

Ecological specialisation and conservation of Australia's Large-footed Myotis: a review of trawling bat behaviour

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ABSTRACT

Increasing exploitation of natural systems by humans is the driving force behind global devastation of biodiversity. Extinction risk is however not apportioned evenly across all taxa and specialist species are inherently more vulnerable compared to generalists. World-wide, 16 species of microchiropterans exhibit adaptations for specialist trawling foraging behaviours. Approximately half of these species are relatively well represented in the literature. Amongst these, the Large-footed Myotis, *Myotis macropus*, exhibits typical trawling bat behaviour; spending the majority (~88%) of foraging time over water, feeding predominantly on aquatic prey items and selecting roosts close (<500m) to permanent water. These traits are broadly representative of all trawling bats and reflect convergence of the group on common, specialised behaviours. Such convergence places trawling bats at risk of very similar conservation threats, primarily disruptions to water-ways used for foraging, disturbance at cave roost sites and the possible reduction of suitable foraging habitat associated with aspects of human-enhanced climate change. These overarching conservation issues are highlighted by several studies of just a few species, but likely represent the same threats faced by all trawling bats, including those for which there is currently little published research available. Conservation of trawling bats world-wide will therefore benefit from actions that, in the least, address the common threats identified throughout this review.

Key words: bat, conservation, *Myotis*, trawling, specialisation.

Principles of ecological specialisation

Species are currently being lost from Earth at a rapid rate, comparable to that recorded for the last five mass extinctions in geological history (Regan *et al.*, 2001). This current devastation of biodiversity has a single predominant cause, the exploitation of natural systems by humans (Lacy, 1997; Lewis, 2006). However, extinction risk is not uniformly distributed across taxa, and a species' ability to persist and flourish in the face of ever increasing anthropogenically-induced change will reflect its extent of behavioural, morphological and evolutionary plasticity (Walker & Preston, 2006). Studies on a diverse range of taxa, including plants (Aguilar *et al.*, 2006), coral reefs (Munday, 2004), tropical butterflies (Koh *et al.*, 2004), marine fish (Dulvy *et al.*, 2004), reptiles (Foufopoulos & Ives, 1999; Attum *et al.* 2006), primates (Harcourt, 2006), marsupials (Fisher *et al.*, 2003), rats (Wijesinghe & Brooke., 2004) and bats (Jones *et al.*, 2003; Safi & Kerth, 2004), have all highlighted the increased risk of extinction faced by specialist species.

Specialist species exhibit adaptations for specific habitat variables, and consequently show greater fidelity to a particular environment (Attum *et al.*, 2006). In comparison, generalist species exhibit fewer adaptations to a particular environment, are defined by less stringent habitat requirements, and are therefore likely to be more successful in a greater variety of environments. Most specialists are typically defined by narrow ecological

niches, and are characterised by small geographic ranges and / or low population densities (Harcourt, 2006). These defining characteristics can act synergistically to render specialists more vulnerable to extinction threats (Davies *et al.*, 2004) including climate change (Walther *et al.*, 2002; Thomas *et al.*, 2004) and habitat loss (Tilman *et al.*, 1994; Henle *et al.*, 2004).

Fragmentation of natural habitats is recognised as one of the principal driving factors behind the current loss of biodiversity (Tilman *et al.*, 1994; Henle *et al.*, 2004). In the absence of large tracts of suitable habitat, fragmented remnants typically support small populations of specialist species. Such small populations often exhibit decreased genetic variability via genetic drift and inbreeding depression (loss of heterozygosity). The consequences of these events on the reduced viability and resilience of populations are well documented (e.g., Frankham *et al.*, 2002; Keller & Waller, 2002; Conner & Hartl, 2004). Furthermore, by definition, there is a greater chance that the matrix surrounding suitable habitat patches will be more inhospitable for specialist species compared to generalists. Where distances between suitable patches exceed those typically covered during dispersal and/or commuting events, the deleterious effects of population isolation and reduced gene flow are further enhanced (Brouat *et al.*, 2004), ultimately increasing the likelihood of extinction.

Similarly, the ability to disperse and move throughout the landscape is cited as a critical requirement for a species ability to persist in the face of climate change (Walther *et al.*, 2002). Even under modest climate change scenarios, modelling predicts that changes to temperature and precipitation will cause shifts in the geographic location of many species' tolerance ranges for these variables (their 'climate envelope', Walther *et al.*, 2002; Hughes, 2003; Thomas *et al.*, 2004). For a species to succeed in 'moving with' their shifting 'climate envelope' (be it to higher altitudes or pole-ward latitudes), a number of requirements must be met, not least of all that 1) suitable alternative habitat exists, 2) that the species can reach this alternative habitat without being blocked by dispersal barriers and that 3) the community from which the species originated can also move and be supported by the alternative habitat without excessive competition from other resident or invasive species (Hughes, 2003). In reality, suitable habitat, particularly for specialist species, is likely to be limiting and the probability of encountering barriers to dispersal such as cleared agricultural land, urban settlements or natural barriers is increasingly high with ongoing human development.

Ecological specialisation in microbats

Bats (Order Chiroptera) form the second most species-rich order of mammals (following rodents), consisting of approximately 1110 extant species traditionally divided between two suborders, the Megachiroptera ('megabats', ~180 species) and the Microchiroptera ('microbats', ~930 species; Simmons, 2005). However, the higher order classification of bats is currently in a state of flux and Teeling *et al.* (2005) proposed division of the Chiroptera into Yinpterochiroptera (megabats and Rhinolophoidea) and Yangochiroptera (remaining microbats) based on molecular phylogenetics. Nonetheless, bats are important members of many ecological communities. For example, pollinators and seed dispersers in tropical systems are keystone species, and insectivores feed extensively on nocturnal insect populations (Mickleburgh *et al.*, 2002), several of which may be perceived as pests and their control by bats confers economic benefits to agriculture (e.g., Federico *et al.*, 2008). Absent only from the poles, microbats have radiated throughout temperate and tropical zones. Their evolutionary success across the globe primarily reflects the group's ability to exploit a myriad of trophic niches (Zubaid *et al.*, 2006) aided by several fascinating behavioural characteristics that include (but are not limited to) the use of flight, torpor and echolocation.

The vast ecological diversity of microbats reflects the specialisation of many species for specific roosting and foraging strategies. Microbats are characterised by a strong reliance on suitable day-roosts, where they can spend over 50 % of their lives (Kunz & Lumsden, 2003). Day-roosts include foliage, tree cavities, caves, and a wide array of artificial structures including buildings, bridges, mine shafts and tunnels (Kunz & Lumsden, 2003). The Disk-winged bat *Thyroptera tricolor* is an oft-cited example of a species with highly specialised morphology that reflects its roosting behaviour. These neotropical bats

have circular suction pads at the base of their thumbs and hind feet which are highly adapted for adhering to the sides of the smooth, furled leaves within which they roost (Wilson & Findley, 1977). Similarly, the threatened Orange Leaf-nosed bat *Rhinionictis aurantia* and Ghost bat *Macroderma gigas* have narrow physiological tolerances and are adapted to the stable, warm and humid microclimates of underground roost sites in rocky outcrops in northern Australia (Worthington Wilmer *et al.*, 1994, 1999; Armstrong, 2006).

Many species also show numerous adaptations for specific foraging niches. Microbats have evolved feeding forms as diverse as nectarivory, sanguivory, carnivory, insectivory and piscivory (Kunz & Fenton, 2003). The elongated heads and tongues of nectarivorous Phyllostomid bats are clear examples of adaptations for a specialised foraging mode. They also reflect a close coevolution between the Phyllostomid bats and the food plants on which they feed and subsequently pollinate (Patterson *et al.*, 2003). However, some of the most striking morphological, echolocation and behavioural adaptations are seen in trawling microbats that are specialised for foraging over water.

Trawling bats

Phylogeography

Although only two truly piscivorous microbat species are recognised (the Greater Bull-dog bat *Noctilio leporinus* and the Mexican Fishing-bat *Myotis vivesi*), numerous species possess hind-feet that are enlarged relative to body size compared to other microbat species (Table 1). Possessing relatively enlarged hind-feet is the principal morphological adaptation for a 'trawling' lifestyle. 'Trawling' is used here to describe the action of capturing prey directly from, or beneath, water surfaces. The majority of trawling microbats belong to the genus *Myotis* and until recently this genus was classified into three recognised sub-genera; *Myotis*, *Selysius* and *Leuconoe* (Findley, 1972). The members of each of these three sub-genera were characterised by their distinct foraging modes; gleaning, aerial insectivory and trawling, respectively. Members of the latter group, *Leuconoe*, were characterised by enlarged hind-feet, hairy legs, strengthened calcar (cartilage that extends from the ankle along the trailing edge of the tail membrane) and shorter tails, which were all seen as adaptations to an aquatic mode of foraging (Findley, 1972). Findley (1972) recognised the broad geographic distribution of the *Leuconoe* sub-genus, and suggested that radiation of large-footed bats from the neotropics into Asia may have occurred via dispersal around the northern rim of the Pacific basin during the early Cenozoic. However, recent concurring phylogenies based on both mtDNA and nuclear markers, have highlighted the lack of a common, close ancestor to the *Leuconoe* group (Ruedi & Mayer, 2001; Stadelmann *et al.*, 2004, 2007). Convergent, or parallel, evolution is now recognised as the principal mechanism responsible for the presence of the strikingly similar ecomorphs that have arisen over a wide geographic range (Ruedi & Mayer, 2001; Stadelmann *et al.*, 2004, 2007; Fig 1).

Similar clades of trawling *Myotis* were identified in the phylogeographic assessment published by Stadelmann *et*

al., (2007) and are highlighted in Fig. 1 by common symbols next to species' names. For example, *M. ricketti* and *M. macrodactylus* in Asia are closely related to each other (closed circles), and their most closely related trawling-cogener in the palearctic is *M. daubentonii* (open circle). *Myotis capaccinii* (open star) belongs to the same clade as the *Myotis* species found in the Australasian region, but those with a solid star (*M. macrotarsus*, *M. hasseltii*, *M. macropus*) are more closely related to each other. *Myotis stalkerii* was not included in the phylogeographic revision by Stadelmann *et al.*, (2007), presumably however it would also belong to the Australasian region clade (closed stars). *Myotis ruber* and *M. vivesi* both belong to the neotropical subclade of *Myotis* bats, however despite the morphological and behavioural similarities between the two, they are not sister-species (Stadelmann *et al.*, 2004).

A review of the available literature on microbat foraging behaviour revealed 16 species (Table 1) that possess enlarged hind-feet relative to their body size and to those of other microbat species. These species are cited throughout their range as foraging primarily over waterways such as large streams, rivers, coastal strips or lakes, but rarely narrow, cluttered waterways (e.g. Anderson *et al.*, 2006). Although riparian zones, with their associated higher abundance of insects, are often the favoured foraging grounds for numerous insectivorous microbats (e.g. Bradbury & Vehrencamp, 1976; Barclay, 1991; Russo & Jones, 2003; Fukui *et al.*, 2006), only the species listed in Table 1 conform to the definition of 'trawling' microbats provided above. The current IUCN red-list category for each species and some of the common threats facing trawling bats are also summarised in Table 1. As a result of the convergence of morphology and behaviour among the species, the threats facing this

group have also converged on common themes that include the degradation of waterways, climate change and disturbance at cave roost sites.

Foraging behaviour

As a result of their highly modified morphology and behaviour, trawling bats successfully exploit a unique, nutritiously rewarding foraging niche that can include fish. *Noctilio leporinus* exhibits a suite of characteristics that optimise this bats ability to capture and handle fish, including large body size, long hind legs and large feet with laterally compressed claws and toes (Schnitzler *et al.*, 1994). Even though *N. leporinus* is considered to be a true piscivore, the proportion of fish in its diet varies seasonally. During the height of the wet season in Puerto Rico, fish may represent only 12–16 % of the diet, whereas during the dry season when fewer insects are available, fish may constitute up to 84 % of the diet of *N. leporinus* (Brooke, 1994). Access to a nutritious prey source that is potentially less seasonally variable in its availability compared to insects, can impact on the life-history tactics of some trawling bats. For example, in the Middle East, the Long-fingered bat *M. capaccinii* avoids hibernation over winter by exploiting introduced populations of the Western Mosquito fish *Gambusia affinis* in fishery ponds located within 800 m of the species cave roost (Levin *et al.*, 2006). Therefore, preying on fish may be important when insect activity is low during mid-latitude winters, or similarly during the dry season in the tropics.

The unique foraging mode of trawling bats results in energetic savings arising from what is referred to as the 'ground effect', where reduced drag over water confers energetic savings during flight (Siemers *et al.*, 2001). Multi-flash photography has been used to capture the



Figure 1. Global distribution of the trawling microbats listed in Table 1; refer to text for selection criteria. The symbols adjacent to each species' name are positioned to show the approximate location for the core of each species' distribution; see Table 1 for more detail on distributions. Symbols associated with each of the trawling *Myotis* species indicate the degree of relatedness among species based on the phylogeographic assessments published by Stadelmann *et al.* (2007). Like symbols indicate membership of the same or similar (unfilled, but same symbol) clade, see text for further explanation.

Table 1. Summary of the species of trawling microbats worldwide. Locality refers to the broad distribution of each species taken from the IUCN red-list (IUCN, 2010). This site also provides IUCN classifications: LC least concern, NT near threatened, Vu vulnerable and En endangered. Primary conservation concerns are the local threats identified by researchers that have the potential to impact on species foraging and / or roosting ecology. The analyses of species diet varies among studies; however the following categories were adopted to convey a relative comparison of the extent of piscivory: *Unknown* = No diet studies published; *None confirmed* = entirely insectivorous; *Very low* = Principally (>95 %) insectivorous, takes fish in captivity; *Low* = Predominantly (70 – 95 %) insectivorous; *Moderate* = flexible insectivores, fish may constitute 30 – 60 % of diet; *Great* = Predominantly (> 60 %) piscivorous. These categories are arbitrary and were scaled such that the best known piscivore *N. leporinus* fell into the highest category, although multiple categories for some species arise on the basis of variation among studies.

Species	Common name	Locality	IUCN	c. body size (g)	Primary roost-type	Extent of piscivory	Primary conservation concerns	References
<i>Noctilio albigentris</i>	Lesser Bulldog bat	Central & South America	LC	30	Tree hollows & buildings	Very Low	Loss of large, older roosting trees, pollution and fouling of water ways.	1, 2, 12, 54
<i>Noctilio leporinus</i>	Greater Bulldog bat	Central & South America, Caribbean	LC	55	Caves, tree hollows & abandoned buildings	Moderate–Great	Water pollution, degradation and loss of riparian vegetation	3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 53, 57
<i>Macrophyllum macrophyllum</i>	Long-legged bat	Central & South America	LC	6–9	Caves	None confirmed	Roost disturbance, water pollution	13, 14, 51, 63
<i>Myotis adversus</i>	Large-footed bat	Indonesia	LC	9–12	Unknown	Unknown	Unknown, likely to include loss of roosting habitat and water pollution	
<i>Myotis capaccinii</i>	Long-fingered bat	Europe, Middle East & Russia	Vu	6–10	Caves	Low	Degradation of habitat in and around known caves, canalization of rivers, modification of flow rates, competition with <i>M. daubentonii</i>	15, 16, 22, 50, 52, 56, 58
<i>M. dasycneme</i>	Pond bat	Russia & Europe	Vu	14–20	Building, bat boxes, caves	None confirmed	Persecution at roost sites, water fouling and pollution	17, 22, 61, 67
<i>M. daubentonii</i>	Daubenton's bat	Europe & Asia	LC	6–12	Tree hollows, rock crevices & caves	Very Low	Removal of riparian vegetation, water fouling and pollution, disturbance at hibernacula	18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 55, 62, 68, 69
<i>M. hasseltii</i>	Lesser Large-footed bat	Asia	LC	7–8	Unknown	Unknown	Largely unknown	29
<i>M. horsfieldii</i>	Horsfield's bat	Asia	LC	5–8	Caves & crevices	Unknown	Largely unknown	29
<i>M. macrodactylus</i>	Japanese Large-footed bat	Japan & Russia	LC	6–11	Caves	None confirmed	Roost disturbance and destruction, loss of foraging habitat	30, 31
<i>M. macropus</i>	Large-footed myotis	Australia	LC*	9–12	Caves, tree hollows, bridges, tunnels, disused mud nests	Low	Loss of riparian vegetation and associated roosts, drought, water fouling and pollution	32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 64, 65, 66, 70

Table 1. (Cont'd) Summary of the species of trawling microbats worldwide. Locality refers to the broad distribution of each species taken from the IUCN red-list (IUCN, 2010). This site also provides IUCN classifications: LC least concern, NT near threatened, Vu vulnerable and En endangered. Primary conservation concerns are the local threats identified by researchers that have the potential to impact on species' foraging and / or roosting ecology. The analyses of species diet varies among studies, however the following categories were adopted to convey a relative comparison of the extent of piscivory: *Unknown* = No diet studies published; *None confirmed* = entirely insectivorous; *Very low* = Principally (>95 %) insectivorous; takes fish in captivity; *Low* = Predominantly (70 – 95 %) insectivorous; *Moderate* = flexible insectivores, fish may constitute 30 – 60 % of diet; *Great* = Predominantly (> 60 %) piscivorous. These categories are arbitrary and were scaled such that the best known piscivore *N. leporinus* fell into the highest category, although multiple categories for some species arise on the basis of variation among studies.

Species	Common name	Locality	IUCN	c. body size (g)	Primary roost-type	Extent of piscivory	Primary conservation concerns	References
<i>M. macrotarsus</i>	Philippine Large-footed myotis	Borneo & Philippines	NT	25	Caves	Unknown	Largely unknown, likely to include small island population sizes, disruption to cave roosts	42, 43
<i>M. ricketti</i>	Rickett's Big-footed bat	China	NT	20–30	Caves	Moderate–Great	Roost disturbance, water fouling and pollution	44, 45
<i>M. ruber</i>	Red myotis	South America	Vu	6–9	Foliage?	Unknown	Small populations, habitat destruction	46, 59, 60
<i>M. stalkerii</i>	Moluccan Mouse-eared bat	Indonesia	En	17	Caves	Unknown**	Reasons for rarity unknown, but likely to reflect threats faced by other trawling species	47
<i>M. vivesi</i>	Mexican Fishing bat	Mexico	Vu	25	Caves & rock crevices	Moderate***	Introduced predators, water fouling and pollution, small island populations	5, 48, 49

*There is currently no IUCN listing for *M. macropus*, the category given here is for *M. adversus* which is the previous name for the Large-footed myotis species present in Australia (see Cooper *et al.*, 2001).

**Cited as a 'fish-eating' bat in Flannery (1995), however there have been no diet studies published on this species.

***Although typically considered one of the two 'truly piscivorous' species, the majority of *M. vivesi*'s diet consists of marine crustaceans.

References: Kalko *et al.* (1998),²Fenton *et al.* (1993),³Schnitzler *et al.* (1994),⁴Brooke (1994),⁵Altenbach (1989),⁶Wenstrup & Suthers (1984),⁷Novick & Dale (1971),⁸Campbell & Suthers (1988),⁹Suthers (1965),¹⁰Bordignon (2006a),¹¹Bordignon (2006b),¹²Aguiar *et al.* (2002),¹³Meyer *et al.* (2005),¹⁴Hamison (1975),¹⁵Levin *et al.* (2006),¹⁶Almenar *et al.* (2006),¹⁷Britton *et al.* (1997),¹⁸Kalko & Schnitzler (1989),¹⁹Jones & Rayner (1988),²⁰Warren *et al.* (2000),²¹Rydell *et al.* (1999),²²Siemers *et al.* (2001),²³Kokurewicz (1995),²⁴Russo (2002),²⁵Siemers *et al.* (2001),²⁶Boonman *et al.* (1998),²⁷Warren *et al.* (2000),²⁸Britton & Jones (1999),²⁹Payne & Francis (2005),³⁰Funakoshi & Takeda (1998),³¹Fukui *et al.* (2004),³²Cooper *et al.* (2001),³³Jones & Rayner (1991),³⁴Seebeck & Hamilton-Smith (1967),³⁵Dwyer (1970),³⁶Law & Urquhart (2000),³⁷Thompson & Fenton (1982),³⁸Lloyd *et al.* (1999),³⁹Barclay *et al.* (2000),⁴⁰Anderson *et al.* (2006),⁴¹Robson (1984),⁴²Esselestyn *et al.* (2004),⁴³Turner *et al.* (2003),⁴⁴Ma *et al.* (2006),⁴⁵Ma *et al.* (2003),⁴⁶Lopez-González *et al.* (2001),⁴⁷Flannery (1995),⁴⁸Stadelmann *et al.* (2004),⁴⁹Blood & Clark (1998),⁵⁰Almenar *et al.* (2008),⁵¹Brinkløv *et al.* (2009),⁵²Biscardi *et al.* (2007),⁵³Börk (2006),⁵⁴Dechmann *et al.* (2009),⁵⁵Luan *et al.* (2009),⁵⁶Papadatou *et al.* (2009),⁵⁷Dias *et al.* (2008),⁵⁸Sbragia & Pessôa (2008),⁵⁹Smimov *et al.* (2008),⁶⁰Todd & Waters (2007),⁶¹Weinbeer & Kalko (2007),⁶²Campbell (2009),⁶³Papadatou *et al.* (2009),⁶⁴Waters (2007),⁶⁵Campbell (2007),⁶⁶Campbell *et al.* (2009),⁶⁷Ciechanowski *et al.* (2009),⁶⁸Akasaka *et al.* (2008),⁶⁹Kapfer *et al.* (2008),⁷⁰Schulz (1998).

intricate movements of three species of trawling bats, and images have been matched to concurrent echolocation recordings to gain an intimate insight into the methods of prey capture used by each species (e.g., Schnitzler *et al.*, 1994). Using these methods, several hunting strategies have been revealed for the predominantly piscivorous *N. leporinus*; high search flight, low search flight, and random, directed and memory-directed rake modes (Schnitzler *et al.*, 1994). The raking modes of *N. leporinus* are similar to the foraging strategies reported for both *M. daubentonii* (Jones & Rayner, 1988; Kalko & Schnitzler, 1989; Britton & Jones, 1999), and the Large-footed Myotis *M. macropus* (Jones & Rayner, 1991) where bats take prey from the water surface with their tail membrane (often for smaller prey) or their large feet (for bigger prey items). Kalko & Schnitzler (1989) describe the hunting behaviour of *M. daubentonii* as consisting of a search phase, approach flight, tail down stage (capture of prey) and finally head down stage where the bat transfers the prey from either its feet or tail membrane, to its mouth during flight. Each of these stages is accompanied by distinct frequency modulated (FM) echolocation call patterns typical of trawling myotis bats, whereas *N. leporinus* emits a combination of constant frequency and FM pulses depending on the type of hunting pattern it adopts (Schnitzler *et al.*, 1994). All of these characteristics combine to define a remarkable group of microbats which have converged on similar foraging behaviour as a result of their common morphology.

There is considerable variation in the amount of information available on trawling bats. Species such as the Greater Bulldog bat *Noctilio leporinus* (e.g. Suthers, 1965; Altenbach, 1989; Brooke, 1994; Schnitzler *et al.*, 1994; Bordignon, 2006ab) and Daubenton's bat *Myotis daubentonii* (e.g. Kokurewicz, 1995; Jones & Rayner, 1988; Britton & Jones, 1999; Siemers *et al.*, 2001; Russo, 2002) have been comprehensively studied in both field and laboratory settings, the former from as early as the first half of the last century (Suthers 1965, and references therein). In comparison, little to no ecological research has been undertaken on several of the Asiatic species including the Lesser Large-footed bat *M. basselii* and Horsfield's bat *M. horsfieldii*. Similarly, the Moluccan Mouse-eared bat *M. stalkerii* was only recently re-discovered on the South Moluccan Islands in Indonesia by Flannery (1995) and very little is known of its ecology. Although the local challenges and concerns facing each species will be unique, the broader conservation issues identified by studies of a few species are also likely to threaten the persistence and viability of less well-known trawling bats.

Australia's Large-footed Myotis

Myotis macropus is a 9–12 g trawling bat whose distribution extends in a broad coastal band across northern and eastern Australia (Richards *et al.*, 2008). Found in both coastal and inland regions, *M. macropus* is uncommon and has a patchy distribution, predominantly at elevations < 300 m (Lumsden & Menkhorst 1995; Law & Anderson, 1999; Churchill, 2008). Prior to 1995, a single large-footed species of Myotis was recognised in Australia, *Myotis adversus*, with two sub-species; *M. a. molucarrum* and *M. a. macropus*. Based on comparisons of

cranial, external and bacellar morphology, Kitchener *et al.* (1995) elevated *M. a. molucarrum* and *M. a. macropus* to species status, with the former occurring predominantly throughout northern Australia, and *M. macropus* restricted to southern and eastern Australia (New South Wales, Victoria and South Australia; Richards, 1995). However, based on more recent mtDNA analyses, a single species of *Myotis* is again recognised in Australia (*M. macropus*), with the boundary between northern and southern mtDNA clades occurring in the vicinity of mid-Queensland (Cooper *et al.*, 2001). Until recently, the majority of studies of *M. macropus* (= *M. adversus* prior to 1995) in Australia came from populations in southern Queensland and northern NSW, where the bats were shown to forage directly over waterways (Dwyer, 1970; Thompson & Fenton, 1982; Jones & Rayner 1991; Barclay *et al.*, 2000), and feed predominantly on aquatic insects and also on fish (Robson, 1984; Law & Urquhart, 2000). Like other trawling bats that are adapted for foraging over water, *M. macropus* has long, pointed wings with slightly high aspect ratio and low wing loading (Norberg & Rayner, 1986; Jones & Rayner, 1991). The discontinuous distribution of *M. macropus* and the species close association with waterways, has the potential to create isolated, locally-adapted populations that may exhibit different behavioural traits.

Convergent evolution: parallel conservation concerns?

Disruptions at foraging sites

Some of the most important issues facing a group of bats that depend on waterways for foraging are those that impact on the quality and availability of suitable waterbodies. Trawling bats cannot detect submerged objects (Suthers, 1965) and instead rely on the echolocation glints returned from surface irregularities such as ripples, jumping fish or emerging insects. The ability to initially detect prey objects using echolocation has been shown to depend on the surface properties of the water, including the presence of surface clutter and the extent of surface turbulence (Boonman *et al.*, 1998; Rydell *et al.*, 1999; Siemers *et al.*, 2001). In the U.K., *M. daubentonii* can mistake floating duckweed (Lemnaceae) for prey, and unnaturally large amounts of duckweed can inhibit the trawling action of *M. daubentonii* (Boonman *et al.*, 1998). In contrast, clutter echoes returned from floating debris do not appear to disrupt the foraging behaviour of *N. leporinus* when hunting for fish along the Costa Rican shoreline (Schnitzler *et al.*, 1994). The preference for smooth over rippled water surfaces by foraging *M. macropus* remains to be quantified, however there is evidence that this species exhibits limited feeding behavioural plasticity.

Between 2002 and 2005, 134 *M. macropus* individuals were fitted with glowing chemiluminescent light-tags and their foraging behaviour was observed over an inland river, inland reservoir and two estuarine coastal areas (Campbell, 2007). At each of these sites bats spent an average of 88% of foraging time within 45 ± 9.0 cm (median) of the surface, frequently contacting the water surface (average 4 contacts/min). Bats foraged over relatively still pools, along bank edges, as well as over

shallow ripples and more turbulent water, exhibiting combinations of zig-zag patterned foraging, concentric circles and a J-shaped foraging mode; where bats would hover approximately 1 m above the surface before diving down to trawl the surface, then flying straight up again to repeat the process. Following behaviour, where up to four individuals were observed flying within a meter of each other and performing identical foraging patterns, is also common amongst *M. macropus* (Campbell, 2007). Group foraging may be an important factor for the evolution of sociality and *N. albiventris* also practices group foraging amongst social units, facilitated by 'eavesdropping' on the echolocation calls of kin (Dechmann *et al.*, 2009). The foraging behaviour of *M. macropus* was consistent among the different site types where bats were observed, and also among individuals (males and females, adults and juveniles) within single populations (Campbell, 2007). In contrast, *M. daubentonii* foraging at different altitudes in North Wales, U.K., adjusts the proportion of time it spends aerial hawking *v* trawling for prey over water in response to varying extents of inedible, aquatic material accumulated on the water surface (Todd & Waters, 2007). Again, such fine scale behavioural flexibility in foraging behaviour remains to be quantified for *M. macropus*.

Despite the potential negative consequences resulting from the proliferation of surface plants, moderate rises in nutrient levels may increase the foraging efficiency of trawling bats (e.g., Kokurewicz, 1995; Abbot *et al.*, 2009). All the species listed in Table 1 are also adept at aerial capture of insects over water and could therefore exploit increased densities of prey resulting from eutrophication events (Kokurewicz, 1995; Vaughan *et al.*, 1996; Law & Urquhart, 2000; Safi & Kerth, 2004). Like the majority of trawling bats, the diet of *M. macropus* predominantly consists of prey associated with the aquatic environment (Robson, 1984; Law & Urquhart, 2000; Campbell, 2007; Table 2). Therefore, the potential for biomagnification of toxicants up the food chain and accumulation of harmful products in bat tissue is great (Clark, 1978; Reinhold *et al.*, 1999; Clark & Shore, 2001) and trawling bats face an increased risk of these processes as polluted run-off from urban, industrial and agricultural areas invariably ends up in waterways. In Ireland, the Environmental Protection Agency has identified eutrophication (increased nutrient loads in waterways associated with decreased dissolved oxygen levels, excess plant and organic matter, resulting in altered invertebrate and fish communities) as the foremost threat to water surface quality (Abbot *et al.*, 2009). The foraging activity of *M. daubentonii* has both benefited (Kokurewicz, 1995) and suffered (Abbot *et al.*, 2009) from anthropogenic alterations to water nutrient levels, which likely reflects the subsequent changes (positive or negative) to preferred local aquatic prey abundance (Kalcounis-Rueppell *et al.*, 2007). *Myotis capaccinii* also shows a strong preference for foraging at sites with higher water quality (expressed by macro-benthic bioindicators, Biscardi *et al.*, 2007), and it is likely that all trawling bats are benefited by foraging over unpolluted waters.

The foraging efficiency of trawling bats may also be compromised by the adjustment of flow rates (e.g. canalisation of streams) and the lowering of water surface

levels such that rocks or other objects are exposed (e.g. due to diversions of large amounts of water for irrigation). Both *M. daubentonii* (Rydell *et al.*, 1999; Warren *et al.*, 2000; Siemers *et al.*, 2001) and *M. capaccinii* show a preference for foraging over smooth water surfaces; *M. capaccinii* concentrates 85% of foraging time over smooth surfaces, compared to only 15% over rippled water (Almenar *et al.*, 2006). Although based on small samples of captive individuals, similar conclusions have been drawn from flight cage experiments where *M. daubentonii*, *M. dasycneme* and *M. capaccinii* could easily detect and capture meal worms placed on linoleum screens (simulating smooth water surfaces). In comparison, prey placed on a 'clutter screen' could not be detected easily because return echolocation calls were scattered (Siemers *et al.*, 2001).

Table 2. The frequency of occurrence and average % volume (\pm S.E.) for each of the 14 potential prey categories identified in faecal pellets collected from 148 *Myotis macropus* during the summers between October 2002 and March 2005 at five sites in Victoria (from Campbell, 2007). Megaloptera and Orthoptera were collected in light-traps and sieve nets, but were not identified in *M. macropus* faecal pellets. Prey categories that were predominantly represented by aquatic taxa are denoted with asterisks.

Prey category	% frequency occurrence	Average % volume
Lepidoptera	41.2	21.6 \pm 2.9
*Diptera (mosquito)	38.5	21.1 \pm 2.7
*Trichoptera	38.5	18.7 \pm 2.6
*Diptera (other)	29.1	10.1 \pm 1.8
*Coleoptera	28.4	11.4 \pm 2.0
Araneae	10.8	6.2 \pm 1.8
*Hemiptera	10.1	4.0 \pm 1.4
*Osteichthyes (fish)	6.8	3.1 \pm 1.2
Hymenoptera	5.4	1.7 \pm 0.7
*Crustacea	4.1	0.6 \pm 0.2
*Odonata	2.7	0.5 \pm 0.2
Ephemeroptera	2.0	0.6 \pm 0.4
Megaloptera	0	0
Orthoptera	0	0

Climate change

The availability of suitable water bodies as foraging sites for trawling bats may further be affected by events associated with human-induced climate change. Whilst much debate still surrounds the finer details of exactly how climate change will manifest, several predictions are common throughout (Walther *et al.*, 2002 and see Hughes (2003) for a review of impacts in Australia,) and their impact on trawling bats may be hypothesised (Table 3). In many areas, including south-eastern Queensland, increasing aridity and persisting drought conditions associated with climate change (Hughes, 2003) will undoubtedly reduce the availability and abundance of suitable waterways for trawling bats. One conspicuous pattern evident in the distribution of these species throughout the world is the paucity of trawling bats in both Africa and Australia (Fig. 1). Currently, *M. macropus* is the only *Myotis* species recognised in Australia (Cooper *et al.*, 2001). Furthermore, only three *Myotis* species are present in Africa, one of which, the Rufous Mouse-eared

bat *M. bocagei*, is known to be active over waterways but does not have enlarged hind-feet. Whilst further research may reveal additional *Myotis* species in these continents, the predominance of woodland savannah with limited waterways in sub-Saharan Africa and arid landscapes in Australia likely explain the depauperate status of trawling bats in these regions (Fenton *et al.*, 1977) and may be indicative of the selection pressures that could be faced by trawling bats worldwide with decreased annual rainfall and warmer temperatures.

Disturbance at roost sites

The majority of trawling bats roost in caves (Table 1). Several species also roost in tree cavities (e.g., *M. daubentonii*; Encarnacao *et al.*, 2005) and the Lesser Large-footed bat *M. hasseltii* has been recorded roosting in bamboo culm (Kunz & Lumsden, 2003). Researchers have tended to focus on the unique and intriguing foraging behaviour of trawling bats, and consequently the specifics of their roosting requirements have received less attention. However, one commonality among most species is the close vicinity of roost sites to water. For example, the Japanese Large-footed bat *M. macrodactylus*

forages in both riparian woodland and over waterways immediately surrounding its summer cave roost that has a brook flowing directly outside the front entrance (Funakoshi & Takeda, 1998). In the Netherlands, the vulnerable Pond bat *M. dasycneme* roosts in buildings next to the artificial canals along which it commutes to its main foraging grounds over a lake (Verboom *et al.*, 1999). Furthermore, in southern Australia, most known roosts of Australia's *M. macropus* are located within 500 m of waterways (Caddle, 1998; Law *et al.*, 2001; Anderson and Law 2006; Campbell, 2009), although Schulz (1998) recorded the species roosting in culverts and disused fairy martin *Hirundo ariel* mud nests > 1 km from permanent water. At an inland reservoir in northeastern Victoria, Australia, 31 *M. macropus* were radiotracked to 17 tree roosts that were all located within 100 m of the water's edge. In addition, maternity roosts were found in both trees and between the basalt blocks that formed a tunnel in an aqueduct that leads into the reservoir (Campbell, 2009). Interestingly, *M. macropus* at this site did not switch roosts frequently, utilising only 1.3 ± 0.1 roosts during the tracking period (average 6.2 ± 0.6 days). Furthermore, the roost trees and cavities utilised by

Table 3. Summary of the possible influences of predicted climate-change induced scenarios on trawling bats. Information on the likely events associated with climate change was gathered from Walther *et al.* (2002) and Hughes (2003).

Possible climate-change induced event	Possible consequences	Likely impact on trawling bats + positive -ve negative
Increase in extreme hot weather events (i.e., longer, harsher droughts).	Increased evaporation leading to decreased water surface availability and associated changes in aquatic prey availability and abundance.	-ve
Changes to fire regimes.	Increased risk of extreme fire events leading to 1) decreased water quality from silt and other run-off, 2) loss of hollow bearing trees, 3) localised reductions in prey availability and abundance.	1,2 and 3) -ve
Decreased diurnal temperature ranges with minimum temperatures rising ~twice as fast as maximum temperatures.	Warmer nights potentially leading to 1) increased insect activity, 2) improved foraging efficiency and reduced thermoregulation costs, 3) less efficient entry into torpor if roosts are warmer, 4) social changes if the thermoregulatory benefits of clustering are lost due to naturally warmer roost microclimates.	1) + 2) + 3) -ve 4) -ve /+
Increase in storm events and number of rainy summer days.	1) Flooding. 2) Increase in surface water availability.	1) -ve if bats cannot forage efficiently over fast flowing, turbulent flood waters, + if flood waters are retained in wetlands and increases in local prey availability and abundance can be exploited by existing, nearby trawling bat populations. 2) +
Decrease in rainfall.	Increased aridity leading to decreased availability of permanent surface water and reduced prey availability and abundance.	-ve
Increase in sea surface temperature.	Alterations to coastal and / or estuarine invertebrate communities.	- ve/ + depending on diet specialisation and the direction of change in prey availability and abundance.
Increased sea levels.	1) Inundation of coastal cave roosts. 2) Increased surface area of coastal waters for foraging.	1) -ve 2) +
Increase in the number of intense tropical cyclones	Destruction of roosting habitat and fouling of foraging grounds with debris.	-ve

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M. macropus did not differ from paired available habitat trees and cavities, except that roost cavities had on average a smaller entrance area ($182 \pm 49 \text{ cm}^2$) compared to paired available cavities ($328 \pm 62 \text{ cm}^2$, $t = -2.327$, $P = 0.034$, Campbell, 2007). Seemingly, so long as roosts are near water, *M. macropus* successfully breeds in a wide variety of roosts including caves (Hamilton-Smith, 2001; Campbell, 2009), trees (Caddle, 1998, Law *et al.*, 2001; Campbell, 2009), bridges and tunnels (Dwyer, 1970; Barclay *et al.*, 2000; Law *et al.*, 2001). Roosts located close to water may decrease the commuting time to foraging sites, however they may also allow bats to exploit linear landscape elements like streams and rivers as navigation aids during commuting flights (Verboom *et al.*, 1999).

Nonetheless, distance *per se* does not appear to be a major consideration for some species. For example, the 6–9 g Phyllostomid *Macrophyllum macrophyllum*, commutes up to 7.5 km from day roost to foraging grounds, and can travel 35–47 km per night during foraging bouts in Panama (Meyer *et al.*, 2005). Furthermore, *M. macropus* has been recorded regularly commuting 10 km between a day roost and lake in Queensland (Barclay *et al.*, 2000). Similarly, the “Bat Cave” that houses 1000–2000 *M. ricketti* in northern China is located 8 km from a permanent reservoir where the bats forage (Ma *et al.*, 2006), suggesting that commuting costs may not be the principal factor determining roost location. Additional factors may help explain the generally close vicinity of day roosts to waterways including the temperature and humidity inside the roost, which may be influenced by the vicinity of mesic environs.

Regardless of location, however, it is reasonable to assume that colonies of trawling bats in caves that are accessible to humans are likely to suffer similar levels of disturbance as other cave roosting species (e.g. Tuttle, 1979; Hamilton-Smith, 2001). Furthermore, given the propensity for human settlements to converge on land near waterways, the anthropogenic risk posed to populations of trawling bats may be further enhanced by the loss and modification of riparian habitats. Riparian vegetation directly influences water quality and temperature (Sweeney *et al.*, 2004) and the clearance and degradation of riparian areas can, in addition to eliminating potential roost sites for tree-hole roosting species (e.g. *N. albiventris*, *M. macropus*, *M. daubentonii*; Table 1), also influence local insect abundance (Subramanian *et al.*, 2005) and negatively impact on foraging efficiency (Warren *et al.*, 2000; Fukui *et al.*, 2006). In addition, a newly emerging anthropogenic threat is the rapid proliferation of wind-energy farms throughout the landscape (Kunz *et al.*, 2007). Particularly when these facilities are located on bat migration or regular commuting paths, severe impacts on bat populations, including trawling bats, may be expected (Furmankiewicz, 2009; Tellería, 2009).

Intact riparian vegetation is also important for connectivity and gene-flow between populations of trawling bats. This fact was highlighted dramatically for *M. macropus* populations in Victoria when 175 individuals from five populations were genotyped at five novel (Genbank accession numbers EF605605 – EF605609) and two existing (Genbank AF203675 and AF203667) nuclear microsatellite loci (Campbell *et al.*, 2009). The global F_{ST} estimate across all populations was high and significantly different from zero (0.221; 99% CI 0.163–0.302), indicating limited gene flow and population differentiation (Campbell *et al.*, 2009). Accordingly, pairwise F_{ST} values among pairs of populations were also high, ranging from 0.021 ($P < 0.003$; between populations only 15 km apart on the same river) to 0.239 ($P < 0.003$; between populations ~700 km apart, when distances were calculated as the shortest distance between two populations via connecting water-ways). These findings suggest relatively low dispersal of *M. macropus* in Victoria, even among sites that are only 15 km apart on the same river, yet separated by agricultural areas and a small city (population ~14,000). A large proportion of riparian sites in south-eastern Australia occur on private land where stocking and grazing has a long history (Jansen & Robertson, 2001). These sites are typically in poor condition and lack structural complexity due to pressures from domestic stock use. The degradation of riparian habitats, particularly the loss of hollow bearing roost trees from riparian zones, may further contribute to the significant genetic isolation of *M. macropus* populations. A formal comparison of the genetic structuring of *M. macropus* populations occupying more contiguous native habitat would help confirm the affect of habitat degradation on gene flow in this species.

Conclusions

Detailed ecological studies on single species, such as *M. macropus*, are important for identifying processes operating at fine scales that may be of immediate threat and require detailed knowledge of species-specific requirements. However, such studies can also illuminate processes that may impact on similar, less well-studied species, such as many of the Asiatic trawling *Myotis* bats that share common morphological, echolocation and behavioural characteristics. As a consequence of human population growth and development, processes such as deforestation, habitat modification, climate change and the use of pesticides impact on a global scale. Consequently, overarching conservation issues raised from species-specific studies, primarily the protection of cave roosts, preservation of native riparian vegetation and prevention of harmful toxin accumulation in waterways, may highlight threats faced by all trawling bats and therefore benefit their conservation.

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Ecological specialisation and conservation of Australia's Large-footed Myotis

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