

Microbats in a 'leafy' urban landscape: are they persisting, and what factors influence their presence?

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Abstract Urbanization is an extreme form of habitat modification, but retention of native vegetation in bushland reserves may improve the ecological sustainability of cities. We focused on bats (Microchiroptera) and investigated the use of the urban matrix and surrounding bushland in a region of Sydney, Australia, where remnant bushland persists and gardens often support large trees. Ultrasonic surveys were conducted at 40 sites over one summer season in the backyard matrix, bushland remnants and surrounding National Parks to determine which species were present, and the influence of landscape elements and habitat characteristics on activity, species richness and presence of individual species. In total, 15 of the 17 microbat species known from the Sydney region were recorded in the study area. Yet only three of these species, *Chalinolobus gouldii*, *Mormopterus* species 2 and *Miniopterus schreibersii* were present in more than 40% of sites. Bat activity was significantly higher in remnant bushland on shale soils and in backyards, compared with sandstone gully and ridge remnants, or reference sites in nearby National Parks. Furthermore, species assemblages in urban areas were different from assemblages in reference sites. Of all the habitat characteristics examined, the amount of bushland within 0.5–3 km surrounding a site and tree density were the most common predictors of individual species presence, particularly rare species. Area of bushland, hollow abundance and average tree diameter were positively correlated with species richness, while tree diameter was the strongest predictor of total microbat activity. The proximity of large areas of bushland and the many trees remaining in residential areas of the northern 'leafy' suburbs of Sydney allowed the persistence of a range of bat species. The higher bat activity on fertile shale soils indicated that bushland remnants embedded within cities can have high conservation value for bats. Surveys in more urbanized areas of Sydney are needed to test predictions of the models derived in this study.

Key words: Insectivorous bats, urbanization, spatial heterogeneity backyards.

INTRODUCTION

Urbanization results in an extreme form of habitat modification, as the original habitat is almost completely removed, making the matrix alien and inhospitable to many species (Burgman & Lindenmayer 1998; McKinney 2002). Species that require large areas of habitat, that cannot disperse from outlying areas or are intolerant of disturbance, are rare in urban landscapes (Dickman 1987; McKinney & Lockwood 1999; Van der Ree & McCarthy 2005). Species that do persist are likely to be those that can cross the matrix or exploit resources within it (Catterall *et al.* 1989; Laurance 1991; Evelyn *et al.* 2004; Van der Ree & McCarthy 2005).

Microchiropteran bats (henceforth 'bats') are a diverse group of small, insectivorous bats and are often a major component of regional mammal diversity (Schulz & de Oliveira 1995). Roost and foraging

sites are two essential habitat components for bats (Findley 1993). Under natural situations bats will commute between roost and foraging sites (Lunney *et al.* 1985; Taylor & Savva 1988) if they are linked by traversable habitat (Lambeck & Saunders 1993). Some bats are highly mobile and may be more tolerant of fragmentation than terrestrial mammals, which often decline in fragmented landscapes (Kitchenner *et al.* 1980). In particular, tolerance of fragmentation has been demonstrated for some species in agricultural and forested landscapes (Estrada *et al.* 1993; Lumsden *et al.* 1995; Law *et al.* 1999). Some bats fly between remnants and utilize resources spread over a wide spatial scale, while others utilize resources in the matrix by foraging around isolated paddock trees in farmland (Law *et al.* 2000; Lumsden & Bennett 2005). However, habitat use, flight characteristics and mobility vary considerably among species (Aldridge & Rautenbach 1987), with only some species using resources within the matrix (Estrada *et al.* 1993).

Urbanization appears to have greater effects than rural land use on bats. One study in Townsville,

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Queensland found that with increasing urbanization there was a decline in species richness and total foraging activity (Hourigan *et al.* 2006). In that study, distance from natural vegetation had the largest influence on the individual foraging preferences of bats. The use of urban areas for foraging also depends on the foraging mode (Aldridge & Rautenbach 1987; Findley 1993). Species with the ability to exploit open and edge habitats created by urban development were more widespread, especially one species of *Mormopterus* in Townsville (Hourigan *et al.* 2006). In North and Central America, some bats that naturally forage in open areas now also forage around streetlights (Geggie & Fenton 1985; Avila-Flores & Fenton 2005). Furthermore, suitable roosts may be limited in urban environments. In the northern hemisphere, urban bats display stronger roost fidelity and travel further between consecutive roosts (Evelyn *et al.* 2004) and appear later after sunset than rural bats, probably because they do not roost in urban areas and have to travel in from outlying areas (Gaisler *et al.* 1998), but this was not evident in Townsville (Hourigan *et al.* 2006). Although some studies have found that urban bat communities have lower diversity and reduced reproductive success compared with bats from their natural habitat (Kurta & Teramino 1992), others have found high diversity in urban areas, especially in low density residential areas (Hourigan *et al.* 2010). It is therefore likely that some species will cope better with urbanization than others, with the degree and scale of urbanization also being important.

Efforts to build more ecologically sustainable cities in part rely on green zones, where native vegetation is protected in bushland reserves or the matrix is softened with street plantings. But little information is available to guide urban planning on the relative value of protecting and restoring habitat in urban areas (Garden *et al.* 2006). In this study, we investigated the use of a patchwork of urban areas in the northern suburbs of Sydney, Australia's most populous city. We focused on this region of Sydney because there are large areas of remnant bushland in steep gullies and 'leafy' suburbs renowned for large gardens and tall trees. While clearly different from higher density urban areas, this part of Sydney offers an opportunity to test the hypothesis that bat diversity is maintained where bushland reserves are more extensive. Seventeen bat species are known from the Sydney region (DEC 2005), and while it is likely that not all species would persist in urban landscapes, we predicted that bat species persistence will be relatively high because of the patchwork of bushland reserves and garden trees within these suburbs.

Our first aim was to compare bat activity (total calls of all bat species), species richness (number of species) and the presence of individual species among backyards (matrix), remnant bushland and surrounding

National Parks. Remnant bushland was stratified by topography and soil fertility, because some bat species roost in gullies near water (Law & Anderson 2000), while soil fertility can be associated with the distribution of species (Braithwaite *et al.* 1989). Second, we aimed to determine what habitat characteristics influenced bat activity, species richness and the presence of individual species. Habitat quality for bats depends on vegetation characteristics, the amount of bushland near a site, and avian predation and competition. Some avian predators and hollow-dwelling birds have increased with urbanization (Smith & Smith 2001; Major & Parsons 2010) and these birds may influence site quality for bats (Young 1980; Start 1998).

METHODS

Study area

The study was undertaken in northern Sydney, New South Wales, Australia ($-33^{\circ}74'S$, $151^{\circ}13'E$). Sydney is a large coastal city supporting nearly 4 million people. Sydney's extremities are bounded by National Parks and the urban area supports a diversity of suburbs that range in their degree of urbanization and residential density. We focused on northern Sydney as these suburbs contain large areas of contiguous bushland adjoining considerable areas of urban development and remnants of varying sizes and degrees of isolation. The area is often referred to as the 'leafy' northern suburbs because of its large gardens and tall trees (some > 30 m). Local government areas sampled included Pittwater, Warringah, The Hills, Hornsby and Ku-ring-gai, with the latter forming the core area sampled. Ku-ring-gai supports 11.6 people per hectare and a very low density of dwellings of 4.2 per hectare, calculated after excluding the 1100 ha of bushland reserves (Ku-ring-gai Council 2010). The 136 bushland reserves in Ku-ring-gai represent 12.8% of its land area. Ku-ring-gai also adjoins larger blocks of bushland within Garigal and Lane Cover River National Parks. Most remnant bushland in the area occurs on low fertility soils of the Hawkesbury Sandstone Complex; however, there are also remnants on more fertile soils derived from Wianamatta Shale. This facilitated comparison between remnants on sandstone and shale sites. Vegetation communities are predominantly Sydney Sandstone Ridgetop Woodlands and Gully Forests, with smaller remnants of Blue Gum High Forest and Turpentine-Ironbark Forest growing on shale soil (Benson & Howell 1994).

Site categories

Sites were stratified into five categories, representing combinations of landscape element, topography and soil fertility. These were: (i) reference areas; (ii) sandstone gully remnants; (iii) sandstone ridge remnants; (iv) shale remnants (mostly less than 10 ha, although usually with connectivity to bushland on sandstone); and (v) backyards (gardens associ-

ated with a dwelling, split evenly between shale and sandstone). Reference areas were the large National Parks (NP) and Nature Reserves (NR) occurring on sandstone to the north of Sydney (Muogamarra NR, Marramarra NP, Berowra Valley Regional Park, Ku-ring-gai Chase NP), and these were surveyed to provide an indication of likely bat assemblages and activity levels in undisturbed parts of the northern Sydney Basin. Backyards represent the most commonly developed component of the landscape, that is, the matrix. Other components of the urban matrix that we did not sample included parks, golf courses, industrial areas and shopping precincts. Gully (e.g. Darling Mills State Forest) and ridge (e.g. Angophora Reserve) remnants were bushland growing on sandstone, sometimes with linear connections to other bushland, but predominantly surrounded by suburbs. Gullies were defined as sites on a lower slope, with a creek running through the site. Ridges were ridge-tops or upper-slopes with no drainage line within at least 200 m. There were eight replicate sites in each category, giving 40 sites in total. Sites were not stratified by patch area, as is typical for studies of remnants, because bat activity/species richness is not closely linked to patch area (Estrada *et al.* 1993; Lumsden *et al.* 1995; Law *et al.* 1999). Sites were chosen to give a range of connectivity and isolation from larger bushland areas. Sites directly adjacent to a motorway or freeway were not selected in order to avoid any potential influence of heavy traffic on bat activity (Hoye & Spence 2004).

Bat surveys

Bat activity was surveyed by remotely recording calls with an Anabat II detector (Titley Electronics, Ballina). At each site a single detector was placed on the ground, pointing up at a 45° angle to optimize airspace sampled. Detectors received calls from most bats echolocating within approximately 20 m, and after passing through a Zero-Crossings Interface Module (ZCAIM), calls were recorded as files on a laptop computer. As detection range of survey equipment decreases with vegetation density (Kalcounis *et al.* 1999; Patriquin *et al.* 2003), surveys were conducted along bat flyways, such as wide walking trails (approximately 2 m wide) or narrow fire trails (approximately 3 m wide) (Law *et al.* 1998; O'Farrell *et al.* 1999; Law & Chidel 2002). As flyways were absent in backyards, detectors in backyards faced into relatively open areas that were not blocked by shrubs or trees. Detectors in gully sites were not placed over water because bat activity can be up to three times higher over water (Law *et al.* 1998). To ensure comparable methodology at each site, surveys were conducted along flyways close to the creek.

Each site was surveyed for 2 consecutive nights, unless inclement weather caused the second night to be postponed (Fischer *et al.* 2009). Surveys occurred for the entire night (1 h before sunset to 1 h after sunrise) to ensure that species active at different times throughout the night were recorded (Law *et al.* 1998). Surveys were conducted between late January and late March 2005 in order to optimize bat activity by surveying in the warmest part of the year and to avoid seasonal variation in bat activity. Up to six sites were surveyed each night, and replicate sites within a category were surveyed across different nights to prevent confounding effects of weather.

Call identification

Recorded calls were manually identified using Anabat (Corben 2000a) and Analook (Corben 2000b) software. A call sequence (also commonly referred to as a pass, hereafter calls) was defined as a sequence of at least three pulses of similar frequency (Law *et al.* 1998) and species identification was based on pulse characteristics using an identification guide developed specifically for Sydney (Pennay *et al.* 2004) and a reference call library for Sydney, which contained up to 66 calls for each species (Pennay *et al.* 2004), so as to avoid potential geographic variation in calls (Law *et al.* 2002). Bat echolocation calls are mostly species-specific, although overlapping call characteristics between some species can cause problems with confident identification. Calls of *Nyctophilus geoffroyi* and *Nyctophilus gouldi* could not be distinguished using Anabat/Analook software so were pooled as *Nyctophilus* spp. Bat trapping at Cumberland State Forest (located in the study area), during this study recorded both species. It is unknown whether both or only one species was present at other sites.

Each call was assigned an identification confidence rating of either definite, probable, possible or unidentified (Mills *et al.* 1996). To ensure that identifications were consistent, 100 calls were randomly chosen and re-identified, of which 100 were assigned the same identification and 97 given the same confidence rating. Only definite and probable identifications were used in analyses of species activity. The inclusion of probable identifications introduces a small degree of potential error, but this classification of calls is still conservative in its allocation of species.

Weather considerations

Surveys were not conducted on rainy or windy nights, nor for 1 week around the full moon, as bat activity and detection probability may be influenced by these factors (de Oliveira 1998). Hourly records from northern Sydney (Terrey Hills Bureau of Meteorology site) were used to determine the average nightly temperature and humidity for each survey night, calculated from the hour before sunset to the hour after sunrise.

Habitat surveys

To characterize habitat, 15 vegetation variables (canopy, shrub and ground layer height both on and off the flyway, percentage cover of each layer on and off the flyway, tree density, tree diameter and hollow abundance), one predation variable (predatory birds) and one competition variable (hollow-nesting birds) were recorded at the location of the detector.

Vegetation density (or clutter) influences bat behaviour by impeding maneuverability and prey detection for some species (Crome & Richards 1988; Brigham *et al.* 1997; Law & Chidel 2002; Schnitzler *et al.* 2003). To determine clutter, vegetation in the range of the detector was measured within the width of the track at 5-m intervals for 20 m along the track in the direction that the microphone faced. The per-

centage cover and height of the canopy (tallest vegetation layer), shrub (understorey shrubs, saplings) and ground (grasses) layers were recorded at each point. Percentage cover was visually estimated using categories 1 (very sparse, <10%), 2 (sparse, 10–29%), 3 (moderate, 30–49%), 4 (mid-dense, 50–69%) and 5 (dense, >70%). Height was measured to the nearest 0.5 m for shrub and canopy layers using a digital range finder. Ground cover was measured to the nearest 0.1 m using a tape measure. The average percentage cover was weighted (multiplied) by height to give the final clutter score for each layer. This survey was repeated 5 m off the track on one randomly chosen side of the track to estimate vegetation density off the flyway.

The point-quadrat transect method (Brower & Zar 1984) was used to estimate tree density. Trees were defined as woody plants at least 4 m high and with a diameter at breast height of at least 10 cm. Two 50 m transects (based on the size of the smallest remnant site) were established at each site, both starting within approximately 200 m of the detector site. Sites were randomly selected from a subset of possible transects based on accessibility. If a creek was present at the site, one transect ran perpendicular to this. At five randomly chosen points along each transect, the distance to the nearest tree in each quadrant was measured with a measuring tape. On each of these four trees, diameter at breast height over bark was measured, and the number of hollows visible with binoculars per tree was counted. From these trees, the average diameter of trees and number of hollows per hectare at each site were calculated. This method was varied for backyards because of the impossibility of walking 50 m through numerous yards. Transects were established along the footpath and the diameter of trees in yards often had to be estimated. This technique counted more street trees (which are sometimes larger than trees in yards) than if the survey had been in backyards; however, these trees may still be used by bats in the matrix.

Bird surveys were conducted at each site for 15 min in the late afternoon and again in the early morning for the first night that the detector was set. Surveys occurred from a stationary point at the detector site and all birds seen or heard within approximately 50 m from this point were counted. Care was taken to count individuals only once. Tallies were kept for the number of diurnal birds seen and heard of each species thought to potentially prey on bats or compete with hollow-roosting bats for roosts. Potential avian predators of bats in urban Sydney mainly included grey butcherbird, pied currawong, laughing kookaburra and Australian raven. Potential roost competitors included lorikeets (e.g. rainbow lorikeet, musk lorikeet), cockatoos (e.g. sulphur-crested cockatoo, galah), parrots (e.g. king parrot), rosellas (e.g. eastern rosella, crimson rosella) laughing kookaburra, common starling and common myna. These species typically occur in high numbers in Sydney (Basham *et al.* 2005, pers. obs.) and were readily recorded by our method.

Area of bushland surrounding each site

Remnant area may not be indicative of the amount of bushland available to bats because remnants are often connected to larger remnants. Determining isolation of a remnant is especially problematic for bats that are highly mobile and

may use the suburban matrix (e.g. backyards). Therefore, the amount of bushland within a certain radius was used as a surrogate variable for remnant area and isolation. Indeed, this is considered the most reliable method for quantifying isolation (Bender *et al.* 2003). Two radii (500 m and 3 km) were chosen to be indicative of local and landscape scales, and were chosen to cover the nightly movements of mobile and less mobile species. Smaller species of *Vespadelus* show movements of less than 500 m in a night (Law & Anderson 2000), while more mobile species such as *Chalinolobus morio* will fly 2.5 km or more in a night (Taylor & Savva 1988). It should be noted that *Tadarida australis* has been known to fly more than 100 km in a night (Rhodes & Catterall 2008). Site locations were marked onto a geographic information system vegetation layer for the Sydney region (Benson & Howell 1994, digitized) using ArcView software (Esri, California). The area of bushland, defined as any mapped native vegetation (minimum size = 1 ha), within each circle was calculated using the Xtools extension function for ArcView.

Statistical analyses

The ANCOVA was used to compare species richness and total activity between site categories, with the co-variate being the amount of bushland surrounding a site at either 500 m or 3 km radius. Data for activity were first log transformed to meet the assumptions of ANCOVA (normality, homogenous variances). Species were then divided into two groups; 'common' (present in more than 40% of sites) and 'uncommon', and an ANCOVA was performed on each group to compare total activity between site categories. A nMDS plot (using presence/absence and Bray Curtis distance) was used to visually compare bat assemblage structure in *a priori* defined categories. Differences among site categories were then tested by ANOSIM (Clarke 1993). Similarity Percentages – species contributions (SIMPER) analysis was used to determine which species were responsible for differences between site categories.

Generalized linear modeling (GLMs) was used to determine which habitat, isolation and site category variables best predicted activity and species richness. For all models, step-wise addition and deletion of variables using the Step-AIC function in S-Plus (Version 7, Insightful Corp.) was used to determine the final model. The final model was based on the smallest Akaike's Information Criteria (AIC) and the change in AIC (ΔAIC). To avoid model over-parameterization and ensure there were substantially more replicates than predictor variables (Quinn & Keough 2002), inter-correlated variables ($r > 0.6$) in a correlation matrix were excluded by retaining the most easily interpretable variable. Also, the average number of calls per night showed no relationship with temperature and humidity ($r^2 < 0.06$), so these variables were excluded from analyses. Variables with almost no variation (flyway ground clutter and flyway shrub clutter) were also excluded. For cave-roosting species (*Miniopterus australis*, *Miniopterus schreibersii* and *Rhinolophus megaphyllus*) the variables 'hollow density' and 'competitive birds' were not included in analyses as these variables are unimportant for such species. Using these variable selection approaches, 10 variables were used in the models (Table 1) and separate models were run for bushland within 500 m and bushland

Table 1. Variables used in statistical models. Means \pm SE (range) of variables are shown for five site categories

Variable	Description	Mean \pm SE of values (range)					Reference
		Sandstone gully	Sandstone ridge	Shale	Backyard		
Average tree diameter	Average diameter (in centimetres) of trees surveyed at each site.	32 \pm 3 (25–44)	31 \pm 3 (24–39)	38 \pm 3 (28–51)	35 \pm 3 (21–42)	28 \pm 3 (15–38)	
Tree density	Estimated tree density per hectare at the site.	571 \pm 94 (163–1038)	672 \pm 135 (246–1228)	504 \pm 74 (151–826)	112 \pm 28 (17–237)	736 \pm 114 (424–1343)	
Hollow density	Estimated hollow density per hectare at the site.	46 \pm 16 (0–101)	30 \pm 12 (0–82)	49 \pm 15 (0–102)	6 \pm 2 (0–20)	71 \pm 14 (0–116)	
Competitive birds	Number of birds seen within 50 m of the microphone that are potential hollow competitors with bats.	16 \pm 4 (2–39)	15 \pm 7 (2–60)	24 \pm 6 (12–66)	12 \pm 3 (2–27)	6 \pm 2 (0–15)	
Predatory birds	Number of birds seen within 50 m of the microphone that are potential predators of bats.	4 \pm 2 (0–13)	4 \pm 1 (0–11)	3 \pm 1 (1–6)	3 \pm 1 (0–10)	2 \pm 1 (0–8)	
Flyway canopy clutter	Estimate of vegetation density based on canopy cover and canopy height along the flyway.	37 \pm 11 (0–110)	45 \pm 11 (8–95)	107 \pm 22 (0–165)	13 \pm 11 (0–93)	16 \pm 5 (0–40)	
Offtrack ground clutter	Estimate of vegetation density based on ground cover and ground layer height parallel to the flyway but off the track.	2.8 \pm 0.3 (1.7–4.1)	2.5 \pm 0.4 (0.6–4.9)	2.1 \pm 0.6 (0.2–4.4)	0.1 \pm 0.04 (0–0.3)	1.5 \pm 0.5 (0.4–4.3)	
Offtrack shrub clutter	Estimate of vegetation density based on shrub cover and shrub height parallel to the flyway but off the track.	9.0 \pm 1.5 (2.1–15.6)	8.6 \pm 2 (2.8–16)	9.0 \pm 2.8 (0–19)	2.5 \pm 1.4 (0–11.6)	7.6 \pm 2.3 (2.3–21.5)	
Bushland within 500 m	Amount of bushland (hectares) within a 500 m radius of the site.	37 \pm 7 (11–61)	37 \pm 8 (2–71)	12 \pm 4 (3–36)	11 \pm 5 (0–46)	75 \pm 2 (63–78)	
Bushland within 3 km	Amount of bushland (hectares) within a 3 km radius of the site.	798 \pm 136 (163–1329)	896 \pm 230 (82–2047)	489 \pm 38 (318–647)	755 \pm 221 (227–2195)	2183 \pm 75 (1854–2438)	

Clutter was assessed within 20 m of the detector microphone and tree density was recorded along two transects within 200 m of the detector.

Table 2. Species detected in the present study; total calls recorded across all sites (those identified as definite or probable), the number of sites that each species was detected in (from a maximum of 40 sites) and conservation status pursuant to the *NSW Threatened Species Conservation Act, 1995*

Species	Common name	Total call sequences	Number of sites detected	Conservation status (NSW TSC Act 1995)
<i>Chalinolobus dwyeri</i>	Large-eared pied bat	1	1	Vulnerable [†]
<i>Chalinolobus gouldii</i>	Gould's wattled bat	505	30	
<i>Chalinolobus morio</i>	Chocolate wattled bat	129	12	
<i>Falsistrellus tasmaniensis</i>	Eastern falsistrelle	6	2	Vulnerable
<i>Miniopterus australis</i>	Little bent-wing	80	9	Vulnerable
<i>Miniopterus schreibersii</i>	Eastern bent-wing	738	16	Vulnerable
<i>Mormopterus norfolkensis</i>	East-coast freetail	47	6	Vulnerable
<i>Mormopterus</i> species 2	Eastern freetail	285	17	
<i>Nyctophilus</i> species (<i>N. gouldi</i> and <i>N. geoffroyi</i>)	Lesser and/or Gould's long-eared bats	21	8	
<i>Rhinolophus megaphyllus</i>	Eastern horseshoe bat	34	9	
<i>Saccolaimus flaviventris</i>	Yellow-bellied sheath-tail bat	14	6	Vulnerable
<i>Scotorepens orion</i>	Eastern broad-nosed bat	7	4	
<i>Tadarida australis</i>	White-striped freetail	24	9	
<i>Vespadelus darlingtoni</i>	Large forest bat	86	8	
<i>Vespadelus vulturnus</i>	Little forest bat	233	7	

[†]Indicates vulnerable at the Federal level pursuant to the Environment Protection and Biodiversity Conservation Act.

within 3 km. One shale site, Sheldon Forest, was considered an outlier, having 4 times as many calls as the second highest site. Hence, the model on activity was re-run without Sheldon Forest, to remove its influence.

The GLMs were also used to identify variables that influenced the presence of individual species which were present in at least 20% of sites. As the relationship between the number of calls and actual abundance is unknown, individual species models were run using a binomial distribution based on the presence/absence data and a logit link function.

Model validation using independent data was beyond the scope of this project. The fit to the original data of each species model was tested by comparing the observed presence/absence of each species with the predicted probabilities of occurrence produced by the model (Ferrier *et al.* 2002). The area under the curve (AUC) of the receiver operating curve (ROC) was calculated using a ROC-AUC program (University of Potsdam 2004). The AUC tests model discrimination, which is the ability of the model to correctly distinguish between presence and absence sites (Pearce & Ferrier 2000). An AUC of 0.5 indicates a discrimination ability equivalent to a random guess, while values higher than 0.8 are considered excellent (Hosmer & Lemeshow 2000, cited in University of Potsdam 2004). The ROC plots and model discrimination plots show how well the model fits the data that were used to construct it. The ROC plots are a measure of overall model discrimination. Good model discrimination ability is shown if present and absent lines are far apart. Poor model discrimination occurs when observed presences do not increase with model prediction probabilities, and when observed absences do not decrease with increasing model prediction probabilities.

RESULTS

The Anabat detectors recorded a total of 2834 calls from 15 species, including 6 threatened species (Table 2). A total of 22% of calls could not be identified to species because of poor quality or similarity with other species. These calls were included in total calls as an index of total activity, but not in individual species tallies. Sites recorded a total of 0–878 calls over the 2 nights. At each site an average of 35 calls was recorded (SD = 139.9) per night of sampling, and there was an average of 3.6 species (SD = 2.3). The highest number of taxa in any one site was nine and three sites recorded no bat calls.

Chalinolobus gouldii was the most widespread species and occurred in 30 of the 40 sites (Table 2). Other common species were *Mormopterus* species 2 (17/40 sites) and *M. schreibersii* (16/40 sites). These three species also recorded the highest number of calls, and together accounted for 69% of identified calls. Twelve species were present in less than 30% of sites.

Landscape element

Shale and backyard sites recorded the most calls (Fig. 1a) (ANCOVA, $F = 2.95$, d.f. = 4, 34, $P = 0.03$) and the number of calls increased with the amount of bushland within 500 m (ANCOVA, $F = 4.20$, d.f. = 1, 34, $P = 0.05$). Both of these results were non-significant when the amount of bushland within 3 km

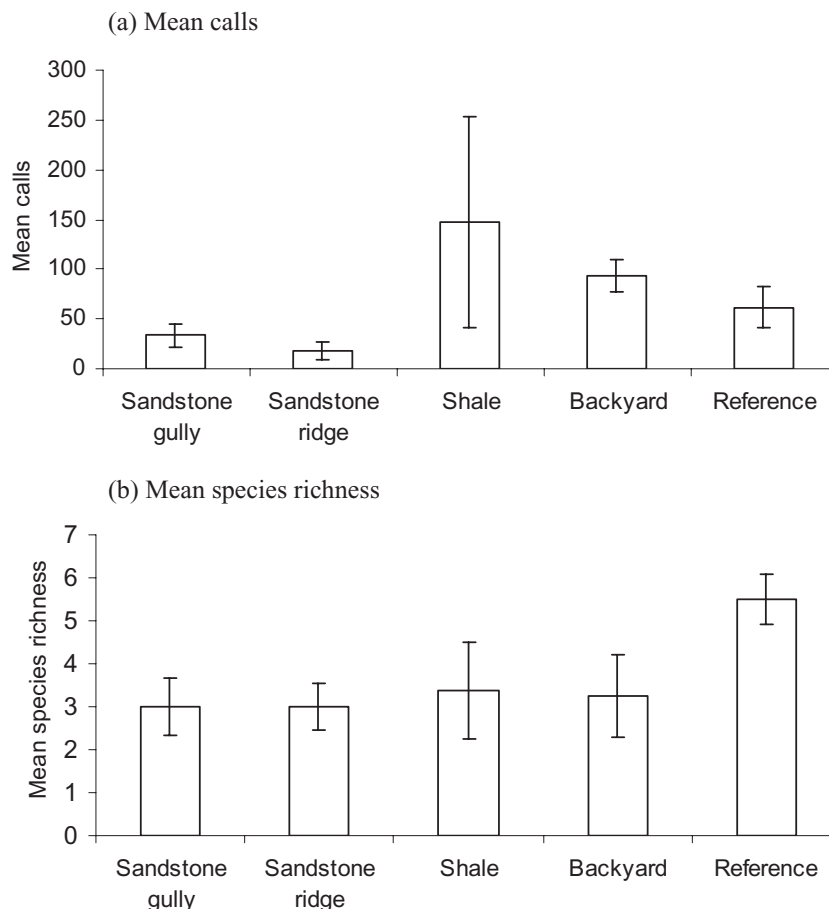


Fig. 1. Mean (with standard error) (a) number of calls for all species per night and (b) number of species per night, recorded in each site category over 2 nights of Anabat recording.

was used instead of 500 m or if the co-variate was omitted from analyses. Reference sites were the most species rich (Fig. 1b), although both this difference (ANCOVA, $F = 1.74$, d.f. = 4, 35, $P = 0.16$) and the bushland co-variables were not significant. Activity in backyards on shale soil was higher (107 calls) than backyards on sandstone (79 calls), but the difference was not significant ($t = 0.83$, $P = 0.44$).

The three common species (*C. gouldii*, *Mo.* species 2 and *M. schreibersii*) were most active in shale sites and backyards (ANCOVA, $F = 3.06$, d.f. = 4, 34, $P = 0.03$ – Fig. 2a), although neither bushland within 500 m nor 3 km showed a relationship with the activity of common species (ANCOVA, $F = 1.53$, d.f. = 1, 34, $P = 0.22$). Uncommon species did not differ significantly in activity across the five site categories (ANCOVA, $F = 0.10$, d.f. = 4, 34, $P = 0.98$ – Fig. 2b), but the number of their calls increased with both the amount of bushland within 500 m (ANCOVA, $F = 6.65$, d.f. = 1, 34, $P = 0.01$) and 3 km (ANCOVA, $F = 1.81$, d.f. = 1, 34, $P = 0.04$).

An ANOSIM of species composition (global R -statistic 0.059, significance level 4.5%) revealed that reference sites had significantly different species composition from backyards and shale sites. The negative R -values of most other comparisons indicated that differences within those groups were greater than differences between groups (Quinn & Keough 2002). Visual assessment of the nMDS plot, which had adequate stress (0.13 – Clarke 1993), suggested that shale, sandstone gully, sandstone ridge and backyard sites were subsets of the reference sites because they occupied a smaller portion of the 2-dimensional space compared to reference sites (Fig. 3). Backyards formed the smallest cluster, suggesting that backyards do not hold the full complement of species present in reference sites. The SIMPER analysis revealed that differences between reference sites and other categories were largely because of reference sites generally having lower activity of *M. schreibersii* and *C. gouldii*, but higher activity of *M. australis* and *Vespadelus vulturinus*.

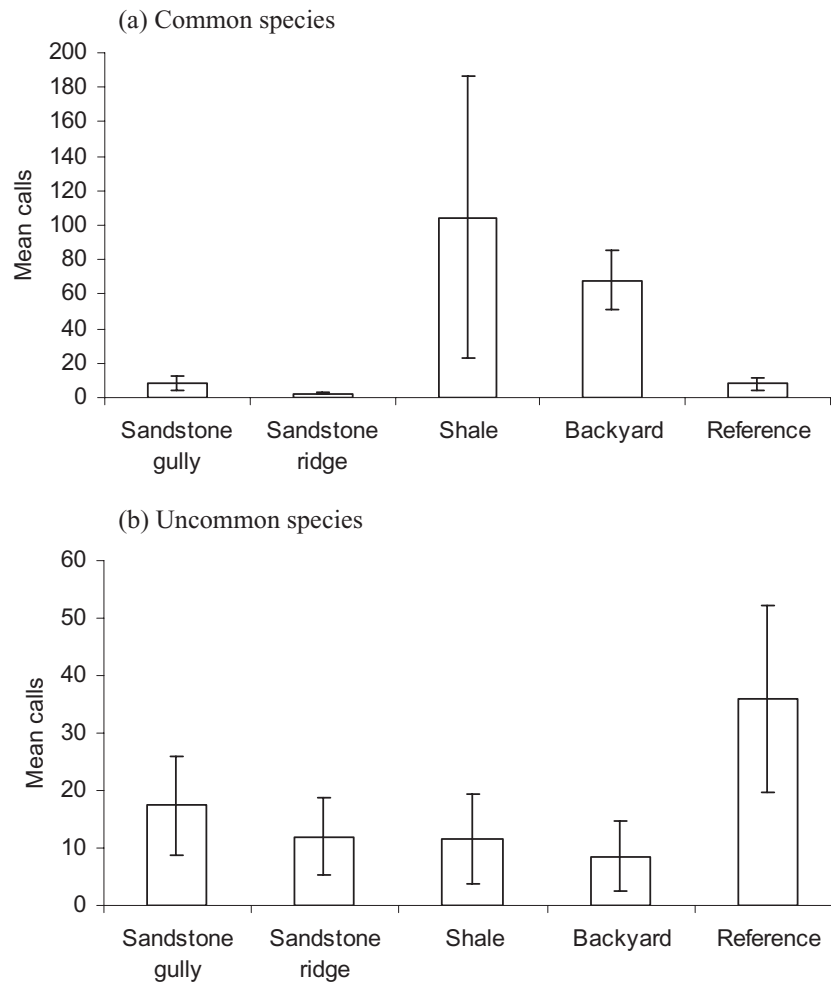


Fig. 2. Mean number of calls (with standard error) per night across each category for (a) common species (species present in 40% of sites or more – *Chalinolobus gouldii*, *Miniopterus schreibersii* and *Mormopterus* species 2) and (b) uncommon species (*Chalinolobus dwyeri*, *Chalinolobus morio*, *Falsistrellus tasmaniensis*, *Miniopterus australis*, *Mormopterus norfolkensis*, *Nyctophilus* spp., *Rhinolophus megaphyllus*, *Saccolaimus flaviventris*, *Scotorepens orion*, *Tadarida australis*, *Vespadelus darlingtoni* and *Vespadelus vulturinus*).

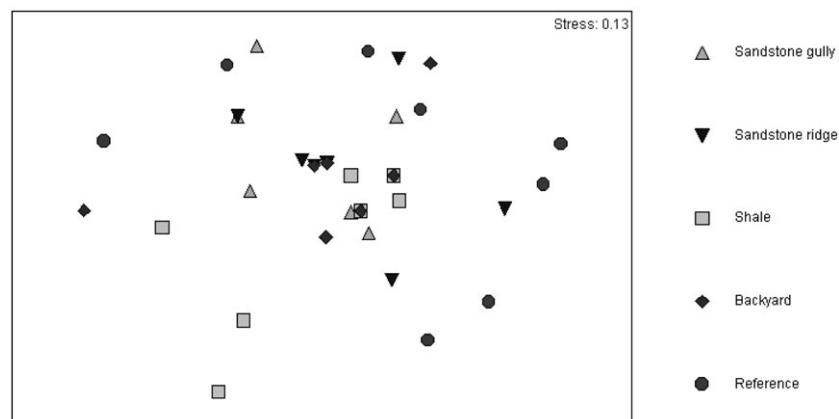


Fig. 3. The nMDS plot for species composition based on site category.

Table 3. Equation of the preferred model for total activity, species richness and each species. Only species that occurred in >20% of the sites were modelled

Model	Equation	AIC	ΔAIC
Total activity	Total activity $\sim -193.31 + 8.06$ Average tree diameter	651 396.4	267 187.4
Total activity without Sheldon Forest	Total activity $\sim 14.17 - 2.46$ (SC1 v SC2) -1.02 (SC1vSC3) $+ 2.98$ (SC1vSC4) $+ 18.40$ (SC1vSC5) $+ 0.92$ Hollow density	46 766.7	11 941.9
Species richness	Species richness $\sim -2.40 + 0.12$ Average tree diameter $+ 0.02$ Hollow density $+ 0.001$ Bushland within 3 km	137.2	69.1
<i>Chalinolobus gouldii</i>	<i>C. gouldii</i> $\sim -3.48 + 1.88$ (SC1vSC2) $+ 1.57$ (SC1vSC3) -0.05 (SC1vSC4) $+ 0.90$ (SC1vSC5) $+ 0.11$ Hollow density $+ 0.16$ Competitive birds	37.5	7.4
<i>Chalinolobus morio</i>	<i>C. morio</i> $\sim -8.38 + 0.12$ Average tree diameter $+ 0.002$ Tree density $+ 0.002$ Bushland within 3 km.	44.9	13.53
<i>Miniopterus australis</i>	<i>M. australis</i> $\sim -2.24 + 0.003$ Tree density -0.62 Off-track ground clutter	40.39	13.07
<i>Miniopterus schreibersii</i>	No model	55.84	0
<i>Mormopterus</i> species 2	<i>Mo. species 2</i> $\sim -7.48 + 0.19$ Average tree diameter $- 0.02$ Hollow density $+ 0.001$ Bushland within 3 km.	51.83	14.02
<i>Nyctophilus spp.</i>	<i>Nyctophilus spp.</i> $\sim -1.87 + 0.03$ Hollow density $- 0.10$ Competitive birds	34.69	16.84
<i>Rhinolophus megaphyllus</i>	<i>R. megaphyllus</i> $\sim -5.36 - 0.003$ Tree density $+ 0.15$ Off-track shrub clutter $+ 0.003$ Bushland within 3 km	29.24	7.2
<i>Tadarida australis</i>	<i>T. australis</i> $\sim -2.61 + 0.09$ Average tree diameter $- 0.15$ Competitive birds	41.12	18
<i>Vespadelus darlingtoni</i>	<i>V. darlingtoni</i> $\sim -3.76 + 0.003$ Tree density $- 1.15$ Off-track ground clutter $+ 0.002$ Bushland within 3 km	30.61	12.86

The AIC is the AIC value at the final model. The ΔAIC is the change in AIC from the null model. The 'SC' component of the equation results from modelling categorical variables in a multiple regression. 'SC1vSC2', for example, is a comparison between Site Category 1 and Site Category 2. Categories are (1) Reference sites (2) Sandstone gully (3) Sandstone ridge (4) Shale and (5) Backyards. The size of the coefficient indicates the relative size of the difference between categories. AIC, Akaike's Information Criteria; ΔAIC, the change in AIC.

Predictors of bat activity and species richness

Of the 10 initial habitat variables, the model selection process recommended one predictor for activity, and three predictors for species richness. Both activity and species richness were positively related to average tree diameter in a site. Species richness was also positively related to hollow density and the amount of bushland surrounding a site (Table 3). The final models for both activity and species richness were significant ($P < 0.001$, $r^2 = 0.24$ and 0.51 , respectively).

A second model was run for activity and richness which included 'Bushland within 500 m' instead of 'Bushland within 3 km' to determine whether the amount of bushland within different distances affected bats. The same final model was chosen for activity, but one more variable (ground clutter) was added to the model for species richness.

The shale site, Sheldon Forest, was considered a statistical outlier (value of more than 1.5 times the interquartile range, as revealed by a box plot (Quinn & Keough 2002)). When the activity model was re-run without Sheldon forest, the final model included two different variables; site category and a positive rela-

tionship with hollows (Table 3). Activity was higher in backyards and shale sites than reference areas, and lower in sandstone gully and ridge sites than reference sites. The model was significant ($P < 0.001$, $r^2 = 0.65$). The same final model was reached with the 500 m bushland window.

Individual species models

The GLMs were only run for the nine species that were present in at least 20% of sites to ensure a reasonable ratio of presences to absences. Of the 10 initial predictors (Table 1), the model selection process generally resulted in a subset of 0–3 predictors for each species for the 3 km window around each site (Table 4). The most common variables selected were the amount of bushland (*C. morio*, *Mo. species 2*, *R. megaphyllus* and *Vespadelus darlingtoni*) and tree density (*C. morio*, *M. australis*, *R. megaphyllus* and *V. darlingtoni*). Hollows (*C. gouldii*, *Mo. species 2* and *Nyctophilus*), competitive birds (*C. gouldii*, *Nyctophilus* and *T. australis*) and tree diameter (*C. morio*, *Mo. species 2* and *T. australis*) were also selected often. Site

Table 4. Deviance explained by the final model for each species and model discrimination as represented by the area under the curve (AUC)

Species	Predictors	Null deviance	Residual deviance	DF	D ²	AUC
<i>Chalinolobus gouldii</i>	SC, H, CB	44.99	23.51	36	47.75	0.94
<i>Chalinolobus morio</i>	D, T, B	48.87	36.90	36	24.48	0.83
<i>Miniopterus australis</i>	T, OG	42.65	34.39	37	19.37	0.54
<i>Miniopterus schreibersii</i>	None	53.84	53.84	39	0	
<i>Mormopterus species 2</i>	D, H, B	54.55	43.83	36	19.66	0.79
<i>Nyctophilus</i> spp.	H, CB	40.03	28.69	37	28.32	0.85
<i>Rhinolophus megaphyllus</i>	T, OS, B	42.65	21.24	36	50.20	0.93
<i>Tadarida australis</i>	D, CB	42.65	35.12	37	17.65	0.77
<i>Vespudelus darlingtoni</i>	T, OG, B	40.03	22.61	36	43.53	0.89

Lower residual deviances indicate a better model. The AUC values greater than 0.8 indicate an excellent ability to discriminate presence/absence sites. Values less than 0.5 have a discrimination ability equivalent to random guess. Key to predictors: SC, Site category; H, hollow abundance; CB, competitive birds; D, average tree diameter; T, tree density; B, bushland within 3 km; OG, offtrack ground clutter; OS, offtrack shrub clutter. DF: degrees of freedom and D² is analogous to r².

category was only important for *C. gouldii*, which was more likely to be present in backyards, sandstone ridges and gullies than reference areas. Two variables, flyway canopy clutter and predatory birds, were not included in any final model. For *M. schreibersii*, no variable predicted its presence/absence better than chance. The amount of variation explained by the final models ranged from 18% for *T. australis* to 50% for *R. megaphyllus* (Table 4). The best models were for *R. megaphyllus*, *C. gouldii* (48%) and *V. darlingtoni* (44%). The models that explained the least variation were for *T. australis* (18%), *M. australis* (19%) and *Mo. species 2* (20%).

When models were re-run using the 500 m window, the same model was reached as with the 3 km window for all but three species. The final 500 m model for *C. morio* included negative relationships with competitive birds and off-track shrub clutter, as well as positive relationships with the three variables of the 3 km model. Tree diameter (positive relationship) became the only predictor for *Mo. species 2*. The 500 m model for *V. darlingtoni* had one less predictor than at the 3 km window, including only off-track ground clutter (negative relationship) and bushland (positive relationship).

Model evaluation and discrimination ability for individual species models

Five species models with excellent discrimination ability were *C. gouldii*, *C. morio*, *Nyctophilus* spp., *R. megaphyllus* and *V. darlingtoni* (Table 4). However, the model for *M. australis* had discrimination ability only slightly better than a random guess (Table 4). The ROC plots and discrimination plots were supportive of the AUC score (see Fig. 4 for example). Model discrimination was generally good (except for *M. austra-*

lis), being able to discriminate presence/absence at high and low predicted probabilities. Discrimination was poor at predicted probabilities of around 0.2 and 0.6–0.7 for *C. gouldii*, 0.3–0.5 for *C. morio*, all probabilities for *M. australis*, 0.3–0.5 for *Mo. species 2*, 0.2–0.7 for *Nyctophilus* spp., 0.3–0.7 for *R. megaphyllus*, 0.2–0.4 for *T. australis* and 0.4–0.6 for *V. darlingtoni* (Fig. 4). Some models such as *Nyctophilus* spp. predicted absence quite well; however, less adequately predict presence. In comparison, the model for *C. gouldii* better predicts presences.

DISCUSSION

Our study was the first systematic acoustic study of bats in urban Sydney, with a focus on the 'leafy' northern suburbs. We found backyards and the fertile shale sites supported the highest bat activity levels and that activity increased with the amount of bushland at a local scale (500 m radius). This part of Sydney containing low-density residential areas is characterized by large areas of remnant bushland in steep gullies and large gardens (often > 0.1 ha) with tall trees. We expect that our results will be most applicable to similar urban areas where native vegetation still exists in a patchwork of reserves. In the mosaic urban landscape of Brisbane, low-density residential areas also supported a high diversity of bats, while high-density residential areas and natural bushland supported lower bat diversity (Hourigan *et al.* 2010). Treeless suburbs of Brisbane supported lower bird richness and abundances than large remnants, but suburbs with many trees had an intermediate assemblage (Sewell & Catterall 1998). Bat activity has also been found to be correlated with heterogeneous urban landscapes in the northern hemisphere (Gehrt & Chelvig 2003), with diversity declining with the amount of urban development (Duchamp

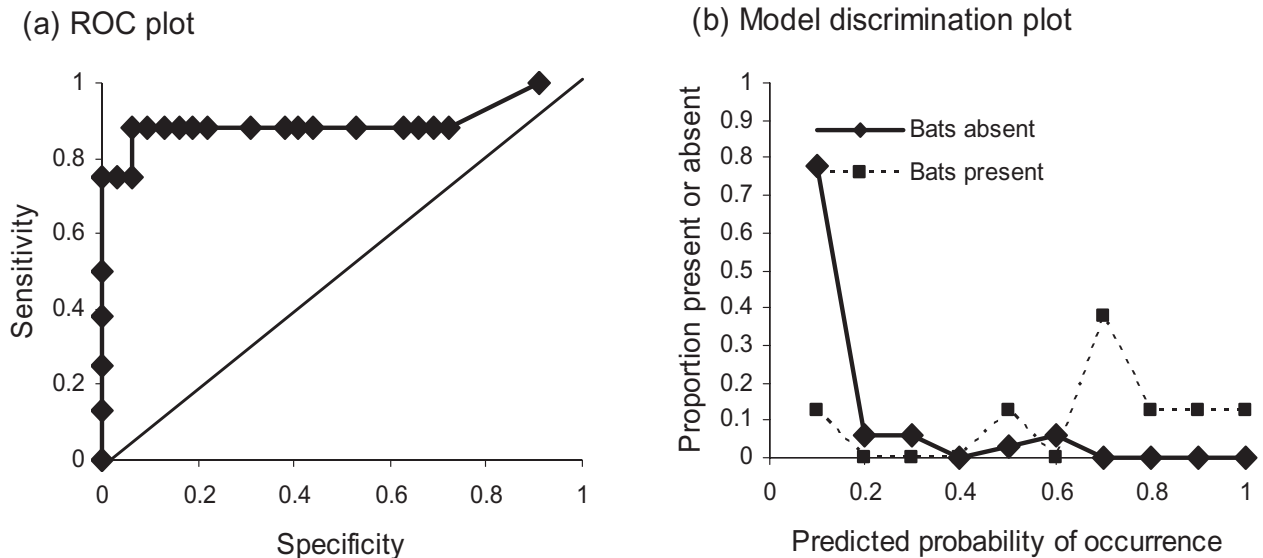


Fig. 4. (a) Receiver operating curve (ROC) plot and (b) model discrimination plot for *Vespadelus darlingtoni*.

& Swihart 2008). This would suggest that the patchwork of bushland and the 'leafy' nature of the northern Sydney suburbs aids the persistence of bats. However, it should also be noted that bat activity in our study (mean of 35 calls per night) was considerably lower than has been recorded elsewhere in New South Wales, such as in forests (50–200 calls/night – Law & Chidel 2002; Lloyd *et al.* 2006) or remnant vegetation in agricultural landscapes (100–300 calls/night – Law *et al.* 1999; Law & Chidel 2006).

Of the 17 microbat species known from the northern Sydney region, all but two were recorded in the remnant bushland, backyards and reference areas in this study, slightly greater than the 14 species recorded in Brisbane (Hourigan *et al.* 2010). Some significant regional records were produced, including the presence of six threatened species and the first records of *M. australis* for northern Sydney, the latter not being recorded during ultrasonic surveys 10 years previous (Turton 1996). However, 12 species were detected in less than a third of all sites. Only three species could be considered common (*C. gouldii*, *Mo. species 2* and *M. schreibersii*), as these were present in 75%, 43% and 40% of sites, respectively. These common species were most active in backyards and shale remnants irrespective of the extent of local bushland, while the activity of rarer species increased as the area of bushland increased. Thus, it appears that bats are persisting in northern Sydney's urban landscape, but most species were recorded in low numbers during 2005. This conclusion needs to acknowledge that some species were under-sampled. Bats with quieter calls, such as *Nyctophilus*, need to be close to the detector to be recorded (Woodside & Taylor 1985) and trapping is needed to distinguish

which of the two species are present (Schulz & de Oliveira 1995; Duffy *et al.* 2000). In addition, the calls of some species are more easily identifiable than others because of minimal overlap with other species (Duffy *et al.* 2000), and therefore species with similar calls may be under-counted because of the inability to confidently identify them. Species that may have been under-counted could have included *V. darlingtoni* (calls are sometimes similar to *M. schreibersii*) as well as *Scotorepens orion* and *Falsistrellus tasmaniensis* (the latter two can be confused with each other and *Scoteanax rueppellii*). Bats previously recorded in Sydney, but not recorded in this study are *S. rueppellii* and *Myotis macropus*; however, *M. macropus* forages over water (Dwyer 1970) and no detectors were placed over water in our study.

Some Australian studies have suggested that many bat species are tolerant of forest fragmentation and clearing (Lumsden *et al.* 1995, 2002; Law *et al.* 1999), but it appears that urbanization may be influencing the rarity of some species, and may facilitate the commonness of others. This pattern was observed in some northern hemisphere cities; species diversity in urban reserves was half that of rural areas, and one species dominated urban areas (Kurta & Teramino 1992; Avila-Flores & Fenton 2005). Almost every species occurred in fewer numbers and at fewer locations in urban sites (Kurta & Teramino 1992). Bats in urban landscapes of northern Sydney showed varying tolerances of urbanization, but our modelling suggests that their occurrence and activity at a site are influenced partly by the broad habitat and spatial context (i.e. soil fertility and extent of local bushland) and partly by its microhabitat features (e.g. tree density and hollow abundance).

Landscape element: effect of habitat type

It was predicted that if bats were negatively affected by urbanization, reference sites should have the highest activity and species richness because of larger areas generally providing more habitat diversity and hence more foraging niches (Law *et al.* 1999). Backyards, which constitute the matrix, should have had the lowest. But overall activity was not higher in reference sites, which is consistent with the study by Hourigan *et al.* (2010) in Brisbane. However, we found trends towards higher species richness and activity of uncommon species in reference areas. Species composition in reference sites was also different from backyards and shale sites, largely because of the high activity of *M. schreibersii* and *C. gouldii* and the rarity of *V. vulturnus* and *M. australis* in backyards. Hence it appears that species we rarely recorded in backyards may be strongly affected by urbanization.

One reason for lower activity in reference sites could be their location within National Parks surrounding Sydney, which are restricted to infertile sandstone geology (Benson & Howell 1990), and so may yield fewer flying invertebrates. In comparison, the backyards sampled in northern Sydney were a mix of either shale or sandstone geology and activity did not differ significantly between the two. This might indicate that backyards on sandstone are modified by the addition of top soil, fertilizers and water all of which could contribute to higher numbers of invertebrates. Clearly this hypothesis warrants testing. It is also worth noting that the backyards we sampled were surrounded by a moderate amount of bushland (mean = 14% of the 500 m radius, Table 1).

Backyards supported moderate levels of activity and every taxa was present in at least one backyard. Furthermore, when Sheldon Forest was removed from the activity model, site category was a partial predictor and backyards had the highest relative activity levels. However, most species were detected in only one or two backyards. The three most common species in backyards were also those most active overall in this study and showed no particular association with landscape element suggesting that they are habitat generalists. *Chalinolobus gouldii* and *M. schreibersii* have similarly been found to be habitat generalists within a fragmented forest landscape, in that both forage in open areas with few trees (Law *et al.* 1999, 2000; Lumsden *et al.* 2002). These species also forage at streetlights (Kirsten & Klomp 1998; Hoyer & Spence 2004), where insects aggregate and attract bats (Fenton 1982; Geggie & Fenton 1985; Furlonger *et al.* 1987; Blake *et al.* 1994). These generalist species have similar ecomorphology; narrow wings, medium-frequency calls and fast flight which dictates a preference for open areas (Rhodes

2002; Duchamp & Swihart 2008). Finally, although these two species have different roost requirements, both commonly roost in human-made structures (Kirsten & Klomp 1998; Hoyer & Spence 2004). Yet even for these species there is the potential for urban impacts. *Miniopterus schreibersii* is often detected in Sydney, but it experiences cat predation at its subterranean roosts and flooding events in stormwater drains, and suffers high injury rates because of urban factors such as vehicle impact (Hoyer & Spence 2004).

Bushland along ridges and gullies on infertile sandstone supported lower bat activity than fertile sites on shale. However, gullies can be important to bats as many species prefer to roost in the larger trees associated with gullies (Lunney *et al.* 1988; Law & Anderson 2000; Evelyn *et al.* 2004) and sites near water are important as bats drink frequently (Findley 1993). Gullies may need streams with a wide flyway before bat activity levels increase (Lloyd *et al.* 2006). Given the large flight distances of many species, bats may rely on roosts in large gully trees, but travel elsewhere to forage, which is one explanation for the equal activity across sandstone categories in this study.

The more fertile shale remnants were expected to have higher activity and richness than sandstone remnants as productivity could be associated with flying invertebrate biomass, thus leading to a higher abundance and diversity of bats (Law 1996). Historical patterns of land clearing in Sydney mean that no large forested shale areas remain to determine whether shale reference areas would have higher activity and diversity. However, the three larger shale sites, Cumberland State Forest, Sheldon Forest and Dalrymple-Hay Nature Reserve did have higher activity and species richness and a different composition than many other sites. This suggests that shale sites may once have been highly valued by bats, and that these larger remnants still are. Many shale remnants are now so small (<10 ha), isolated and degraded (Smith & Smith 2001) that they no longer supported high bat activity. As bat activity increased with the area of local bushland, it is likely that increasing linkages and tree cover near existing small reserves would benefit a range of bat species.

Habitat element: microhabitat predictor variables

The nine species that were modelled (as they occurred in at least 20% of sites) responded to different combinations of habitat quality characteristics, probably reflecting different roosting requirements and ecomorphology. Notably, the models sometimes

explained little variance, and highlight the difficulty in finding variables that are important for determining distributions.

Roosting variables – hollows, tree diameter, competitive birds

A positive relationship with hollow abundance and average tree diameter at a site indicated that some bats may be confined to areas within the urban landscape that have abundant roost sites in large trees. Five of the six species which are known to roost in hollows (Churchill 1998) were partially predicted by one of these variables, and some species prefer to roost in trees with diameter greater than 80 cm (Lunney *et al.* 1988; Taylor & Savva 1988; Law & Anderson 2000), which are more likely to have hollows (Mackowski 1984). Individual bats can roost under bark or in cracks in the trunk (Tidemann & Flavel 1987), but these characteristics are still correlated with tree diameter (Lindenmayer *et al.* 1993). Bats in North American cities rely strongly on hollows for roosting, display higher roost fidelity, and travel further between consecutive roosts than bats in outlying areas (Geggie & Fenton 1985; Evelyn *et al.* 2004), suggesting that roosts are limited in the urban environment. The only study of roosting behaviour in an Australian city found *T. australis* to roost in late senescent trees with many hollows, located within parklands rather than large forest reserves (Rhodes and Wardell-Johnson 2006).

A negative relationship with competitive birds for three species indicated that there may be competition for tree roosts between urban bats and hollow-dwelling birds. Numerous hollow-dwelling birds, particularly rainbow lorikeets and other parrots, have increased in Sydney's urban areas (Smith & Smith 2001; Major & Parsons 2010), and may place pressure on urban bats. Indeed an instance of lorikeets evicting bats from hollows has been reported in Western Australia (Start 1998). Lorikeets and bats (*T. australis*) have also been found to use the same hollows, although at different times of the year (Rhodes and Wardell-Johnson 2006). Models containing this variable also included either hollows or tree diameter, which further supports the theory of hollow competition.

Artificial roost sites such as buildings and bridges in urban areas may have facilitated some species (Fenton 1997) and may explain why the three species known to roost in such structures, *M. schreibersii*, *Mo.* species 2 and *C. gouldii* (Churchill 1998; Hoye & Spence 2004; SOPA 2004) were the most common. However, other species will only roost in buildings if trees are not available (Brigham 1991) and roosting in buildings is not ideal as such roosts are likely to be disturbed (Brittingham & Williams 2000).

Foraging variables – clutter, bushland and tree density

Access to foraging resources was the other major determinant of local bat activity, and the ability to travel among resource patches and across open areas varies between species (e.g. Pavey 1998; Law *et al.* 1999). Some species may have difficulty accessing resources in the urban environment, whereas others may more easily cross or even exploit the matrix, as suggested by the positive relationship with the amount of bushland surrounding a site. *Rhinolophus megaphyllus*, *C. morio* and *V. darlingtoni* all showed positive relationships with bushland (500 m and 3 km). *Rhinolophus megaphyllus* avoids open areas and will only fly 250 m or so across cleared matrix, and tends to react poorly to fragmentation (Pavey 1998). It was detected in only one backyard, in Berowra, which was <100 m from bushland. Similarly, *C. morio* is sensitive to fragmentation because it does not forage in the open (Law *et al.* 1999). Interestingly, *V. darlingtoni* is widespread in farmland, even in open paddocks (Law *et al.* 1999), suggesting that it responds differently to fragmentation in urban compared to agricultural areas. In contrast, *Mo.* species 2 was one of the most common species in this study, and it is also one of the most common species at paddock trees in farmland (Law *et al.* 2000); yet its presence was still related to the amount of bushland nearby. Even species that use some aspects of urban landscapes may rely on natural vegetation, for instance foraging around streetlights increases with the amount of tree and shrub cover nearby (Blake *et al.* 1994). Also, buildings used as roosts in one European urban study had a considerable amount of bushland nearby (Entwistle *et al.* 1997). *Tadarida australis*, which forages in open areas (Churchill 1998), is an interesting exception. It was a common habitat generalist in a fragmented forest landscape of southern New South Wales (Law *et al.* 1999) and urban Townsville (Hourigan *et al.* 2006), but was only recorded in nine sites in this study. Rhodes and Catterall (2008) found that this species roosted across the urban landscape of Brisbane, but preferentially foraged above cleared and grassy floodplain habitat, which was not sampled in our study.

Bushland also showed a positive relationship with overall species richness, suggesting that many bat species rely upon remnant bushland in urban areas (Hourigan *et al.* 2006). The amount of bushland surrounding a site will reflect the influence of both foraging and roosting opportunities. While some species may variably occur in backyards or isolated remnants, richer communities and uncommon species depend on more extensive areas of bushland. Indeed, some small patches of bushland in this study (e.g. Stony Range Flora Reserve, Dee Why) that were isolated by more than one km from other bushland recorded no

bats. The importance of surrounding bushland for bats is similar to the relationship between richer bird communities and remnant size in southern Sydney, with a threshold of 50 ha of bushland for forest interior species (Drinnan 2005). These patterns contrast with agricultural areas where proximity to bushland has not been found to strongly influence bat activity (Law *et al.* 1999; Law & Chidel 2006). It is not clear what is driving this difference, but the extensive use and availability of scattered hollow-bearing trees in the farmland matrix may be important (Lumsden & Bennett 2005).

The density of vegetation in long-established Townsville suburbs did not substantially reverse the trend for urban areas to have fewer bat species than original habitats (Hourigan *et al.* 2006). Yet in our study, tree density showed a positive relationship with *M. australis*, *C. morio* and *V. darlingtoni* and all forage between shrub and canopy layers (Dwyer 1965; Kutt 1995). Positive relationships with tree density could also indicate that these bats find backyards unfavourable and notably these species were only present in one backyard each. *Rhinolophus megaphyllus* showed a positive response to shrub clutter as a partial predictor and has been classified as a clutter-tolerant species because of its gleaning foraging style (Norberg & Rayner 1987). Habitats with higher tree and shrub density are likely to be reduced in an urban environment (e.g. Hourigan *et al.* 2006).

Conclusions

The proximity of large areas of bushland and the many trees remaining in residential areas of the northern 'leafy' suburbs of Sydney (Benson & Howell 1990) appear to allow bats to persist in a reasonably intact assemblage. Even though backyards are typically perceived as cleared land, the leafy nature of the northern Sydney suburbs may allow the area to act as a corridor between bushland remnants for uncommon species and provide foraging habitat for the more common species. Barrett *et al.* (1994) recognized that some landscapes should be considered variegated, rather than strictly fragmented, as the matrix contains resources such as scattered trees and small habitat remnants. This may be true in northern Sydney. Nevertheless, the maintenance of bat species diversity as Sydney's population grows in the future will rely on landscape planning to ensure that forest remnants and linkages are retained and restored. Because this region retains many of the landscape features upon which bats rely, our models should be tested in other areas of Sydney to determine whether these predictors are applicable across other urban areas. Further studies are also required on the 12 uncommon species to provide the detailed understanding of species-specific habitat

requirements that is essential for effective conservation and management in fragmented urban landscapes.

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