have been interpreted as a consequence of predation driven extinction in North America (Kerr 2003). Unfortunately, blitzkrieg has often been confused with rapid anthropogenic extinction by any means (e.g. Potts & Behrensmeyer 1992, Alroy 1999). This has produced confusion, with rapid extinctions that involved human influences other than direct predation being misidentified as blitzkrieg and then invoked as support for the global overkill model. The flipside is that arguments against climate as the causal factor are also often cited as evidence for blitzkrieg (see Alroy 1999). However, while effective dismissal of climate would strengthen the case for a human role, it is not specific support for overkill, which is

only one of various models incorporating human impacts.

A related problem is that arguments against blitzkrieg are commonly misconstrued as arguments against a human hand in megafaunal extinction, but many specialists who reject blitzkrieg still consider it likely that human activity, including predation, was a significant or decisive factor, including some authors of the present manuscript.

## Naiveté

The argument that taxa not previously exposed to human predation are exceptionally vulnerable to colonising humans is the linchpin of blitzkrieg theory. Both qualitative and numerical models are critically reliant on this assumption. As observed by Brook & Bowman (2002), complete naiveté is assumed in all computer simulations supporting overkill. More specifically, these models presuppose a Type II Functional Response in which hunting ability is only influenced by prey density and search efficiency (Alroy 2001), or else treat off-take as independent of prey density (Holdaway & Jacomb 2000). Effectively, absolute naiveté is assumed in Type II Functional Responses. But if more realistic models incorporating the capacity to develop anti-predator behaviours (i.e. Type III Functional Response) are employed, then the possibility of extinction decays rapidly (Brook & Bowman 2002). Consequently, the blitzkrieg model is strongly undermined by any evidence that extinct megafauna had, or were likely to develop, anti-predator behaviours that diminished their vulnerability to human predation.

Most megafaunal extinctions occurred in the Americas and Australia, but there are no observed instances of human-naïve megafauna on continents responding to predation with which to test the concept (Martin 1984). By way of support, proponents of overkill draw on examples of humans killing animals on remote oceanic islands, a process typically accomplished with chilling ease (Flannery 1994, Diamond 1998). That species on remote islands fail to recognize humans as a threat and can be easily killed is beyond dispute. However,

the analogy is incomplete because island endemics are typically naive with respect to any form of terrestrial predation and entirely lack anti-predator behaviours. Consequently, they fail to recognise any land-based threat and this renders them singularly vulnerable to any immigrating terrestrial carnivore, human or otherwise (Soulé 1983, Quammen 1997, Grayson & Meltzer 2003).

Mounting evidence discredits the assertion that continental faunas with long histories of terrestrial predation would have responded to colonisation by humans, or any other taxa, in a way comparable to that of remote island species. Prior engagement with any terrestrial predator significantly improves the resistance of island taxa to over-exploitation by colonising humans and other exotics. For example, Steadman *et al.* (1999) suggested that previous exposure to predation from rodents buffered native species on New Ireland (Melanesia) against human arrival and the translocation of six other potentially destructive taxa, including pigs and dogs. Although human-driven extinctions occurred in this instance, they were less complete than on more remote locales and took place over tens of millennia (Steadman *et al.* 2002). Blumstein (2002) and Blumstein & Daniel (2002) posited that in insular kangaroo populations, the continued presence of a single predatory species acts to maintain a generalised suite of anti-predator behaviours that would otherwise be lost. Moreover, extant species preyed upon by native taxa are far less susceptible to hunting by evolutionary novel predators, while some island populations historically exposed only to native carnivores retain a generalized response that is transferred to evolutionary novel carnivores (Griffin *et al.* 2000). Blumstein *et al.* (2000) showed that Tammar Wallabies (*Macropus eugenii*), separated from endemic Australian as well as exotic predators for 9,500 years on Kangaroo Island, showed anti-predator responses to two evolutionarily novel predators (*Vulpes vulpes* and *Felis catus*), as well as a reconstructed thylacine (*Thylacinus cynocephalus*). Blumstein *et al.* (2001) showed that island quokkas (*Setonix brachyurus*), unaffected by terrestrial predators for 7,000 years, also exhibit

typical anti-predator behaviours. Not only can marsupials rapidly learn to avoid novel predators, but learned responses can be socially transmitted to predator-naïve companions (Griffin & Evans 2003). These data suggest that continental taxa insulated against predation for historically significant periods do not display naiveté of the degree hypothesized by advocates of overkill. Such behaviour is only likely to appear in species that have existed in circumstances entirely devoid of terrestrial predators for evolutionarily significant time spans.

Populations that have been completely isolated from mammalian carnivores can learn to avoid colonising predators within a single generation (Dickman 1992, McLean 1996, Berger *et al.* 2001). This extends to entirely novel predator species (McLean 1996). In parts of North America and Eurasia, wolves and brown bears are recolonising areas from which they were eliminated decades ago (Berger *et al.* 2001). Along recolonisation fronts, predator-naïve moose are vulnerable to re-invading carnivores, but behind this front, surviving populations quickly adjust and are no more susceptible than populations that have always known bears and wolves. Berger *et al.* (2001) contend that their results provide an analogy for Martin's blitzkrieg model, mirroring the hypothesized extinction of human-naïve prey along an advancing front of human colonisers. An obvious problem with this analogy is that unlike the fossil megafauna, the predator-naïve moose populations did not go extinct. Berger *et al.* (2001) note that in order for naiveté to be maintained, all generations of megafaunal prey must have been eliminated simultaneously along the crest of the colonising wave. We further note that regarding herding species, nearly all members of the group would have had to be killed if vertical and horizontal transmission of anti-predator skills was to have been shut down. Berger *et al.* (2001, p. 1039) conclude that '...perhaps species that failed to survive post-Pleistocene hunters were simply not quick learners.' However, neither of these caveats apply to at least some extinct megafauna for which blitzkrieg has been posited. Evidence of selective rather than general predation on young proboscideans in North America has been used as

evidence for human hunting (Ward 1997), and it is unlikely that mammoth were incapable of learning to associate humans with threat.

Two further inconsistencies negate the validity of transferring the findings of Berger *et al.* (2001) to human colonisation models. Firstly, the moose populations along wolf-bear colonisation fronts were completely predator-naïve, i.e. they had not been subject to predation by any taxa. This was not so for continental megafauna that faced human colonisation. Secondly, if megafauna were extinguished along a colonising front, this should be reflected in the chronology of human expansion and megafaunal extinction, but this is not the case (Beck 1996).

Although continental taxa are not as vulnerable to evolutionarily novel predators as remote island species, novel predators often hold an advantage. In Australia, introduced carnivores have undoubtedly contributed to range reductions and extinctions among native species. However, isolating the roles of each of these predators from each other, as well as from translocated placental herbivores and other human influences remains impossible. The introduction of the dingo, around 4,000 years ago (Gollan 1984) did not initiate any known extinctions among potential prey, although it is implicated in the disappearance of mainland thylacines around 3,000 years ago and Tasmanian devils (*Sarcophilus harrisii*) around 430 years ago (Archer & Baynes 1972, Archer 1974; but see Johnson & Wroe 2003). More recently, the introduction of foxes and cats by Europeans has clearly played a role in the decline of native species (Morton 1990). A lack of appropriate behavioural responses may have been significant (Short *et al.* 2002), but historic extinctions in Australia are complex phenomena. Correlation between the expansion of cats and declines among native faunas has been questioned (Abbot 2002). In western New South Wales localized extinctions correlate more strongly with the spread of pastoralism (Lunney 2001). Land-clearing and the introduced herbivores have also had significant impacts. In addition to competition with endemics and habitat destruction, introduced herbivores have probably facilitated the maintenance and expansion

of feral predator populations. Suppression of dingo populations has produced a skewed predator guild, benefiting the fox across much of its range (Short *et al.* 2002). It is not clear that any novel predator is singularly responsible for the extinction of any native species, although there is no doubt that recent extinctions in Australia are ultimately the product of human interference.

With respect to human predation, a bipedal 'carnivore' does not fit the generalized, quadrupedal, morphotype of predators. Humans also introduced entirely novel hunting behaviours and technologies. However, this must be balanced against the fact that in some respects *Homo sapiens* is typically carnivore-like. Forward-facing eyes are a feature that many prey animals may instinctively identify with threat (Blumstein *et al.* 2000), as are flattened ears (Janis pers. comm.). Similarly, scents produced by carnivores and their droppings may carry universal signatures. Voles on European islands display avoidance to tiger urine, a very novel predator in this instance (Stoddart 1982a-b), and predator-experienced herbivorous marsupials do modify their behaviour in the presence of predator scents (Blumstein *et al.* 2002). Lastly, animals of the Americas, and possibly Australia, had been subject to predation by large bipedal hunters. Gigantic, Terror Birds (Phorusrhacidae) stalked the South American continent throughout most of the Cretaceous and invaded North America in Pliocene times (Chandler 1994, Marshall 1994). The 150 kg *Titanis walleri*, was present in the Pleistocene and may have persisted in North America until the late in this period (Baskin 1995; J. Baskin pers. comm.). In Australia, giant dromornithids may have included meat in their diets (Wroe 1999a-b).

The presence of large terrestrial carnivores unambiguously divides continents from the only landmasses for which rapid anthropogenic extinction of megafauna (but not necessarily overkill) is widely accepted, i.e. remote islands, New Zealand's being the largest. Ranging from around 20 to 117 kg in mean body mass (Holdaway & Jacombs 2000, Burness *et al.* 2001, Grayson 2001) moas were small megafauna. Of 12 species, most were under 75 kg (Anderson 1989). The giant eagle,

*Harpagornis moorei*, at up to 13 kg (Holdaway 1989), preyed on at least some species, although it is known only from the South Island (Worthy 2000). No terrestrial endemic preyed on moa (Williams 1984).

Among islands, Madagascar is of special interest because terrestrial predators were present when humans arrived. The biggest endemic carnivore was the fossa, *Cryptoprocta ferox*, large sub-fossils are sometimes given species status as *C. spelea*. Its origins are enigmatic. It is commonly placed within the Viverridae, Veron (1995) treats it as the sister taxon to Felidae, but it may be more closely related to herpestids (Yoder *et al.* 2003). Taxonomy aside, *Cryptoprocta* is cat-like in overall proportions (Kohncke & Leonhardt 1986). Extant *Cryptoprocta* range between seven and 12 kg in weight, with measurements of 138 mm and 152 mm for two skulls attributed to *C. spelea* (Kohncke & Leonhardt 1986). Felid regression data, based on skull length (Van Valkenburgh 1990), gives an average body mass estimate of 20 kg for *C. spelea*. At this size it may not have been an effective predator of Madagascar's larger extinct endemics, inclusive of gigantic birds and lemurs, as well as intermediate-sized *Hippopotamus* (Dewar 1984, Faure & Guerin 1990), but it is significant that on this island populated by endemic carnivores, the question of whether human or climatic influences drove extinctions remains open (Dewar 1984, Culotta 1995).

In contrast to the position on remote islands, when humans colonised continents they arrived on territory long occupied by large terrestrial carnivores. Large American predators, including sabre-toothed cats, the giant short-faced bear and American lion, undoubtedly took megafauna and taphonomic evidence suggests that juveniles of even the largest species may have constituted regular prey (Anyonge 1993, Turner & Anton 1997, Christiansen 1999).

In Australia evidence for active predation on the biggest species is stronger still. In addition to indirect evidence (De Vis 1883, Case 1985, Nedin 1993), partially healed damage inflicted by a marsupial lion (*Thylacoleo carnifex*) on the femur of a large, sub-adult diprotodontid, testifies to the fact that *T. carnifex* preyed on megafauna (Scott &

Lord 1924). The near-complete domination of the cheektooth row by huge vertical shearing blades in this species leaves it singularly unsuited to a scavenging role (Wells *et al.* 1982). Massively built averaging around 104 kg and with the most extreme carnivorous dentition of any mammal, the marsupial lion was formidable by any standard (Wroe 1999a, 2000, 2002; Wroe *et al.* 1999, 2003a). Found continent wide, it was also relatively abundant and widespread (Wroe 2002). Other large, wide-ranging terrestrial mammalian carnivores included the thylacine and *Sarcophilus lanianus*, a 'Tasmanian' devil much larger than the extant species (Wroe 2002). Australia's megafauna may also have suffered the attention of at least one giant terrestrial reptile. Its habitus remains the subject of speculation, but with an average length of around 3.5 m and mean body weight of 97-158 kg (Wroe 2002, 2003), the giant varanid, *Megalania prisca*, was certainly capable of taking big prey as does its closest living ecomorphological analogue, the Komodo dragon, *Varanus komodoensis* (Auffenburgh 1981). As noted above, Australia's giant terrestrial birds (Dromornithidae) may also have eaten meat (Wroe 1999b).

Another problem with citing lack of human-specific anti-predator responses as the facilitator of overkill, is that although some mammals have innate responses specific to non-human predators (Dickman 1993), no such behaviours have been documented with respect to humans, and this extends to African species. Interestingly, it appears that the dynamics of species undergoing range contraction in present-day Africa are unique, but not restricted to large species that are hunted by humans. Channell & Lomolino (2000) have argued that a singular pattern of contraction extends to a wide range of extant African species: large and small, avian and mammalian, terrestrial and volant. These authors invoke Martin's (1984) concept of co-evolution with humans to account for the unique response of African taxa. This explanation is unsatisfactory for two reasons. Firstly, the blitzkrieg concept applies to a model of selective and direct human predation on large, terrestrial and almost exclusively mammalian species. Many of the species considered by Channell & Lomolino (2000) fit none

of these criteria. This sits uncomfortably with Martin's model wherein the perceived lack of human impact on non-megafaunal taxa is commonly used as supporting data (Alroy 1999). Secondly, no known extant megafauna are 'naive' in the context used by Martin (1984), i.e. having no previous experience with humans. While hominids have clearly inhabited Africa for longer than any other landmass, *Homo* has been present in Eurasia for almost as long (see below). If coexistence with humans that hunt large prey is critical, as forwarded in overkill theory, then the dynamics of range contraction in Eurasia should be most similar to those of Africa. They are not. The results presented by Channell & Lomolino (2000) are significant precisely because they suggest that factors other than the development of human-specific anti-predator behaviours have insulated African faunas against mechanisms driving extinctions elsewhere. And there are many alternative possibilities because Africa is unique in many respects, including greater available habitat area, greater long-term climatic stability, greater equatorial exposure and extraordinary mammalian diversity (Ambrose 1998, Berger 2000). The influences of these attributes may explain the resistance of African species to extinction more adequately than gradual acclimation to human predation.

Studies extending the antiquity and geographic spread of early European and Asian *Homo* bear strongly on how we interpret the significance of naiveté in the megafaunal extinction debate. Two predictions inherent to Martin's hypothesis are: 1, there should be a clear relationship between the duration of exposure of megafauna to human

populations and levels of extinction; and 2, in all instances where modern humans did colonise pristine environments extinctions should have rapidly followed. Chronologies in Asia are too poor for meaningful analysis (Martin 1984), but these predictions do not hold for Europe. At around 60% (see Table 1), megafaunal extinctions in Europe approached those of the Americas and Australia. While even the broad chronology of megafaunal extinctions in the Americas and especially Australia remain contentious (Grayson & Meltzer 2003, Wroe *et al.* 2002; and see below), in Europe the process was clearly staggered over tens of millennia (Martin 1984, Stuart 1999). Until recently it was thought that humans did not colonise Europe before 500,000 years ago (Balter 2001), but it is now clear that humans were present in Western Europe by 800,000 years BP (Balter 2001, Roebroeks 2001). In some instances inferred increases in human population correlate with increased large mammal species richness (Palombo & Mussi 2001). A figure of around 1.7 million years is now widely accepted for hominid remains assigned to *Homo ex gr. ergaster* from Dmanisi, Republic of Georgia (Gabunia *et al.* 2000, Vekua *et al.* 2002). This approaches the 1.79 million year age of the earliest *Homo ergaster* in Africa (Asfaw *et al.* 2002). Of course, much older hominid remains are known from Africa, but with respect to the acquisition of human-specific anti-predator behaviours, the duration of coexistence is only relevant for the period over which humans hunted megafauna. Although debate continues over the diet of the oldest *Homo*, the importance of meat and whether it was hunted or scavenged Lupo & O'Connell 2001, Dominguez-Rodrigo 2002,

	Extinct	Living	Total	% Extinct	Landmass km <sup>2</sup>
Africa	7	42	49	14.3	30.2 x 10 <sup>6</sup>
Europe	15	9	24	60.0	10.4 x 10 <sup>6</sup>
North America	33	12	45	73.3	23.7 x 10 <sup>6</sup>
South America	46	12	58	79.6	17.8 x 10 <sup>6</sup>
*Australia	19	3	22	86.4	7.7 x 10 <sup>6</sup>

Table 1. Late Quaternary (last 100,000 years) extinct and living genera of terrestrial megafauna >44 kg adult body weight of five continents. Adapted after Martin (1984). Data for extinct and living European megafauna from Martin (1984). For Australia it may be that as many as eight genera were already extinct before human arrival (Roberts *et al.* 2001). If so, this reduces both the number and percentage of megafaunal extinctions that could conceivably be attributed to human activity.



O'Connell *et al.* 2002), there has been no suggestion that any hominid predating *H. ergaster* or *H. erectus* had developed the capacity for big-game hunting (Ragir 2000). Consequently, any hominid occupation in Africa or Europe before the appearance of these species is irrelevant to discussion of human-specific anti-predator behaviours. The only humans likely to have preyed on large game have been in Europe for almost as long as Africa. If co-evolution with predatory humans is the critical factor explaining differences in numbers of extinctions at a global level, then why does Europe display levels of extinction that are closer to those of Australia and the Americas than Africa?

Expanding knowledge of the colonisation of Europe by behaviourally modern humans is also inconsistent with overkill. At such latitudes these people were probably obligate big-game hunters (Harris 1992, Mason *et al.* 1994). This process began before around 40,000 years ago (Pavlov *et al.* 2001, Roebroeks 2001). Various Eurasian sites testify to a modern human presence at latitudes greater than 50° by 40,000 BP (Dolukhanov *et al.* 2002) and people had extended their range to within an ice-free, grassy European Arctic by 35,000 years ago (Pavlov *et al.* 2001, 1994). Thus, in Europe and most of Asia, megafauna were exposed to a novel human predator over a relatively short period. In regions where *H. neanderthalensis* and other archaic *Homo* were eliminated/absorbed by *H. sapiens*, it might be argued that survival of megafauna was due to their co-evolution with the earlier *Homo*, but *Homo sapiens* introduced new technologies and novel hunting techniques. Consequently, to some degree, most Eurasian megafauna were naive to these new hunters, while those at latitudes beyond the range of *neanderthalensis* were naive in the strict sense of Martin (1963). However, no colonisation by modern humans correlates with any extinction event in Eurasia (Stuart 1999, Grayson *et al.* 2001). On the other hand, there is clear evidence of climate-induced extinction. The Irish Elk (*Megaloceros giganteus*) went extinct in Ireland during the late Pleistocene in the absence of humans (Moen *et al.* 1999), while *Megaloceros* persisted into the early

Holocene on the Isle of Man, in pre-human times (Gonzales *et al.* 2001).

These arguments do not disprove the proposition that human hunting contributed significantly to the disappearance of late Pleistocene megafauna. However, they suggest that the presence or absence of human-specific anti-predator responses developed through co-evolution were not necessarily critical and that other mechanisms must be considered. In addition, this evidence shows that we cannot simply divide fauna into naive and predator-hardened categories. We also conclude that because neither initial naivety, nor the rate at which large continental taxa might have learned to effectively respond to a human presence, can ever be assigned a meaningful value based on analysis of extant taxa, the results of computer simulations that model continental megafaunal extinction can never claim to reliably approximate reality.

## Landmass area and megafaunal extinction

There remains no landmass exceeding 150,000 km<sup>2</sup> (the South Island of New Zealand), for which human activity is widely accepted as the cause of megafaunal extinctions. New Zealand accounts for 0.54 % of the total land area for which blitzkrieg has been proposed. Widespread extinctions took place soon after the arrival of Maori people, although just how rapidly is contested (Anderson 2000, Wilkes 2000). Moa were extensively hunted, but many scientists cite translocations and habitat disturbance as significant factors in the extinction of these and many smaller island species (Anderson 2000, Grayson 2001). 'Blitzkrieg' describes the rapid extinction of large species solely through selective predation. Until the roles played by introduced species, land clearing, agriculture, and burning have been identified, the significance of evidence from remote islands in predicting the form of human influence on landmasses where these other influences were absent or unknown remains limited. Huge differences in area enforce further limitations.

Island biogeography treats area, together with temporal and geographic isolation, as fundamental

to the susceptibility of species to extinction (MacArthur & Wilson 1967, Terborgh *et al.* 2001, Whittaker *et al.* 2001). The shape of a landmass may also impact on extinction (Williams 1997). Rates of extinction on oceanic islands in the wake of human colonisation vary greatly, but area, together with isolation and topography are critical predictors. On tiny, remote islands, large-scale extinctions have immediately followed human arrival (Steadman *et al.* 2002). On larger, less isolated islands extinctions have been less rapid and total (Steadman *et al.* 1999).

The inverse relationship between susceptibility to extinction and area must also be considered with respect to continents. Africa is around 25% larger than North America, the largest continent for which blitzkrieg has been proposed and 400% larger than Australia, the smallest, but Australia is more than 45 times larger than the most extensive landmass for which rapid anthropogenic extinction is generally conceded. Partly because of its greater equatorial exposure, climate change has more significantly restricted the effective area available to megafauna in the Americas and Australia than in Africa, which accounts for around one-third of earth's habitable area (Ambrose 1998, Berger 2000, McBrearty & Brooks 2000). Glaciers have encompassed as much as 56% of North America over this time and as much as 60% of Australia has been overrun by windswept sand-dunes (Bowler 1982, White 1998). Many large African taxa underwent major range contractions during Pleistocene Glacial Maxima (Klein 1984). However, Africa can suffer vast loss of habitable area and still sustain refugia extensive enough to sustain large species. Put simply, most African species could survive a climatic catastrophe that rendered 7,000,000 km<sup>2</sup> uninhabitable, most Australian taxa would not.

Of further interest regarding landmass area and megafaunal extinction is recent work by MacPhee *et al.* (2002) on late Pleistocene megafauna in north Asia. Results suggest that many north Asian megafauna suffered massive range contractions broadly contemporaneous with latest Pleistocene extinctions in North America. These contractions flagged extinctions in some north Asian species

and populations, for others they heralded extended hiatuses from which they rebounded in Holocene times. The maintenance of refugia was paramount in these instances of survival and the likelihood of refugia persisting is inextricably linked with landmass area.

Lastly, throughout the Quaternary, Africa, Europe and Asia formed a single super-continent amounting to around 57% of the world's continental land surface. On a landmass of this size, continent-wide extinctions could be replaced by immigration of the same, or ecologically similar taxa. To a lesser degree, and through a filter barrier that clearly excluded taxa not adapted to high latitudes, this also applies to the Americas through intermittent connection to Eurasia-Africa and each other. Area correlates positively with species richness and maximal body mass (Wroe *et al.* 2004a) and communities with higher species richness are less susceptible to invading species (Case 1990). On the basis of size and isolation, the faunas of the Americas and Australia were inherently more vulnerable to stress than those of Afro-Eurasia. This may have acted to facilitate blitzkrieg, but could also explain how climate and/or other factors, human or otherwise, might account for the differential pattern of late Pleistocene and Holocene extinctions. One point is incontestable: island species are far more vulnerable than continental taxa and the only clear cases of rapid mass extinction driven by colonising societies have occurred on islands that are dwarfed by the smallest continent (Soulé 1983, Simberloff 2000, Grayson 2001). Demonstrating rapid faunas extinctions on small remote islands in response to human interference says little about the likelihood of similar events on continents. A lower rate of megafaunal extinction in Africa would be predicted from biogeographical first principles, regardless of any hypothesized human activity.

## Climate

Martin (1984) and Diamond (1998) argued that if oscillations in global climate were the primary force driving late Pleistocene extinctions, then events should have occurred simultaneously and previous

climatic oscillations should have correlated with mass extinctions on a comparable scale. We reiterate that if it was unequivocally demonstrated that for each landmass the Last Glacial Maximum was not the most severe, then this is not specific support for blitzkrieg over other anthropogenic models, and even the broader case for human driven extinction is valid only if two additional assumptions are proven: (i) global climatic change was manifested in identical or very similar ways on each landmass; and (ii) the varied faunas and floras responded similarly to climate change.

Each of these assumptions remains undemonstrated. Broad global temperature trends have been reasonably well established (Ambrose 1998; Alroy *et al.* 2000). However, high amplitude short duration events have received relatively little attention (Ambrose 1998), while extrapolation to predicting climate at local levels and more importantly, specific effects on vegetation within individual landmasses, remains imprecise (Lear *et al.* 2000, Schrag & Linsley 2002). Often oscillations in global climate have had markedly different effects on each continent (Nichol 1999, Elenga *et al.* 2000, Thompson & Anderson 2000, Williams *et al.* 2000, Walther *et al.* 2002) and many global trends have locally reversed (Moen *et al.* 1999). In the American tropics during the LGM, precipitation decreased in the north, but increased in the South (Baker 2002). Geographic and temporal variability also extends to the rapidity of climate change (Alley 2000). The LGM may not have been the most severe in North America or Africa (Alroy 1999, Nichol 1999), but in Australia, evidence is highly equivocal if not contrary (Horton 2000, White 1998). Nanson *et al.* (1992) draw attention to pluvials and dust flux in the Australian region conflating with the Xifeng loess sequence in Asia (Pye and Zhou 1989), which in turn reflects an overall trend toward increased aridity in the mid to late Pleistocene (that is, over the last five glacial cycles). Moreover, wetter conditions lag by about 15 ka behind sea-level and temperature highs (Nanson *et al.* 1992). If correct Australian megafauna were subjected to increasingly severe and frequent episodes of regional aridity over the last three glacial cycles, with the last being the driest.

The long lead up to the LGM in Australia was prefaced by a decline in overall humidity from around 45,000 years ago (Turney *et al.* 2001). This may have been exacerbated by the onset of intense variability in the El Niño Southern Oscillation (ENSO) at around 40,000 BP, although most hold that this was a Holocene event (Kershaw *et al.* 2000).

We posit that the last two glacial cycles in Australia were particularly harsh and that the majority of Pleistocene megafaunal extinctions were driven by these events, with a possible temporary reprieve during the Stage 5 pluvial (120 ka - 90 ka). Consistent with this interpretation are results of a recent analysis suggesting that eight genera of megafauna may have become extinct by 80 ka, i.e. almost certainly prior to settlement of the Australian continent by *Homo sapiens* (Roberts *et al.* 2001).

## Other exotic taxa

On all landmasses for which global blitzkrieg has been suggested, excepting Australia, humans arrived in company. On oceanic islands where human induced extinctions have been documented, various exotic species were also translocated. These include the Pacific rat, pig and the domestic dog. We concur with Grayson (2001) in his conclusion that it is presently impossible to apportion blame to human hunting as the sole or primary cause of extinctions under such circumstances. However, non-human arrivals at least roughly contemporaneous with human colonisation were not restricted to islands.

Through much of the late Pleistocene the fauna of North America was isolated within two distinct refugia divided by huge ice sheets. In what is now Alaska, the Beringian refugium contained many taxa that were, to all intents and purposes, Eurasian and discrete from those of the southern refugium (Brown & Lomolino 1998). Beringian species included the modern moose, wapiti, Eurasian-Alaskan bison, brown bear and musk oxen. Evidence of blood residues on projectile points from eastern Beringia has been used to argue that most of these species

were utilized in the late Pleistocene by Arctic Americans (Loy & Dixon 1998). Southern taxa comprised all of the endemic North American megafaunal species, including almost all of those that went extinct (Edwards 1967, Flannery 2001).

Just when humans made footfall in North America has attracted much scholarly energy. The classical view that Clovis peoples arriving at around 13,000 years BP were the first is now a minority position (Goebel 1999, Flannery 2001). Evidence from Monte Verde, suggesting human arrival at least 1,000 years before Clovis times has been widely accepted (Dillehay 1997, 1999) and ongoing analyses suggest still earlier dates (Watanabe *et al.* 2003). Goebel (1999) considers it possible that overland dispersal occurred before onset of the Last Glacial Maximum at around 25,000 to 20,000 years ago, but unlikely because archaeological sites above 60° latitude do not appear in northeastern Siberia until 25,000. However, sites near or beyond this latitude have now been dated at older than 30,000 years (Dulokhanov *et al.* 2002), while Mandryk *et al.* (2000) argue that the first humans used watercraft to skirt regions of ice-water contact. Most recently, Pitulko *et al.* (2004) showed that humans had pushed deep into the Siberian arctic by 27,000 BP. Advocates of human occupation before 13,000 BP accept that earlier economies did not revolve around systematic big-game hunting (Roosevelt 2000). Pre-Clovis human presence does not discount the possibility that Clovis people rapidly hunted megafauna to extinction following their arrival or descent from an earlier culture (Martin 1984). However, it emasculates the prediction that rapid mass extinction inevitably follows human interaction with human-naïve megafauna. This is a salient point because the argument for blitzkrieg on landmasses lacking evidence of predation and established chronologies rests on this assumption.

Late Pleistocene North America is characterised by high faunal turnover between north and south, but traffic was one-way. Beringian taxa expanded into the southern refugium with great success. Southern species held on where they were or went extinct. Historically, advocates of blitzkrieg have argued that Beringian taxa prevailed because they

were not naïve with respect to human hunters and that southern endemics disappeared for the reverse reason (Martin 1984). It is not this simple, even if no prior human presence is assumed. Other explanations can wholly or partially account for these biogeographical phenomena. Firstly, in both an historical and ontogenetic sense, the Beringian taxa were naïve with respect to human predation. For thousands of years the fauna of Beringia had been isolated not only from their Eurasian conspecifics, but human big-game hunters as well. Flannery (2001) argues that these animals may have been 'hard-wired' with respect to specific anti-predator responses and behaviours that allowed them to coexist with people, but as noted above no direct evidence supports this contention.

An important factor that seems to have been largely overlooked is the potential impact that southwardly mobile megafauna themselves might have had on the taxa of the southern refugium. Regardless of any hypothesized human impact, this event in itself may have resulted in the extinction of many species in the southern communities. We dispute the implication of Stuart (1991), that the effect of these non-human invasions would have been limited to competitive exclusion of close ecological equivalents. The results of such interactions are difficult to predict (D'Antonio & Kark 2002, Dickman 2002, Roemer *et al.* 2002) and the addition or loss of 'keystone' species can have catastrophic impacts (Terborgh *et al.* 2001). Whether invading species initiated trophic cascades that caused the extinction of many more taxa than those that they 'replaced' is impossible to calculate at present. However, where two landmasses collide, the fauna of the larger is more likely to prevail (Beard 1998). Recent evidence for Asia as the point of origin for the major mammalian radiations of the Tertiary (Bowen *et al.* 2002) is consistent with this hypothesis. As part of the Eurasian megafauna, Beringian taxa were advantaged. For most of these taxa neither the timing of extinctions or arrivals is well-documented (Flannery 2001, Grayson & Meltzer 2003). Some colonising species probably arrived well before the appearance of Clovis people, while others, such as the moose, were contemporaneous (Flannery 2001).

If it is shown that the chronologies of arrival and extinction do not correlate tightly, this does not eliminate a role for invading Beringian species in the disappearance of southern endemics. Invasion-driven extinctions may take place over tens of millennia (Steadman *et al.* 1999). Sole *et al.* (2002) describe a model they call Self-organized Instability (SOI), wherein they posit that feedback between immigration, diversity, connectivity and extinction lead an ecological system to SOI. Based on analysis of the Hawaiian avifauna, Keitt & Marquett (1996) argued that through immigration, avian diversity in Hawaii reached a saturation point beyond which the addition of a single species forced mass extinction.

Forster (2003) invoked this and SOI to explain megafaunal extinction in Australia: increased immigration from the Pliocene onwards brought Australian ecosystems to saturation point, then increased connectivity following human arrival drove an extinction process in which predation played a minor role. However, immigration during the Quaternary in Australia was low compared to that of North America and we suggest that this mechanism is more likely to apply to the American continent. Whether fast or slow, mass extinctions of endemic species in North America could have been the product of a cumulative process, driven by successive invasions of multiple taxa. Humans may have been one of the last and most significant, but this does not mean we can discount others and Clovis people were perhaps not the only big-game hunters that arrived in the late Pleistocene. At this time the grey wolf (*Canis lupus*) vied with *Homo sapiens* for the title of world's most successful and pervasive large mammalian hunter. It had been thought that *C. lupus* was present within the southern refugium prior to the Last Glacial Maximum. However, FAUNMAP lists no occurrences of the grey wolf prior to the LGM, only two are Full Glacial in age, and evidence before 13,000 BP has been questioned (Flannery 2001). The arrival of Clovis hunters and *C. lupus* may have been broadly synchronous, but if *C. lupus* did arrive before the LGM, this does not mean that it can be dismissed as a significant factor in late Pleistocene extinctions. Either way, southern

endemics encountered two successful, mobile social hunters within a constrained time frame. Wolves were probably incapable of bringing down proboscideans, but most other late Pleistocene North American taxa were within the size range of prey dispatched by living *C. lupus*.

Another large canid, *Canis dirus*, was present in North America in the late Pleistocene. However, *C. dirus* filled a different niche, being both slower and less social (Kurten & Anderson 1980). Prior to the arrival of *C. lupus*, American endemics may have never encountered a large, social, pursuit-predator, although it is possible that this role had once been occupied by the Plio-Pleistocene hyaenid, *Chasmoporthetes* (Janis & Wilhehn 1993). If over-hunting by novel predators contributed to megafaunal extinction in North America, then in many ways *C. lupus* fits the stereotype more snugly than *Homo sapiens*. Humans are omnivorous, whereas the grey wolf is a hyper-carnivore (Van Valkenburgh 1991). Moreover, its extreme mobility and higher birth-rate endow *C. lupus* with a greater capacity for rapid range expansion. In Southern Europe, the arrival of the grey wolf at the Plio-Pleistocene transition correlates with a major loss in species richness of large mammals (Torre *et al.* 2001) and changes in grey wolf behaviour have been shown to cause population declines in prey and initiate trophic cascades (Post *et al.* 1999).

The appearance of human big-game hunting specialists in the southern refugium of North America broadly coincided with that of various other exotic megafauna, including a very large omnivore (grizzly bear) and possibly another, highly efficient and intelligent, large-prey-specialist with novel hunting behaviours (*Canis lupus*). Range expansions of Beringian species into the southern refugium might be more accurately described as a large-scale, staggered invasion by Eurasian species that included humans. Greater resolution of the chronologies of arrival and extinction, together with more data on range expansions and contractions is needed before the role of invading taxa can be determined. Even in Australia and South America, where late Pleistocene immigration was far less pronounced, earlier immigration may have been

sufficient to achieve Self-organized Instability and mass extinction.

## Hunter-gatherer technologies, traditions and predation on megafauna

Proponents of blitzkrieg have claimed that the disproportionately high rate of species loss among large taxa in the late Pleistocene is explained by preferential selection by human hunters. It may be energetically more efficient for hunter-gatherers to select prey of greater body-mass, to a point, and there is archaeological and ethnographic evidence to support this (Winterhalder & Lu 1997, Duncan *et al.* 2002). Large species with low reproductive rates may be more prone to extinction via human predation and this also has been demonstrated, at least with respect to birds (Owens & Bennett 2000).

However, resource depression is commonly determined on the basis of observed or inferred capture rates and changes in hunting success need not reflect fluctuations in prey population sizes (Hill *et al.* 1997). Confounding variables include behavioural changes among prey, as well as short-term migration. Whether predation using traditional technologies alone can effect extinction remains contested (Hill *et al.* 1997, Choquenot & Bowman 1998) and it is difficult to account for limitations imposed by differing human technologies and biologies of extinct species. Ethnographic studies are often not inclusive of societies that prey on species within the size range of most extinct late Pleistocene megafauna. Demonstrating that Amazonian Indians select tapirs of 110 kg over smaller game (Vickers 1991, 1994), does not show that Palaeolithic hunters selected the largest contemporaneous animals, including taxa with mean body-masses of up to 6,000 kg (Burness *et al.* 2001). No analysis we know of has demonstrated that the selective hunting of proboscideans or rhinocerines is an economically optimal strategy. Difficulties using ethnographic data as analogy in this instance are compounded by the fact that many modern hunter-gatherers use technology that ranges from shotguns to poisoned, metal arrow-points (Hill *et al.* 1997, Lupo 2001).

Below we consider specifics of culture and predation on megafauna in more detail, but firstly we note that evidence for an extinction event that preferentially selected larger species is not strong evidence for human influence. The palaeontological record attests to many mass extinctions that show size-related bias. The disappearance of non-avian dinosaurs and most other large archosaurs at the Cretaceous-Tertiary boundary is a text-book example, but both temperature falls and glacial terminations have been correlated with the selective extinction of large mammalian taxa in Palaeogene (Bown *et al.* 1994) and Neogene (Webb 1984) deposits of North America, although Webb treats animals >5 kg as large. High faunal turnover and extinction among megafauna has also been demonstrated across the Plio-Pleistocene boundary in Europe (Torre *et al.* 2001, Agusti & Anton 2002).

## Hunting tool-kits and strategies

The significance of technology in the dispatch of large prey is widely acknowledged (Edwards 1967, Smith 1975, Kusimba 1999, Ashler & Geib 2000, Shea *et al.* 2001, Schmitt & Churchill 2003) and this extends to advocates of blitzkrieg (e.g. Smith 1975, Martin 1984). In the Americas, the presence of specialised big-game hunting technology, particularly stone-tipped projectile points, is often cited in support of overkill, while in Eurasia its absence is invoked as a limit on its temporal and geographical extent (Martin 1984, Diamond 1998, Flannery 2001). If this reasoning is upheld, then where such technology is lacking the argument for rapid overkill is diminished. The absence of big-game hunting technology in Middle Stone Age sites of Africa has been invoked to explain low levels of predation on large game (Klein & Cruz-Urbe 2000, Henshilwood *et al.* 2001). Martin (1984, p. 363) considers the appearance of people in North America prior to 13,000 BP as irrelevant to arguments against rapid overkill, unless it can be demonstrated that earlier cultures possessed big-game specific tools. The unambiguous implication is that rapid mass extinction of North America's megafauna was

impossible without appropriate technology. We concur on this point, a prior human presence does not eliminate the possibility that the more recent Clovis people rapidly exterminated megafauna and the presence of an appropriate tool-kit is important. However, demonstration of a prior culture in North America eats deeply into the efficacy of the overkill model. Blitzkrieg explains megafaunal extinction as a direct function of naiveté with respect to human predation (Martin 1963, 1984). Unless pre-Clovis societies entirely abstained from hunting animals >44 kg, a pre-Clovis presence means that the American fauna were not naïve to human predation when ultimately beset by more efficient hunters. *Thus, if a second society did rapidly hunt North American taxa to extinction, the critical factor was not the naiveté of the prey, but the traditions and technology of the culture itself.* This suggests that the theory's underlying mechanism is flawed with respect to North America, but it also strongly influences the likelihood of a human hand in megafaunal extinction where colonising cultures lacked a big-game hunting tradition and technology, at least on continents.

Before advancing further, we stress that an absence of stone-tipped projectiles or other specialised technologies does not indicate that a past society did not hunt large animals. Evidence for hafting stone points does not extend beyond 80,000 years ago (Koller *et al.* 2001), but humans undoubtedly killed large animals before this date. Equivocal evidence for the hunting of large animals using wholly wooden spears extends back perhaps half a million years in Europe. In Germany, hunting spears have been found in deposits 400,000 years old, along with horse remains (Thieme 1997, Roebroeks 2001). These weapons are up to 2.3 metres long and similar to Olympic javelins, although they were more likely hand-held thrusting weapons (Schmitt & Churchill 2003). In deposits possibly 500,000 years old at Boxgrove, England, damage to the shoulder blade of a horse has been interpreted as evidence that this animal was dispatched with a wooden spear (Pitts & Roberts 1997). However, this claim has been greeted with some skepticism (McNabb 2000), and the significance of megafauna in the diet of Middle

Palaeolithic humans remains debatable (Klein 1995, Ardbas & Palmqvist 1999, Roebroeks 2001).

While an absence of specialised technology does not preclude predation on large taxa, it undeniably influences hunting ability or predation efficiency and hence the probability of rapid overkill (Smith 1975). It also affects both the optimal and maximal body-mass of potential prey species (Edwards 1967). Consequently, limitations imposed by technology strongly impact the results of predator-prey modelling (Smith 1975). Hunting ability was the single most important influence on results derived from recent computer simulations presented by Alroy (2001). In this analysis, reducing the arbitrarily defined hunting ability constant from 36 to 28, cut the number of predicted extinctions among large North American taxa from 21 species to 0. Moreover, just as, the Type II Functional Response model incorporated by Alroy (2001) does not allow for learning behaviour in prey species (Brook & Bowman 2002), it also fails to accommodate differences in technology. Nor can it account for the learning of specialised behaviours or technologies in predators. Increases in the efficiency of hunting or prey handling can shift the functional response curve from Type II to Type III (Orians 1969, Real 1977). Type II models effectively, but unrealistically assume that the efficiency of hunting technologies and behaviours is maximal. For a Type III functional response, accounting for sub-optimal hunting technology has precisely the same affect on the probability of overkill as allowing for 'predator-hardened' prey, i.e. rapid decay. A further limitation imposed by assuming a Type II response is that it does not allow for the predator to switch to alternative food sources as prey density declines (Real 1977). This would be unusual for any predatory terrestrial vertebrate (C. Dickman, pers. comm.) and for humans the suggestion is contradicted by analyses showing that hunter-gatherers do shift to other foods where large taxa become less common (Vickers 1991, 1994).

On islands where megafauna were relatively small, lacking anti-predator responses, and disadvantaged by small populations and restricted ranges, technology may not have imposed a significant limit on predation efficiency and

something approaching a Type II Functional Response appears possible. However, the argument that technology would not have limited predation efficiency becomes less convincing as targets become larger and more aggressive or vigilant, as well as more numerous and widespread. It is one thing to efficiently dispatch 75 kg moas with wholly wooden spears or clubs, it is another to kill 6,000 kg *Mammuthus primigenius*. Thus, our argument is not that megafauna could not be hunted without big-game specific tool-kits, but that without it, optimum prey size and predation efficiency are significantly reduced. This deduction is accepted by proponents of overkill and is especially relevant with respect to continents, most notably Australia.

Projectiles with stone points are far more lethal than wholly wooden weapons with respect to the dispatch of large animals (Christenson 1986, Ellis 1997, Boeda *et al.* 1999, Villa & d'Errico 2001). Toth (1987) corroborates the assertion of Jones (1980) by showing that bifacially flaked tools are more effective than informal artefacts regarding the butchery of big-game. In a study of 79 American societies Ellis (1997) showed that societies that systematically hunted big game invariably used stone-tipped projectiles, while societies that rarely killed large animals used wooden ones. At >40 kg, the definition of 'large' in these instances closely corresponds with that of 'megafauna' as widely applied in the megafaunal extinction debate (i.e. >44 kg). Stone spear points do not appear in the Australian record until the mid-Holocene, tens of millennia after the arrival of humans (Flood 1999, Mulvaney & Kamminga 1999).

A more recent invention was the spear-thrower, also known as an atlatl (Mexican) or woomera (Australian Aboriginal). This device increases a spear's velocity, range and impact and hence the range of taxa that can be hunted (Churchill 1993). A projectile thrown with a spear-thrower can release four times the kinetic energy of a modern compound bow, massively increasing penetration and providing a four to sevenfold increase in range over hand thrown spears (Hutchings & Bruchert 1997, Schmitt & Churchill 2003). Many consider it likely that the atlatl was instrumental in the hunting of megafauna

by Palaeoindians, although the earliest unequivocal evidence in North America is from the early Holocene (Sheppard *et al.* 1987, Hutchings & Bruchert 1997). The oldest spear-throwers from Europe are less than 20,000 years old (Knecht 1994). The woomera in Australia is thought to date to around 5,000 years ago (Flood 1999), although Tacon & Brockwell (1995) suggest early Holocene.

Entrapment through the use of topographic relief has been advanced as one method employed by palaeoindians (Frison 1998) and Upper Palaeolithic Europeans (Straus 1993). The use of similar techniques has been reported for at least some indigenous Australians in pursuit of relatively small animals (Cosgrove & Allen 2001). Straus (1993) argues that a correlation between Upper Palaeolithic sites and regions with hills and canyons demonstrates the importance of relief to these peoples in the dispatch of large animals. On the world's flattest continent such opportunities are more limited and, having cornered concentrations of megafauna, early Australians would still have been faced with using wooden spears to kill animals that may have weighed several tonnes.

Other relevant ethnographic studies are those concluding that hunter-gatherers from tropical grassland habitats typically use single animal encounter techniques, while tactical landscape strategies that produce mass kills and surpluses are characteristic of peoples from cold grassland ecosystems (Marean & Assefa 1999). Churchill (1993) demonstrates that among modern day hunter-gatherers the dispatch of very large animals, i.e. mean body mass of 327 kg, is most commonly associated with tactical landscape strategies as well as specialised weapons and dogs. Alternatives such as snares and pitfall traps constitute an unlikely means of effecting rapid overkill. These are typically used by sedentary groups in pursuit of solitary game as a means of dietary supplementation (Holliday 1998).

The use of dogs is inextricably linked with hunting among present day hunter-gatherers. It has been argued that the use of domestic dogs significantly increased big-game hunting efficiency (Diamond 1984, Tacon & Pardoe 2002) and the dog is ubiquitous among modern hunter-gatherer



societies (Tacon & Pardoe 2002). Dogs arrived with humans on most islands (Grayson 2001) and probably in the Americas also, although this has yet to be confirmed with the oldest fossils being early Holocene in age (FAUNMAP), but humans and dogs did not arrive together in Australia. Molecular biologists have suggested an origin for the domestic dog prior to 100,000 years ago (Villa *et al.* 1997), although this is more properly interpreted as evidence for the lineage split and not domestication (Janis pers. comm.), it is also *contra* evidence tendered by Epstein (1971) showing that the morphological traits of domestic dogs arise quickly. The first appearance of domestic canids remains at 12,000 years BP (Villa *et al.* 1997) and the Australian dingo arrived around 4,000 years BP, long after humans (Gollan 1984).

As alluded to above, other relevant factors rarely considered in debate are the relative sizes and behaviours of the megafauna. Yet these are important because, all else being equal, the larger and better able to defend itself an animal is, the more difficult it is to kill. Average body-masses of megafauna that figure in this debate range from between 44 kg to 6,000 kg (Burness *et al.* 2001), a difference exceeding two orders of magnitude. Modern day Australian Aborigines can kill the largest living native species without stone or metal projectile tips (although a spear-thrower is commonly used). Larger exotics are also preyed on. At approximately 750 kg, the largest is the water buffalo (*Bubalus bubalis*), introduced from Indonesia around 1825 (Nowak & Paradiso 1983, Suaban 1995, Choquenot & Bowman 1998). They are now generally hunted with firearms, vehicles and dogs, but historically Aborigines have hunted them with iron-tipped spears and spear-throwers (Altman 1982). However, we have found no evidence that any were killed using wholly traditional projectiles (stone or wooden tipped), or without woomeras. In an account of a buffalo hunt by Aborigines using large, shovel-headed, iron-tipped spear heads, the dispatch of the animal took from first light to mid afternoon and required ten separate spearings before the animal finally succumbed to blood loss (Bowman 1993). This is significant, because wooden

projectiles induce less trauma and loss of blood. The hunting of water buffalo remains a dangerous activity. It may take up to eight hits with a shotgun to immobilise the animal and severe injuries to the hunters are not uncommon. Killing water buffalo lends kudos to the hunters, but groups rarely kill more than one per month (Altman 1982). Using *B. bubalis* as an analogue, Choquenot & Bowman (1998) questioned the potential of Aboriginal hunters to hunt megafauna to extinction. With respect to nineteenth century attacks by Aborigines on cattle in north-eastern New South Wales, one observer wrote that '...the blacks soon began to be troublesome and many head of cattle were speared. It was a common sight in those days to see fine bullocks roaming about with spears sticking through their necks....' (Kemp 2000), but there can be no doubt that cattle were killed using wholly wooden spears - our point is that these were relatively inefficient in such a role.

Among native Australian species, the heaviest is the red kangaroo (*Macropus rufus*) with an average adult body mass of 66 kg for males and 26.5 kg for females (Strahan 1995). Assuming an equal abundance of the sexes, the mean mass is then around 46 kg, slightly above the minimum 44 kg as typically defined in the megafaunal extinction debate (Martin 1984). Two other extant Australian taxa are also sometimes treated as megafauna (Martin 1984) the eastern grey kangaroo, *Macropus giganteus*, and the emu, *Dromaius novaehollandiae* (mean body mass 34 kg, Eastman 1968). Mean body-mass data is unavailable for *M. giganteus*, but it is significantly smaller than *M. rufus* (Strahan 1997). Allowing for a good deal of error in predictions such as those of Flannery & Roberts (1999), at 46 kg the extant red kangaroo remains much smaller than most extinct late Pleistocene taxa, including conspecifics of Pleistocene age.

Overall, Australia's extinct megafauna were smaller than those of other continents, but quantitatively determined weight estimates for Australian fossil species are few and this makes meaningful comparison difficult. Although empirically determined estimates have been attempted for some (Myers 2001, Wroe *et al.* 2003,

Wroe *et al.* 2004b), most estimates for Pleistocene Australian taxa remain the product of guesswork (Wroe 2001, 2002). Notably, among the few quantitatively based predictions available is the figure of 2,786 kg for average body mass in *Diprotodon optatum* (Wroe *et al.* 2004b). *Diprotodon* was comparable to rhinoceros and hippopotamus with respect to general body proportions, but larger than any extant species of either group (Wroe *et al.* 2004b). Although this pouched giant had no obvious defensive weapons such as horns, tusks or hypertrophied canines, given the presence of known big-game specialists such as *Thylacoleo*, it must have had anti-predator responses. Of course, *D. optatum* was the largest of Australian megafauna and it is likely that killing smaller taxa would have been less technically challenging. Of around 54 of Australia's late Pleistocene extinct species typically referred to as megafauna, as many as 14 may have averaged less than 44 kg (Flannery & Roberts 1999). However, while the lack of quantitatively determined body-mass estimates for most taxa remains problematic, it is certain that most were much larger than the heaviest species known to have been regularly hunted using wholly wooden weapons by modern Australian Aborigines. If current estimates are any guide (Flannery & Roberts 1999), then at least seven late Pleistocene Australian herbivores exceeded the average body-mass of the red kangaroo by more than an order of magnitude.

## Megafauna and subsistence diets

The relative significance of large-game, small-game and plant foods in human diets is an important factor in this debate and can produce very different outcomes for mathematical models that address the problem (Smith 1975). While global overkill assumes predictability and uniformity for the behaviours of colonizing hunter-gathers, it is increasingly clear that variability is the rule (Foley 1999). Different cultures place different emphases on different foods and these may or may not reflect economic rationales (Rick & Erlandson 2000).

Hunter-gatherers can specialise as big-game hunters even though it is an economically sub-optimal choice. Edwards (1967) suggests that in North America, the prestige value of big-game hunting may have contributed to megafaunal extinction by sustaining male hunting practices in the face of diminishing returns. Elegant studies by Hawkes (1991) and Hawkes *et al.* (2001) conclude that big-game hunting by Hadza men is better understood as a form of mating competition, i.e., showing-off, than as an economically optimal strategy. These authors show that the children of successful hunters gain no immediate nutritional advantage, but because their status allows them access to more productive wives, their offspring fair better. Male Indians of middle Holocene California may have increased their investment in large prey, despite diminishing returns for similar reasons (Hildebrandt & McGuire 2002). The 'showing-off' hypothesis has undoubted merit and is likely to variably apply to other hunter-gatherer economies. Its significance with respect to megafaunal extinction will change with interrelated factors including technology, group size, seasonality and whether single encounter or tactical landscape strategies are favoured, but it is not universally applicable. The Batek Negritos of Malaysia are nomadic hunter-gatherers that exclusively hunt small prey of around 4.7 kg, despite the presence of large animals ranging from pig to elephant and access to long-bladed iron spear-points. The explanation given by the Batek is that big animals are too dangerous (Endicott 1979). However, exceptions aside, as a generality, big-game hunting unquestionably draws kudos and this could elevate predation rates on megafaunal taxa beyond those predicted on purely economic grounds.

Failure to conform with predictions grounded on economic rationales is evidenced in many other examples. Tasmanian Aborigines abandoned eating fish by 3,000 years ago, despite a long fish-eating tradition and no measurable decline in the resource (Mulvaney & Kamminga 1999). In North America some tribes focused on smaller prey and plants, while others focused on big-game for reasons not clearly based on availability (Ellis 1997). With some exceptions (see Alberdi *et al.* 2001), late

Pleistocene archaeological sites in South America evidence economics based on plants and small animals (Roosevelt *et al.* 1996, Dillehay 1997, 1999; Gnecco & Mora 1997). In the North American Great Basin, among societies thought to concentrate on large prey, small game (when easily obtained) may well have been favoured to the point at which big-game hunting was abandoned altogether (Madsen & Schmitt 1998).

While ethnographic data must be treated with caution where we project so far into the past, some broad trends must have applied then as now. Particularly relevant in this debate is the relationship between big-game hunting and latitude. At high-latitudes ( $>40^{\circ}$ ) big-game is a more important source of nutrition, with plants and small-game playing a lesser role. At lower latitudes small-game and plants become progressively more significant (Hiatt 1974, Binford 1981, Speth & Speihnan 1983, Mason *et al.* 1994, Harris 1992, Marean 1997, Hardy *et al.* 2001). This trend is reflected in an increased female contribution in more temperate, through to tropical climates. Although the existence of these trends has not been questioned, relative proportions have. Reversing the long dominant 'man the hunter' paradigm that treated big-game hunting at all latitudes as the primary source of nutrition for hunter-gatherers, Hiatt (1974) argued that, at low-latitudes, plants and small animals procured by women constituted the bulk of human subsistence. Merwe (1992) claims that plants account for up to 90% of hunter-gatherers' diets and a study based on 58 hunter-gatherer societies concluded that hunting was the dominant only at latitudes above  $60^{\circ}$ , with fishing at the forefront between  $40^{\circ}$  and  $59^{\circ}$  and gathering dominant below  $40^{\circ}$  (Harris 1992). However, ongoing ethnographic analyses suggest that these figures understate the importance of meat. Marlowe (2001) argues that in societies where mean temperate exceeds  $13^{\circ}$  C, men contribute around 55% of food. Similarly, in an investigation of ten hunter-gatherer communities, Kaplan *et al.* (2000) found that male contribution to diet exceeded 50% in eight instances (the great majority obtained as meat) and others have concluded that animal foods contributed 45-65% of energy requirements (Cordain

*et al.* 2000, 2002). Still, some maintain that plant foods constituted the bulk of pre-agricultural subsistence (Lee 1968, Milton 2000).

In the context of the megafaunal extinction debate, it is not simply the proportion of meat to plants, or male contribution to female contribution, but the relative importance of megafauna that is significant. Unless species with mean body-masses over 44 kg amount to almost all male contributions among low-latitude peoples, which typically include small-game, fish, carrion and honey (Marlowe 2001), then the proportion of hunted megafauna in their diets is likely to be small. In some instances, game exceeding 44 kg could not be commonly acquired because taxa exceeding this mean are rare or not present. For Australian and South American societies, native species exceeding this figure are very few; one in Australia and two in the neotropics (Hawkes *et al.* 2001). Hawkes *et al.* (2001) stress the inverse relationship between hunting success and prey size, reporting that for the Ache of Paraguay, no prey exceeding 40 kg were taken in observations over 674 hunter-days. In a study of Ache hunters in Mbaracayu Reserve, conducted over seven years between 1980 and 1996, animals exceeding 44 kg in body-mass amounted to less than 7% of total caloric intake (Hill *et al.* 1997). This holds true in environments where many large species are present. Lee (1979) observed that for the African !Khung-speaking Bushmen, no large antelope were taken and only 22% of kills exceeded 10 kg over 83 hunter-days.

There is also a significant relationship between latitude and hunting strategy. Single animal encounter techniques are the hallmark of low-latitude hunter-gatherers from tropical grasslands. Tactical landscape strategies that produce mass kills are more widely used in cold grassland habitats at high latitudes (Marean & Assefa 1999). Geographical boundaries varied with climatic change and during Glacial Maxima the latitudinal range over which plants and small-game were dominant foods would have shrunk. The reverse would have applied during warmer periods. In Australia at the peak of the LGM mean temperatures were as much as  $8^{\circ}$  C lower than today (McKenzie

2002). This may bolster the case for higher levels of big-game hunting at this time, but the period over which the first humans are thought to have arrived in Australia, 43,000 to 62,000 years ago, is thought to have been relatively warm (Johnson *et al.* 1999).

Although diet and foraging behaviour among late Pleistocene societies probably followed some broad trends shared with those of modern hunter-gatherers, there were major differences, some imposed by technology. These might be construed as evidence for or against rapid overkill in different areas and landmasses. Certainly, the respective importance of meat and plants in the diet of Palaeolithic societies remains contentious (Mason *et al.* 1994, Hardy *et al.* 2001, Mithen *et al.* 2001). Analyses of stable isotopic data some have suggested that human diets were meat-based in a number of European locales (Bocherens *et al.* 1999, Richards *et al.* 2000) and that animal protein was largely acquired from hunted, rather than scavenged carcasses (Marean 1999). However, stable isotope analysis is a fallible, if useful tool (Witt & Ayliffe 2001) and results need to be interpreted cautiously. Human  $\delta^{15}\text{N}$  values are usually high relative to both carnivores and herbivores. Levels for European Neanderthals are no more elevated relative to carnivores than are those of maize agriculturalists in the US southwest (Schoeninger 1995). Based on analysis of isotopic data, Sponheimer & Lee-Thorpe (2001) suggest that early *Homo* in Africa consumed no more meat as a proportion of diet than did *Australopithecus africanus*. While these authors conclude that *A. africanus* may have been more carnivorous than previously thought, plant foods were the dominant source of nutrition for both hominids. Further complicating the issue is the possibility that termites contributed significantly to the animal protein intake of Plio-Pleistocene hominids (Brain & Read 2002). Likewise, the importance of predation versus scavenging among Palaeolithic societies remains contentious (Lupo & O'Connell 2002) and some remain doubtful that animals were the dominant source of nutrition in Ice Age Europe (Milton 2000). Nonetheless, meat probably constituted a *relatively* high proportion of

intake in Pleistocene Europe because most of the continent is at high-latitude (although high meat intakes need not translate into a reliance on megafauna). For much of the Pleistocene, environmental conditions were even less conducive to the continuous growth of high nutrient-value plant foods than at present (Hardy *et al.* 2001). Ultimately, evidence for or against high levels of meat consumption in Pleistocene Europe has limited bearing on like arguments for societies from below 40° latitude.

In tropical rainforests, all modern subsistence societies use domesticated sources of carbohydrates and Bailey *et al.* (1989) argue that permanent occupation of rainforests was impossible until recent times. If correct, this eliminates humans from the equation regarding late Pleistocene extinctions in these habitats. Marean (1997) concludes that late Pleistocene hunter-gathers inhabiting open environments at low-latitudes in Africa are unlikely to have been dependent on big-game or to have used specialized tactical hunting techniques to pursue and kill such prey. Additionally, for a number of Middle Palaeolithic / Middle Stone Age peoples, where evidence of big-game hunting exists, a single species is often the overwhelmingly dominant target (Marean *et al.* 1998, Marean & Assaref 1999). Such evidence counts against the likelihood that humans eliminated many species of megafaunal taxa simultaneously through predation. However, in other European sites, analyses evidence a wide range of prey taxa (Grayson & Meltzer 2003).

Technology restricted the variety of plant foods accessed by late Pleistocene societies relative to Holocene peoples (Edwards & O'Connell 1995), but just how the appearance of new plant processing technologies affected human-megafaunal interaction was probably not straight forward. Without more advanced plant-processing tools, earlier societies may have been more dependent on meat, and subsequently their affects on fauna would have been greater. However, there is tension in the interplay between technology, dietary breadth, population levels, habitat range and impact on megafauna. With the appearance of new technologies and renovations

allowing access to a greater range of plant and animal foods, human population densities and the variety of habitats occupied expanded. Consequently, the overall off-take of megafauna could increase, despite a decline in the proportion of big-game included in individual diets. Impact on megafauna would be further exacerbated where advances allowed human populations to permanently settle areas that previously could only be accessed seasonally, or not at all, thereby denying megafauna important refugia. For example, the development of new technologies may have increased the off-take of small prey in the Upper Palaeolithic of southern Europe (Pringle 1997). Because this appears to correspond with declining availability of large game, it may represent a response to dwindling megafaunal populations. Alternatively, we suggest that greater predation efficiency on small to medium sized prey would have promoted human population growth and hence contributed to an increased impact on megafauna.

The archaeological record can evidence human population trends through increases in the number of sites over time, as well as through changes in artefact discard rates. Following this reasoning, increases in human population densities and range expansions have been suggested for many parts of the world in the Pleistocene and Holocene. It is widely held that human population and range increased significantly in Australia during the mid-Holocene, a time when new technologies, as well as the dingo, first appear in the Australian record (Morwood 1987, Bird & Frankell 1991, David & Lourandos 1997). The disappearance of the thylacine and Tasmanian devil (*Sarcophilus harrisii*) from the mainland might be due to mid-Holocene intensification of land usage, rather than competition with dingoes (Johnson & Wroe 2003).

The development of special knowledge and new technologies is time-dependent, especially where new environments are colonised. The greater the differences between the point of origin and final destination, the more time will be required to acquire new knowledge and tools. This is significant with respect to Australia. The habitats encountered by the first Australians were probably very different to the environments they left (Bowdler 1983), and it is

unlikely that they arrived as skilled hunters of megafauna in open country (Owen-Smith 1999). Given that their arrival demonstrates sophisticated seamanship, a fish-based economy is probable. At present we cannot predict how long these people took to adapt to this foreign environment. However, in the context of the blitzkrieg debate any period exceeding a single generation of prospective prey is significant because continental taxa may have quickly learned to avoid humans. Evidence for a pre-Clovis human presence in America further supports the significance of origin, tradition and technology in this debate and underscores the fact that we cannot assume that colonising societies will immediately and catastrophically impact on megafauna.

A final cultural component that is at once both impossible to quantify or dismiss, is the role of self-regulation by subsistence peoples. Ethnographic evidence attests to widespread strictures on the harvesting of replenishable resources by hunter-gatherer societies (Heizer 1955). As observed by Smith (1975, p.743) 'Among primitive peoples that have invented property-rights systems, there are instances of sophistication that would rival the modern property deed.' Of course, whether societies implicated in global blitzkrieg used such practices remains entirely speculative, but at present we can neither assume that they did, nor that they did not. Models invoking overkill assume the latter.

## Australian evidence and its significance

Debate continues over when people first arrived in Australia. Thorne *et al.* (1999) and Grün *et al.* (2000) argue for a date of 62,000 years ago for a human burial at Lake Mungo. Roberts *et al.* (2001) dismiss this figure, claiming that two sites dated by Roberts at around 56,000 are older. Allen (2001) criticised the methodology used by Roberts to derive these dates and observed that there is no consensus on Aboriginal arrival in Australia beyond approximately 43,000 years ago. Most recently, Bowler *et al.* (2003) have also contested the findings

of Thorne *et al.* (1999) and argued that the burial took place between 42,000 and 45,000 years ago. Argument over the timing of megafaunal extinctions has been similarly spirited and inconclusive (Roberts *et al.* 2001, Wroe & Field 2001a, Brook & Bowman 2002).

In Australia there is no direct evidence of predation by humans on extinct megafauna and the flaked stone assemblages typically associated with big-game hunting elsewhere in the world are absent until around 6,000 years ago (Mulvaney & Kamminga 1999), a minimum of 36,000 years after human arrival. The spear-thrower is unknown prior to the Pleistocene-Holocene transition or more recently still (Tacon & Brockwell 1995).

All Pleistocene stone tool assemblages in Australia were described as the 'Core Tool and Scraper Tradition' by Bowler *et al.* (1970). Recently, regional variations have been identified, as in Tasmania (Allen 1996, Hiscock & Allen 2000). No tool kits for hunting large animals are known, but there is evidence for early use of plant-processing technology (Head 1996, Fullagar & Field 1997, Field & Fullagar 1998). Despite some heterogeneity, there is also evidence for a general trend toward the manufacture of increasingly efficient stone tools through the late Pleistocene and into the Holocene. Jones (1977) calculated that, on average, the ratio of working edge length to mass increased eight-fold between around 25,000 and 5,000 years ago.

An ancient lake-bed in southeastern Australia called Cuddie Springs is the only Australian site with an *in situ* association of megafauna and cultural material (Field & Dodson 1999, Field *et al.* 2002). Functional studies of flaked stone artefacts from one horizon (AL 1) show that they are from predominantly middle stages of manufacture and were primarily used for butchering (Furby 1995; Field, Fullagar & van Gijn unpublished results). The flaked stone assemblage from AL 1 is consistent with some expedient tools with modification (e.g., Frison & Todd 1986). The large stone tool assemblages from Cuddie Springs (>5000) have yielded no evidence for any specific hunting technology (Field & Dodson 1999) and formal tools, such as bifacially flaked axes and stone spear points

are absent.

The proposition that the rapidity of blitzkrieg would count against the likelihood of many kill-sites or butchery sites being preserved does not apply to the preservation of stone projectile points and butchery tools. Stone artefacts are far more likely to be preserved than faunal remains. For example, while kill-sites are exceedingly rare in North America, the stone spear-points of palaeoindians are found in hundreds of sites, over 100 in Texas alone (Largent 1995). Humans might have developed this technology then lost it after the megafauna became extinct, but this is unlikely. Stone spear-tips (and spear-throwers) remain valuable tools in the dispatch of remaining medium-large native fauna. Perhaps more importantly, they have great utility in warfare (Ellis 1997). Megafauna aside, any population that unilaterally dispensed with these weapons would be seriously disadvantaged.

Because of the absence of kill-sites or specialised technology, as well as uncertainty over the chronologies of human arrival and megafaunal extinctions, Australia has long been a weak link in the case for global overkill (Martin 1984, Martin & Steadman 1999). Consequently, a recent claim to have pinpointed megafaunal extinction in Australia to around 46,000 years ago (Roberts *et al.* 2001), well before climate change peaked at 22,000 to 18,000, has generated considerable interest, the implication being that extinctions and human arrival were closely correlated. The evidence from Cuddie Springs presents a major departure from this assertion.

Methodology employed in the Roberts *et al.* study has been criticised (Field & Fullagar 2001, Wroe & Field 2001a-b, Wroe *et al.* 2002). Wroe & Field (2001a-b) query the veracity of only accepting the dates for human arrival of around 56,000 years ago (Roberts *et al.* 1998), while current reports suggest human arrival anywhere from around 42,000 to 62,000 years ago. Also contested is the efficacy of the approach applied by Roberts *et al.* (2001) to select their sample of megafaunal sites. Twenty-eight late Pleistocene sites were dated, but the six that were younger than 46,000 years old were excluded *a priori*. The statistical analysis was based

on around nine sites, although the actual number was not explicitly given. For Cuddie Springs, their work constituted the third separate confirmation of an age of 36,000 years or younger for three strata containing megafauna.

Roberts *et al.* (2001) applied a single selection criterion to establish the strength of association between fossils and the material being dated, i.e. whether or not sites contained articulated skeletal remains. Sites without articulated remains were dismissed. In support of this general approach they refer to a conference abstract (Baynes 1999) and a more substantive work by Mead & Meltzer (1985). Baynes (1999) argues that many carbon dates should be treated with circumspection because they approach the C14 barrier, and applies the selection criteria of Mead & Meltzer (1985) in an analysis of 91 mostly unnamed sites. The method advanced by Mead & Meltzer (1985) and adopted by Baynes (1999) differs significantly from that of Roberts *et al.* (2001) in that it advocates the use of multiple criteria, but presence-absence of articulated remains is not among them. A criterion that is forwarded by Mead & Meltzer (1985, p. 162) is whether the charcoal being dated is: 'from a stratigraphic layer that is entirely capped on lower and upper layers by different sediments'. Baynes (1999) posits that megafaunal sites as young as 28,000 ka may be reliably dated, including Cuddie Springs (Baynes

pers. comm.), where upper and lower layers are indisputably capped (Figure 1). Applying the criteria of Meltzer & Mead (1985) gives a stronger association between megafauna and material dated for Cuddie Springs than most, if not all of the sites included in the analysis of Roberts *et al.* (2001).

Meltzer & Mead (1985) consider 'strong' associations to be those in which skeletal are directly dated. Short of that, and this is true of Optical Dating as well as C14, the association between the dated and target items must be inferred, and is automatically by their rating system either 'medium' or 'weak', depending on the strength of the evidence behind that inference. Roberts *et al.* provide no argument to support the implication that the presence of articulated remains provides greater assurance of correct dating than other criteria, such as whether deposits are capped. Articulated skeletal material can move and dates taken from material surrounding articulated remains can differ significantly in age to the fossil material itself (Meltzer pers. comm.). Roberts *et al.* do not define 'articulated remains' and we have found only one definition in the literature. Lyman (1994:150) describes 'articulated' as '....two or more skeletal parts in their proper anatomical positions relative to one another, and within a centimetre of each other if not in fact touching.'. By this definition, many bones from the lowest archaeological horizons at Cuddie

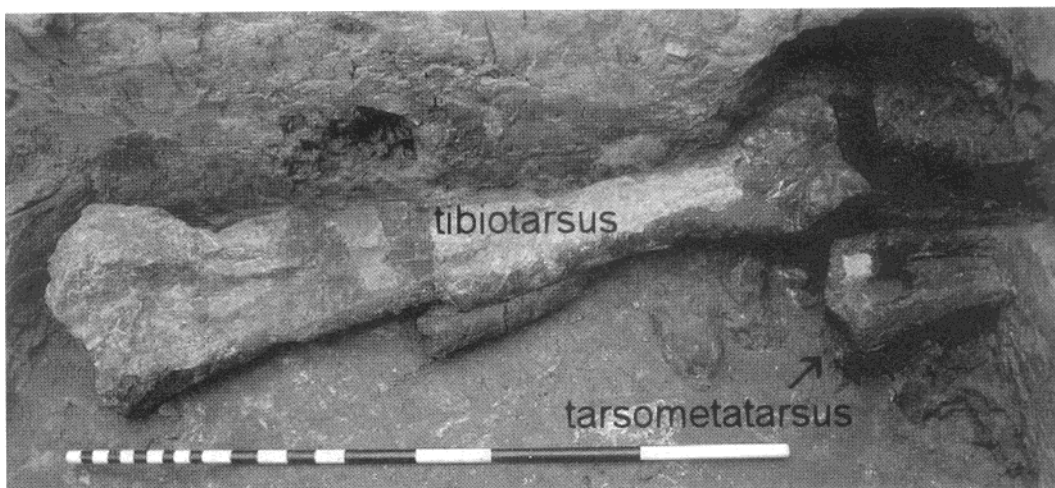
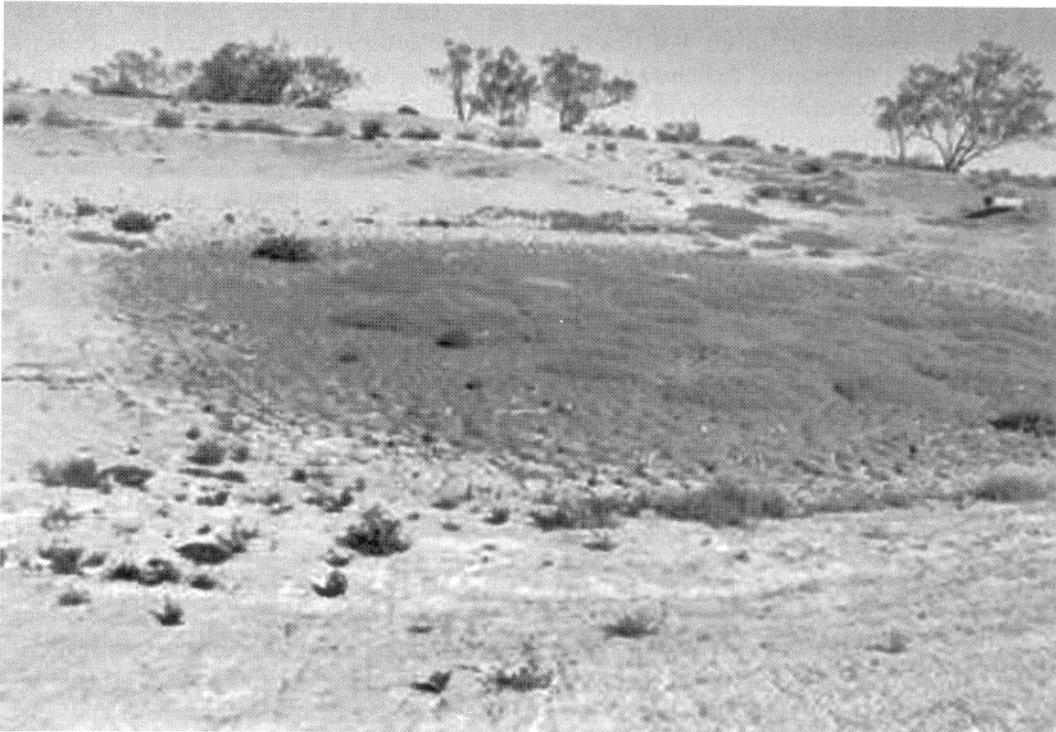


Fig. 1. *Genyornis newtoni* elements, *in situ* at the Cuddie Springs site in southeastern Australia. The tarso-metatarsus and the tibio-tarsus are shown here in juxtaposition in levels dated to around 36,000 years. (Scale = 50cm).





Springs are articulated (Figure 2; and see Field & Dodson 1999).

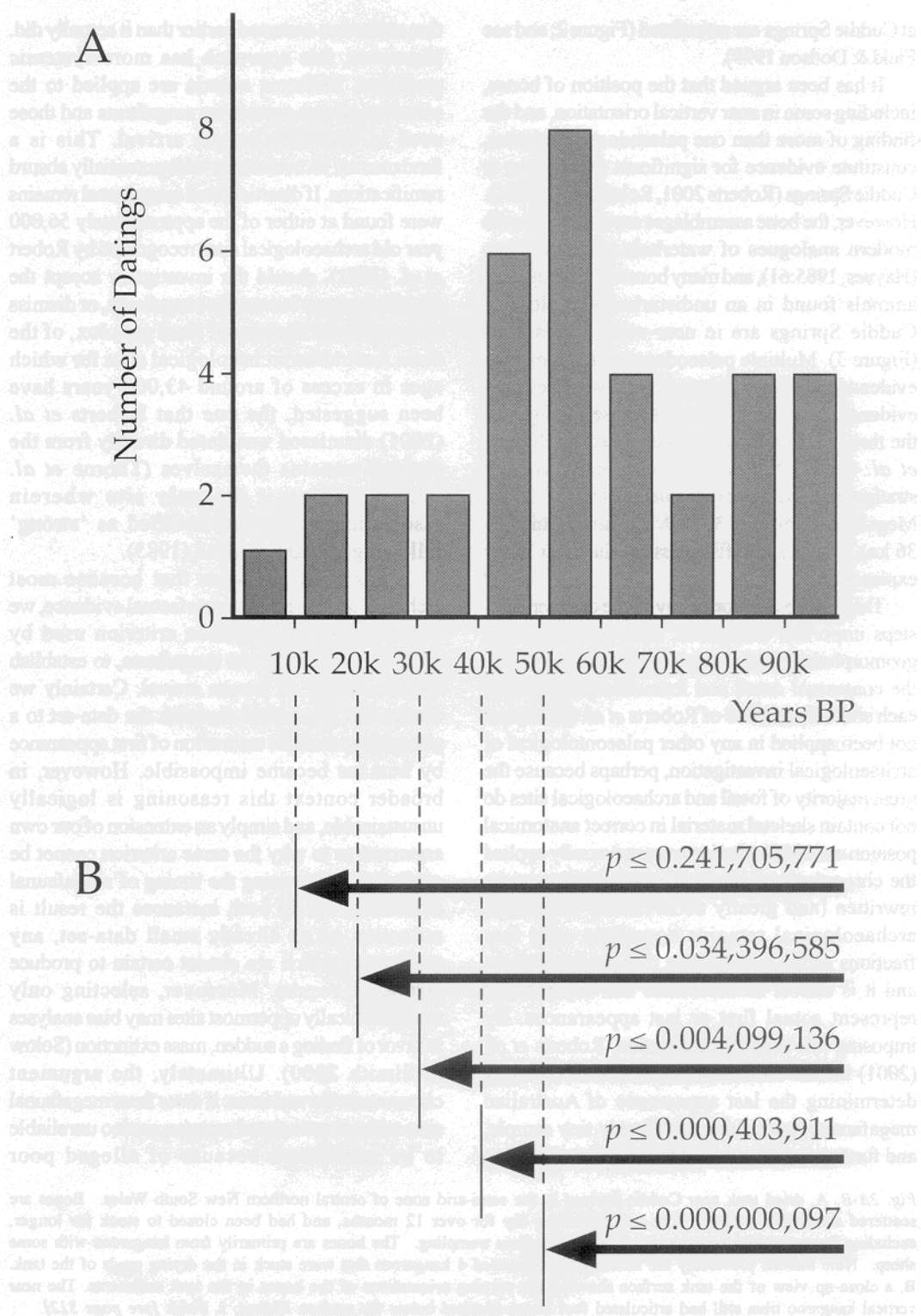
It has been argued that the position of bones, including some in near vertical orientation, and the finding of more than one palaeodose population, constitute evidence for significant disturbance at Cuddie Springs (Roberts 2001, Roberts *et al.* 2001). However, the bone assemblages are consistent with modern analogues of waterhole accumulations (Haynes, 1985:61), and many bones of recently dead animals found in an undisturbed site close to Cuddie Springs are in near-vertical positions (Figure 3). Multiple palaeodose populations may evidence sediment mixing, alternatively they may evidence procedural flaws. Because the ages of the three Cuddie Springs strata dated by Roberts *et al.* (2001) fall in chronologically correct stratigraphic sequence (Megafaunal Unit 5 = 27 ka, Megafaunal Unit 6a = 30 ka, Megafaunal Unit 6b = 36 ka), procedural difficulties are the most likely explanation.

The rigid application of any single criterion side-steps important disciplines, such as taphonomy, geomorphology and archaeology, that can establish the contextual detail and formation processes of each site. The method of Roberts *et al.* (2001) has not been applied in any other palaeontological or archaeological investigation, perhaps because the great majority of fossil and archaeological sites do not contain skeletal material in correct anatomical position and if this criterion were universally applied the chronology of life history would have to be rewritten (and greatly abbreviated). Fossil and archaeological remains constitute only tiny fractions of the populations that produced them and it is almost inconceivable that any remains represent actual first or last appearances. By imposing this arbitrary restriction, Roberts *et al.* (2001) further reduce the likelihood of correctly determining the last appearance of Australian megafauna, diminishing the already tiny sample, and further stacking the odds in favour of finding that extinction

occurred earlier than it actually did. Moreover, this approach has more systemic problems. Different criteria are applied to the selection of sites containing megafauna and those used to establish human arrival. This is a fundamental inconsistency with potentially absurd ramifications. If disarticulated megafaunal remains were found at either of the approximately 56,000 year old archaeological sites recognized by Roberts *et al.* (2001), should the investigator accept the date for humans but not the megafauna, or dismiss or accept both? By way of final paradox, of the three Australian archaeological sites for which ages in excess of around 43,000 years have been suggested, the one that Roberts *et al.* (2001) dismissed was dated directly from the skeletal remains themselves (Thorne *et al.* 1999), making it the only site wherein association would be classified as 'strong' following Meltzer & Mead (1985).

It has been put to us that because most archaeology is centred on artefactual evidence, we cannot apply the selection criterion used by Roberts *et al.* (2001) for megafauna, to establish the chronology of human arrival. Certainly we concur that this would diminish the data-set to a point where realistic estimation of first appearance by humans became impossible. However, in broader context this reasoning is logically unsustainable, and simply an extension of our own argument as to why the same criterion cannot be applied to determining the timing of megafaunal extinction, i.e. in both instances the result is reduction of an already small data-set, any analyses of which are almost certain to produce erroneous results. Moreover, selecting only stratigraphically uppermost sites may bias analyses in favour of finding a sudden, mass extinction (Solow & Smith 2000). Ultimately, the argument circumvents the real issue: if dates from megafaunal sites without articulated remains are too unreliable to be considered because of alleged poor association, why should we accept dates from archaeological sites without articulated remains? Alternatively, if

Fig. 2A-B. **A**, dried tank near Cuddie Springs in the semi-arid zone of central northern New South Wales. Bones are scattered across the surface. The tank had been dry for over 12 months, and had been closed to stock for longer, excluding the possibility of extensive bioturbation from trampling. The bones are primarily from kangaroos with some sheep. Nine months previously the farmer had euthenased 4 kangaroos that were stuck in the drying muds of the tank. **B**, a close-up view of the tank surface showing the varying orientations of the bones in the tank sediments. The near vertical kangaroo tibia still had articulated foot bones attached below the surface. Photos: J. Field. [see page 312].



other criteria are sufficient to permit confidence in dates from archaeological sites without articulated remains, then why are these criteria not applicable to megafaunal sites? In short, we cannot apply the selection process of Roberts *et al.* (2001) to dating megafaunal disappearance for precisely the same reasons that we cannot apply them to dating human arrival.

Roberts *et al.* (2001) concluded that humans and megafauna coexisted in Australia for around 10,000 years, but did not articulate the obvious corollary that this counted against blitzkrieg in Australia. Instead, they argued that their data do not rule out blitzkrieg. Of course, strictly speaking this is correct. It is even possible that Australia's megafauna went extinct before humans arrived (Wroe & Field 2001a). Indeed, at localized level, there is evidence that this was the case in Tasmania (Cosgrove 1989, Cosgrove & Allen 2001). But in our view it is incumbent on authors to state explicitly the more likely hypothesis supported by their results.

Criticism aside, the data presented by Roberts *et al.* (2001) contribute significantly to the extinction debate and warrant re-analysis. This was done by Brook & Bowman (2002), but these authors accepted the flawed selection process of the prior investigators and unsurprisingly their analysis generated similar results.

The study by Roberts *et al.* (2001) assumed that fossil deposits become more common in progressively younger strata. As a generality this is true. However, the reverse may be applicable to late Pleistocene Australia. Although the 28 sites dated by Roberts *et al.* (2001) span around 170,000 years, there is a heavy concentration of sites within a narrow 20,000-year stretch. To some degree this reflects the site selection process, but the concentration of sites within this band may also reflect changes in the availability of water, a critical factor in fossil formation.

Between around 65,000 and 45,000 years ago

Australia was relatively wet, but these humid conditions were winding back by between 45,000 and 50,000 years ago (Johnson *et al.* 1999, Turney *et al.* 2001, Bowler *et al.* 2003). Increasing aridity affected central Australia first, browning the continent from the inside-out in a process that was more tumultuous and drawn out than had been previously thought (White 1998, Lambeck & Chappell 2001, Bowler *et al.* 2003). Lambeck & Chappell (2001) argue that the LGM itself was in full swing almost 10,000 years earlier than previously supposed. Evidence from Lake Mungo suggests that climate began to fluctuate widely between 50,000 and 40,000 years ago, before descending into a period of sustained aridity between 40,000 and 30,000 years ago (Bowler *et al.* 2003). Violent swings in ENSO from around 40,000 years ago (Kershaw *et al.* 2000) may have contributed to deteriorating circumstances that peaked with the Last Glacial Maximum (22,000–18,000) when as much as 85 % of the continent was denuded of tree cover (Dodson & Wright 1987, White 1998). The shift from a depositional to erosional regime would have limited the formation of new fossil deposits and increased the rate at which previously formed sites disappeared. Consequently, an accelerating decline in the number of fossil sites from between around 50,000 to around 22,000 years ago would be predicted, irrespective of other influences (Wroe & Field 2001a). Preservational bias can impact greatly on how we view mass extinctions and perceived events may be artefacts of fluctuation in depositional regimes (Peters & Foote 2002). If we include all the data obtained by Roberts *et al.* (2001) for sites under 100,000 years old, results are consistent with the interpretation that aridification over many millennia accounts for declining rates of fossilization (Figure 3). More data is needed to test this assertion. This pattern could also be influenced by human predation and/or habitat modification over a longer time flume. However, a climate-based model also predicts that fossil sites containing smaller taxa

Fig. 3A-B. **A**, distribution of the estimated ages of late Quaternary Australian sites (<100,000 years BP) containing megafauna examined by Roberts *et al.* (2001). **B**, the inferred probability that Australian megafauna had gone extinct 10,000 years BP, 20,000 years BP, 30,000 years BP, 40,000 years BP, and 50,000 years BP.

would likewise decline with increasing aridification from 45,000 years ago. Brook & Bowman (2002), propose a further test would be to expand the database to include sites with articulated non-megafaunal as well as megafaunal remains. We would expand on this by including all sites for which medium or greater evidence of association was demonstrated.

A comprehensive drop in the incidence of fossilisation correlating with declining rainfall would not eliminate a role for human hunting, but it would point to climatic disintegration as primary in the extinction of Australia's megafauna. If aridification did drive the process then local extinctions within the arid and semi-arid zones would have predated extinctions outside this region (Horton 2000). Sample sizes are currently too small to provide strong support, but the results obtained by Roberts *et al.* (2001) are certainly congruous with this hypothesis. Also consistent is evidence based on the dating of eggshells by Miller *et al.* (1999) suggesting that the gigantic terrestrial bird *Genyornis newtoni* disappeared from three sites within this region around 50,000 years ago. More recently, McColluch *et al.* (2000), also based on eggshell dating studies, have observed that while abundance of *Genyornis* decreases markedly from 50,000 years ago, last appearances are at 40,000 years. Dates of around 30,000 years for *G. newtoni* at Cuddie Springs suggest differential rates of extinction for this species in different parts of the continent (Field & Boles 1998).

More evidence is required to evaluate these hypotheses, but we can test whether the underlying data are consistent with the argument that megafauna had gone extinct by 45,000 years ago. Monte Carlo simulations (1,000,000,000 using software developed by LSJ and available on request), run with the data from Roberts *et al.* (2001), were used to determine the probability of megafaunal extinction at five 10,000 year intervals starting at 10,000 BP. The results are presented in Fig. 3. The frequency distribution in the upper part of Fig. 3 was used to infer the probability that a randomly chosen fossil came from one of the 10,000 year periods of concern. The lower part of Fig. 3 shows the probability that the Australian megafauna had gone

extinct in each time period listed above, with the optimum period of extinction at 10,000-20,000 BP (0.241,705,771  $> p > 0.034,396,585$ ). The analysis also shows that it is extremely unlikely that megafauna went extinct between 40,000-50,000 BP (0.000,403,911  $> p > 0.000,000,097$ ). On this basis humans and megafauna probably coexisted in Australia for between 23,000 and 42,000 years, dependent on whether humans arrived at 43,000 or 62,000 years ago.

As alluded to previously, an interesting result obtained by Roberts *et al.* (2001) was evidence to the effect that much of Australia's late Pleistocene megafauna went extinct before human arrival. As many as eight genera may have disappeared by 80,000 years ago, meaning that humans might be implicated in a maximum of 60% of the late Pleistocene megafaunal extinctions at a generic level, and theoretically as few as 25% at the species level.

If eight genera had disappeared by 80,000 years ago, it supports claims that few prehistoric extinctions can be explained by obvious causes, climatic, human or otherwise (Kerr 2001, Barnes *et al.* 2002). A mounting body of evidence suggests that mono-factorial catastrophes are rarely, if ever, sufficient to account for mass extinctions and that most communities can resist extraordinary levels of devastation by single events (Racki & Wrzolek 2001). This brings into focus a double-fallacy often used in support of blitzkrieg. That is, that extinction can only be explained by conspicuous disaster, and, *ipso facto*, that demonstration of a single extinction amounts to evidence that there were other contemporaneous disappearances. Using evidence for the disappearance of *Genyornis newtoni* from three sites in south-central Australia at 50,000 years ago, Miller *et al.* (1999) strive to implicate humans in continent-wide mass extinction. Several leaps of faith are required to arrive at this conclusion. These are: 1. localised extinction of *G. newtoni* indicates continent-wide extinction; 2. without evidence for major climatic change we are left with no alternative but people; and 3. if humans wiped-out *G. newtoni*, then they must have been responsible for all other extinctions. However, there is evidence for younger *G. newtoni* outside the area they considered (Field & Boles 1998) and extinction in the absence of

obvious climate change is the norm. Moreover, Miller *et al.* accept that the localized extinction of this bird did coincide with the onset of climate change. Their reasoning being that the degree was insufficient to cause localised extinction of *Genyornis*. However, how much climate change would have been required to drive this, or any other fossil species out of part of its range, or to extinction, is unknown. The food source the authors considered primary for *G. newtoni* (browse) was likely to have declined in the face of the climate change they acknowledged. Lastly, as noted above, Bowler *et al.* (2003) show that major climatic change did occur between 50,000 and 40,000 years ago within the region examined by Miller *et al.* (1999).

Similar logic is used to support overkill in North America, where it has yet to be established that most extinct genera were still present at the time of human arrival, but in this instance there is uncontested evidence of coincident major climate change (Stafford *et al.* 1999, Grayson & Meltzer 2003). Interestingly, Barnes *et al.* (2002) and Guthrie (2004) suggested that two species of Beringian megafauna, brown bears and horses became locally extinct before human arrival.

The flip-side of arguments predicated on catastrophism are presumptions that only climatic changes perceived as detrimental in a narrow, anthropocentric sense, can cause extinction. Alroy (1999, 2001) contends that rather than go extinct, megafaunal species should have benefited from climatic change during the terminal Pleistocene in North America, because rising temperatures and rainfall increased productivity. Superficially, this makes sense, but the relationship between climate, productivity and species richness is not simple (Kondoh 2001, Wroe 2004a) and global-warming, as well as cooling, have precipitated widespread extinctions in past and present biomes (Bown *et al.* 1994, McLaughlin *et al.* 2002). Global warming may locally increase or decrease productivity (Knapp *et al.* 2002), but the imposition of a more productive environment can spell doom for species that are not adapted to newly emerging habitats.

## Conclusions

(1) Human-related extinctions of both large and small taxa have occurred on many remote islands. The length of time over which these took place varies from decades to tens of millennia. For some larger island species human predation was certainly significant or primary, although hunting has not been established as the sole cause in any instance. On the three continents for which rapid overkill has been suggested, chronologies of megafaunal extinction and human arrival are contested, as is the likelihood or mode of human involvement. But on these much larger landmasses, the significance of blitzkrieg relative to various other factors, anthropogenic and otherwise, can be predicted on the basis of other evidence.

(2) The argument that continental megafauna were completely vulnerable to colonising human hunters is misrepresented by analogy with remote island taxa not subject to terrestrial predation of any kind. Furthermore, extrapolations based on evidence from islands must be heavily qualified given the well-demonstrated relationship between area and extinction risk (Kennedy *et al.* 2002). Negative support for human causation (not necessarily blitzkrieg) hangs on the assertion that climate change cannot explain these phenomena because previous climatic disturbances did not cause extinctions on a comparable scale. However, this inference presupposes that the local effects of previous glacial maxima were, in each case, locally more severe than those of the Last Glacial Maximum. This proposition remains conjectural. Also overlooked are the roles of other invading and translocated species.

(3) The significance of cultural differences between colonising human populations is often overlooked in the megafaunal extinction debate, but a number of conclusions with direct bearing can be drawn from ethnographic and archaeological data. They include the following:

- (a) specialised technologies, such as stone projectile tips and spear-throwers significantly influence predation efficiency and the optimal body-mass of prey and hence the probability of rapid overkill;
- (b) plant foods and small-game are more significant contributors to hunter-gatherer diets at low-latitudes than high;

(c) at low-latitudes, hunter-gatherers are likely to employ single encounter hunting behaviours that do not produce mass kills or surpluses;

(d) improved technologies for the procurement of plants and small-game are likely to have negatively impacted on megafauna by increasing human population densities and range, even where *per capita* consumption of megafauna declined;

(e) colonisers not originating among big-game hunting societies are less likely to have become efficient systematic predators of megafauna.

(4) While we posit that overkill as a global model is probably invalid, its explanatory potential cannot be discounted on localised levels. Rapid mass extinctions of megafauna on remote islands are the most likely to fit the hypothesis, facilitated by extreme naïveté to terrestrial predation, small population sizes and highly restricted ranges.

Among continents the case for rapid extinction through over hunting is probably strongest, although still weak, in North America. Certainly spirited debate continues over the role of Clovis Indians in the disappearance of the continent's megafauna (Alroy 2001, Grayson & Meltzer 2003). Clovis people had megafauna specific tools, used them to kill and butcher at least some extinct megafaunal species, arguably hailed from a big-game hunting tradition, used tactical landscape hunting strategies (Slayman 1996; but see Roosevelt 2000), and their appearance overlaps with the rapid loss of at least 15 of 35 extinct late Pleistocene genera. However, in light of escalating evidence for pre-Clovis cultures in North America that were not big-game dependent, we argue that the process that took place was not overkill as advanced by Martin (1963). That is, it was not facilitated by naivety to humans, the cornerstone of Martin's theory, but by technological and cultural change against a backdrop of intense climatic fluctuation and invasion by other species. Either way, unless clear chronological separation is established between extinctions, major climatic change and invasions by various exotic taxa into the southern refugium, then the extinction debate in North America is likely to remain unresolved.

Moreover, the evidence for pre-Clovis cultures eats into the proposition that colonisation by hunter-gathers inevitably leads to rapid mass-extinction of large animals not previously exposed to humans and underscores the significance of tradition and technology in the megafaunal extinction debate.

In South America evidence for overkill is more equivocal still. There are no confirmed kill-sites for extinct taxa and although chronologies are relatively poor, at least some localised extinctions occurred in the absence of humans (Coltori *et al.* 1998). While many palaeoindian economies do not appear to have been based on big-game hunting, some were characterised by specialised technologies associated with taking large prey (Roosevelt 2000, Alberdi *et al.* 2001).

Regarding Australia, we argue that available data is strongly inconsistent with overkill, or *rapid* anthropogenic mass extinction through any means. Coming from and arriving at low-latitudes and leaving no evidence of big-game specific technology or kill-sites, the most parsimonious conclusion is that neither the first Australians nor their immediate ancestors and descendants hunted megafauna with the efficiency required to effect geologically instantaneous mass extinction. The size of the Australian landmass and the presence of large native carnivores also count further against the probability of rapid overkill. No compelling evidence exists for fire-stick farming as a primary cause (Bowman 1998, 2000), whereas the fact that people did not translocate exotic predators, competitors or associated pathogens, diminishes arguments that rapid extinctions were prosecuted through other anthropogenic means. Because Bowler *et al.* (2003) also argue that human remains previously dated at around 62,000 years old are in fact 45,000 or less, their results will be heralded as supportive evidence by proponents of blitzkrieg, narrowing the potential gap between human arrival and megafaunal extinction. However, in finding that major climate change in Australia began around 50,000 years ago, Bowler *et al.* (2003) in fact undermine a primary argument for blitzkrieg and anthropogenically driven extinction in general, i.e. that because no major climate change occurred at the time of megafaunal extinction on this continent

human activity is the only explanation. Thus, even if it was shown that human-megafaunal overlap in Australia was brief, these results effectively put the megafaunal extinction debate in Australia on similar footing to that in North America, where it remains impossible to convincingly separate the respective influences of climate change and human activity in the megafauna's demise. Lastly, although there is still far too little data to permit prediction with great confidence, two recent analyses have put human-megafaunal coexistence in Australia at 10,000 years or more.

(5) The concept of rapid global extinction of large animals, solely through violent human activity, evokes sensational imagery and its mass appeal is strengthened by its simplicity (Wroe *et al.* 2002, Grayson & Meltzer 2003). However, while monofactorial models can be heuristically valuable, they are unlikely to explain extinctions, past or present. The oversimplification of complex phenomena may generate misconceptions and constrain the development of effective conservation strategies for living taxa. Many species are currently disappearing for reasons that are unclear and untangling the significance of various, mostly anthropogenic influences in the decline of living taxa remains a daunting challenge (Bowman 2001, Manlius 2001). There may even be fundamental limits to our ability to explain ecological phenomena (Castelli & Casper 2001).

(6) Lastly we stress that although rapid overkill, facilitated by naïveté to human predation, is unlikely to accurately describe most megafaunal extinction - this most certainly does not exclude decisive human roles in the loss of many, even most late Quaternary species.

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