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Foraging strategies determine the effect of traffic noise on bats

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Anthropogenic noise is a concern in many ecological systems. One important source of noise pollution is traffic noise as it can dominate the soundscape in urban and peri-urban environments. Taxa that rely on acoustics for behavioural strategies are likely to be especially susceptible to noise, as noise can inhibit the perception of informational sounds. Bats use echolocation to hunt prey while foraging and are therefore prime candidates for adverse effects. Captive studies have shown that foraging efficiency can be significantly reduced in noisy environments for some bat species, and that these species actively avoid noisy areas. However, it remains unclear how this selective sensitivity manifests in urban environments. Given that mode of flying and use of echolocation is entwined with foraging strategies, we hypothesised that different foraging guilds (i.e. fast flyers versus slow flyers) may show different levels of sensitivity to noisy roads. We used transects running perpendicular to a major traffic route in Sydney, Australia, to record bat activity and traffic noise levels. Noise amplitude levels across each frequency band dropped by over 50% in the first 50 m, with high frequency components (> 10 kHz) being especially soft at this distance. Furthermore, all traffic noise above 5 kHz was lost within the first 150 m from the road. Fast flying bats flew close to the road, despite the traffic noise. In contrast, slow flying species appeared to fly more often away from the road. However, few calls of slow flyers were recorded, probably reflecting their difficulty in detecting them using acoustic surveys as well as their earlier decline in these peri-urban environments.

Key words: bats, noise, peri-urban, roads, frequency, foraging, traffic

INTRODUCTION

Anthropogenic noise has become a significant problem in many ecological systems. This is particularly true in urban environments, where anthropogenic noise can arise from a multitude of sources. In urban landscapes, traffic noise often dominates the soundscape (Botteldooren *et al.*, 2006), and excessive traffic noise has been shown to cause physiological stress and changes in behaviour in animals (Halfwerk *et al.*, 2011; Morgan *et al.*, 2012). While chronic noise exposure can directly impact on animal health, noise can also inhibit other vital functions, such as the perception of informational sounds — an effect called acoustic masking (Barber *et al.*, 2009). Taxa that rely on acoustics as part of their behavioural strategies are likely to be highly susceptible to anthropogenic noise masking. Acoustic masking can prevent prey from avoiding predators (Chan *et al.*, 2010), can impact on foraging efficiency (Siemers and Schaub, 2011), and can impact on courtship behaviour and the successful rearing of offspring (Parris *et al.*, 2009; Halfwerk *et al.*, 2011).

While the focus of research has mostly been on birds and amphibians to date, there is growing recognition that the implications for bats may be considerable.

Two contrasting factors appear relevant to bats in urban environments: high mobility appears to enable persistence by reducing fragmentation effects (Threlfall *et al.*, 2011); while urban areas in general have been shown to reduce species richness and promote adaptable species (Duchamp *et al.*, 2004; Avila-Flores and Fenton, 2005; Hourigan *et al.*, 2006, 2010). The effect of human-modified landscapes on bats has received much attention (e.g., Law *et al.*, 1999; Erickson and West, 2003; Duchamp and Swihart, 2008; Law *et al.*, 2011), leading to growing concern for their persistence in urban areas (Duchamp *et al.*, 2004; Avila-Flores and Fenton 2005; Hourigan *et al.*, 2006; 2010; Basham *et al.*, 2011; Threlfall *et al.*, 2011; 2012). Although some species show the ability to adapt to the urban environment, it seems that many more show at least some level of sensitivity to urbanisation (Threlfall *et al.*, 2011). Dispersion of resources, lack of roosts, and disturbance all contribute to this effect, but less

is known about how human disturbance alters the behaviour of bats in urban environments (but see Speakman *et al.*, 1991) and what the implications may be in contributing to the susceptibility of bats to urban development. Research to date suggests that noise pollution (Schaub *et al.*, 2008; Siemers and Schaub, 2011) and other impacts on sensory modalities, like artificial light (Stone *et al.*, 2009; Threlfall *et al.*, 2013), can impact on the foraging efficiency and choice of foraging areas in bats. Because bats largely rely on hearing whilst foraging, it is assumed that noise pollution is likely to disrupt their foraging efficiency (Siemers and Schaub, 2011). Noise has the potential to mask echolocation calls; and high-frequency anthropogenic noise such as that produced by ultrasonic amplifiers has been shown to be a deterrent to foraging bats (Szewczak and Arnett, 2008). Rydell *et al.* (1999) observed bats avoiding foraging over water that had ripples, postulating that the ripples disrupted echolocation, either by masking call echoes or creating acoustic clutter. Bats have also been shown to avoid road environments (Berthinussen and Altringham, 2011), however, because the reduction in bat activity occurred at distances much greater than the reduction in noise levels (i.e. traffic noise dropped 89% within the first 50 m from road), the role of traffic noise in this avoidance has been suggested to only occur within the first 100 m.

Where new roads are created in previously untouched landscapes, it could be expected that sensitive species may gradually decline and tolerant species persist, or indeed increase from reduced interspecific competition. However, where roads have existed for a period of time, it could be expected that this adjustment in bat diversity and dispersion is well established. If this was the case, tolerant species should show either positive selection for roads or no avoidance, while sensitive species should show avoidance and be less abundant. To investigate the effect of traffic noise on bats, we examined the influence of a major road through bushland on bat activity. We presumed that sensitivity might be linked to the different foraging strategies of bats. It is likely that species that glean (i.e., slow-flying species that hunt by passive listening to sounds produced by prey, as opposed to actively using echolocation) are more sensitive to the lower frequency components of anthropogenic noise masking the prey-produced sounds they listen for whilst foraging. We hypothesised that foraging strategy should be a good indicator of sensitivity. To do this, we quantified traffic noise levels and measured bat

activity (for fast versus slow flying guilds) at different distances from the road, throughout multiple nights. We predicted that traffic noise would dissipate rapidly with increasing distance from the road and that activity levels would differ between species guilds, with the activity of slow flying species being reduced close to the road.

MATERIALS AND METHODS

Study Design

We conducted acoustic surveys in late summer/early autumn 2012, along seven sampling transects that ran perpendicular to a major traffic route, the Wakehurst Parkway, NSW, Australia (Fig. 1). The Wakehurst Parkway is one of the major traffic routes from Sydney's central business district (CBD) to northern Sydney, carrying over 25,000 vehicles daily (Roads and Maritime Services, 2012) with a speed limit of 80 km/h. The road bisects bushland and is predominantly unlit. It is typical of peri-urban environments, where residential housing and thoroughfares traverse, and are adjacent to, remnant vegetation. The area is primarily a mix of Hawkesbury Sandstone Open-forest and Sydney Sandstone Ridgetop Woodland communities, with isolated patches of Coachwood Closed Forest surrounding small streams (Pittwater Council, 1997). The road traverses the alluvial flats along a bushland creek, and the presence of water and fertile soil might suggest that bat activity would be biased toward the location of the road.

We sampled bats and traffic noise along seven transects that ran perpendicular to the road on unlit sections of bushland. Lights were also absent along the road where transects were located. Sampling was carried out on weekdays only (Monday to Friday) to coincide with weekday traffic levels. Sites were selected from Google Earth imagery by assessing the accessibility of areas at least 250 m from the road. GPS coordinates of sites were extracted from Google Earth and entered into a hand-held GPS (Garmin 60CSx, Olathe, KS, USA), which allowed us to locate sampling points in the field. Geology and vegetation communities were further identified using GIS layers provided by both Pittwater and Warringah Councils. This was to identify any potential confounding factors caused by differences in natural habitat or soil productivity within and between transects.

The total number and location of sampling points along each transect varied, depending on factors such as topography and the extent of urbanisation. All transects were sampled at points 10 m and 50 m from the road, and then subsequent distances increased by 100 m. Four transects were sampled up to a distance of 450 m, while the remaining three were only sampled to 250 m due to topographical constraints. Tree height and canopy cover were also recorded at each detector site, while vegetation density was estimated between the road and first (10 m) sampling point at each transect.

Acoustic Surveys

We recorded bat activity over two consecutive nights at each sampling point with Anabat II detectors (Titley Electronics, Ballina, NSW, Australia). We set the detectors to a division ratio of 8 and set them on a timer to begin recording one hour before sunset and conclude one hour after sunrise. A single detector was placed at each sampling point, with the microphone

positioned one metre off the ground, facing up at a 45° angle and towards vegetation gaps to optimise sampling of unobstructed air space. Microphones were housed in short s-shaped PVC pipes to provide protection from rain.

We captured traffic noise levels using automatic Song Meter recorders (16 bit, 192 kHz sample rate — Wildlife Acoustics Inc., Concord, MA, USA). Song Meter microphones had a sensitivity of -36 ± 4 dBV Pa⁻¹ (1 Pa = 94 dB SPL) at 1 kHz, with a flat frequency response (20 Hz–20 kHz). Devices were set to record in half hour blocks throughout the night, simultaneously with Anabats, to record traffic noise at each distance relative to

the road. Song Meters were placed in trees two meters from the ground at all sampling points, with the recording microphone pointed towards the road.

Peak amplitude of a passing vehicle at its closest point to the microphone was measured in dB relative to full scale (dBFS). We also measured the average amplitude over the time period of a vehicle passing (any noise from start to finish of a single vehicle heard at 10 m) because traffic noise remained at constant levels at distances above 50 m from the road. To convert traffic noise amplitude from dBFS to dB sound pressure level (dB SPL), we recorded sound levels of vehicles passing a known

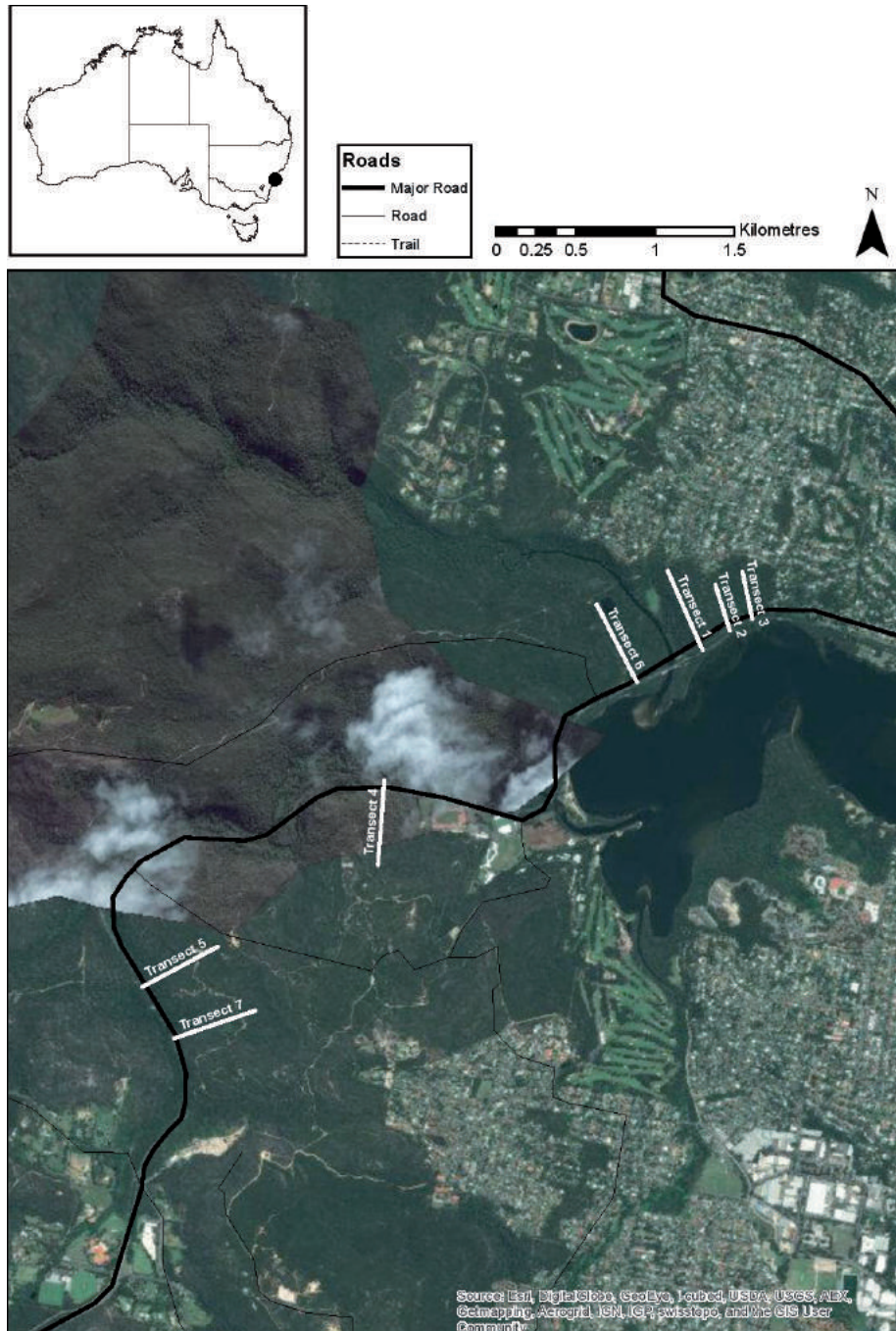


FIG. 1. Map of study area showing the seven sampling transects (white lines) along the Wakehurst Parkway

10 m sampling point using a sound level meter (Sper Scientific model 840013 — Scottsdale, Arizona, USA) with an A-weighted filter. Amplitude levels (in dB SPL) were then deduced from peak amplitude values of the digital recordings from the same site.

We analysed activity and noise levels in hour blocks throughout the night. We used traffic volume as well as peak and average amplitude levels of passing vehicles to quantify traffic noise. Traffic volume was estimated by recording the number of vehicles passing the microphone in three 5-minute blocks per hour (e.g., 20:45–20:50 h, 20:55–21:00 h, 21:05–21:10 h) over three weeknights.

Acoustical Analyses

The Anabat detection system uses zero-crossings analysis to process information from the dominant harmonic of calls, with a frequency bandwidth of 10–200 kHz (Adams *et al.*, 2010). A bat ‘pass’ is defined as a sequence of at least three echolocation calls (or pulses) of similar shape and frequency, separated by brief pauses of less than one second (Law *et al.*, 1998). Call identification was automated using Anascheme software (M. Gibson, Ballarat University, Ballarat, Victoria, Australia) with an identification key specific to the Sydney region (Adams *et al.*, 2010). Anascheme models calls recorded by the Anabat using regression analysis and extracts call parameters from both raw and modelled data (Adams *et al.*, 2010). A standard protocol was implemented within Anascheme to identify test calls and sequences. Identification of individual calls was only made when model quality (R^2) was > 0.9 (or > 0.8 for *Mormopterus* species). For a call sequence to be identified as a species, more than 50% of the calls in the sequence and at least three calls in total, had to be identified to the same species. Any files that Anascheme could not match to these conditions were placed in an ‘unknown’ category. Unknowns were then classified as either bat calls or noise, with noise files being discarded.

Most species could be identified to species level in Anascheme with the exception of *Nyctophilus* (*N. geoffroyi* and *N. gouldi*), hence both species were pooled as ‘*Nyctophilus* spp.’. Threatened species (e.g., *Chalinolobus dwyeri*) were assessed manually using Analook software (C. Corben, version 4.8) and compared to an identification key for the area (Pennay *et al.*, 2004) to ensure correct identification.

Feeding buzzes were manually distinguished from normal search phase calls using Analook, and were used to estimate foraging activity. We differentiated feeding buzzes from normal calls by identifying short sequences of steep linear calls with increased repetition rates (i.e., shorter interval between pulses). Foraging activity was assessed using the number of bat passes containing feeding buzzes.

We used Adobe Audition CS6 (Adobe® Systems, Mountain View, CA, USA) to analyse amplitude levels of traffic noise. Analyses were reduced to four separate frequency bands: 0–1 kHz, 1–5 kHz, 5–10 kHz and 10–20 kHz. An upper limit of 20 kHz was set as ultrasonic frequencies (i.e. > 20 kHz) were quiet at 10 m, and negligible at distances greater than 10 m from the source.

Statistical Analyses

A Poisson generalised linear mixed model (GLMM) was used to analyse bat activity data from the Wakehurst Parkway road transects, performed using the software package R, ver. 2.15.1 (R Core Team, 2012). Independent variables were

standardised to have means of 0 and standard deviations of 1 so as to make interpretation among variables equivalent. Three variables included in the model were distance from road (m), tree height (m) and canopy cover (%), with transect treated as a random factor. As noise and distance from road were highly negatively correlated ($r = -0.833$) and we did not have noise data for all points, noise was not included in the model as a variable. GLMM models were run for total calls across all species, and then separately for species grouped as fast flying or slow flying according to Churchill (2008). To determine whether bat distribution differed along transects throughout the night, a second GLMM was run with time (h) as a factor. Bat passes were pooled into hour blocks throughout each night (i.e., 20:01–21:00 h, 21:01–22:00 h). Predictor variables were time and distance, with transect as a random factor.

We used Spearman’s rank correlation to investigate a direct relationship between traffic noise and activity between 20:00 and 21:00 h when bat activity levels were at their peak and traffic was relatively constant. Noise data were based on the average amplitude of the lowest frequency band (to avoid confounding effects from other noise sources) across the whole hour, quantified using Audition. One-way analysis of variance (ANOVA) was used to detect significant differences in sound attenuation in the four frequency bands at 10 m from the road along a vegetation density gradient. The peak amplitude (mean across 15) of passing cars at each of the three levels of vegetation density was recorded for analysis. Tukey’s HSD post-hoc tests were used to examine any pair-wise differences between vegetation categories in each frequency band. Data did not require transformation to meet the assumptions of ANOVA (normality and homogeneity of variances) as confirmed by Kolmogorov-Smirnov and Levene’s tests. Tests were performed in the SPSS statistical package 19 (IBM Ltd., St Leonards, NSW 2065, Australia).

RESULTS

Levels of Traffic Noise and Volume

Traffic noise levels gradually decreased with distance from the road in each of the four frequency bands (Fig. 2). Amplitude levels across each frequency dropped by over 50% in the first 50 m, with high frequency components > 10 kHz being especially soft at this distance. Furthermore, all traffic noise above 5 kHz was lost within the first 150 m from the road. The entire audible traffic noise recorded at distances of 250 m or more was contained within the < 1 kHz frequency band. Vegetation density had a significant inverse effect on traffic noise attenuation (Table 1), with sound levels decreasing as vegetation density increased (Fig. 3). Attenuation by vegetation was not homogenous among frequencies.

Traffic volume along the Wakehurst Parkway peaked at dusk and dawn (Fig. 4). Volume remained high at 20:00 and 21:00 h with a mean (\pm SE) of 50 ± 3 and 40 ± 1 vehicles passing every five

minutes, respectively. By 23:00 h, traffic volume reduced to a mean of 6 ± 1 vehicles per five minutes and continued to decrease further into the night. Traffic volume began rising at 04:00 h until morning peak hour (06:00 h), which was the busiest period with a mean of 95 ± 4 vehicles per five minutes.

Bat Activity and Diversity

A total of 1,288 bat passes from at least 11 species were detected across 38 nights of recordings, and bat activity was recorded at 34 of the 36 sampling points (Table 2). Forty-eight percent of passes could be identified to either species or a species complex (i.e., *Nyctophilus* spp.). The remaining 52% were pooled in an unknown category and were included in total calls as an index of activity. *Chalinolobus gouldii* had the greatest number of passes (247) and was recorded at the largest number of sampling points (29 of 36). Other frequently recorded species were *Miniopterus schreibersii* with 123 passes recorded at 23 sampling points, and *Mormopterus ridei* with 93 passes from 16 sampling points. Species that were recorded at less than 10% of the total sites were classed as rare and not included in graphical representation. A total of 110 feeding buzzes were recorded (8.5% of total calls) from 23 of the 36 sampling points.

The majority of recorded bat passes occurred at 10 m from the road (Fig. 5A). Foraging activity was also highest, with 53.6% of total feeding buzzes being recorded at 10 m. Fast flying species (excluding *M. ridei*) were found to contribute to the higher activity levels at this distance, with *C. gouldii*, *M. schreibersii* and *Tadarida australis* calls being more common at 10 m than at any other distance

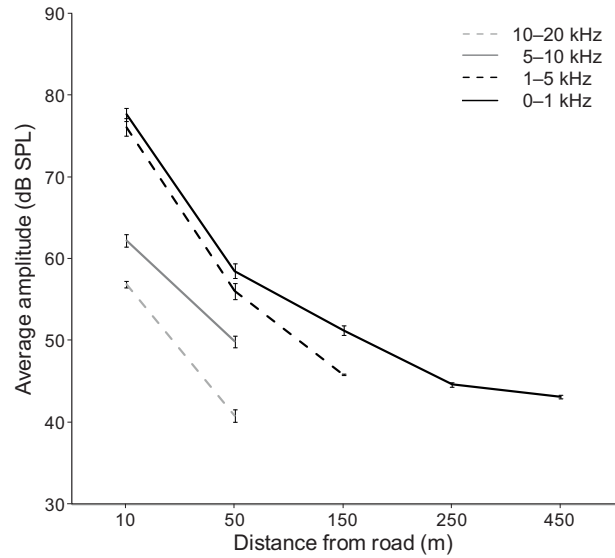


FIG. 2. Average amplitude levels ($\bar{x} \pm SE$; dB SPL, decibels sound pressure level) of traffic noise recorded at five distances perpendicular to Wakehurst Parkway. Note: noise above 20 kHz was excluded from analyses

from the road (Fig. 5B). More than 50% of calls from *C. gouldii*, and 75% from *T. australis*, were recorded in the first 10 m from the road. Interestingly, 17 passes were recorded at 10 m from the road for the vulnerable and rare Large-eared pied bat (*Chalinolobus dwyeri*) and this was the highest number of passes recorded from this species at any sampling point. Distance from road and canopy cover were negatively correlated with total bat activity, while tree height positively influenced total bat activity (deviance explained, DE = 54.75% — Table 3), however, this was not consistent among species guilds. Decreasing canopy cover and distance from the road significantly influenced the activity of fast

TABLE 1. Summary of results of one way ANOVAs testing for differences in sound attenuation between all pairs of vegetation categories (No = significant gap in vegetation between traffic and microphone, moderate = some vegetation between traffic and microphone, dense = dense vegetation between traffic and microphone) within each of four frequency bands

Frequency band	Vegetation category	d.f.	F	P-level
0-1 kHz	No vs. moderate	42	144.6	< 0.001
	No vs. dense			< 0.001
	moderate vs. dense			< 0.050
1-5 kHz	No vs. moderate	42	57.10	< 0.001
	No vs. dense			< 0.001
	moderate vs. dense			< 0.050
5-10 kHz	No vs. moderate	42	34.33	< 0.001
	No vs. dense			< 0.001
	moderate vs. dense			< 0.010
10-20 kHz	No vs. moderate	42	19.16	0.106
	No vs. dense			< 0.001
	moderate vs. dense			< 0.001

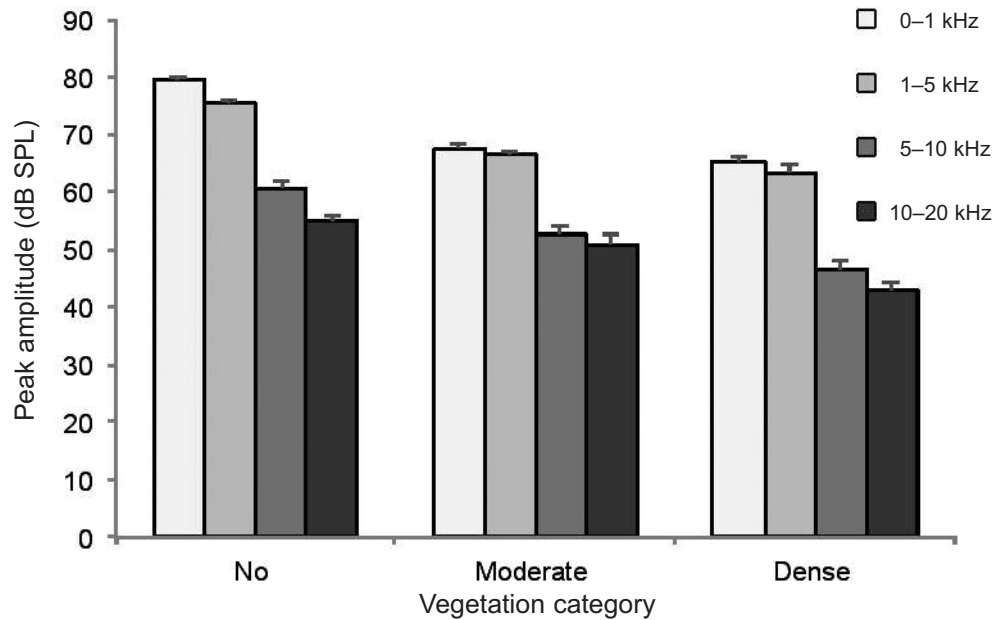


FIG. 3. Peak amplitude levels ($\bar{x} \pm SE$) of traffic recorded at 10 m from the edge of Wakehurst Parkway across three vegetation categories (No = significant gap in vegetation between traffic and microphone, moderate = some vegetation between traffic and microphone, dense = dense vegetation between traffic and microphone; examples in Fig. 2)

flyers, while tree height negatively influenced activity (DE = 43.19%). In contrast, tree height was positively correlated with the activity of slow flying species, and there was no relationship between activity and distance from the road and canopy cover (DE = 14.19% — Fig. 5C).

Bat activity levels across all recorded species were highest early in the night (2000–2100 h) and then decreased (Table 4), however, the relationship between bat activity and distance from the road weakened when time was included as a factor (total calls DE = 17.15%). This was also the case for fast flyers with a weaker negative relationship between

activity and distance from the road with time being a factor (DE = 11.38% — Fig. 6A). Additionally, with time included as a factor, there was a weak positive relationship between the distribution of slow flying species and distance from the road (DE = 13.16% — Fig. 6B). Zero passes were recorded from slow flying species at 10 m until after 2100 h when traffic volumes begin to decline, however activity was recorded at this distance between 0600 and 0700 h when volumes are at their peak. Unlike overall activity, there was no relationship between foraging activity and time, with feeding buzzes being distributed at any time throughout the night. Spearman’s rank correlation confirmed that there was no direct relationship between traffic noise and activity across all species (Spearman’s rho = 0.145, $P = 0.203$) and across species guilds (fast flyers: Spearman’s rho = 0.184, $P = 0.145$; slow flyers: Spearman’s rho = 0.069, $P = 0.347$, in all cases $n = 35$).

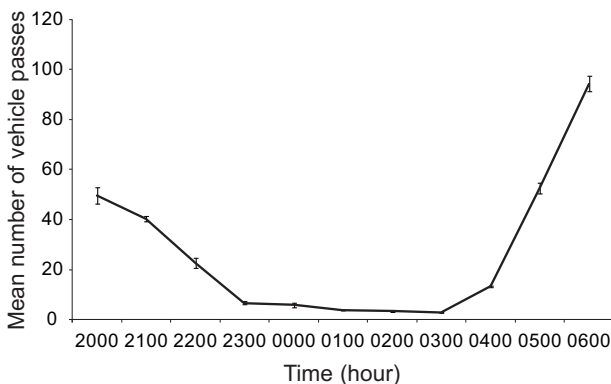


FIG. 4. Mean number of vehicles passing per five minutes as measured each hour over an 11-hour period (values are means of three 5-minute blocks per hour over three nights $\pm SE$)

DISCUSSION

Contrary to a priori expectations, we found no evidence of road avoidance in bats. In fact, we found overall activity to be highest within the first 10 m from the road, with the vast majority of calls being produced by three fast flying species (*C. gouldii*, *M. schreibersii* and *T. australis*). These species

TABLE 2. Species detected in transect study with total passes across all sites and the total number of sites (n) in which each species was recorded in (36 in total). * — rare species

Species	Common name	Total passes	n
<i>Chalinolobus dwyeri</i> *	Large-eared pied bat	26	3
<i>C. gouldii</i>	Gould's wattled bat	247	29
<i>C. morio</i> *	Chocolate wattled bat	2	2
<i>Miniopterus australis</i> *	Little bent-wing	5	3
<i>M. schreibersii</i>	Eastern bent-wing	124	24
<i>Mormopterus ridei</i>	Eastern freetail	93	16
<i>Nyctophilus</i> spp.	Lesser and/or Gould's long-eared bats	6	5
<i>Rhinolophus megaphyllus</i>	Eastern horseshoe bat	12	8
<i>Tadarida australis</i>	White-striped freetail bat	71	9
<i>Vespadelus darlingtoni</i> *	Large forest bat	2	2
<i>V. vulturnus</i>	Little forest bat	26	13

preferred to forage in productive areas with a significant gap in the canopy. Fast flying species, such as these, tend to use open areas such as roads (Abbott *et al.*, 2012) and quiet forest tracks (Lloyd *et al.*, 2006) as flyways while foraging. Recent studies have revealed that bat activity is highest in areas of high productivity, where invertebrate numbers are high (Basham *et al.*, 2011; Threlfall *et al.*, 2011). Throughout suburban Sydney, insect biomass is highly influenced by landscape and geology variables (Threlfall *et al.*, 2011). Suburban bushland habitats in sandstone landscapes support significantly lower insect biomass than suburban bushland habitats with shale geology, as well as open space and riparian habitats on either geology. Within our study area, a gradient exists between low productivity sandstone ridges and the productive moist gullies and alluvial flats (Collins *et al.*, 2012), consisting of open space and riparian habitats, on which the road is located. We recorded high foraging activity at one 450 m sampling point excluded as an outlier from analyses. Unlike the other sampling points far from the road that were located on sandstone

ridges, this point was located in a low-lying productive alluvial flat with a significant gap in the canopy.

Because of the location of the Wakehurst Parkway in relation to soil productivity and, therefore, insect biomass, we predicted that bats would forage close to the road. Unexpectedly, however, we found activity to be highest at times of high traffic volume. This finding is supported by Abbott *et al.* (2012), who recorded high incidences of foraging bats crossing motorways coincident with passing vehicles. In addition, it is possible that bats hunt insects that are attracted to vehicle headlights (Adams *et al.*, 2005). Lentini *et al.* (2012) found that bat activity on country roads was unaffected by estimated traffic volume, however, bitumen road surface reduced activity in nearby remnant vegetation. This suggests that the amount of traffic may not deter bats from foraging if resources are present. In addition, bats are most active at dawn and dusk (e.g., Law *et al.*, 1998), which in our study coincides with peak traffic levels. One consequence of not avoiding traffic noise could be increased vulnerability of foraging bats colliding with cars (Lesiński *et al.*, 2011).

TABLE 3. Summary from GLMM analysis of transect variables from seven transects. SE — standard error; * — significant at $\alpha = 0.05$

Species guild	Variable	Coefficient	SE	z	P -level
Total calls	(Intercept)	3.102	0.318	9.757	< 0.001*
	Distance	-0.356	0.041	-8.670	< 0.001*
	Canopy cover	-0.582	0.048	-12.010	< 0.001*
	Tree height	0.176	0.051	3.396	< 0.001*
Fast flyers	(Intercept)	2.176	0.340	6.411	< 0.001*
	Distance	-0.583	0.070	-8.288	< 0.001*
	Canopy cover	-0.888	0.084	-10.600	< 0.001*
	Tree height	-0.151	0.082	-1.835	0.066
Slow flyers	(Intercept)	0.387	0.295	1.315	0.189
	Distance	-0.050	0.141	-0.359	0.720
	Canopy cover	-0.164	0.165	-0.994	0.320
	Tree height	0.555	0.185	2.994	0.002*

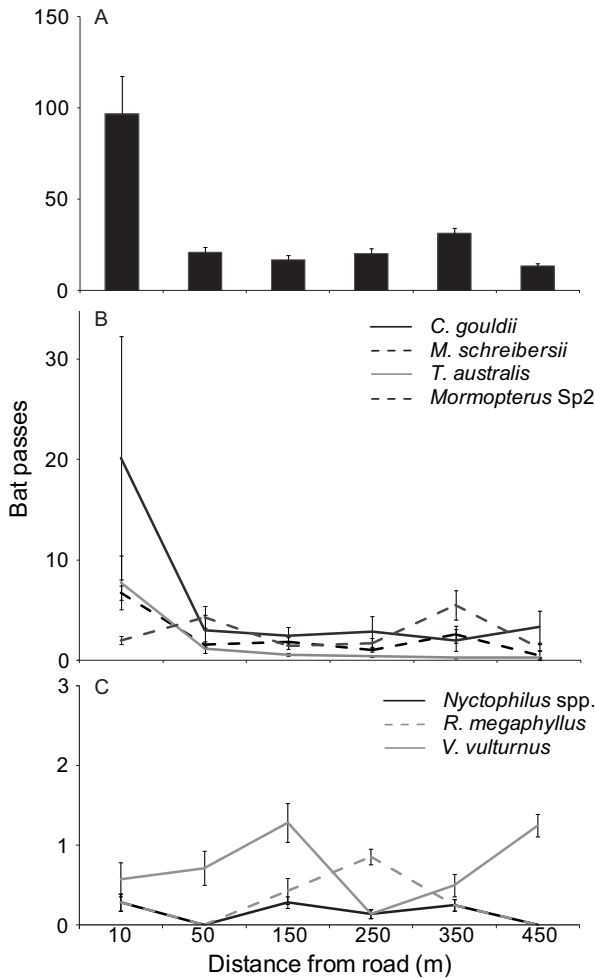


FIG. 5. Number of passes ($\bar{x} \pm SE$) from (A) all bat species, (B) fast flyers and (C) slow flyers recorded at six perpendicular distances from the edge of Wakehurst Parkway

We recommend this as an important subject for further research, particularly for vulnerable species such as *C. dwyeri*.

We predicted that bats would show a level of avoidance of foraging near busy roads because of acoustic disruptions caused by traffic noise (Schaub *et al.*, 2008), but found no evidence of this. In con-

trast, Berthinussen and Altringham (2011) did report a decrease in activity in proximity to a major road. These differences point to a role for habitat, landscape elements, and spatial scale in altering effects. At small spatial scales, roads through forested landscapes like the Wakehurst Parkway provide a contrast of resources for bats, attracting those that can exploit those resources. In other environments, where resource distribution is not driven by road proximity, bats may choose to avoid roads because they are a disturbance, not because they prevent foraging. Thus, it is possible that traffic noise does not disrupt the high frequency calls of echolocating bats. The majority of sound energy in traffic noise lies within low frequency ranges (< 5 kHz), with ultrasonic components (> 20 kHz) being soft and attenuating rapidly over short distances. Even at 10 metres from the road, we found that ultrasonic components were often negligible. As most species echolocate far above this frequency, it is unlikely that their calls would be masked by traffic noise. However, the call of *T. australis* lies between 10 and 15 kHz (Pennay, 2004); a frequency range in which traffic noise is highly detectable at 10 m. *T. australis* is widespread throughout urban Sydney (Threlfall *et al.*, 2012) and tends to forage in areas high above the canopy, potentially at altitudes of over 100 m (Rhodes and Catterall, 2008). At altitudes this high, traffic noise is largely attenuated, and therefore unlikely to have any effect on echolocation. But even at 10 m from the road, it is possible that traffic noise is unable to mask the high intensity of echolocation calls. Surlykke and Kalko (2008) recorded the calls of eleven fast flying species in full-spectrum, and found that the intensity of calls was above 115 dB SPL for all species. At 10 metres from the road, traffic noise recorded in the lowest (i.e. loudest) frequency band (0–1 kHz) was below 80 dB SPL, where noise recorded in the highest measured band (10–20 kHz) was below 60 dB SPL. Therefore, it is unlikely that the low amplitude levels of traffic

TABLE 4. Summary from GLMM analysis with bat passes grouped in hour blocks across the night. SE — standard error; * — significant at $\alpha = 0.05$

Species guild	Variable	Coefficient	SE	z	P
Total calls	(Intercept)	2.606	0.285	9.140	< 0.001*
	Distance	-0.002	0.000	-8.806	< 0.001*
	Time	-0.263	0.010	-26.760	< 0.001*
Fast flyers	(Intercept)	1.961	0.263	7.461	< 0.001*
	Distance	-0.002	0.000	-7.408	< 0.001*
	Time	-0.264	0.014	-18.330	< 0.001*
Slow flyers	(Intercept)	-1.018	0.454	-2.244	0.025*
	Distance	0.003	0.001	4.285	< 0.001*
	Time	-0.298	0.039	-7.709	< 0.001*

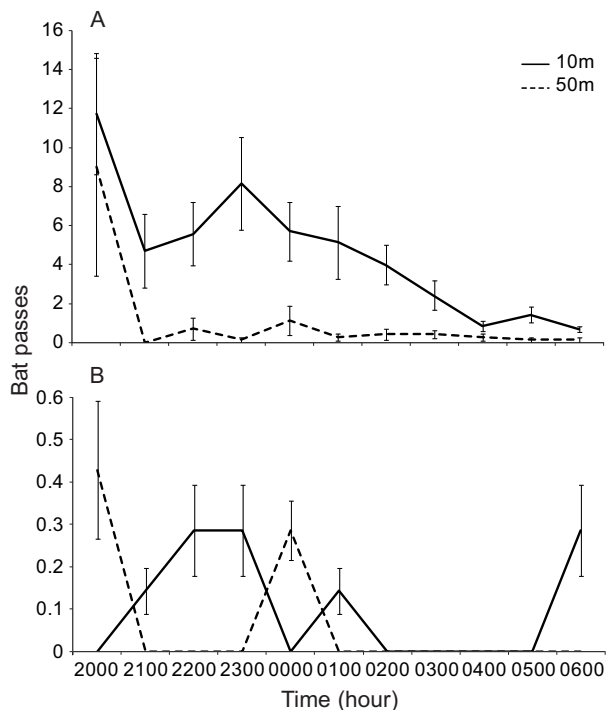


FIG. 6. Activity of (A) fast flying species and (B) slow flying species across hourly blocks throughout the night within the first 50 m from the road (values are means across transects \pm SE)

noise would be able to effectively mask a call above 115 dB SPL.

Nonetheless, not all species rely on high frequency and high intensity echolocation calls whilst foraging. Slow-flying gleaning species, such as *Nyctophilus* spp., largely rely on passive listening to sounds produced by prey (Grant, 1991). These species are likely to be more sensitive to noise, due to the masking of low intensity sounds produced by prey animals. Previous studies observed decreased foraging efficiency (Siemers and Schaub, 2011), and even avoidance of noisy areas (Schaub *et al.*, 2008) in the gleaning *Myotis myotis*. Therefore, we assumed that *Nyctophilus* spp. would show similar avoidance behaviour in the field; noting that this would only likely be noticeable near the road.

We determined that the majority of traffic noise was lost within the first 50 m from the road, due in part to the dense vegetation surrounding Wakehurst Parkway. This allows us to assume that the potential of traffic noise masking prey-produced sounds is significantly reduced by 50 m. Kerth and Melber (2009) found that the gleaning *Myotis bechsteinii* often foraged within 50 m from the edge of a busy motorway, but these bats totally avoided crossing the road, apart from a few that used an underpass.

Capacity to test this hypothesis in situ was difficult as only a low number of *Nyctophilus* spp. calls were detected. These species are often under-represented in acoustic surveys (Law *et al.*, 1999) as they have soft calls and rely on vision and passive listening (Grant, 1991; Hosken *et al.*, 1994). Future field research should target such species with more suitable methods where ultrasonic detectors do not suffice, such as the use of infrared cameras (Szewczak and Arnett, 2008), radio tracking (Kerth and Melber, 2009) or greater acoustic sampling effort. Threlfall *et al.* (2012) found that these species are less abundant in urban bushland than more extensive bushland, which is possibly in part due to their sensitivity to noise around roads or other anthropogenic effects such as lights (Threlfall *et al.*, 2013).

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LITERATURE CITED

- ABBOTT, I. M., F. BUTLER, and S. HARRISON. 2012. When flyways meet highways — the relative permeability of different motorway crossing sites to functionally diverse bat species. *Landscape and Urban Planning*, 106: 293–302.
- ADAMS, M. D., B. S. LAW, and K. O. FRENCH. 2005. Effect of lights on activity levels of forest bats: increasing the efficiency of surveys and species identification. *Wildlife Research*, 32: 173–182.
- ADAMS, M. D., B. S. LAW, and M. S. GIBSON. 2010. Reliable automation of bat call identification for eastern New South Wales, Australia, using classification trees and AnaScheme software. *Acta Chiropterologica*, 12: 231–245.
- AVILA-FLORES, R., and M. B. FENTON. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal of Mammalogy*, 86: 1193–1204.
- BARBER, J. R., K. R. CROOKS, and K. M. FRISTRUP. 2009. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25: 180–189.
- BASHAM, R., B. LAW, and P. BANKS. 2011. Microbats in a 'leafy' urban landscape: are they persisting, and what factors influence their presence? *Austral Ecology*, 36: 663–678.

- BERTHINUSSEN, A., and J. ALTRINGHAM. 2011. The effect of a major road on bat activity and diversity. *Journal of Applied Ecology*, 49: 82–89.
- BOTTELDOOREN, D., B. DE COENSEL, and T. DE MUER. 2006. The temporal structure of urban soundscapes. *Journal of Sound and Vibration*, 292: 105–123.
- CHAN, A. A. Y., P. GIRALDO-PEREZ, S. SMITH, and D. T. BLUMSTEIN. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters*, 6: 458–461.
- CHURCHILL, S. 2008. *Australian bats*, 2nd edition. Allen & Unwin, Crows Nest, NSW, Australia, 254 pp.
- COLLINS, L., R. A. BRADSTOCK, E. M. TASKER, and R. J. WHELAN. 2012. Can gullies preserve complex forest structure in frequently burnt landscapes? *Biological Conservation*, 153: 177–186.
- DUCHAMP, J. E., and R. K. SWIHARD. 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecology*, 23: 849–860.
- DUCHAMP, J. E., D. W. SPARKS, and J. O. WHITAKER, JR. 2004. Foraging-habitat selection by bats at an urban-rural interface: comparison between a successful and a less successful species. *Canadian Journal of Zoology*, 82: 1157–1164.
- ERICKSON, J. L., and S. D. WEST. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation*, 109: 95–102.
- GRANT, J. D. A. 1991. Prey location by two Australian long-eared bats, *Nyctophilus gouldi* and *N. geoffroyi*. *Australian Journal of Zoology*, 39: 45–56.
- HALFWERK, W., L. J. M. HOLLEMAN, C. K. M. LESSELLS, and H. SLABBEKOORN. 2011. Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48: 210–219.
- HOSKEN, D. J., W. J. BAILEY, J. E. O'SHEA, and J. D. ROBERTS. 1994. Localisation of insect calls by the bat *Nyctophilus geoffroyi* (Chiroptera: Vespertilionidae): a laboratory study. *Australian Journal of Zoology*, 42: 177–184.
- HOIRIGAN, C. L., C. JOHNSON, and S. K. A. ROBSON. 2006. The structure of a micro-bat community in relation to gradients of environmental variation in a tropical urban area. *Urban Ecosystems*, 9: 67–82.
- HOIRIGAN, C. L., C. P. CATTERALL, D. JONES, and M. RHODES. 2010. The diversity of insectivorous bat assemblages among habitats within a subtropical urban landscape. *Austral Ecology*, 35: 849–857.
- KAKU, J., M. HIROE, S. KUWANO, and S. NAMBA. 2004. Sleep disturbance by traffic noise: an experimental study in subjects' own houses using a portable CD player. *Journal of Sound and Vibration*, 277: 459–464.
- KERTH, G., and M. MELBER. 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation*, 142: 270–279.
- LAW, B. S., J. ANDERSON, and M. CHIDEL. 1998. A bat survey in State Forests on the south-west slopes region of New South Wales with suggestions of improvements for future surveys. *Australian Zoologist*, 30: 467–479.
- LAW, B. S., J. ANDERSON, and M. CHIDEL. 1999. Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. *Biological Conservation*, 88: 333–345.
- LAW, B. S., M. CHIDEL, and P. TAP. 2011. Bat activity in ephemeral stream-beds in the Pilliga forests: clarifying the importance of flyways and buffer widths in open forest and woodland. Pp. 308–321, in *The biology and conservation of Australian bats* (B. LAW, P. EBY, D. LUNNEY, and L. LUMSDEN, eds.). Royal Zoological Society of NSW, Mosman, NSW, Australia, 498 pp.
- LENTINI, P. E., P. GIBBSON, J. FISCHER, B. LAW, J. HANSPACH, and T. G. MARTIN. 2012. Bats in a farming landscape benefit from linear remnants and unimproved pastures. *PLoS ONE*, 7: e48201.
- LESIŃSKI, G., A. SIKORA, and A. OLSZEWSKI. 2011. Bat casualties on a road crossing a mosaic landscape. *European Journal of Wildlife Research*, 57: 217–223.
- LLOYD, A., B. LAW, and R. GOLDINGAY. 2006. Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biological Conservation*, 129: 207–220.
- MORGAN, G. M., T. E. WILCOXEN, M. A. RENSEL, and S. J. SCHOECH. 2012. Are roads and traffic sources of physiological stress for the Florida scrub-jay? *Wildlife Research*, 39: 301–310.
- PARRIS, K. M., M. VELIK-LORD, and J. M. A. NORTH. 2009. Frogs call at a higher pitch in traffic noise. *Ecology and Society*, 14(1): 25. Available at <http://www.ecologyandsociety.org/vol14/iss1/art25/>.
- PENNAY, M., B. LAW, and L. REINHOLD. 2004. *Bat calls of New South Wales: region based guide to the echolocation calls of microchiropteran bats*. NSW Department of Environment and Conservation, Hurstville, NSW, Australia, 87 pp.
- PITTWATER COUNCIL. 1997. *Urban bushland inventory and action plan, South Ward Reserves. Volume 2*. Pittwater Council Natural Resources Unit, Warriewood, NSW, Australia, 101 pp.
- R CORE TEAM. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/>.
- RAIMBAULT, M., and D. DUBOIS. 2005. Urban soundscapes: Experiences and knowledge. *Cities*, 22: 339–350.
- RHODES, M., and C. P. CATTERALL. 2008. Spatial foraging behavior and use of an urban landscape by a fast-flying bat, the molossid *Tadarida australis*. *Journal of Mammalogy*, 89: 34–42.
- ROADS AND MARITIME SERVICES. 2012. *Average daily traffic volume*. Roads and Maritime Services, NSW Government. Available online at: <http://www.rms.nsw.gov.au/documents/about/corporatepublications/statistics/nsw-traffic-volumes-2012.pdf>.
- RYDELL, J., L. A. MILLER, and M. E. JENSEN. 1999. Echolocation constraints of Daubenton's bat foraging over water. *Functional Ecology*, 13: 247–255.
- SCHAUB, A., J. OSTWALD, and B. M. SIEMERS. 2008. Foraging bats avoid noise. *Journal of Experimental Biology*, 211: 3174–3180.
- SIEMERS, B. M., and A. SCHAUB. 2011. Hunting at the high-way: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society*, 278B: 1646–1652.
- SPEAKMAN, J. R., P. I. WEBB, and P. A. RACEY. 1991. Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology*, 28: 1087–1104.
- STONE, E. L., G. JONES, and S. HARRIS. 2009. Street lighting disturbs commuting bats. *Current Biology*, 19: 1123–1127.

- SURLYKKE, A., and E. K. V. KALKO. 2008. Echolocating bats cry out loud to detect their prey. *PLoS ONE*, 3: e2036.
- SZEWCZAK, J. M., and E. B. ARNETT. 2008. Field test results of a potential acoustic deterrent to reduce bat mortality from wind turbines. An investigative report submitted to the Bats and Wind Energy Co-operative. Bat Conservation International, Austin, TX, USA. Available at <http://www.batsandwind.org/pdf/2007DeterrentPondStudyFinal.pdf>.
- THRELFALL, C. G., B. LAW, and P. B. BANKS. 2012. Sensitivity of insectivorous bats to urbanization: implications for suburban conservation planning. *Biological Conservation*, 146: 41–52.
- THRELFALL, C. G., B. LAW, and P. B. BANKS. 2013. The urban matrix and artificial light restricts the nightly ranging behaviour of Gould's long-eared bat (*Nyctophilus gouldi*). *Austral Ecology*, 38: 921–930.
- THRELFALL, C., B. LAW, T. PENMAN, and P. B. BANKS. 2011. Ecological processes in urban landscapes: mechanisms influencing the distribution and activity of insectivorous bats. *Ecography*, 34: 814–826.
- WATSON, D. M. 2011. A productivity-based explanation for woodland bird declines: poorer soils yield less food. *Emu*, 111: 10–18.

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