Ethology

Behavioural Response of Bats to Perceived Predation Risk While Foraging

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Received: October 20, 2005
Initial acceptance: December 14, 2005
Final acceptance: February 26, 2006
(S. Foster)

doi: 10.1111/j.1439-0310.2006.01249.x

Abstract

The ability to detect and respond to predation risk while foraging may have important fitness consequences for prey organisms. Anti-predator behaviours may reduce the probability of mortality because of predation, but they may also be associated with reduced foraging efficiency. Several behaviours of bats have been suggested to serve as anti-predator responses, and there is evidence that predation, particularly by avian predators such as owls, may be an important cause of bat mortality. Previous studies have attempted to determine whether predator presence affects bat behaviour when emerging from roost sites, but few have examined effects of predator presence on bat behaviour while foraging. In this study, we investigated whether foraging bats respond to predator cues by presenting bats with an acoustic cue simulating the presence of an owl. Within matched trials, which were conducted at different locations each of 18 nights, significantly fewer bat detections were recorded at owl playback stations than at control stations (no auditory cue), suggesting an avoidance response by bats. An acoustic control (i.e. station playing woodpecker calls), however, did not have significantly more detections than the stations playing the owl calls, suggesting that bats may simply be avoiding noise and more detailed investigation is warranted. Although evidence for owl predation on bats is minimal in North America, results of this study may indicate that the perceived presence of owls may represent a factor influencing the behaviour of bats while foraging.

Introduction

Many prey organisms are capable of assessing and responding to cues signalling the presence of a predator. These cues may be visual (McGowan & Woolfenden 1989), chemosensory (Van Buskirk & McCollum 1999) or auditory (Berger 1999), depending on the characteristics of the environment and adaptations of the prey organism. Prey organisms may detect predators by using sensory cues other than those used for activities such as foraging. Echolocating bats emit signals directionally for spatial orientation and foraging; however, to scan for predators over a wider perceptual field, foraging bats may also rely on auditory or visual cues (Schnitzler & Kalko 1998). Regardless of the perceptual cues used, once a bat has detected a predator the most common response exhibited is one of avoidance (Twente 1954; Fenton et al. 1994). Bat behaviours such as coloniality (Barclay et al. 1982; Kunz 1982), clustered roost emergence (Swift 1980; Duvèrge et al. 2000) and nocturnality (Fenton 1974; Speakman 1991a) have been suggested to function as mechanisms for predator avoidance, indicating that predation may be an important factor influencing bat mortality (Speakman 1991b). Relatively few studies, however, have examined the response of bats to detection of predators.

Prey species may alter their behaviour in response to the perceived threat of predation, but often at the expense of other fitness-related activities such as feeding or finding mates (see reviews Lima & Dill 1990; Lima 1998). Birds of prey such as hawks, falcons and owls are predatory threats to bats in temperate zones (Gillette & Kimbrough 1970; Speakman 1991b; Hamilton & Barclay 1998). Hawks and falcons are predominantly diurnal predators, but near large bat roosts they may feed at dawn and dusk when bats are returning to, or emerging from, the roost (Baker 1962). In northern temperate regions, owls represent a more likely predator of bats as they are also nocturnal. Evidence for this has been accumulated mainly through sporadic observations of predatory events at roost sites (Twente 1954; Baker 1962; Barclay et al. 1982) and through analysis of owl pellets (Vaughan 1954; Marti 1974; Swengel & Swengel 1992). Studies examining behavioural responses of bats to owl predators have done so by placing a predator (Petrželková & Zukal 2003), a predator model (Speakman et al. 1992), or a model in combination with predator call playbacks (Kalcounis & Brigham 1994; Petrželková & Zukal 2001) near roosts. Conclusions of these studies were inconsistent, because bats did not always appear to alter their emergence behaviour in response to perceived presence of an owl predator.

Away from roost sites, bats may experience the greatest predation risk from owls while commuting or foraging in open habitats (Speakman 1991a), both because of increased conspicuousness and reduced cover (Verboom & Huitema 1997). Consistent with this hypothesis, bats appear to be unwilling to cross large gaps (Limpens & Kapteyn 1991), and instead concentrate their activity along forest patch edges (Furlonger et al. 1987; Grindal & Brigham 1999). We are not aware of any studies, however, that have examined the effect of predator presence on bat foraging behaviour away from roost sites and thus the extent to which foraging behaviour of bats may be influenced by avian predators is not known. The objective of this study was to determine whether foraging bats modify their activity in response to the perceived presence of an owl. We predicted that, if bats use auditory cues as signals indicating the presence of predators such as owls, and avoid areas of perceived predation risk while foraging, the number of bat detections along forest edges would be reduced in the presence of owl call playbacks.

Methods

This study was conducted in central British Columbia, Canada (51°51′N, 121°50′W) over 18 nights at different trial sites from 23 June to 25 Aug. 2004 in Sub-boreal pine-spruce (SBPS) and Interior Douglas Fir (IDF) biogeoclimatic zones (Meidinger & Pojar 1991). The SBPS region is characterised by cold, dry winters and cool summers (mean annual temperature ranges from 0.3 to 2.7°C) and forests dominated by even-aged stands of lodgepole pine (*Pinus contorta*). Moist sites, or those that have missed several fire cycles, are dominated by white spruce (*Picea glauca*). The IDF is slightly warmer (mean annual temperature ranges from 1.6 to 9.5°C) and forests are dominated by open to closed canopies of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine and hybrid white spruce (*P. glauca x engelmannii*). Forest harvesting and livestock grazing are predominant anthropogenic disturbances in both zones. Bat species known to occur in the forests of this region include the long-eared myotis (*Myotis evotis*), little brown myotis (*Myotis lucifugus*), long-legged myotis (*Myotis volans*), big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*) and hoary bat (*Lasiurus cinereus*; Nagorsen & Brigham 1993).

Bats often travel within narrow corridors such as tree lines and skidder trails (Menzel et al. 2002) to maximise their energy intake (Lewis & Dibley 1970; Kusch et al. 2004), to exploit higher insect densities while minimising energy expenditure navigating through cluttered environments (Brigham et al. 1997; Grindal & Brigham 1999), to obtain shelter from the wind, and to reduce their vulnerability to predation associated with open habitats (Verboom & Huitema 1997). We therefore conducted nightly trials in corridors bounded by intact, continuous forest edges. We selected trial sites that had continuous edges of similar tree species composition, age class and moisture regime to minimise potential influence of habitat preference by foraging bats; different trial sites were selected each night and no sites were used more than once. On any night, site locations were separated by a minimum of 1.5 km to reduce the probability of detecting the same bats between nightly trials (Brigham 1991; Henry et al. 2002; Duchamp et al. 2004).

Because owls are silent flyers and visually cryptic, the most obvious way that one can reveal its presence is through territorial calls (Eilam et al. 1999). Thus, at each trial site, we presented bats with the territorial calls of three owls common to the study area, including the great horned owl (*Bubo virginianus*), barred owl (*Strix varia*) and northern saw-whet owl (*Aegolius acadicus*). To test the alternative hypothesis that bats were simply avoiding the area because of an interfering acoustic signal, we also presented calls of the pileated woodpecker (*Dryocopus* *pileatus*), hairy woodpecker (*Picoides villosus*) and black-backed woodpecker (*Picoides arcticus)* at a second playback station. Owl and woodpecker call-playback stations, along with a silent control station, were separated by 200 m and bat activity was recorded simultaneously for each station. Our experimental design, therefore, consisted of 18 different trial sites of relatively homogeneous edge habitat separated by a minimum of 1.5 km, where we had each an owl playback, woodpecker playback and a silent control station at 200-m intervals on any one night. Treatments at each station within site were randomly determined for each nightly trial. The influence of habitat and weather, therefore, was similar for each station on a given night.

Calls were broadcast using tape recorders. Recordings from each of the three species of owls and each of the three woodpeckers were repeated consecutively with 10-s pauses between calls. Volume on each tape recorder was calibrated so that broadcasted calls were not easily detected by human ears between stations.

To detect the presence of bats, we used three Anabat II detector systems coupled with storage ZCAIM devices (Titley Electronics, Ballina, NSW, Australia), which allowed data to be directly stored to flash disk. Anabat detectors use frequency division to transform echolocation calls into audible signals and zero-crossing analysis (i.e. the frequency of call is calculated and graphed against time) to view spectral content (Corben 2004). We used ANALOOK software to identify echolocation signals, but made no attempt to distinguish between species. At each of the three treatment stations, detectors were placed on posts 1.3 m off the ground with microphones at an upward angle of 45° directed towards the forest edge. Nightly trials began 30 min after sunset and continued for 1 h; we did not sample on evenings with precipitation as many bats reduce their activity in the rain (Grindal et al. 1992). The total number of bat passes detected was used as a measure of the activity at each treatment station. We defined a pass as a minimum of two echolocation calls that were easily identifiable as originating from a bat (i.e. minimum and maximum frequency and slope were recognisable; Fenton 1970; Thomas & West 1989). Few passes, however, consisted of less than six consecutive calls. Because these passes are not an independent estimate of the number of bats in the area (Thomas & LaVal 1988), we report the total number of pass detections at each station as an indication of overall bat activity.

Statistical Analysis

Bat activity data, as measured by the total number of passes at each treatment within site, were examined for normality as well as for homogeneity of variance (Bartlett's test; Sokal & Rohlf 1995). To control for possible effects of sampling location and weather conditions on nightly differences in bat activity, and because assumptions of normality and homogeneity of variance were not met, we analysed the bat-detector data with a Friedman's two-way ANOVA (Sokal & Rohlf 1995) matching the data collected on a given night (i.e. owl, woodpecker, control) using a significance level of 0.05. Significant overall differences between individual pairs of treatments (i.e. control vs. owl-playback, etc.) were then examined with paired t-tests on log-transformed data (to normalise differences) provided that there was an overall effect among treatments. We adjusted our level of significance for individual comparisons using a Bonferroni's correction to account for multiple comparisons ($0.05/3 = 0.0167$). All statistical analyses were performed with STATA (Release 9.0; StataCorp 2005). Unless otherwise noted, all values are reported as untransformed $\bar{x} \pm 1$ SE.

Results

The total number of detections recorded on any one night was highly variable ($\bar{x} = 28.1$, $n = 18$, $SD = 22.3$ range = 5–86) with 0 detections recorded on the detector monitoring the owl-playback treatments at three sites (both control and woodpecker playback had at least one detection on every night). Consequently, there was considerable variation around the treatment means; overall, we recorded 505 detections, with 256 at the control stations ($\bar{x} = 14.2 \pm 4.1$), 144 at the woodpecker stations ($\bar{x} = 8.0 \pm 1.4$) and 105 detections at the owl stations ($\bar{x} = 5.8 \pm 1.2$). When detections among treatments were matched by night, there was a significant treatment effect (Friedman's $\chi^2 = 31.88$, $p = 0.0156$; Fig. 1). Individual multiple comparisons indicated that number of detections at owl-playback stations was less than at control stations ($p = 0.0167$). There were no differences between control and woodpecker playback stations ($p = 0.182$) and between woodpecker-playback and owl-playback stations ($p = 0.0813$), however, which confound the interpretation of the effect. Although our analysis accounts for within-night variation, the magnitude of the effect varied greatly by night (Fig. 1).

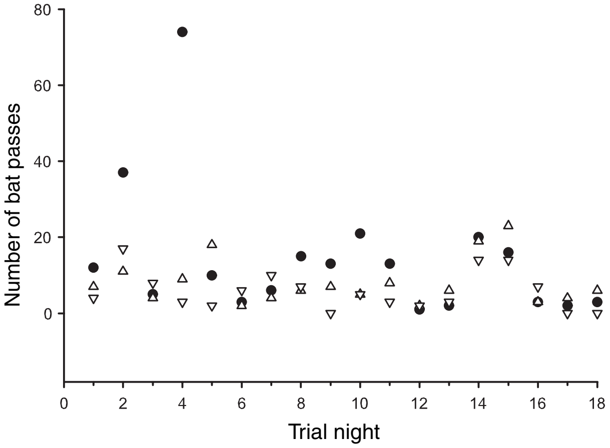

Fig. 1: Number of bat passes recorded at each treatment station for all trial nights. On a given night the control (●), woodpecker playback (△) and owl playback (▽) were placed 200 m apart in similar habitat and bat activity was recorded simultaneously. Different sites were used for every trial night. We tested for treatment effects with Friedman's two-way ANOVA matching the data collected on a given night to control possible effects of weather and habitat (see text)

Discussion

Several prey species have been shown to respond to acoustic cues signalling the presence of a predator (Bshary & Noë 1997; Hendrie et al. 1998; Durant 2000). Our results suggest that bats modify their foraging activity in response to perceived predation risk, as fewer bats were detected in the presence of owl calls than at control stations (with no acoustic cue). To our knowledge, this is the first study to demonstrate that bats respond to an acoustic predator cue while foraging; however, because activity at the woodpecker and owl playback stations was not different, avoidance may be because of the acoustic interference alone and caution should be taken in the interpretation of the results as exclusively predator avoidance.

The most conspicuous examples of bat predation by avian predators are found at large roost sites, when bats are emerging from or entering roosts (Baker 1962; Fenton et al. 1994). Results of studies investigating bats under predation risk at roosts sites, however, have been inconsistent (Speakman et al. 1992; Kalcounis & Brigham 1994; Petrželková & Zukal 2001, 2003). Because insectivorous bats are constrained by the emergence times of their prey, they may not be capable of varying their own emergence time (Jones & Rydell 1994), except at the potential expense of foraging efficiency. In contrast, once a bat has left the roost area its behaviour may be more variable, because it can potentially alter movement patterns and selection of foraging areas. Results of our study support this prediction, because movement patterns of bats at foraging locations were altered in response to acoustic stimuli.

Upon detection of a predator, the most adaptive strategy for a prey organism is to move away from or reduce its conspicuousness to the predator (Blanchard & Blanchard 1989). In our study, the reduction in number of bat detections at owl stations, relative to no sound controls, suggests that bats implemented an avoidance response. The lack of a significant difference between the woodpecker and owl treatments confounds these results, however, and suggests that the avoidance response could also be because of acoustic disturbance. Acoustic disturbance caused by a musical festival delayed emergence of a colony of Daubenton's bats (*Myotis daubentonii)* in England (Shirley et al. 2001) and can also interfere with a bat's passive listening, which many species of bats use to detect and locate prey in structurally cluttered environments (Schnitzler & Kalko 2001). Further, woodpeckers are diurnal and do not typically vocalise at night; therefore, bats are not likely exposed to woodpecker calls while foraging. Other species have been shown to modify behaviour in response to novel stimulus or non-lethal disturbance (see review in Frid & Dill 2002). Future studies may consider using an acoustic control of a sound common at night (e.g. frogs in northern regions) as our results cannot distinguish between a predator avoidance response or acoustic disturbance alone.

It is also possible that bats were still present at all stations during the trials, but responded to perceived predator cues by switching off their echolocation as some species do just before capturing their prey (Anderson & Racey 1991; Faure & Barclay 1992). It is unlikely, however, that bats are silent for extended periods because they also use echolocation to orient themselves spatially while foraging (Altringham 1996; Schnitzler et al. 2003). Further, predators such as owls generally do not locate prey using the auditory frequencies emitted by foraging bats, and appear to rely on visual cues to detect bats (Baker 1962). For this reason, bats would not reduce the probability of their detection by reducing the number of echolocation signals emitted. Thus, it is more probable that bats in our study responded to a perceived risk of predation, or noise in general, by spatial avoidance.

Mortality of northern insectivorous bats because of avian predation is generally believed to be low (Speakman 1991b). In the British Isles, however, avian predation has been estimated to account for 11% of all bat mortality (Speakman 1991b), and in North America, incidents of bat predation by avian predators, though rarely observed, have been shown to occur (Baker 1962; Barclay et al. 1982; Hamilton & Barclay 1998). Evidence of predation has also been gathered through bat remains in the pellets of a variety of owl species (Marti 1974; Dodson & Wexlar 1979; Swengel & Swengel 1992). There are errors, however, associated with estimating the incidence of bat predation using owl pellet analysis. For example, observations of the type and size of prey brought to nest sites by owls may be biased, because smaller prey such as bats are consumed by adults upon capture, while larger prey are taken to the nest to feed young (Speakman 1991b). Bats may therefore constitute a greater proportion of owl diets than have been estimated by pellet analysis. Our results further support this hypothesis, because bats appeared to modify their behaviour more so in response to owl calls than acoustic interference alone relative to the control station.

Spatial avoidance of predators, noise, or other perceived risks while foraging may be associated with substantial energetic costs for bats. In other species, predator avoidance reduces the amount of time invested in other behaviours such as thermoregulation (Stapley 2004) or hunting (Durant 2000), and may lead prey species to occupy habitats that provide fewer foraging opportunities than habitats associated with high predation risk (Lima & Dill 1990; Abrahams & Healey 1993; Cowlishaw 1997; Lima 1998). For bats, detection and avoidance of predators such as owls may similarly reduce the amount of time spent foraging, and may result in selection of low-risk foraging habitats with lower prey densities, thereby compromising foraging efficiency. Thus, avoidance of avian predators may be an important component of bat behaviour, and future studies should investigate movements and habitat selection of bats when exposed to predation risk while foraging.

To our knowledge, this is the first study to suggest that bats respond to an acoustic predator cue while foraging, however, acoustic interference alone cannot be excluded as a cause for the reduced activity. These results suggest that consideration to the quality of the acoustic environment may be necessary when studying habitat preferences of foraging bats.

Acknowledgements

We are indebted to C. Hotson and H. Jack for their assistance with the data collection. This work was facilitated by a British Columbia Forest Science Program grant to M. Gillingham (FSP Project Number Y051058) and was conducted on Riverside Ltd's IFPA tenure.

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