Australian bats: differential responses to Cenozoic climate change

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ABSTRACT

Bats represent approximately a quarter of Australia's living land mammals. Their sensitivity to current climate change has prompted global recognition of them as bellwether species. The Australian fossil record is rich in bats from a period of sequential climate changes over the last 25 million years of the Cenozoic. Long-term, overall trends apparent from fossil and modern records in the Riversleigh World Heritage Area, northern Australia include an increase in diversity in vespertilionids, pteropodids and emballonurids, decline in hipposiderids and mystacinids, and relatively stable diversity in megadermatids and molossids. This deep-time record indicates that individual bat families have responded differently to past changes in Australia's climate and environments, with those responses ranging from diversification to decline and extirpation. Extinction is a normal part of the process of evolution but the speed with which anthropogenic global warming is occurring threatens to disrupt that natural balance.

Key words: bats, fossils, Australia, climate change, Cenozoic, Riversleigh

Introduction

Bats comprise one fifth of the world's extant mammals and a quarter of Australia's native terrestrial mammals. Australia's 80 or so living bat species are widely distributed from the tropics to cool temperate regions in habitats ranging from rainforests to deserts (Churchill 2008; Van Dyck and Strahan 2008). Predictions about the effects of current global warming on bat populations in Australia (e.g. Climate Watch 2010) and worldwide (Burns *et al.* 2003) have been made on the basis of what is known about bat biology. Robinson *et al.* (2005) predict that continuing climate change may affect a bat's fertilization and parturition dates, hibernation periods, favoured hibernation roost sites, increased or decreased distance between suitable winter and summer roosts, suitable migration stopovers, or result in complete cessation of migration. Robinson *et al.*'s (2005) report also suggests that bat community structure is likely to be affected through changes in species composition, pressure on specialist species, and the uncoupling of complex phenologies and synchronies in interactions with food, prey and predators.

However, long-term monitoring of regional bat distributions, abundance, breeding and movements is rare and there are few derivative reports on the actual effects of current anthropogenic global warming on bats (e.g. Sachanowicz *et al.* 2006; Lundy *et al.* 2010) as opposed to ecological niche modelling of likely effects (e.g. Machado and Aquiar 2010; Rebello *et al.* 2010).

Riversleigh: the bat-rich fossil deposits

From a different perspective, bat-rich fossil deposits in the Riversleigh World Heritage Area, northwestern Queensland (Figs 1-3) provide an opportunity to study changes in diversity and abundance of bats in northern Australian bat communities through climate change cycles over the last 25 million years of the Cenozoic, the geological era in which we live.

Figure 1. The early Miocene fossil deposit Bitesantennary Site in the Riversleigh World Heritage Area, northwestern Queensland, represents a fossilised cave floor where the walls and ceiling have eroded away. Photo: H. Godthelp.

Figure 2. A reconstruction of the fauna and palaeoenvironment of Bitesantennary Site cave in the early Miocene. Eight hipposiderid species have been recovered from this deposit. Reconstruction: D. Dunphy.

Figure 3. Bat bones bristle from a block of limestone from the cave floor preserved at Bitesantennary Site, Riversleigh. Photo: R. Arnett.

For this interval of time, studies of marine foraminifera occurrence, vegetation, sea level changes and rainfall (e.g. Frakes *et al*. 1987; McGowran and Li 1994; McGowran *et al*. 2004; Martin 2006) have been used to infer a sequence of changing climatic conditions in Australia – from relatively cool and dry icehouse conditions in the late Oligocene, to warm and wet greenhouse conditions in the early and middle Miocene, increasingly dry icehouse conditions in the late Miocene, a brief greenhouse phase in the early Pliocene before many rapid and severe climate fluctuations in the Pleistocene with an overall decline in temperature and rainfall (Fig. 4).

The Riversleigh fossil deposits occur in freshwater limestones covering an area of >40 sq km of Boodjamulla (Lawn Hill) National Park in the Gulf of Carpentaria, Queensland (19°S, 130° 40'E). The deposits range in age from late Oligocene (c.25 Ma) to modern, and include tufa, cave, fissure-fill and lake deposits (Archer *et al*. 1989, 1994). More than 250 different fossil assemblages (local faunas) have been recorded and these preserve the remains of >300 species of fish, frogs, reptiles, birds, monotremes, marsupials, bats and rodents, as well as rarer invertebrates and plants (Archer *et al*. 1994, 2006). Palaeohabitats sampled by these assemblages range from open forests in the late Oligocene and late Miocene, closed forests in the early and middle Miocene, and in the Quaternary savannah grass- and woodlands which now characterise the area (Travouillon *et al*. 2009).

Today eight bat families occur in Australia: Pteropodidae (flying foxes, fruit and blossom bats), Emballonuridae (sheathtail bats), Rhinolophidae (horseshoe bats), Hipposideridae (leaf-nosed bats), Megadermatidae (false vampires), Vespertilionidae (common bats or vespers), Miniopteridae (bentwing bats) and Molossidae (freetail bats). Fourteen bat species have been recorded in the Riversleigh area today (White and Mason 2011), with another five species expected to occur there (Van Dyck and Strahan 2008).

From Riversleigh's Oligocene to Pliocene fossil deposits c.57 bat species have been identified (Table 1) and include representatives of five of Australia's eight extant
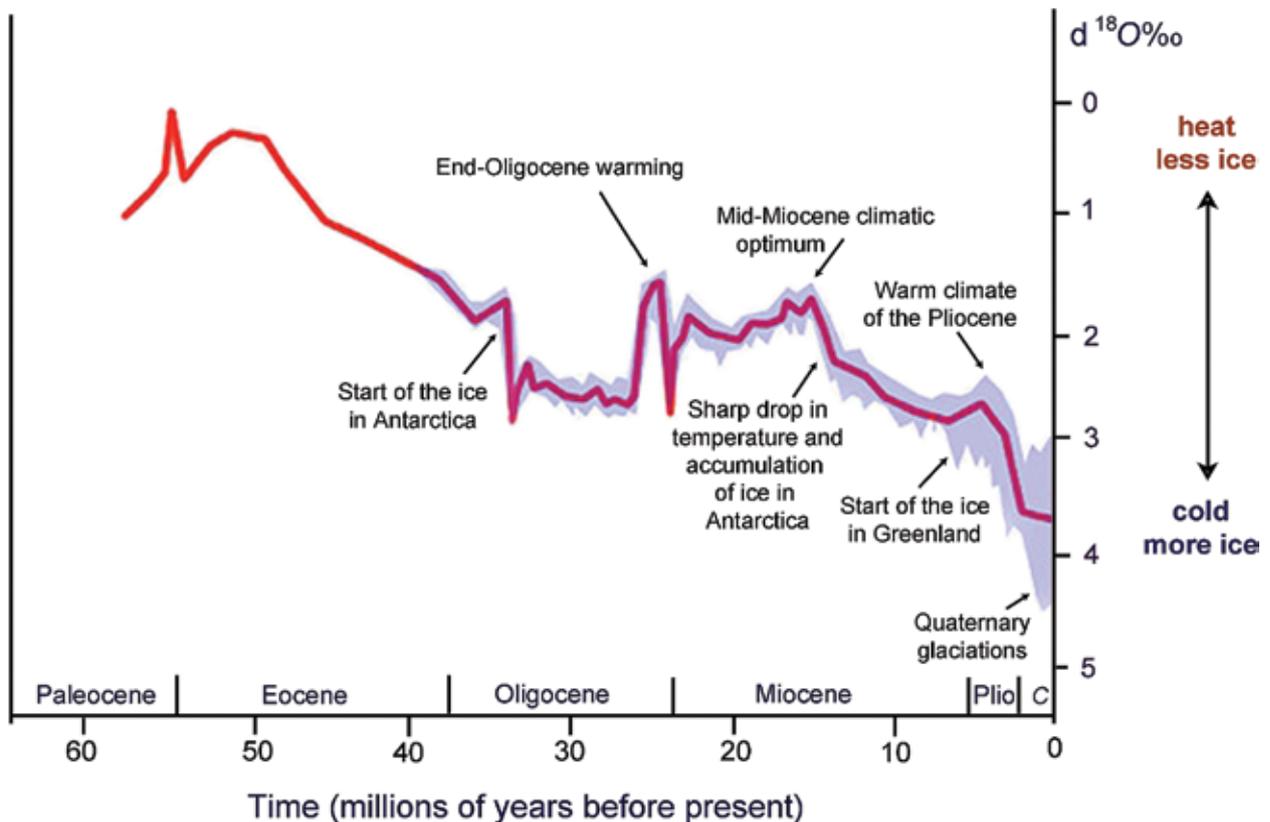
Figure 4. Climate change throughout the Cenozoic as measured by the palaeotemperature proxy oxygen-isotopic composition of benthic foraminifera (redrawn from Uriarte 2009).

Table 1. List of bats recovered from Oligocene to Pliocene fossil deposits in the Riversleigh World Heritage Area, northwestern Queensland. Numbers are minimum values; indet.= indeterminate (yet to be assigned to family).

Family	No. of Species
Hipposideridae (leaf-nosed bats)	28
Megadermatidae (ghost bats)	7
Vespertilionidae (vespers)	5
Molossidae (freetail bats)	4
Mystacinidae (burrowing bats)	4
Emballonuridae (sheathtail bats)	3
Rhinolophidae (horseshoe bats)	0
Pteropodidae (fruit bats)	0
Miniopteridae (bentwing bats)	0
Chiroptera indet.	6
TOTAL	57

bat families. Additionally represented are the family Mystacinidae (burrowing bats now surviving only in New Zealand; Hand et al. 2001, 2005) and several taxa yet to be assigned to family.

Long-term trends

Changes in Riversleigh bat communities over the period sampled are apparent at species, genus and family levels. Long-term trends in species-level diversity (Fig. 5) include an increase in vespertilionids include an increase in diversity in vespertilionids, pteropodids and emballonurids, decline in hipposiderids and mystacinids, and relatively stable diversity in megadermatids and molossids (Hand et al. 2010).

Hipposiderids dominate the Riversleigh fossil deposits (Table 1). Today 60 living hipposiderid species in eight genera are restricted to lowland tropical and subtropical regions of the Old World. They generally have short, broad (low aspect) wings and are slow, weaving fliers that forage for insects near or within vegetation by hovering and gleaning, hawking from observation perches, or by aerial pursuit. In the early to middle Cenozoic, 50 to 20 million years ago (Ma), their distribution extended to Europe where hipposiderids were the most common cave bats, with as many as five species occurring in an individual fossil deposit (Remy et al. 1987). Their disappearance from European fossil deposits during the later Neogene coincides with regional and global falling temperatures and precipitation (Legendre 1982, Zachos et al. 2001).

In the Riversleigh deposits, a minimum of 28 hipposiderid species in ten genera are recorded, with some taxa represented by many hundreds of individuals. In some deposits, as many as eight hipposiderid species of four genera appear to have co-existed in the one cave (Fig. 2). In early Miocene Riversleigh (c.20 Ma), at least 11 hipposiderid species were evidently syntopic (Hand and Archer 2005).

The abundance of hipposiderids in Riversleigh's limestone deposits is perhaps not surprising considering the cave-dwelling habits of most members of this bat family, but the diversity is significantly greater than the highest recorded globally today (e.g. 5-6 sympatric species in tropical karst systems in Borneo and New Guinea; Payne et al. 1985, Flannery 1995).
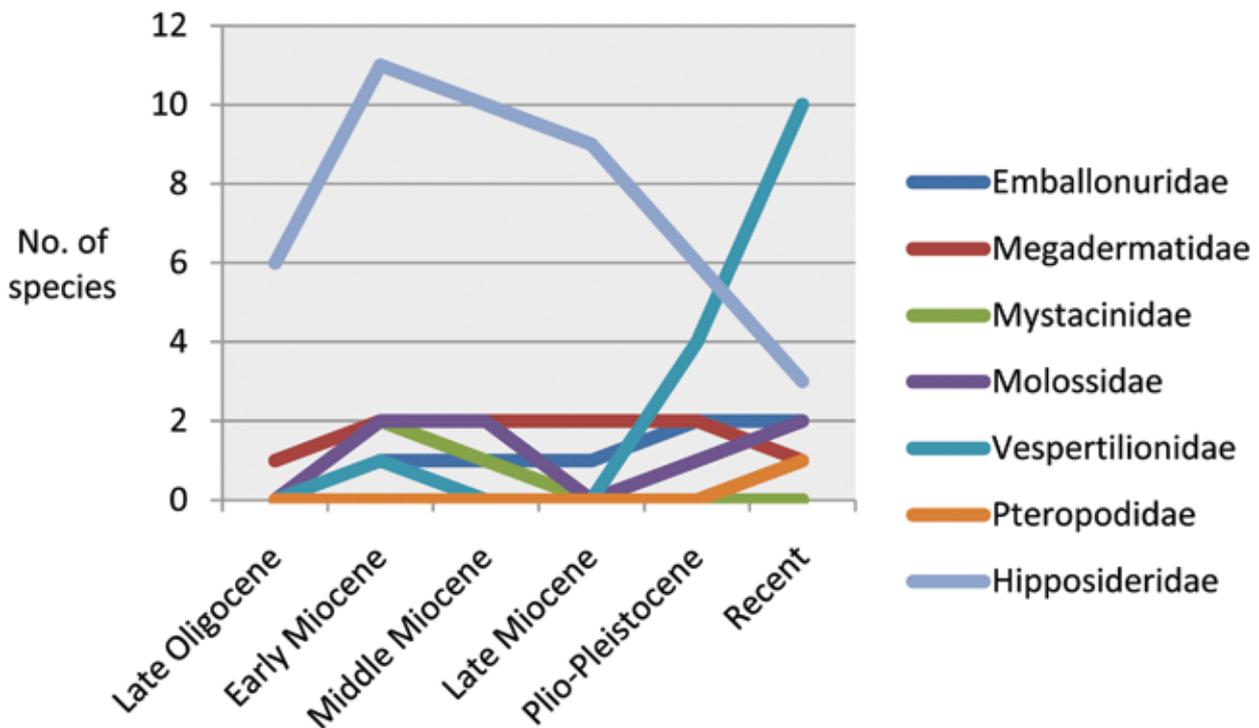

Figure 5. Graph showing trends in bat diversity over time in the Riversleigh area of northwestern Queensland. Species numbers shown are for representative bat faunas in those time intervals (e.g. Hand and Archer 2005) and exclude taxa unassigned to family. Modern bat diversity in the Riversleigh area is from Van Dyck and Strahan (2008) and White and Mason (2011).

The fossil record shows significant loss in Australian hipposiderid diversity in the later Cenozoic with only two of ten genera (*Rhinonicteris* and *Hipposideros*) surviving in Australia.

In relative terms, hipposiderids dominate all Riversleigh bat deposits (representing half to two-thirds of all bats identified), including in late Oligocene and late Miocene deposits, but by the Pliocene they represent only one-third of bats recovered (four of 12 bats in the Rackham's Roost Local Fauna; Archer *et al.* 1994). Today hipposiderids comprise three of 19 bat species occurring in the Riversleigh area and four of 35 bat species in the Wet Tropics rainforests of northern-eastern Australia.

Hipposiderid diversity appears to track changes in climate

Comparing trends in total number of Riversleigh hipposiderid species over time (Fig. 5) with that of changing palaeotemperatures (Fig. 4), diversity appears to track changes in climate over the last 25 million years, peaking in the warmer, wetter early Miocene following a brief thawing of the Antarctic ice-sheets, and falling after reglaciation in the drier (and arguably cooler) later Miocene (Zachos *et al.* 2001, 2008; McGowran *et al.* 2004). Nevertheless, throughout this period hipposiderids remain the most common bats in all Riversleigh deposits, with overall bat diversity also being generally lower in late Oligocene and late Miocene Riversleigh deposits.

The Riversleigh record shows a clear increase over time in diversity of vespertilionids, the common bats in the region today (10 of 19 species). Worldwide the Vespertilionidae is the largest and most widely distributed bat family with 325 living species found from tropical to arctic zones and on many oceanic islands. Like hipposiderids, vespertilionids have a fossil record dating back to the early Cenozoic (50 Ma) of Europe, but also have middle Cenozoic records from North America and South America as well as Europe, Asia, Africa and Australia (Hand 1984; Eiting and Gunnell 2009). Today 38 vespertilionid species constitute almost half of the modern Australian bat fauna (Churchill 2008; Strahan and Van Dyck 2008).

Despite their living diversity and old record elsewhere, vespertilionids have a poor fossil record in Australia. As yet the only pre-Pliocene vespertilionid known from Australia is a single tooth, from an early Miocene Riversleigh site (c. 20 Ma; Menu *et al.* 2002). This rarity may relate to actual scarcity of vespertilionids in the Riversleigh region of northern Australia during the Oligo-Miocene, preservational biases resulting from the roost and habitat preferences of such taxa in the past, or possibly both.

Nevertheless, cave-dwelling has not been a prerequisite for preservation in the Riversleigh deposits, as testified by the overwhelming majority of the >30,000 fish, frog, turtle, crocodile, lizard, snake, bird, monotreme, marsupial and rodent fossils collected so far (e.g. see Archer *et al.* 1994). Among these are bats whose remains tend to be more fragmentary than those of interpreted cave-dwelling species (Hand and Archer 2005) and which were probably tree-dwellers (e.g. mystacinids; Hand *et al.* 2005). In

cave deposits accumulating in northern Australia today, similarly fragmented bones and teeth of tree-dwelling (e.g. blossom) bats occur alongside the more abundant, better-preserved remains of cave-dwelling bats (pers. obs.) and have evidently been washed or brought in by predators from the immediate surrounds.

By Pliocene time (c.4 Ma), vespertilionids had increased in diversity and abundance in the Riversleigh record with at least four species represented in the Rackham's Roost deposit, two of which may be referrable to the modern Australian genera *Chalinolobus* and *Scotorepens* (Archer *et al.* 1994; Hand 1999). Today, vespertilionids are the most diverse of Australia's bats, including in the Riversleigh region (Van Dyck and Strahan 2008).

Extinction of mystacinids

While the Riversleigh fossil record charts a reversal of evolutionary fortunes for the families Hipposideridae and Vespertilionidae during the later Cenozoic, it also documents the loss from Australia of the family Mystacinidae. Mystacinids are omnivorous bats that feed on nectar, flowers, fruit, and flying and terrestrial invertebrates on the wing, in tree branches and on the ground. They occur today only in New Zealand, primarily in closed forests (Lloyd 2005). They lived in Australia from at least 26 to 12 Ma but had disappeared from the Riversleigh area by 3 to 5 Ma (Hand *et al.* 2005).

The decline and, ultimately, extinction of mystacinids in Australia may reflect the intense drying of Australia since the late Miocene which resulted in the replacement of wet forests by open woodlands and grasslands over much of the continent (McGowran and Li 1997; Martin 2006). In Oligo-Miocene Australian bat communities, mystacinids probably partially occupied the frugivore and nectarivore roles (Hand *et al.* 2005). Today, they occupy those niches in New Zealand (Lloyd 2005), while their relatives (noctilionoids) do so in South and Central America (Nowak 1999).

The global record

The global Cenozoic record for bats (Eiting and Gunnell 2009) shows a striking rise in vespertilionid generic diversity similar to that observed in the Riversleigh fossil record. It also shows a sharp rise in pteropodid diversity in the later Cenozoic as in the Australian record. Today, up to six pteropodid species occur sympatrically in northern Australia (one in the Riversleigh area and six in the Wet Tropics). Pteropodids appear to have been late arrivals to the Australian continent, the earliest Australian records being late Pleistocene remains from archaeological deposits (e.g. White 1967; Archer and Brayshaw 1978; Aplin 1985).

In its high hipposiderid diversity, the early to middle Miocene Riversleigh bat fauna differs strikingly from its modern counterpart. However, it may differ less in overall diversity and trophic structure (Hand and Archer 2005). In both the modern northern Australian fauna and Riversleigh's early Miocene bat communities, six of seven trophic categories for bats defined by Wilson (1973)

– carnivore, sanguinivore, piscivore, foliage gleaner, aerial insectivore, frugivore and nectarivore – are represented, with only the sanguinivore niche unrepresented. By comparison, in modern southern Australian bat faunas the carnivore niche is also unfilled, and in Tasmanian faunas only the aerial insectivore and foliage gleaner categories are represented (Hand and Archer 2005). Vespertilionids show a greater diversity of wing shapes and foraging styles than do hipposiderids with individual species feeding within cluttered vegetation, in open areas, in forest gaps, above water or above the canopy (e.g. Churchill 2008; Van Dyck and Strahan 2008). In Miocene northern Australia, hipposiderids may have occupied a wider variety of niches than they do now, or alternatively the forest habitat of the early and middle Miocene might have supported more hawking and gleaning specialists. Wilson (1973) regards the modern bat fauna of the Australian biogeographic region to include less foliage gleaners than anywhere else.

Changes in climate appear to have favoured certain bat lineages

Although overall diversity and trophic structure of northern Australian bat faunas might not have changed dramatically over 25 million years, changes in climate and palaeoenvironments appear to have favoured certain bat lineages over others, with differential responses to Cenozoic climate change being evident in, for example, the decline of hipposiderids, the diversification of vespertilionids, and the extinction of mystacinids.

Extinction is a normal and important part of the inexorable process of evolution, as is biotic response to climate and environmental change, but the rate at which anthropogenic global warming is occurring threatens to disrupt the natural balance between origination and extirpation.

From what we know about modern bat biology combined with the steadily improving fossil record, three conclusions stand out for the conservation of Australia's bat fauna in the face of a rapidly changing climate. The first is to appreciate that the bat fauna is as vulnerable to climate change as any other group of animals. They must be included in all future scenarios of change. Second, the management strategies for our native fauna need to be explicit about conserving bats, their caves, their foraging grounds and the hollow-bearing trees that so many species depend upon. Third, the study of bats, both extant and extinct, is a critical element of all planning programs to conserve our fauna in the face of the inevitable rise in temperatures and increasing aridity, or conversely, regionally increased rainfall. Bats will not evolve within decades to cope with the expected climatic and environmental changes, it is our challenge to confront and address that.

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