

# Do predators influence the behaviour of bats?

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## ABSTRACT

Many aspects of animal behaviour are affected by real-time changes in the risk of predation. This conclusion holds for virtually all taxa and ecological systems studied, but does it hold for bats? Bats are poorly represented in the literature on anti-predator behaviour, which may reflect a lack of nocturnal predators specialized on bats. If bats actually experience a world with minimal anti-predator concerns, then they will provide a unique contrast within the realm of vertebrate ecology. Alternatively, such predator-driven behaviour in bats may not yet be fully understood, given the difficulties in working with these highly mobile and nocturnal animals. We provide a wide-ranging exploration of these issues in bat behaviour. We first cover the basic predator-prey information available on bats, both on potential predators and the ways in which bats might perceive predators and respond to attacks. We then cover work relevant to key aspects of bat behaviour, such as choice of daytime roosts, the nature of sleep and torpor, evening roost departures, moonlight avoidance, landscape-related movement patterns, and habitat selection. Overall, the evidence in favour of a strong influence of predators on bat behaviour is equivocal, with the picture clouded by contradictory results and a lack of information on potential predators and the perception of risk by bats. It seems clear that day-active bats run a considerable risk of being killed by diurnal raptors, which are able to capture bats with relative ease. Thus, bats taking advantage of a pulse of insects just prior to sunset are likely taking risks to gain much-needed energy. Further, the choice of daytime roosts by bats is probably strongly influenced by roost safety. Few studies, however, have directly addressed either of these topics. As a group, insectivorous temperate-zone bats show no clear tendency to avoid apparently risky situations, such as activity on moonlit nights. However, some observations are consistent with the idea that predation risk affects choice of movement paths and feeding areas by temperate-zone bats, as well as the timing of roost departures. The behaviour of tropical bats, on the other hand, seems more generally influenced by predators; this is especially true for tropical nectarivores and frugivores, but also for insectivorous bats. Presumably there are more serious predators on bats in the tropics (e.g. specialized raptors or carnivorous bats), but the identity of these predators is unclear. More information is needed to assess fully the influence of predators on bat behaviour. There is much need for work on the ways in which bats perceive predators *via* auditory, visual, and olfactory cues, and whether bats have some knowledge of the risks posed by different predators. Also needed is information on how predators attack bats and how bats react to attacking predators. Difficult to obtain, but of critical value, will be information on the nature of the predation risk experienced by bats while away from roosts and during the full darkness of night.

*Key words:* anti-predator behaviour, bats, foraging behaviour, habitat use, moonlight avoidance, predation risk, risk perception, roost choice, roost departure, torpor.

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## I. INTRODUCTION

Great strides have been made over the last three decades in understanding the influence of predators on the behaviour of their prey (Sih, 1987; Lima & Dill, 1990; Lima, 1998; Caro, 2005). This body of work indicates that many aspects of animal decision-making are affected by real-time changes in the risk of predation, which may be driven by changes in the environment or predator behaviour. This large literature covers a broad range of topics, such as foraging behaviour (Lima & Dill, 1990; Caro, 2005), sociality (Krause & Ruxton, 2002; Caro, 2005), reproductive behaviour and mate choice (Magnhagen, 1991; Caro, 2005), animal personalities (Sih *et al.*, 2004), and the sensory (Fernández-Juricic, Erichsen & Kacelnik, 2004) and physiological (Creel, Winnie & Christianson, 2009) underpinnings of anti-predator decision-making. A major theme in this work is that observed behaviour often reflects a trade-off between safety and key behavioural objectives, such as gaining energy (Brown, 1988; Houston & McNamara, 1999; Bednekoff, 2007).

Nearly absent from this body of anti-predator work is research on bats. For instance, there is virtually no mention of bats in Caro's (2005) wide-ranging monograph on anti-predator behaviour, and only minimal mention in earlier syntheses (e.g. Lima & Dill, 1990). This situation does not reflect the taxonomic status of bats in the vertebrate world. In fact, bats comprise roughly 20% of all mammalian species, and exhibit a degree of ecological diversity greater than any other mammalian order. This relative lack of anti-predator work may reflect some apparent facts about bats and predators. First, there are few predators that specialize on bats (Gillette & Kimbrough, 1970; Sparks, Roberts & Jones, 2000), which could imply that bats are subject to less risk than other vertebrate taxa. Second, many of the most dangerous predators faced by bats (e.g. diurnal raptors; Speakman, 1991*b*) are not active at night (but see Harris, Dunning & Hoets, 1990; Rejt, 2004), thus many bats may encounter relatively few serious nocturnal predators. Third, and perhaps most importantly, bats are difficult to observe compared to most other vertebrates, thus their anti-predator behaviour is difficult to assess or appreciate fully.

This overall situation raises some interesting and potentially far-reaching questions. Do most species of bats actually experience a world largely free of the risk of predation? Does the existing body of work on anti-predator decision-making not apply to bats in general? If so, then bats would indeed comprise a unique group of vertebrates. Alternatively, the anti-predator behaviour so

typical of other vertebrates may indeed be generally present in bats, perhaps in a more subtle form not well understood at present.

If predators influence the behaviour of bats, then an increase in predation risk should generally lead to a change in behaviour favouring a safer behavioural option, at some cost to foraging efficiency or a similar measure. Such predation-risk-dependent behaviour could be apparent in many aspects of bat behaviour, such as choice of roosts, roost departures, activity and movement patterns, and overall habitat selection. Our exploration of these possibilities begins with some basic information on the potential predators of bats and the ways in which bats might perceive predators and respond to attacks. We then provide a survey of predation-risk-dependent behaviour in bats. Where possible, we synthesize the available literature and attempt to draw generalizations. Overall, our analysis suggests that, at least in some respects, the risk of predation has a major influence on bat behaviour. However, predators may have little influence on certain groups of bats, but firm conclusions here would be premature. We end with a discussion of how future work might address the anti-predator information gap in bats.

## II. PREDATOR-PREY BASICS IN CHIROPTERANS

### (1) Predators and predation

Which animals prey on bats? Just about any sort of animal that might eat bats has been recorded as a predator of bats, including many mammals, birds, reptiles, amphibians, and fish (Gillette & Kimbrough, 1970; Sparks *et al.*, 2000). A thorough treatment of this topic is beyond the scope of this paper, but a unifying theme in this work is that there are few vertebrate predators that specialize on bats. One apparent exception is the bat hawk (*Macheiramphus alcinus*) of the Old World tropics, which preys mainly on bats (Fenton, Cumming & Oxley, 1977*b*; Global Raptor Information Network, 2012*b*). Bat falcons (*Falco rufigularis*) of the New World tropics may occasionally specialize on bats (Black, Howard & Stjernstedt, 1979; Global Raptor Information Network, 2012*a*), but are more likely to feed on birds and insects (Beebe, 1950). Overall, most predation on bats seems to be opportunistic in nature.

Opportunistic predation by owls and other avian predators is prominent in many reports of predation on bats (Sparks

*et al.*, 2000). In fact, individual raptors can be specialized on bats to a significant extent (e.g. Lesiński, Ignaczak & Manias, 2009). Reports of such specialization frequently involve raptors hunting bats as they emerge from roosts at dusk. The best examples involve falcons, hawks, and owls hunting Mexican free-tailed bats (*Tadarida brasiliensis*) as the latter emerge from large maternity colonies in the caves of southern Texas (Stager, 1941; Lee & Kuo, 2001). This sort of roost-focused predatory behaviour by raptors occurs in other cave-based systems (e.g. Rodríguez-Durán & Lewis, 1985), as well as those in which bats roost in buildings (Barclay, Thomson & Phelan, 1982; Fenton *et al.*, 1994) or in the open (Welbergen, 2006).

Little information exists about predation well away from roosts. There are only a few scattered observations on this topic. For example, falcons have been observed hunting bats over drinking sites at dusk (Yosef, 1991) and over large lakes at dawn (Byre, 1990). Also, bats are frequently attacked immediately after release from captivity (Twente, 1954; Fenton *et al.*, 1994; Speakman, Lumsden & Hays, 1994). All of these observations involve diurnal predators hunting in appreciable light, which strongly suggests that bats abroad during daylight hours are at great risk of predation. In fact, Speakman (1991a, 1995) estimated that the predation rate on temperate-zone bats during daylight hours is 100–1000 times higher than the nocturnal rate.

Little is known about potential nocturnal predators that are capable of catching feeding bats on the wing and away from roosts. Nevertheless, many of the studies discussed below (Section III) imply the existence of such predators. The list of potential aerial predators seems fairly small, being most obviously limited to owls and perhaps some of the larger nightjars (see Owre, 1967). However, bat hawks (Old World tropics) may regularly hunt small bats all night (Harris *et al.*, 1990). Furthermore, trawling bats might contend with predation by large fish, and foliage- or ground-gleaning bats might often encounter arboreal or terrestrial predators while feeding.

Some large predatory bats may also take other bats in flight, such as the nycterids of tropical Africa, the megadermatids of tropical Asia and Australia (*Megaderma*, *Macroderma*), and the carnivorous phyllostomids (*Vampyrum*, *Chrotopterus*) of the New World tropics. These bats are known to consume smaller bats (Fenton *et al.*, 1993; Bonato, Facure & Uieda, 2004) and have been observed pursuing the latter in flight (Greenhall, 1968; Vaughan, 1976; Fenton *et al.*, 1993). Indeed, the nycterid *Nycteris grandis* can capture flying bats (Fenton, Gaudet & Leonard, 1983). Non-chiropteran prey may be taken more typically by these carnivorous bats (e.g. Vehrencamp, Stiles & Bradbury, 1977; Medellín, 1988), but chiropteran prey may form a substantial portion of their diets (e.g. Fenton *et al.*, 1993). The existence of substantial bat-on-bat predation would add a new dimension to our understanding of the anti-predator behaviour of tropical bats, especially since most tropical ecosystems harbour one or more carnivorous bat species.

Note that a lack of predators specialized on bats (Gillette & Kimbrough, 1970; Sparks *et al.*, 2000) does not necessarily imply that predators have little impact on bats. Consider the case of nest predation in birds, which is the single greatest source of mortality in the avian life cycle (see Martin & Briskie, 2009). Such nest predation is often driven by generalist and opportunistic predators that, in many cases, are not usually considered to be predators (e.g. mice; Schmidt *et al.*, 2001). A similar situation may exist in bats, in which the effects of predators are transmitted *via* the actions of many unlikely or unspecialized predators rather than a few specialized ones.

## (2) Encounters between bats and predators

The behaviour of predators attacking bats has rarely been described in detail. The most valuable observations derive from diurnal predators attacking molossid bats, especially Mexican free-tailed bats, that leave day roosts before sunset. Free-tailed bats emerge from large roosts in a dense stream of flying bats, often starting before sunset (Lee & Kuo, 2001). Raptors such as peregrine falcons (*Falco peregrinus*) and red-tailed hawks (*Buteo jamaicensis*) launch attacks directly into a stream of bats. Their success rates (sometimes well in excess of 50%; Lee & Kuo, 2001) are high in comparison to those with their typical prey (see also Black *et al.*, 1979). Great-horned owls (*Bubo virginianus*) can achieve similar hunting success on bats (Roberts, Yancey & Jones, 1997), and can presumably hunt well beyond sunset. Notably, *Buteo* hawks and large owls do not normally take prey on the wing, but appear able to do so when hunting bats.

Fenton *et al.* (1994) described the behavior of goshawks and two eagles hunting molossid bats (*Tadarida* spp.) in Africa as they exited roosts in small numbers at sunset. These raptors are also adept at capturing bats (approximately 50% capture rate), which they invariably approach from the rear. Quantitatively similar observations were reported in a system in which merlins (*Falco columbarius*) attacked roost-departing mormoopid bats in Puerto Rico (Rodríguez-Durán & Lewis, 1985). No comparable set of observations exists for any group of post-sunset-emerging bats. Furthermore, to our knowledge, attacks by predators on flying bats during the dark hours of the night have not been described.

Terrestrial predators such as raccoons, cats, and snakes have also been observed to capture bats in flight, mainly at roosts with large numbers of bats and amidst the confusion that large emergences can cause. Raccoons (McCracken, Gustin & McKamey, 1986; Sparks *et al.*, 2003) and cats (Rodríguez-Durán *et al.*, 2010) simply grab or swat bats out of the air, sometimes with much success (McCracken *et al.*, 1986). Observations of terrestrial predators attacking bats away from roosts are rare, but such attacks may be a problem for very low-flying or ground-gleaning bats (Delpietro *et al.*, 1994).

Observations of predators hunting bats within roosts are surprisingly scarce. However, Boinski & Timm (1985) suggest that squirrel monkeys (*Saimiri oerstedii*) routinely hunt tent-roosting bats by pouncing on the tent (bent leaves) in an

apparent effort to dislodge pups which then fall to the ground; the adult bats evade such attacks, but are then easy prey for kites that follow foraging bands of monkeys. Raccoons have also been observed to enter tree cavities in an apparent attack on roosting evening bats (*Nycticeius humeralis*; Sparks *et al.*, 2003); such attacks may be relatively common in tree-cavity-roosting bats (see also Veilleux *et al.*, 2003). Roosting bats attacked while torpid or non-volant would be easy prey for any predator that can reach them (e.g. Estók, Zsebok & Siemers, 2010).

Escape behaviour in bats is even less well described than that of the attacking predators. Once again, observations are largely limited to bats that are willing to exit roosts before sunset, especially the free-tailed bats (*Tadarida* spp.). A surprisingly common observation, however, is an apparent absence of escape manoeuvres by these molossid in the face of attacks from falcons (Black, 1976), owls (Twente, 1954), and larger hawks (Baker, 1962). Observed escape manoeuvres appear limited to aerial dodges or precipitous drops immediately before contact (Black, 1976; Fenton *et al.*, 1994). Despite the highly social roost departures in Mexican free-tailed bats, there are no reports of socially-coordinated escape manoeuvres such as those commonly observed in social birds (Lima, 1993). The few observations from other groups of bats suggest a similar range of escape behaviours in response to diurnal raptors. Aerial dodging and climbing has been observed in three vespertilionids (Twente, 1954; Black, 1976; Negro *et al.*, 1992). No apparent evasive manoeuvres were observed in sooty mustached bats (*Pteronotus quadridens*, Mormoopidae) targeted for attack by falcons (Rodríguez-Durán & Lewis, 1985).

We found no observations of bats escaping into vegetation when pursued by raptors, although we cannot rule out such escape behaviour given the paucity of observations. However, bats released during daylight tend to head for the nearest vegetation (Speakman *et al.*, 1994; Sparks, 2008; see also Byre, 1990). The use of vegetative cover for escape is common in small birds and mammals, and has implications for habitat choice at multiple scales (see Section III.5).

### (3) Predator detection and risk perception

Bats have a variety of sensory modalities that might be used to detect changes in the risk of predation. First, bats are among the most auditory of animals, hence it is reasonable to expect that bats detect predators *via* auditory cues. We suspect that this is indeed the case, but the available studies present a mixed picture. Studies have used owl calls to induce a change in the risk perceived by bats, but with little (Kalcounis & Brigham, 1994), ambiguous (Baxter *et al.*, 2006) or only subtle behavioural effects (Petrželková & Zukal, 2001). This lack of clear responses to owl calls could reflect either a lack of concern about owls, or a general lack of recognition of owl calls themselves. Distress calls from other bats, however, invoke a marked mobbing-like response in several groups of bats (see Section III.6). We know of no work on other auditory cues of predatory danger, but many possible cues could be envisioned.

The role of echolocation in the detection of predators is largely unstudied. Bats may have an ability to use echolocation to identify immobile predators lying in ambush, but we can cite no work to that effect. On the other hand, a roosting bat should have little trouble detecting a predator in motion. A bat in flight can almost certainly detect an oncoming aerial predator (or at least perceive the approach of a large object), but may also be faced with a serious echolocational blind spot to the rear. Perhaps such a blind spot explains the lack of evasive manoeuvring in response to predator attack in some instances (see Section II.2). In any case, many aspects of predator detection *via* echolocation should be amenable to experimental tests.

Vision as mode of predator detection has also received little attention in bats. Given the echolocational abilities of most bats, vision might seem to be unimportant in predator detection. However, several studies suggest that vision may dominate echolocation during navigation in many bats (see Orbach & Fenton, 2010). Hence, vision may also be generally important in predator detection. Furthermore, vision is likely a main mode of predator detection in pteropodid bats, as none use complex echolocation calls (Altringham, 1996). Experimental work on this topic should also be feasible.

Predator detection *via* chemical cues is a hallmark of many mammalian systems (Kats & Dill, 1998), and one would reasonably expect a similar ability in bats. However, two recent studies failed to demonstrate predator scent detection in two vespertilionid bats. Mouse-eared bats (*Myotis myotis*) showed no response to chemicals typically associated with mammalian carnivores (Driessens & Siemers, 2010), and big brown bats (*Eptesicus fuscus*) similarly failed to avoid the scent of raccoons or snakes (Boyles & Storm, 2007). A general lack of sensitivity to predator scents across all vespertilionids (and other bats) would have important behavioural implications (see also Section III.1).

In a more general sense, the observed behavioural responses of bats in many of the studies mentioned below imply an ability to perceive changes in the local risk of predation, but the source of that perception is often not clear. In many cases, the actual spatial and temporal changes in predation risk are either poorly understood or presumed to exist. Presumptions about risk and its perception are not unusual in the study of anti-predator decision-making (Lima, 2002), but the lack of baseline perceptual information on bats limits our ability to interpret some of the behavioural work discussed below.

## III. PREDATOR AVOIDANCE IN AN ECOLOGICAL CONTEXT

We next consider several contexts in which predators may influence the behavioural decisions made by bats. In all cases, we focus on real-time behavioural responses to real-time changes in predation risk. Evolutionarily fixed behavioural or morphological adaptations related to predators are also relevant, but are not our major focus.



### (1) Roost choice

Predators have clearly been a major evolutionary force in shaping the roosting ecology of bats (Kunz, 1982; Kunz & Lumsden, 2003). This fact is especially apparent given that bats are clearly at risk if disturbed into flight during the day (e.g. Boinski & Timm, 1985; Speakman, 1991*b*). In this sense, safety from predators (*via* roosts) is a critical feature in the biology of nearly all bats. However, the question of interest here is whether some aspects of roost choice by bats are influenced by ‘ecological time’ changes in the risk of predation. In other words, will an increase in local predator abundance cause a bat to shift its roost to another site? Do bats make trade-offs in roost choice, such as trading roost safety for a better microclimate?

Manipulative experiments altering predation risk at roosts may provide much insight into the role of predators in roost choice, but such studies are rare. In a quasi-experimental study, Barclay *et al.* (1982) found that the persistent attacks by a screech owl at a little brown bat roost (as bats exited from a building) were associated with a major decline in roost attendance, which was partially reversed when the owl was removed. Similarly, attacks by barn owls during evening roost departures prevented Hildebrandt’s horseshoe bats (*Rhinolophus hildebrandtii*) from returning frequently to the day roost during the night (Fenton & Rautenbach, 1986), which they typically did otherwise. Tent-making phyllostomid bats abandon roosts when discovered by predatory monkeys (Boinski & Timm, 1985); presumably such bats can fairly easily construct another roost. Such roost abandonment may be less likely when roosting sites are more limited.

Two recent experimental studies suggest that some bats cannot directly assess the safety of roosts *via* chemical cues of predators. Boyles & Storm (2007) found that roosting big brown bats showed no spatial avoidance of the scent of raccoons or tree-climbing snakes, and Driessens & Siemers (2010) similarly found no such avoidance in mouse-eared bats. Driessens & Siemers (2010) suggested that mouse-eared bats may occupy a roosting environment (deep caves) in which there is no strong selection for assessing predation risk. However, big brown bats historically roosted in tree cavities where they might readily interact with predators such as raccoons (e.g. Sparks *et al.*, 2003), hence their apparent inability to sense the chemical cues of predators is not so easily explained. If these results are general across vespertilionids and other taxa, then bats may assess roost safety *via* less direct cues about risk, such as roost entrance size, or very direct cues such as actual encounters with predators.

Standard approaches to the study of roost-site selection can provide some insight into the role of predators in roost choice, especially when anti-predator considerations are directly incorporated into the study design. Such studies typically compare roost sites chosen by bats to a random sample of sites in the local landscape, thus yielding insight into factors driving roost-site selection (Kunz & Lumsden, 2003; Barclay & Kurta, 2007). Using this approach, Jenkins *et al.* (1998) found that the roosts of common pipistrelles (*Pipistrellus pipistrellus*) tend to be in buildings that are closer

to substantial vegetation and have linear vegetation elements extending away from them, which presumably allow for safer roost departures and travel (see also Section III.5). Ferrara & Leberg (2005) found that insectivorous bats (mainly Rafinesque bats, *Corynorhinus rafinesquii*) chose the darkest and most obviously protective areas under bridges, but not the very darkest spots, which were near easy access points for predators. Such studies might be enhanced to include measures of local predator abundance, distance to the nearest owl nest, etc., for additional insight into predation-risk-sensitive roost choice.

### (2) Bats at the roost

We consider here some of the ways in which the behaviour of roosting bats might be influenced by predators. We focus on the way in which sleep and torpor might change in response to changes in the risk of predation. Such considerations are particularly relevant to foliage-roosting bats, which sleep in relatively exposed situations (e.g. Shump & Shump, 1982; Boinski & Timm, 1985). Predators probably play a lesser role in the sleep and torpor of cave-roosting bats, but even these bats may face trouble from predators (Estók *et al.*, 2010).

Sleep is a prominent behaviour in bats (Klose *et al.*, 2009; Zhao *et al.*, 2010), as in most mammals (Lesku *et al.*, 2006). Since a sleeping animal is relatively unresponsive to the external environment, time spent asleep is often time spent at risk to predators (Lesku *et al.*, 2006). However, mammals have behavioural control of both the quantity and depth of sleep (e.g. Lesku *et al.*, 2008), thus predation-risk-dependent sleep is a distinct possibility in bats. Along these lines, Zhao *et al.* (2010) suggest that anti-predator considerations might explain differences in the structure of sleep between two pteropodid species that vary in the degree of exposure while roosting. Vigilance has also been shown to detract from sleep in another open-roosting pteropodid bat, and vigilance levels (while low overall) increase substantially for those sleeping at the edge of a roosting colony (Klose *et al.*, 2009), suggesting that their quality of sleep is influenced by the perception of risk. We suspect that bats in general will show real-time changes in sleep characteristics with changing predation risk.

Diurnal torpor is a prominent feature of bat biology, and one that has received much more attention than sleep (Altringham, 1996). As with sleep, a key feature of torpor is a reduced ability to detect and respond to predators (Pravosudov & Lucas, 2000). Accordingly, predation risk might influence the degree of, and time spent in, torpor. Risk-dependent torpor has not received direct study in bats, but big brown bats may use shallow torpor in relatively unsafe roosting sites (Lausen & Barclay, 2006). Genoud & Bonaccorso (1986) also suggest that anti-predator concerns explain why open-roosting emballonurid bats usually remain normothermic, at least down to an air temperature of 20°C.

An important point here is the degree to which torpor compromises a bat’s ability to detect and respond to predators. Several studies have addressed such effects in bats, more than in any other torpor-using endotherm. Many torpor-using species (mainly vespertilionids) are able

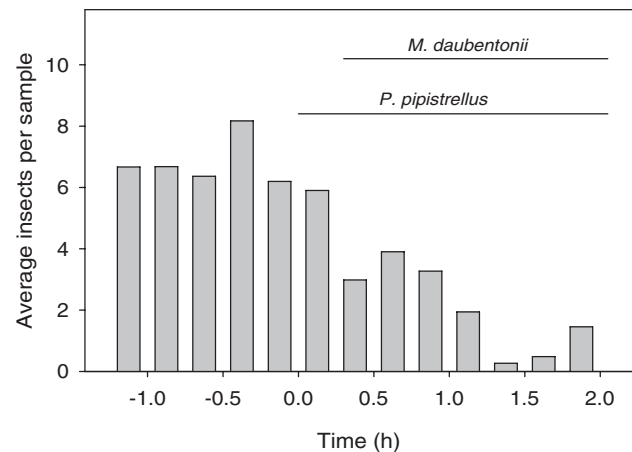
to initiate flight at body temperatures ( $T_b$ ) in the range of 28–30°C, and a few can do so down to 21°C (Studier & O'Farrell, 1972). Choi *et al.* (1998) determined that crawling and biting in the greater tube-nosed bat (*Murina leucogaster*) is limited to  $T_b > 8^\circ\text{C}$ , with flying limited to  $T_b > 29^\circ\text{C}$ . The  $T_b$  limit on flight is probably a key determinant of the degree to which a bat may go hypothermic in a risky situation. Choi *et al.* (1998) also noted that torpid bats can vocalize when cold (see also Speakman, Webb & Racey, 1991). Martin & Fenton (1978) suggest that such vocalizations might be defensive in some way, but the vocalizations of torpid bats can also attract predators (Estók *et al.*, 2010).

Vespertilionid bats in relatively deep torpor are largely unresponsive to non-tactile stimuli such as sound, light, and small temperature changes (Speakman *et al.*, 1991). Torpid bats are responsive to tactile stimuli, but much time is necessary to warm up enough to respond effectively. By contrast, Thomas (1995) found that hibernating *Myotis* bats were responsive to non-tactile predator cues, as measured by the tendency of several bats to engage in flight during the hours after human entries into a hibernaculum. Thomas (1995) suggested that the responsive bats were near the end of a torpor cycle and thus not in deep torpor, and that such bats cause subsequent arousals in other bats. Perhaps these sorts of socially stimulated arousals might act as a social predator detection system in torpid/hibernating bats (see also Section III.6). Such a system is feasible since a predator would not immediately kill all bats in a given roost, thus giving non-attacked bats the time they need to warm up and escape.

### (3) Roost departure

Leaving a roost too early is clearly dangerous, and late-hunting diurnal raptors (Rodríguez-Durán & Lewis, 1985; Fenton *et al.*, 1994) could be avoided simply by delaying roost departure until complete darkness (see also Section II.1). However, the cost of doing so is less time available for feeding, or the loss of food to competitors (Lee & McCracken, 2001; Welbergen, 2006). For some insectivorous bats, a delayed departure may mean missing a pre-sunset peak in insect abundance [Fig. 1; Rydell, Entwistle & Racey (1996); see also Jones & Rydell (1994) and Speakman *et al.* (2000)]. Hence, there is a foraging benefit to early roost departure, but also a substantial risk in feeding under bright conditions. Questions about this trade-off drive many studies of roost departure.

Empirically speaking, many bat species tend to leave roosts just after sunset (Erkert, 1978; see also Welbergen, 2008). Such behaviour may well represent a compromise solution to the timing of roost departures, in which emerging bats miss some but not all of the early foraging opportunities (e.g. Rydell *et al.*, 1996; Speakman *et al.*, 2000). In a comparative study, Jones & Rydell (1994) found that fast-flying bats emerge from roosts earlier than other types of bats, sometimes an hour or more before sunset (e.g. Lee & McCracken, 2001). These bats are presumably able to cope better with diurnal raptors, but evidence suggests that they are still fairly easily

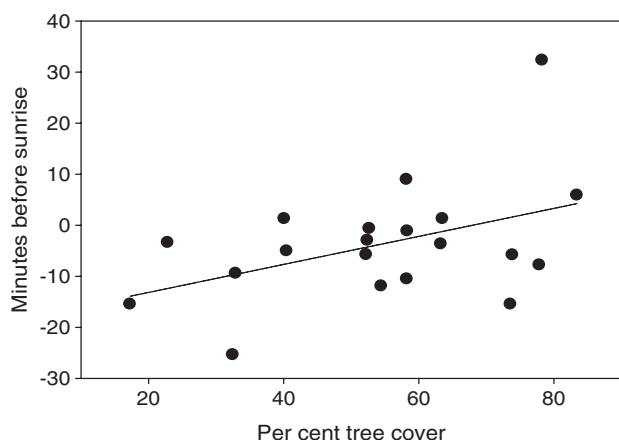


**Fig. 1.** Average insect abundance (appropriate to small insectivorous bats) relative to the onset of feeding activity (zero point) of the common pipistrelle (*P. pipistrellus*) around a pond in northern Scotland. Insects were sampled *via* hand nets; data from suction traps were quantitatively similar. Horizontal lines indicate the presence of feeding common pipistrelles and Daubenton's bats (*M. daubentonii*). These bats largely missed the higher density of insects present earlier in the evening. From data in Rydell *et al.* (1996).

captured (see Section II.2). Furthermore, soprano pipistrelles (*P. pygmaeus*), a bat not in the fast-flying guild, may sometimes leave roosts 30–60 min before sunset (Russo *et al.*, 2011). Vegetation-gleaning bats tend to emerge well after sunset (Entwistle, Racey & Speakman, 1996; Rydell *et al.*, 1996); for these bats, late departures may have lower costs because their insect prey are more active after dark (Jones & Rydell, 1994).

The most direct evidence of anti-predator trade-offs in roost departures would be real-time responses in departure times to observable changes in risk. Some limited observational work suggests such an effect. For instance, the presence of eagles delays emergence in a large roosting colony of grey-headed flying foxes (*Pteropus poliocephalus*; Welbergen, 2006). Common pipistrelles (Jenkins *et al.*, 1998) and barbastelles (*Barbastella barbastellus*; Russo, Cistrone & Jones, 2007) depart roosts earlier as the percent tree cover near roosts increases (Fig. 2). Roost departure in the southern blossom bat (*Syconycteris australis*), a small pteropodid, is delayed when a nearly-full moon is visible at sunset (Law, 1997). However, the available experimental work on this topic is decidedly mixed. In some molossid, roost departures can be brought to a halt by distress calls resulting from simulated bat captures (McWilliam, 1989; Fenton *et al.*, 1994). On the other hand, the simulated or actual presence of owls close to roost exits had no effect on departure times in little brown bats (*M. lucifugus*) (Kalcounis & Brigham, 1994) or serotine bats (*Eptesicus serotinus*) (Petrželková & Zúkal, 2001, 2003). In the latter cases, it is not clear whether the bats could perceive the perched owls.

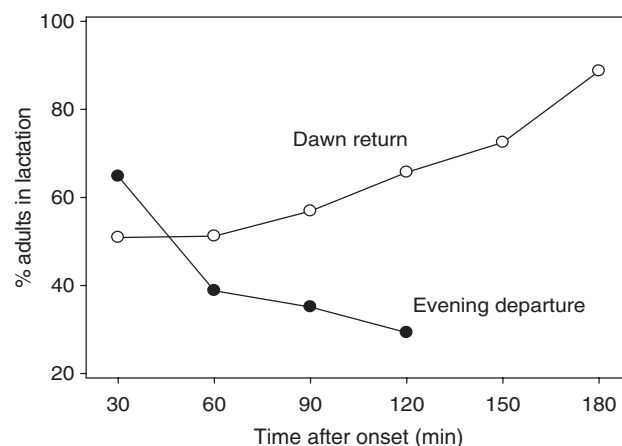
Additional evidence for anti-predator trade-offs comes from studies examining roost departures as a function



**Fig. 2.** Relationship between the timing of roost departure by common pipistrelles and tree cover within 50 m of roost entrances (percent tree cover) in northern Scotland. Departure data are averages for a given roost with more than a single observation (applies to only two points). Negative values indicate departures after sunset. Bats roosting in relatively high-cover sites tended to depart significantly ( $P < 0.05$ ) earlier than those in areas with few trees. From data in Jenkins *et al.* (1998).

of the reproductive state of females. Many studies show that animals with a more immediate need for energy are willing to accept a greater risk of predation to obtain food (Lima, 1998; Caro, 2005), and such 'state-dependent' risk-taking is a hallmark of predation-risk-dependent behaviour (Houston & McNamara, 1999). State-dependent work on roost departures in bats is based on the fact that a female's need for food increases markedly during the reproductive period (see also Barclay, 1989), hence reproductive females should emerge earlier from roosts (i.e. take greater risks) than non-reproductive bats. Such behaviour has been observed in Mexican free-tailed bats (Lee & McCracken, 2001; Reichard *et al.*, 2009) and in grey-headed flying foxes (Welbergen, 2006). Duvergé *et al.* (2000) show that three insectivorous bats (*Eptesicus nilssonii*, *Rhinolophus ferrumequinum*, *R. hipposideros*) emerged earlier as lactation progressed. However, females emerged later as pregnancy progressed, perhaps reflecting the avoidance of risk-taking when heavy and less manoeuvrable in flight (see also Crespo, Burns & Linhart, 1970; Hamilton & Barclay, 1998). Reproductive females may also return to roost later in the morning than other bats (Fig. 3; Lee & McCracken, 2001). We know of no experimental work altering the energetic states of bats prior to roost departure, but such work ought to be feasible where roosts are predictable and bats are accessible.

The temporal clustering of roost departures in insectivorous bats has also been interpreted as an anti-predator strategy (Swift, 1980; Speakman *et al.*, 1992; Speakman, Stone & Kerslake, 1995). The basic idea is that individual bats benefit from a sort of temporal selfish herd effect or simple risk dilution (see Krause & Ruxton, 2002) when leaving roosts if multiple individuals depart in quick succession. Field observations in molossid suggest that such temporal clustering increases after the



**Fig. 3.** Effect of reproductive state on the timing of evening roost departures from, and dawn returns to, a large maternity roost of Mexican free-tailed bats in southern Texas, USA. The percent of adult bats captured that were in a reproductive state (indicated by active lactation) is plotted as a function of time after the onset of roost departures or the dawn return to the roost. Early roost departures were enriched in lactating bats, as were the later dawn arrivals. Each data point represents well over 100 bats captured (range 121–598) during the latter portion of the reproductive cycle. From data in Lee & McCracken (2001).

arrival of bat falcons (Chase *et al.*, 1991) or bat hawks (McWilliam, 1989) at a roost. However, roost departures are also clustered in the Azores noctule (*Nyctalus azoreum*; Irwin & Speakman, 2003), which inhabits predator-free islands. Experimental studies of departure clustering, all in vespertilionids, provide mixed results. Clustering did not increase significantly with owl model presentations (with or without vocalizations) in little brown bats (Kalcounis & Brigham, 1994) or common pipistrelles (Speakman *et al.*, 1992); a minor increase in clustering was seen in another raptor model study (Petrželková & Zukal, 2001). A more substantial increase in clustering was observed in response to a live barn owl (*Tyto alba*; Petrželková & Zukal, 2003). Overall, a general link between predation risk and departure clustering is not yet well established.

#### (4) Foraging activity under moonlight

Little is known about the risk that bats face during much of the night. Presently, our main source of insight into such risk is moonlight avoidance behaviour in foraging bats. The basic idea is straightforward: if feeding bats experience an appreciable risk of predation at night, then they should respond with a drop in activity under brighter nocturnal conditions, assuming that predators are more adept in brighter light (e.g. Kotler, Brown & Hasson, 1991). An avoidance of activity under bright moonlight is well known in other small nocturnal mammals (Caro, 2005; Kotler *et al.*, 2010).

Moonlight avoidance is, in fact, the most routinely addressed anti-predator issue in bat behaviour. Several relevant studies are summarized in Table 1. To gain a



broad perspective on the role of moonlight in bat activity, we were liberal in the inclusion of studies. Moonlight avoidance was not the main focus of many of these studies, hence the effects of moonlight were often summarized briefly in the form of an  $F$ -statistic,  $P$  value, or just a qualitative statement. In some cases, moonlight effects were excluded from full statistical consideration due to early indications of the lack of an effect. We present species-specific results when such information was provided, but many studies combined measures of activity over several species or guilds due to difficulties in species-level identification. Further, some taxonomic and geographical biases are apparent, especially an over-representation of vespertilionids and phyllostomids in the insectivorous and frugivorous/nectarivorous bats, respectively. Table 1 nevertheless represents the best available information on moonlight avoidance.

There is fairly broad support for moonlight avoidance in tropical frugivores and nectarivores, both new world (Phyllostomidae) and old world (Pteropodidae), as well as in tropical carnivores (Table 1). Such support follows from the very earliest formal studies (Erkert, 1974, 1982; Morrison, 1978) to those more recent. Several exceptions to moonlight avoidance have some plausible anti-predator explanations, such as the lack of nocturnal predators capable of taking fairly large phyllostomid bats on the island of Puerto Rico (Gannon & Willig, 1997; Rodríguez-Durán & Vázquez, 2001). Thies, Kalko & Schnitzler (2006) suggested that the relatively small size of chestnut short-tailed bats (*Carollia castanea*) does not allow them to forgo feeding for long periods during full moons, and Mancina (2008) suggested that Leach's single leaf bats (*Monophyllus redmani*) experience low risk due to their flight agility and highly vegetated environment. One study indicated an increase in phyllostomid activity under bright moonlight (Santos-Moreno, Velásquez & Martínez, 2010), a result that is difficult to explain.

The situation in insectivorous bats is not as clear. There are several cases of apparent moonlight avoidance in tropical insectivorous bats (Table 1). Some studies show very clear effects, such as a strong suppression of insectivore activity under full moonlight in central Africa (Fenton *et al.*, 1977a). Usman *et al.* (1980) (see also Singaravelan & Marimuthu, 2002) observed a marked increase in activity during a lunar eclipse in India (Fig. 4), despite a drop in insect activity during the eclipse. Nevertheless, tropical insectivorous bats remain relatively unstudied, and not all studies suggest strong moonlight avoidance (Table 1).

Considering temperate-zone insectivorous bats (Table 1), there are many studies but little support for lowered activity under bright moonlight. This view corresponds with that of Karlsson, Eklöf & Rydell (2002), who claim that no unequivocal cases of moonlight avoidance exist for temperate bats. In fact, this view has become common in the study of temperate bats, to the point where moonlight effects are often not reported in detail (Table 1). However, it is possible that the frequent (often unavoidable) pooling of species in such analyses may obscure moonlight avoidance in some species (e.g. study by Ciechanowski *et al.*, 2007; Table 1).

The reasons for this temperate-tropical dichotomy in moonlight avoidance are not clear. A straightforward possibility is that tropical bats suffer greater predation from raptors, but the lack of information about predation on bats makes it difficult to assess such possibilities. There are tropical raptors that routinely hunt bats, but mainly during brief windows of opportunity at sunset and sunrise (McWilliam, 1989; Chase *et al.*, 1991; Fenton *et al.*, 1994), although bat hawks may hunt on moonlit nights (Harris *et al.*, 1990). Carnivorous bats (see Section II.1) might be driving moonlight avoidance in tropical insectivores, but it is not clear that their hunting efficiency would increase under moonlight.

Comparisons between tropical and temperate bats are also complicated by the taxonomic differences between these two groups. Results from the temperate zone are dominated almost completely by work on vespertilionid insectivores, whereas several families are represented in tropical studies (Table 1). There are, however, no compelling reasons to expect family-specific moonlight avoidance. A related complication is the role that diet might play in moonlight avoidance. For instance, the effect of moonlight on tropical frugivores could reflect a greater diversity of tropical predators on bats or perhaps the predictable feeding locations of such bats. A comparison between tropical and temperate frugivores would be valuable in making such a distinction, but frugivores are absent from temperate bat communities.

Some cases of apparent moonlight avoidance may reflect a drop in prey abundance rather than a response to greater risk (Lang *et al.*, 2006; see also Turner, 1975). Moonlight can suppress the abundance of some types of insects (see Jung & Kalko, 2010), but such effects have not typically been included in studies of moonlight avoidance by bats. Studies that found a drop in prey abundance on moonlit nights often did not find a corresponding reduction in bat activity (e.g. Anthony, Stack & Kunz, 1981; Jung & Kalko, 2010; but see Lang *et al.*, 2006). Furthermore, moonlight avoidance in frugivorous bats is unlikely to reflect a drop in fruit resources on moonlit nights. Note that the idea of prey-driven moonlight avoidance implies that bats have behavioural options more valuable than foraging when prey density is relatively low, otherwise feeding would likely proceed. Such options might include caring for offspring at the roost or torpor if prey density is very low (e.g. Anthony *et al.*, 1981). A large body size might also allow for greater fasting during bright moonlight, as suggested by Erkert (1982) and Law (1997).

## (5) Use of space while foraging

Several studies suggest that predators influence the use of space by bats. A major focus here is the tendency of insectivorous bats to move or feed along tree lines or vegetated fencerows. Other studies address the general avoidance of open habitats where the risk of predation might be high. We first deal with activity focused on vegetated landscape elements through otherwise open habitats.



Table 1. Avoidance of nocturnal activity during bright moonlight

Family	Genera or species	Common name <sup>a</sup>	Avoid?	Comments <sup>b</sup>	Reference
<b>Tropical frugivores (mainly) and nectarivores</b>					
Pteropodidae	<i>Cynopterus sphinx</i>	Short-nosed fruit bat	Yes	Moonlight effect on overall activity, not on roost departure	Elangovan & Marimuthu (2001)
	<i>Rousettus aegyptiacus</i>	Egyptian fruit bat	Yes	In laboratory, exposed to natural moonlight	Erkert (1974)
	<i>Syconycteris australis</i>	Common blossom-bat	Yes	Long delays in roost departure under bright moonlight	Law (1997)
	<i>Nyctimene robinsoni</i>	Eastern tube-nosed bat	Yes	Body temperature used as measure of activity (in field)	Riek <i>et al.</i> (2010)
	<i>Cynopterus sphinx</i>	Short-nosed fruit bat	Yes	Major increase in activity during a lunar eclipse	Singaravelan & Marimuthu (2002)
Phyllostomidae	<i>Phyllostomus hastatus</i>	Greater spear-nosed bat	Yes	Laboratory result related to general level of activity; bats exposed to natural moonlight	Erkert (1974)
	<i>Artibeus lituratus</i>	Great fruit-eating bat	Yes	Laboratory result: bats exposed to natural moonlight	Erkert (1974)
	<i>Artibeus obscurus</i>	Dark fruit-eating bat	No	Little suggestion of moonlight avoidance	Esbérard (2007)
	<i>Artibeus lituratus</i>	Great fruit-eating bat	Yes	Avoid full moon, but mist net captures not maximal on darkest nights	Esbérard (2007)
	<i>Artibeus jamaicensis</i>	Jamaican fruit bat	Yes	Avoid full moon, but mist net captures not maximal on darkest nights	Esbérard (2007)
	<i>Carollia perspicillata</i>	Seba's short-tailed bat	Yes	Avoid full moon, but mist net captures not maximal on darkest nights	Esbérard (2007)
	<i>Sturnira lilium</i>	Little yellow-shouldered bat	Yes	Avoid full moon, but mist net captures not maximal on darkest nights	Esbérard (2007)
	<i>Carollia perspicillata</i>	Seba's short-tailed bat	Yes	Tendency to be at day roost under bright moonlight	Fleming & Heithaus (1986)
	<i>Stenoderma rufum</i>	Red fig-eating fruit bat	No	Suggested no appropriate nocturnal predators in Puerto Rican forests	Gannon & Willig (1997)
	<i>Phyllostomus discolor</i>	Pale spear-nosed bat	Yes	Laboratory result related to general level of activity	Haeussler & Erkert (1978)
	<i>Artibeus lituratus</i>	Great fruit-eating bat	Yes	Laboratory result related to general level of activity	Haeussler & Erkert (1978)
	<i>Carollia perspicillata</i>	Seba's short-tailed bat	Yes	Main effect on distance moved to feed rather than overall activity	Heithaus & Fleming (1978)
	<i>Phyllonycteris poeyi</i>	Poey's flower bat	Yes	Suggested that lesser flying ability leads to avoidance	Mancina (2008)
	<i>Monophyllus redmani</i>	Leach's single leaf bat	No	Attributed lack of response to stronger flight and shrubby (safe?) habitat	Mancina (2008)
	<i>Artibeus jamaicensis</i>	Jamaican fruit bat	Yes	Clear avoidance which correlates to moon rise and set	Morrison (1978)
	<i>Artibeus lituratus</i>	Great fruit-eating bat	Yes	Longer periods of inactivity under moonlight	Morrison (1980)

Table 1. (Cont.)

Family	Genera or species	Common name	Avoid?	Comments <sup>a</sup>	Reference
	<i>Vampyroides caraccioli</i>	Great stripe-faced bat	Yes	Longer periods of inactivity under moonlight	Morrison (1980)
	<i>Artibeus jamaicensis</i>	Jamaican fruit bat	No	Suggested no appropriate nocturnal predators in Puerto Rican forests	Rodríguez-Durán & Vázquez (2001)
	<i>Artibeus</i> spp.	Neotropical fruit bats	No	Captures peaked in second-to-highest moonlight category	Santos-Moreno <i>et al.</i> (2010)
	<i>Choeroniscus godmani</i>	Godman's long-tailed bat	No.	Clear tendency for maximum captures in brightest moonlight	Santos-Moreno <i>et al.</i> (2010)
	<i>Carollia castenea</i>	Chestnut short-tailed bat	No	Suggested that this relatively small bat cannot avoid feeding	Thies <i>et al.</i> (2006)
<b>Tropical carnivores</b>					
Megadermatidae	<i>Megaderma lyra</i>	False vampire bat	Yes	Data from two bats, but clear avoidance	Subbaraj & Balasingh (1996)
Phyllostomidae	<i>Desmodus rotundus</i>	Vampire bat	Yes	Largely stayed in day roosts on bright nights	Crespo <i>et al.</i> (1972)
	<i>Desmodus rotundus</i>	Vampire bat	Yes	Attributed avoidance to the affect of moonlight on cattle	Turner (1975)
Noctilionidae	<i>Noctilio leporinus</i>	Greater fishing bat	Yes	A strong effect; could have been driven by moonlight avoidance in fish	Börk (2006)
<b>Tropical/subtropical insectivores</b>					
Phyllostomidae	<i>Lophostoma silvicolum</i>	White-throated round-eared bat	Yes	Bats stayed at roost under moonlight; was attributed to moonlight avoidance by prey	Lang <i>et al.</i> (2006)
Molossidae	<i>Tadarida pumila</i>	Little free-tailed bat	Yes	Later emergence on moonlit nights	McWilliam (1989)
Vespertilionidae, mainly	Several genera	Several microbat spp.	Yes	Combined activity dropped markedly in bright moonlight	Fenton <i>et al.</i> (1977a)
Vespertilionidae, Molossidae; Emballonuridae	Several genera	Several microbat spp.	No	Combined activity over all species (SS); reported several microhabitat shifts	Jung & Kalko (2010)
Vespertilionidae, Molossidae, Emballonuridae	Bats identified to guild by call characteristics	Open and forest edge guilds – FM-QCF	Yes	Clear tendency to avoid bright moonlight	Meyer <i>et al.</i> (2004)
Vespertilionidae, Nycteridae, Hipposideridae, Rhinopomatidae	Bats identified to guild by call characteristics	Cluttered guild – FM and CF	No	Non-significant tendency for greater activity during brighter moonlight	Meyer <i>et al.</i> (2004)
Several families, mainly Vespertilionidae	Several genera	Several microbats (24 spp.)	Yes	Combined activity suppressed around midnight during full moon	Milne <i>et al.</i> (2005)
Vespertilionidae, Hipposideridae, Rhinopomatidae	<i>Pipistrellus</i> , <i>Hipposideros</i> , <i>Rhinopoma</i>	Several microbat spp.	Yes	Major increase in bat activity during a lunar eclipse	Usman <i>et al.</i> (1980)
<b>Temperate insectivores</b>					
Rhinolophidae	<i>Rhinolophus ferrumequinum</i>	Greater horseshoe bat	No	Excluded moonlight early in analysis (SS)	Wang <i>et al.</i> (2010)

Table 1. (Cont.)

Family	Genera or species	Common name	Avoid?	Comments <sup>a</sup>	Reference
Vespertilionidae	<i>Plecotus townsendii</i>	Virginia big-eared bat	Yes	Moonlight one of the remaining variables in statistical model (SS)	Adam <i>et al.</i> (1994)
	<i>Myotis lucifugus</i>	Little brown bat	No	No change in activity despite moonlight effect on prey (SS)	Anthony <i>et al.</i> (1981)
	<i>Eptesicus serotinus</i>	Serotine bat	No	Non-significant negative effect of moonlight (SS)	Ciechanowski <i>et al.</i> (2007)
	<i>Pipistrellus pipistrellus</i>	Common pipistrelle	No	Non-significant negative trend (SS)	Ciechanowski <i>et al.</i> (2007)
	<i>P. pygmaeus</i>	Soprano pipistrelle	No	Non-significant negative trend (SS)	Ciechanowski <i>et al.</i> (2007)
	<i>P. nathusii</i>	Nathusius' pipistrelle	No	Non-significant negative trend (SS)	Ciechanowski <i>et al.</i> (2007)
	<i>Nyctalus noctula</i>	Common noctule	No	Non-significant positive trend ( $P = 0.06$ , SS)	Ciechanowski <i>et al.</i> (2007)
	<i>N. leisleri</i>	Lesser noctule	No	Non-significant negative trend (SS)	Ciechanowski <i>et al.</i> (2007)
	<i>Myotis daubentonii</i>	Daubenton's bat	Yes	Significant negative trend ( $P = 0.029$ ; SS)	Ciechanowski <i>et al.</i> (2007)
	<i>P. pipistrellus</i>	Common pipistrelle	No	No hint of effect in data	Gaisler <i>et al.</i> (1998)
	<i>Nyctalus noctula</i>	Common noctule	No	No hint of effect in data	Gaisler <i>et al.</i> (1998)
	<i>Eptesicus serotinus</i>	Serotine bat	No	Some suggestion of avoidance in the data	Gaisler <i>et al.</i> (1998)
	<i>Eptesicus fuscus</i>	Big brown bat	No	QS	Geggie & Fenton (1985)
	Mainly <i>Myotis</i> spp.	Several microbat spp.	No	Combined activity; bats were feeding under dense canopy	Hayes (1997)
	Mainly <i>Myotis</i> spp.	Several microbat spp.	No	No effect on activity (QS); suggested microhabitat shift under moonlight	Hecker & Brigham (1999)
	Mainly <i>Plecotus</i> and <i>Myotis</i> spp.	Several microbat spp.	No	Addressed swarming activity at roost entrance	Karlsson <i>et al.</i> (2002)
	<i>Euderma maculatum</i>	Spotted bat	No	Also no effect of cloud cover (SS)	Leonard & Fenton (1983)
	<i>Myotis lucifugus</i>	Little brown bat	No	No hint of effect in data	Negraeff & Brigham (1995)
	Mainly <i>Myotis</i> spp.	Several microbat spp.	No	Addressed swarming activity at roost entrance	Parsons <i>et al.</i> (2003)
	<i>Myotis yumanensis</i>	Yuma bat	No	No overall change in activity; observed shift into shaded microhabitats	Reith (1982)
	<i>Lasionycteris</i> , <i>Lasiurus</i> , <i>Corynorhinus</i> , <i>Eptesicus</i>	A low-frequency acoustic guild	No	Activity combined over species (SS)	Rogers <i>et al.</i> (2006)
	<i>Myotis</i> spp.	Five possible species	No	Activity combined over species (SS)	Rogers <i>et al.</i> (2006)
	<i>Pipistrellus pipistrellus</i>	Common pipistrelle	No	Addressed roost emergence only (QS)	Swift (1980)
	<i>Myotis</i> , <i>Eptesicus</i> , <i>Pipistrellus</i> , <i>Nyctalus</i>	Several microbat spp.	No	Excluded moonlight early in analysis (SS); all bat activity combined	Vaughan <i>et al.</i> (1997)
Vespertilionidae (mainly)	<i>Myotis</i> and <i>Eptesicus</i> , mainly	Several microbat spp.	No	No change despite possible drop in insect abundance under full moon (QS)	Bell (1980)

Table 1. (Cont.)

Family	Genera or species	Common name	Avoid?	Comments <sup>a</sup>	Reference
Vespertilionidae and Molossidae	Mainly <i>Chalinolobus</i> and <i>Mormopterus</i> spp.	Several microbat spp.	No	All bat activity combined (SS)	Scanlon & Petit (2008)
Molossidae	<i>Tadarida</i> and <i>Nyctinomops</i> spp.	Free-tailed bats	No	Activity combined over species (SS)	Rogers <i>et al.</i> (2006)

Observations relate to feeding activity unless otherwise noted. Entries are ordered by family (when possible), and alphabetically by reference within families in order to group entries from the same study.

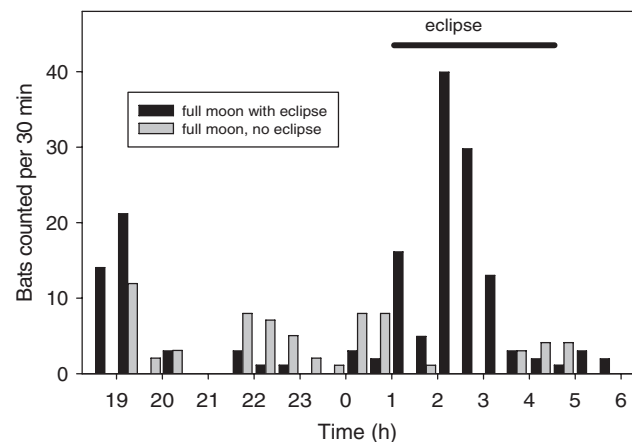
<sup>a</sup>FM denotes steep frequency modulated calls; CF denotes constant frequency calls; QCF denotes quasi-constant frequency calls. Call types defined as per Meyer, Schwarz & Fahr (2004).

<sup>b</sup>SS refers to result given only in the form of a statistical statement, typically a test statistic and/or *P* value. QS refers to observations given only as a qualitative statement.

Many small birds and diurnal mammals move along vegetated fence or tree lines to avoid the higher risk of travelling in the open (Belisle & Desrochers, 2002), and similar 'vegetation hugging' has been noted in several insectivorous bats. For instance, common pipistrelles and other European bats routinely travel along vegetated tree lines (Limpens & Kapteyn, 1991; Schaub & Schnitzler, 2007), sometimes showing a preference for relatively tall vegetation (Limpens *et al.*, 1989; Verboom & Huitema, 1997; Downs & Racey, 2006). These bats also prefer to travel between tree rows lining both sides of a road (Verboom & Spoelstra, 1999; Schaub & Schnitzler, 2007), show similar preferences for positioning their flight paths relative to various landscape elements (Schaub & Schnitzler, 2007), and generally do not feed far from vegetation (Verboom & Spoelstra, 1999; Wang *et al.*, 2010). Such phenomena are not as well documented elsewhere, but North American *Myotis* bats show a similar tendency (Murray & Kurta, 2004; Henderson & Broders, 2008). We know of no reports of such behaviour outside of insectivorous bats.

Vegetation hugging by flying bats seems like a classic example of predator avoidance, which is the hypothesis favoured by most who study this phenomenon. This hypothesis is often proffered as intuitively obvious (Limpens & Kapteyn, 1991; Verboom & Huitema, 1997), but the precise anti-predator benefits in feeding close to vegetation are not clear. For the great majority of birds and diurnal mammals that move within or along vegetation, the vegetation itself provides a refuge from attack (e.g. Belisle & Desrochers, 2002). Escape behaviour is not well studied in bats (see Section II.2), but we know of no observations of bats flying into dense vegetation to avoid attacking predators. Flying under canopy vegetation may thwart the attacks of open-ground raptors like falcons (Rodríguez-Durán & Lewis, 1985), but not necessarily attacks by raptors like *Accipiter* hawks or many owls. Perhaps bats can decrease their overall detectability to predators while flying close to vegetation, but this is difficult to assess with present information.

Other explanations for vegetation hugging exist and cannot easily be ruled out. First, insect abundance might be highest around vegetated landscape elements (Limpens & Kapteyn, 1991; Verboom & Huitema, 1997). Verboom & Spoelstra (1999) provide a thorough examination of this

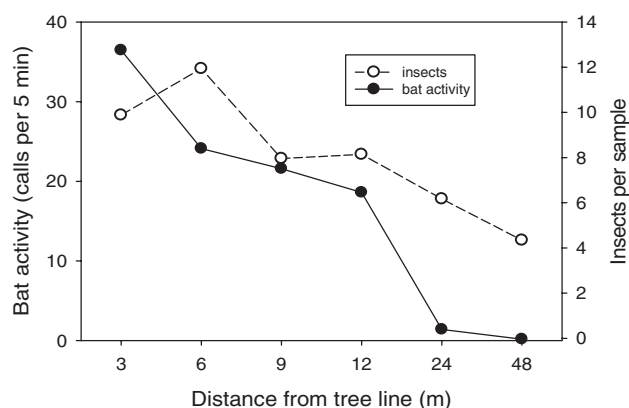


**Fig. 4.** Increase in activity of insectivorous bats during a lunar eclipse in southern India. Data from a full-moon night 1 month after the eclipse are shown as a control. The combined activity of the bats (*Pipistrellus*, *Hipposideros*, and *Rhinopoma* spp.) increased markedly during the height of the lunar eclipse; data from an additional site were qualitatively very similar. From data in Usman *et al.* (1980).

possibility in common pipistrelles, which both commute and feed along tree rows. Insect abundance declined away from tree rows, which was mirrored by a drop in bat activity. Bat activity dropped faster than prey abundance with distance to the tree line (Fig. 5), which can be interpreted as evidence for a predation-risk effect (Verboom & Spoelstra, 1999), but could conceivably reflect a situation where there are relatively few bats in the area (not enough crowding to warrant feeding away from the higher prey densities). A similar study on European vespertilionids (Downs & Racey, 2006) suggested that bat activity declines much faster away from a tree line than do insect resources. More tests of this hypothesis are clearly needed.

A second explanation suggests that vegetated landscape elements are useful landmarks for navigation (Limpens & Kapteyn, 1991; Verboom & Huitema, 1997; Schaub & Schnitzler, 2007). This is a reasonable idea, and the behaviour of commuting pond bats (*Myotis dasycneme*) suggests that they stay in acoustic contact with landscape features as they travel (Verboom, Boonman & Limpens, 1999). On the





**Fig. 5.** Common pipistrelle (*Pipistrellus pipistrellus*) activity and insect abundance as a function of distance from a tree line bordering a meadow in the Netherlands. Both bat activity and insect abundance decreased with distance to the tree line, but bat activity at the 24 and 48 m distance was very low compared to insect abundance. Such a sharp drop in bat activity was not seen in other sites studied, one a similar meadow, and the other an agricultural field. From data in Verboom & Spoelstra (1999).

other hand, it seems unlikely that bats are obliged to navigate *via* landscape pathways. For instance, the relatively strong-flying serotine bat does not hug vegetation to nearly the same extent as bats more specialized for slow flying in clutter (Verboom & Huitema, 1997; see also Sleep & Brigham, 2003). Furthermore, bats that normally hug vegetation may readily cross large, featureless bodies of water in nightly feeding flights (e.g. Ekman & de Jong, 1996). Nevertheless, this navigational hypothesis certainly merits consideration in many insectivorous bats.

Moving beyond the influence of landscape elements *per se*, habitat use might be influenced by predators *via* light levels. In fact, several studies suggest that microhabitat use is sensitive to moonlight (Table 2). A common observation is that insectivorous bats tend to shift to shaded microhabitats or feed closer to vegetation under bright moonlight, although such effects are not always observed (Table 2). As before (see Table 1), there are more such suggestions for tropical bats than temperate bats. Much of the information in Table 2 is rather qualitative in nature, and more quantitative information on this topic would be valuable. Larger-scale studies also suggest that open habitats may be avoided until well after sunset (when darker conditions prevail), which implies a greater risk to feeding in the open under brighter conditions. For instance, early-feeding soprano pipistrelles feed only under the canopy in forested areas until well after sunset (Russo *et al.*, 2011). Similarly, Ciechanowski *et al.* (2009) and Rydell *et al.* (1996) report that *Pipistrellus* bats avoid feeding over open water (staying in open woodland) until well after sunset, and in so doing they miss the greater insect abundance over water during the twilight period (Rydell *et al.*, 1996; see Ekman & de Jong, 1996 for a related example). Frugivorous phyllostomid bats also avoid feeding in relatively open habitats until about an hour after sunset (Fig. 6; Presley *et al.*, 2009); this is an unambiguous

avoidance response, since fruit availability does not vary with light levels.

Experimental studies could provide stronger support for the above anti-predator interpretations, but few exist. Baxter *et al.* (2006) took the straightforward approach of comparing the abundance of bats in areas in which were broadcast the calls of owls, the calls of woodpeckers, and no calls at all. Bats avoided sites with calls more than the silent sites, but there were not significantly fewer bat detections in the owl sites as compared to woodpecker sites (although the trend was in that direction). In another system, taking advantage of quasi-experiments provided by subsistence farmers, Delpietro *et al.* (1994) found a strong tendency for vampire bats (*Desmodus rotundus*) to avoid livestock corrals guarded by cats. This result probably reflects the risks taken by vampire bats in feeding on or close to the ground. More experimental work along these lines ought to be feasible in many systems.

## (6) Sociality and anti-predator considerations

Work on chiropteran sociality deals mainly with the social dynamics of roosting bats (see Kerth, 2008, for a recent review). Bat sociality is rarely considered in an anti-predator context. In marked contrast, many other vertebrate taxa rely on the safety of a group for much of their lives (Krause & Ruxton, 2002; Caro, 2005). Surprisingly, however, scattered observations of social anti-predator defences in bats provide some of the stronger evidence for predation-risk-dependent behaviour in this taxon.

Some bats emit distress calls when captured or restrained, and those calls appear to induce a form of mobbing behaviour (see Caro, 2005, for a discussion of distress calls and their function). Such behaviour involves a gathering of flying bats whose members frequently dive towards and close to the source of the calls. This behaviour has been described in a few species of phyllostomid [*Artibeus* spp. (August, 1979; Ryan, Clark & Lackey, 1985)] and vespertilionid bats [*Myotis lucifugus* (Fenton *et al.*, 1976; McGuire & Fenton, 2010); *Pipistrellus* spp. (Russ, Racey & Jones, 1998; Russ *et al.*, 2004)]. Distress calls attract not only conspecifics but also heterospecific bats. For instance, distress calls by *Artibeus* spp. are known to attract other phyllostomids (August, 1979; Ryan *et al.*, 1985). Russ *et al.* (2004) found that the calls of any one of three European *Pipistrellus* bats attract the other two species; European *Pipistrellus* bats also respond to the distress calls of three vespertilionids and an emballonurid native to Madagascar. This distress-call-induced behaviour may be a widespread phenomenon in bats, since the taxonomic groups implicated thus far (phyllostomids, emballonurids, and vespertilionids) are not very closely related (Teeling *et al.*, 2005).

Since distress calls imply danger, the close approach to the caller is likely an act of risk-taking by the participating bats, and one not necessarily directed towards relatives (see Russ *et al.*, 1998). The effect that such mobbing might have on a given predator is unknown, since true predators were not actually present in any study. We also know of no case in which bats initiate the mobbing of a newly discovered predator in the absence of distress calls. The

Table 2. Moonlight and its effect on microhabitat use by temperate and tropical insectivorous bats

Zone <sup>a</sup>	Family	Scientific name	Common name	Observed shift (if any) <sup>b</sup>	References
Temperate	Vespertilionidae	Mainly <i>Myotis</i> spp.	Several microbats (combined)	Small upward habitat shift in forest under bright moonlight; contrary to expectation	Hecker & Brigham (1999)
	Vespertilionidae	<i>Myotis lucifugus</i>	Little brown bat	No microhabitat shift observed (QS); no overall drop in activity	Negraeff & Brigham (1995)
	Vespertilionidae	<i>Myotis yumanensis</i>	Yuma bat	Shift into shaded microhabitats in bright moonlight (no overall drop in activity)	Reith (1982)
Tropical	Vespertilionidae	<i>Nyctophilus</i> spp. (two)	Long-eared bats	No observed microhabitat shift	Brigham, Francis & Hamdorf (1997)
	Vespertilionidae	<i>Scotophilus borbonicus</i>	Lesser yellow bat	Avoid feeding above canopy in bright moonlight (QS)	Fenton & Rautenbach (1986)
	Molossidae	<i>Tadarida midas</i>	Midas free-tailed bat	No habitat shift; almost always feed well above canopy (QS)	Fenton & Rautenbach (1986)
	Vespertilionidae	<i>Neoromicia (Eptesicus) capensis</i>	Cape serotine	Stay below canopy and avoid open under bright moonlight (QS)	Fenton <i>et al.</i> (1977a)
	Vespertilionidae	<i>Nycticeinops (Nycticeius) schlieffeni</i>	Schlieffen’s bat	Stay below canopy and avoid open under bright moonlight (QS)	Fenton <i>et al.</i> (1977a)
	Vespertilionidae	<i>Scotophilus viridis</i>	Greenish yellow bat	Lesser tendency to avoid open in bright moonlight; flight more swift when bright (QS)	Fenton <i>et al.</i> (1977a)
	Emballonuridae	<i>Cormura brevirostris</i>	Chestnut sac-winged bat	Feed closer to vegetation under new moon (QS)	Jung & Kalko (2010)
	Vespertilionidae	<i>Lasiurus blossevillei</i>	Desert red bat	Feed closer to vegetation under new moon (QS)	Jung & Kalko (2010)
	Vespertilionidae	<i>Myotis albescens</i>	Silver-tipped myotis	Avoid street lights under full moon; speculated due to spatial shift by prey (QS)	Jung & Kalko (2010)
	Molossidae	<i>Eumops</i> spp.	Mastiff bats	Feed closer to vegetation under full moon (QS)	Jung & Kalko (2010)
	Molossidae	<i>Molossus molossus</i>	Velvety free-tailed bat	Avoid street lights under full moon; speculated due to spatial shift by prey (QS)	Jung & Kalko (2010)

Entries are organized alphabetically (by reference) within temperate and tropical zones in order to group entries from the same study.

<sup>a</sup>The tropical designation includes sub-tropical bats.

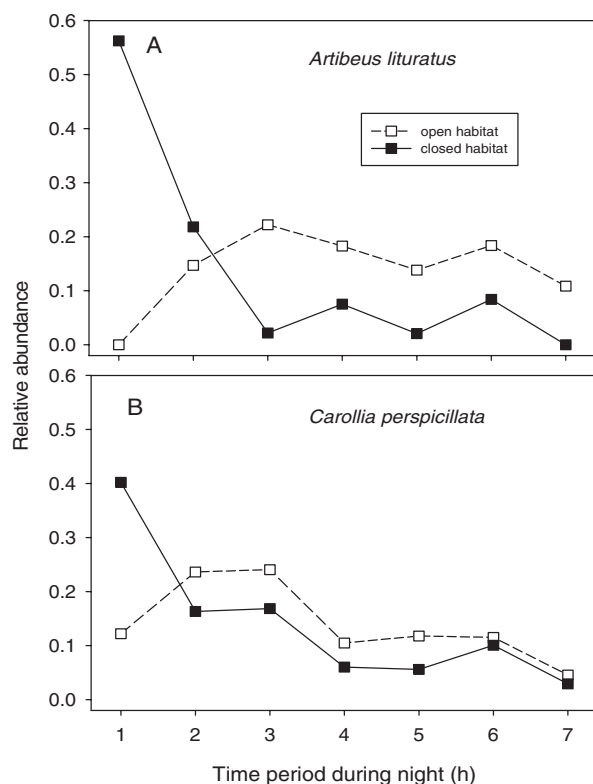
<sup>b</sup>QS refers to observations given only as qualitative statements.

distress calls themselves are relatively low-frequency calls that would enhance long-distance communication (August, 1985; Russ *et al.*, 1998), and are audible to humans and perhaps many types of predators. Examining the response of real predators to mobbing bats would likely provide many insights into this phenomenon.

We can only speculate on other possible anti-predator roles of sociality in bats. We note that the temporal clustering of bats at roost departure (see Section III.3) could be considered a form of social anti-predator behaviour. Some bats remain socially organized well beyond roost departure (see Dechmann *et al.*, 2010), which may have an anti-predator

function (especially if such bats depart prior to sunset). Social hibernation in some bats may function as a form of risk dilution and collective predator detection (see above and Wilkinson, 1985).

The possibility of anti-predator sociality while feeding also exists, since some bat species typically move or feed in groups when outside the roost. Frugivorous phyllostomids are sometimes social while feeding (Wilkinson & Boughman, 1998), and consume food in social night roosts, which Fleming (1988) suggests has a significant anti-predator function. On the other hand, social foraging in the more omnivorous greater spear-nosed bat (*Phyllostomus hastatus*)



**Fig. 6.** Relative use of open and closed habitats by two frugivorous phyllostomid bats in slash-and-burn agricultural areas in Amazonian Peru. Open habitat refers to recently cleared areas (but not devoid of vegetation). Closed habitat refers to early regrowth of forest vegetation for (A) *Artibeus lituratus*, and more mature forest for (B) *Carollia perspicillata*. Each plotted value represents the proportion of bat captures that occurred during a given hour after sunset. Both species showed a significant tendency ( $P < 0.001$ ) to avoid open areas during the first hour of the night (dusk), followed by a greater tendency to use open areas during the darker part of the night. These two species represent the range of responses reported in the eight common phyllostomid species studied. From data in Presley *et al.* (2009).

does not seem to have an anti-predator function (Wilkinson & Boughman, 1998). Organized social feeding appears uncommon in insectivorous bats (see Dechmann *et al.*, 2010), although such bats may benefit from eavesdropping on the feeding calls of nearby bats (Balcombe & Fenton, 1988; Dechmann *et al.*, 2009; but see Loeb & Britzke, 2010). Social anti-predator warning systems, such as those involving vigilance in many other mammals and birds (Caro, 2005), appear completely unstudied in bats.

#### IV. DISCUSSION

Do most bats live in a world in which their behaviour is influenced by predators? Do predators influence decisions about when to leave roosts or where to feed during the night? Does current information about predators influence the

roosts chosen on a given day, or the degree of torpor adopted while at roost? The prevalence of predator-driven decision-making in a variety of vertebrates (Lima, 1998; Caro, 2005) suggests that bats too would be strongly influenced by predators. However, at present, the evidence in favour of this view is equivocal.

One generalization that seems clear is that a bat feeding well before sunset is likely to be in danger from diurnal raptors (Fenton *et al.*, 1994; Speakman, 1995). Comparative work suggests that certain groups of bats are better equipped to deal with this diurnal risk than others, and their behaviour varies accordingly (Rydell *et al.*, 1996). It seems likely that the start of nocturnal activity (relative to ambient light) is largely a fixed evolutionary trait within a species (based on flight ability, etc.) that is adjusted based on the local level of risk and a given bat's energetic state (Speakman, 1991b). However, the few studies that directly manipulated predator presence/absence have not consistently shown a strong effect on roost departures.

Another generalization that bat biologists would likely accept is that roost choice by bats should be influenced (in part) by a real-time assessment of danger. Many comparative aspects of roost choice are clearly driven by roost safety (Kunz & Lumsden, 2003; Barclay & Kurta, 2007). One might thus expect that roost choice by individual bats is sensitive to day-to-day variation in the risk of predation, but there is little information available to support or refute that idea. Given the fitness consequences of choosing a dangerous roost, and likely conflicts between safety and other aspects of roost choice (e.g. favourable microclimates), we suspect that bats are generally sensitive to local changes in predation risk in their choice of roosts.

If any one group of bats is influenced relatively little by predators, then that group is probably temperate-zone bats, but such a conclusion would be premature. The general lack of moonlight avoidance in temperate insectivorous bats (Table 1) does suggest that they do not deal routinely with visually-oriented predators. Yet there are persistent suggestions (e.g. Wang *et al.*, 2010, see also Section III.5) that the choice of movement paths and feeding areas by temperate bats is driven by the danger of feeding in the open. Temperate (and other) bats also respond to distress calls with apparent mobbing behaviour, indicating an ongoing history with predators. A tendency to depart from roosts in social/temporal clusters may also suggest an influence of predators on temperate-zone bats (see Section III.3).

Tropical bats appear to be much more responsive to predators. There are certainly more examples of moonlight avoidance in tropical insectivorous bats than in their temperate counterparts (Table 1). Frugivorous bats (all tropical or subtropical) nearly always reduce activity on moonlit nights (Table 1). This pattern suggests that there are more serious predators on bats in the tropics, but the nature of this greater threat is not obvious from the available studies. Bat hawks are a potentially important bat specialist in parts of the Old World tropics, but no such specialists are apparent in the New World tropics. Perhaps tropical owls are more focused

on bats than their temperate counterparts. Carnivorous bats might also play an important role in the tropics.

A basic limitation in understanding the influence of predators on bats is the lack of information on key aspects of the interaction between bats and their potential predators. Much more work is needed on the ways in which bats perceive predators *via* auditory, visual, and olfactory cues, or *via* their echolocational abilities. This perceptual work ought to be amenable to experimental study, such as that on predator chemical cue perception by insectivorous bats (Boyles & Storm, 2007; Driessens & Siemers, 2010). This sort of work would establish some baseline expectations about how bats might respond to changes in the risk of predation, since they cannot respond to changes in risk that they do not perceive. Information on whether bats respond appropriately to the threats posed by different classes of predators (e.g. owls *versus* mammalian mesopredators) could provide valuable insights into habitat and roost choice. Also needed is much more information on the responses of bats to actual attacks from predators, especially with respect to vegetation and various landscape elements. Such attacks might be difficult to stage with real predators, but should be feasible with model predators. This information would help greatly in interpreting bat movement patterns in various landscapes, as well as patterns in habitat choice.

Solid information about the predators themselves would be especially valuable, but perhaps harder to obtain. Observations of predators at bat roosts are probably the most easily obtained in the field, and indeed, several such examples exist (see Section II.2). More difficult to address will be predation on bats as they feed well away from roosts during the full darkness of night. Owls are still the main suspects as predators on bats in most areas, but their ability or tendency to capture feeding bats at night is unclear. Work on possible bat-on-bat predation in the tropics might add a new dimension to our understanding of the anti-predator dichotomy in tropical *versus* temperate bats.

Future work may reveal that bats are only minimally influenced by predators in their daily lives, and such a realization would provide a unique contrast within vertebrate ecology. We suspect, however, that research focused explicitly on the anti-predator capabilities of bats and the nature of their potential predators will reveal many aspects of bat behaviour that are sensitive to extant risk. Such research may ultimately provide insights into the ecology of bats at the population and community levels (e.g., Howe, 1979; Presley *et al.*, 2009), much as it has in other ecological systems (Preisser, Bolnick & Benard, 2005). But for the present, research focused at the level of individual bats and how they assess and deal with predators will help build the foundation upon which any such larger insights may follow.

## V. CONCLUSIONS

(1) The behaviour of many animal taxa is affected by real-time changes in the risk of predation, but the applicability of this statement to bats is not well established.

(2) Bats are potential prey for many types of opportunistic predators, but few predators specialize on bats.

(3) Apparently, most bats can detect changes in extant risk in at least some circumstances. However, relatively little is known about how bats detect and evade attacks from predators.

(4) The available empirical information does not clearly support the idea that predators strongly influence the behaviour of bats. For instance, tropical bats generally show the classic moonlight avoidance observed in other small nocturnal mammals, but no such tendency is apparent in temperate-zone bats.

(5) Much observational evidence suggests that bats are sensitive to predation risk when departing from roosts, but the experimental evidence on this matter is equivocal. However, bats that become active before sunset face considerable risks from diurnal predators. The nocturnal threats to bats are less clear.

(6) An influence of predation risk on habitat selection and movement paths has frequently been suggested in both temperate and tropical bats, but the predators driving such behaviour are not clear. Roost choice is likely to be sensitive to changes in risk, but little work has addressed this topic.

(7) Several anti-predator topics are presently largely unexplored in bats, including the effects of risk on torpor and sleep while at roosts, the social aspects of predator avoidance, and many aspects of decision-making while foraging in risky situations.

(8) To assess more fully the influence of predators on bat behaviour, future work should address the ways in which bats perceive predators *via* auditory, visual, and olfactory cues. Also needed is information on how predators attack bats and how bats react to attacking predators. Of critical value will be work on the nature of predation risk during the full darkness of night.

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