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Patterns in bat functional guilds across multiple urban centres in south-eastern Australia

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ABSTRACT

Understanding the impacts of landscape change on species behaviour is a major challenge in landscape ecology. A focus on the functional traits of species may improve this understanding if species with similar traits (functional guilds) are impacted by landscape change in similar ways, but this idea has not been widely tested on bat communities in urban landscapes. We examined changes in bat species richness and the activity level of species in different functional guilds within 72 residential neighbourhoods across 18 towns and cities spanning over 250,000 square km in south-eastern Australia. Species richness increased close to native vegetation, declined with increasing urbanization, and had a hump-shaped relationship with neighbourhood vegetation cover. Also, the activity level of all bat species combined peaked at mid-range values of neighbourhood vegetation cover. The activity of species in the open-adapted guild was not strongly related to any urban characteristic, but our results concur with previous findings that the activity of most open-adapted species does not appear to be negatively impacted by urbanization. Conversely, clutter-adapted species appear more sensitive to urbanization and their activity level was negatively related to urban intensity and increased closer to native vegetation, consistent with previous studies. The functional-trait approach may improve the capacity to make generalisations across different landscape contexts for clutter-adapted and open-adapted guilds, but is currently hampered for other bat species owing to variation in the behaviour of different species assigned to the same functional guild, and a lack of ecological knowledge regarding the impacts of different types of landscape change on particular species.

Keywords: Australia; bat activity; bat diversity; Bayesian analysis; functional traits; guilds; Microchiroptera; urban ecology; urban landscapes

INTRODUCTION

The responses of species to landscape change may be dictated by their functional traits (i.e. a morphological, physiological, phenological or behavioural feature of an individual; Violle et al. 2007; Luck et al. 2012). Species with similar functional traits (collectively described as ‘guilds’) may be impacted in similar ways by particular landscape changes (Simberloff and Dayan 1991). Therefore, a focus on functional type rather than species identity may enhance the capacity of ecologists to make broader generalisations about the impact of particular land uses on ecological communities regardless of geographic location or differences in taxonomy.

Urbanization, one of the most pervasive land-use trends of the 21st century (United Nations 2010), creates landscapes with similar structural characteristics and this may result in comparable species assemblages occupying widely separated urban settlements (McKinney 2006). Yet, while research on the ecology of urban landscapes is increasing, knowledge is lacking that enables broad generalisations about the impacts of urbanization on particular taxonomic or functional groups (Gaston 2010). Much of the research on urbanization has focussed on major cities (e.g. Germaine and Wakeling 2001; Niemelä et al. 2002; Crooks et al. 2004; Marzluff 2005) neglecting relations that occur in smaller human settlements. Examination across the full range of settlement types is fundamental to a wider understanding of the impacts of varying levels of urbanization on native ecosystems.

Research on bats in urban areas suggests certain functional guilds may either readily adjust to or be disadvantaged by urbanization (Gehrt and Chelsvig 2003; Avila-Flores and Fenton 2005; Duchamp and Swihart 2008; Basham et al. 2011). For example, a study by Threlfall et al. (2011) in Sydney, Australia, found that open-adapted bat species with low-medium frequency echolocation may be favoured by increasing urbanization, whereas clutter-adapted species with high or linear frequency echolocation tended to avoid urban areas, being recorded more commonly in extensive patches of native vegetation. Although a functional guild approach has been successful in identifying general patterns in bat communities in other environments such as forests and

agricultural landscapes (Law and Chidel 2002; Hanspach et al. 2012), further research is required to determine the usefulness of the approach in urban landscapes, particularly across different types of urban development.

Urbanization is likely to threaten the persistence of some bat species through, for example, the loss or modification of vegetation (e.g. loss of hollow-bearing trees that are used for roost sites; Kunz and Lumsden 2003; van der Ree and McCarthy 2005), a reduction in invertebrate abundance (McIntyre 2000) or alteration in foraging behaviour through increased noise (e.g. traffic; Schaub et al. 2008). Yet, other bat species may be less adversely affected by urbanization if, for example, they are able to roost in urban structures (Duchamp et al. 2004; Neubaum et al. 2007; Coleman and Barclay 2011), take advantage of invertebrate food resources concentrated around artificial lights (Rydell 1992; Blake et al. 1994; Rydell and Racey 1995; Hickey et al. 1996) or commute long distances from roosting to foraging areas (Lumsden et al. 2002). Here, we assess spatial variation in bat communities across towns and cities and compare our results with studies conducted in major metropolitan locations. We examine whether particular functional guilds exhibit similar patterns in activity levels in small-scale vs. large-scale urbanization, testing the usefulness of the functional guild approach in different contexts.

METHODS

Study area

Our work is part of a broader study on urban vegetation and fauna conducted in 18 towns and cities in south-eastern Australia (Fig. 1). The population size of towns ranged from 16,182 to 78,221 (mean: $36,637 \pm 1 \text{ s.e. } 4,305$) and the distance between towns ranged from 6 km to 879 km measured from the centre of each town (see Luck and Smallbone 2011; Luck et al. 2009, 2011, in press for details). All of the towns in our study region were established more than 100 years before present with many greater than 150 years old. Initial settlement would have resulted in the clearing of native eucalypt forests and woodlands, but recent development has primarily occurred on already

cleared agricultural land. Agriculture is the main surrounding land use for most towns (Table S1). However, some areas retain large remnants of native vegetation and all towns have at least small patches of remnant or re-growth native vegetation within the settlement boundary.

We recorded bat species richness and activity levels in four neighbourhoods per town (total $n = 72$). Neighbourhood boundaries were defined by census collection districts (≈ 200 houses; mean neighbourhood area: $69 \text{ ha} \pm 1 \text{ s.e. } 9 \text{ ha}$) and neighbourhoods were selected for surveying using stratified random sampling to capture the full range of variation in neighbourhood characteristics such as housing density (see Luck et al. 2009). Across neighbourhoods, housing density ranged from $0.5\text{--}11 \text{ houses ha}^{-1}$, the cover of woody and non-woody vegetation ranged from $1\text{--}78\%$, and the cover of impervious surfaces ranged from $1\text{--}88\%$. All neighbourhoods were at least 20 years of age at the time of sampling and neighbourhoods in the same town were separated by at least 1 km.

Bat surveys and call identification

We surveyed bats in autumn (March–May), winter (July–August), spring (October–November) and summer (December–February) in nine towns, and spring (September) and summer (December) in the remaining nine towns across 2007–2009. Almost no bat activity was recorded during winter so we discarded the surveys from this period. Most activity was recorded during spring and summer when resource requirements for bats are likely to be high (see below).

Bats were surveyed by placing a single Anabat detector (Titley Electronics, Ballina, Australia) in each neighbourhood. Anabat detectors record the ultrasonic echolocation calls of bats which facilitate species identification from call sequences. These bat calls can be used subsequently to estimate activity levels. To minimise interference by the general public, detectors were located between 3–4 m above the ground, either attached to a tree trunk or on the roof of a building (e.g. house) with the transducer positioned upwards at a 45° angle. For those detectors placed on tree trunks, we avoided possible interference from the tree canopy by placing detectors only on

Eucalyptus trees with an upright habit (so that the canopy did not overhang the transducer). The location of detectors was randomized among neighbourhoods.

We attempted to sample over two consecutive nights in each season in each neighbourhood (maximum of six sampling nights per neighbourhood across autumn to summer). However, faulty survey equipment resulted in no recording on some nights. Nevertheless, we obtained a minimum of four nights of survey data from 71 of the 72 neighbourhoods, with one neighbourhood sampled only during two nights in summer. Hence, our analyses were based on four to six sampling nights for all but one neighbourhood. The total number of nights we sampled is consistent with the findings of Fischer et al. (2009), who concluded that a minimum of four nights of sampling should be sufficient to account for nightly variability in bat activity in agricultural landscapes in south-eastern Australia. However, the Fischer et al. (2009) study focussed on the sampling effort required to minimise variability across consecutive nights, whereas our samples were pooled across seasons. Pooling samples in this way may mask seasonal variation in bat activity. In our study, bat species richness averaged across neighbourhoods was lowest in autumn (mean 5.1 ± 1 s.e. 0.45) compared to spring (5.4 ± 0.23) and summer (5.5 ± 0.25), but this difference was not significant ($F_{2,173} = 0.53$, $P = 0.59$). Similarly, mean bat activity level (bat passes/night) across neighbourhoods was lowest in autumn (94.4 ± 24.4) compared to summer (128.1 ± 20.5) and spring (139.9 ± 26.3), but again the difference was not significant ($F_{2,173} = 1.09$, $P = 0.34$).

Given no significant seasonal differences in species richness or bat activity levels, we believe it is appropriate to pool our samples across seasons to ensure analyses are based on adequate sampling effort (i.e. 4–6 nights). However, it is important to recognise that the activity of certain bat species may vary seasonally. Appropriate analyses of seasonal variation are likely to require multiple nights of sampling in each season to account for both nightly and potential seasonal variation in activity levels. The most appropriate number of nights per season will be context dependent (Hayes 1997; Fischer et al. 2009).

Surveys were conducted from dusk until dawn during suitable weather conditions (e.g. avoiding heavy rain and strong wind). Each of the four neighbourhoods in each town was sampled simultaneously. Before placement, each detector was calibrated to equal sensitivity using a high voltage insect zapper (Mayo Hardware, Rosebery, Australia). The insect zapper emits a high frequency signal that is detected by the Anabat, and we adjusted the sensitivity of each Anabat detector so that all detectors were equally sensitive to this signal (by emitting a ‘buzzing’ sound) at a distance of 1 m. Additionally, the placement of detectors was rotated among neighbourhoods to control for any minor differences in sensitivity among detectors.

Bat passes detected by Anabat were stored as a single file on a CF storage card via a zero-crossing interface (Z-CAIM, Titley Electronics). These data were processed by Anascheme software (Gibson and Lumsden 2003), an automated system of call identification, and checked by the authors or bat-call identification experts (see Acknowledgements) to identify bat species and the number of passes per species (Gibson and Lumsden 2003; Lumsden and Bennett 2005). Recorded bat passes were processed by geographically specific, regional identification keys, which allow for the fact that there is geographic variation in species’ calls and that different suites of species occur in different regions (Law et al. 2002; Adams et al. 2010).

A ‘bat pass’ as defined here comprised a sequence of a minimum of three pulses. In the regional keys used to identify bat species in Victoria, a minimum of five pulses was used to define a pass. The difference in the definition of a ‘pass’ may have resulted in lower recorded activity levels overall and across functional guilds for bats in Victoria, but this should not influence our results of the relationships between bat activity and neighbourhood environments because neighbourhood types were distributed randomly across all towns. Species identifications were only made when at least 50 % of pulses within a pass were identified to the same species. Bat passes that could not be identified to species (owing to insufficient pulses or similarity in calls among species) were recorded as ‘unknown’. These data were used in our analysis only when calculating total bat activity (see ‘Response variables and functional guilds’).

Passes from *Nyctophilus* species (*Nyctophilus gouldi*, *N. geoffroyi* and *N. corbeni*) cannot be identified to species level by Anascheme or manually owing to the similarity in call type; therefore, we combined these into a single species complex (*Nyctophilus* spp.). Some ‘freetail’ bats (*Mormopterus* sp.) remain undescribed and we refer to these as *Mormopterus* species 2, 3 and 4. *Miniopterus schreibersii* may be split into two sub-species (*M. schreibersii oceanensis* or *M. schreibersii bassanii*), but we only recorded *M. schreibersii bassanii* in four of the 72 neighbourhoods so we refer to the species as *M. schreibersii* from here on. Finally, passes from *Scotorepens greyii* cannot be distinguished from undescribed *Scotorepens* species so we included the species complex *Scotorepens* spp.

Response variables and functional guilds

We analysed the relationships between the independent (predictor) variables and the following dependent (response) variables: bat species richness; total activity level (i.e. number of passes from all bat species including passes not identified to species level); and the activity level of the following functional guilds – open-adapted, clutter-adapted, edge-low (call frequency), edge-medium and edge-high. Measures of bat activity across the entire sampling period were divided by the number of nights sampling to give bat activity per night. Although sampling varied between four to six nights across neighbourhoods, total species richness per neighbourhood from these surveys was largely the same as that recorded when the number of sampling nights was controlled to four nights per neighbourhood ($r = 0.92$ comparing richness across neighbourhoods). Therefore, we retained the response variable of total species richness.

The functional traits of bat species were used to assign each species to a guild based on the previous study of Threlfall et al. (2011) and our knowledge of bat ecology. Guild allocation was primarily based on the foraging niche of bats (which reflects morphological traits such as wing loading and forearm length; Aldridge and Rautenbach 1987; Norberg and Rayner 1987) and echolocation frequency (Schnitzler and Kalko 2001). The open-adapted guild forages mostly in

open areas and has a low echolocation frequency (frequency range < 34 kHz). The clutter-adapted guild forages mostly in areas of denser vegetation and has a linear (vertically linear calls) or high echolocation frequency (frequency range > 48 kHz). The ‘edge’ guilds forage mostly at edges of vegetation patches (or in clearings through vegetation) and are further split into the low, medium (frequency range 34–48 kHz) and high echolocation frequencies (see Threlfall et al. 2011 for details).

Neighbourhood characteristics

We measured various neighbourhood characteristics that could reasonably be expected to influence bat communities in urban areas, and assigned these to four categories.

Broad-scale vegetation cover

Overall vegetation cover and/or distance to native vegetation has been shown previously to influence bat species occurrence or activity levels (e.g. Gehrt and Chelsvig 2003; Basham et al. 2011). Therefore, we measured broad-scale vegetation cover in each neighbourhood using remote sensing. We developed a land cover classification for each town using Advanced Land Observation Satellite (ALOS) imagery at a 10 m pixel resolution, and measured the proportional cover of woody and non-woody vegetation (‘vegetation cover’) across the entire area of each neighbourhood. We also measured the distance from the centroid of each neighbourhood to the nearest patch of native vegetation > 5 ha using ArcMap 9.3.1 (ESRI 2009).

Local-scale vegetation characteristics

To measure local-scale vegetation characteristics, we collected field data in each neighbourhood at four randomly located quadrats of 20 m × 100 m, with 20 m × 50 m quadrats nested within these larger quadrats. Using stratified random sampling, quadrats were located in urban greenspaces (e.g. parklands) or aligned along the road edge and projected into house blocks to capture streetscape and

private garden vegetation. In each 20 m × 100 m quadrat, we measured the number of trees > 20 cm in diameter at breast height and the number of native trees. In each 20 m × 50 m quadrat, we measured the proportion of quadrat area covered in understory vegetation (< 2 m in height), midstorey vegetation (2–4 m) and overstorey vegetation (> 4 m) (see Luck et al. 2009, 2011 for details).

Bat species have been recorded using native and exotic trees for roost sites (generally they use hollows for roosting; Kunz and Lumsden 2003) so we included the density of all trees ('tree density') as an independent variable (most of the trees we recorded were native). Using the data for the proportional cover of understory, midstorey and overstorey vegetation, we calculated a 'vegetation complexity' measure based on Shannon's diversity index. We expected increasing vegetation complexity to favour clutter-adapted bat species (see 'Hypotheses, data handling and analysis').

Built environment

Bat species richness can be relatively high in low density urban areas, but species richness and total activity levels may decline with increasing urbanization (Hourigan et al. 2006, 2010; Threlfall et al. 2011). Therefore, it was important to capture variation in the built environment across neighbourhoods, which we measured using housing density/ha (Australian Bureau of Statistics (ABS) 2006 Australian Census) and the proportional cover of impervious surfaces (data from ALOS satellite imagery as above). Housing density (square-root transformed) and impervious surface cover (arcsine(square-root) transformed) were positively correlated ($r = 0.55$) and we created the composite variable 'urban intensity' from these measures using principal component analysis (see Luck et al. in press).

Street lights may favour bats that forage in open areas (Rydell 1992; Rydell and Racey 1995; Avila-Flores and Fenton 2005), but artificial illumination has been shown also to negatively influence clutter-adapted species (Stone et al. 2009) and overall bat richness and activity levels

(Scanlon and Petit 2008). Therefore, we also measured the distance between the Anabat detector and the nearest street light to determine if bat activity varied as a factor of artificial illumination.

Predatory and competitive birds

Bird species that are potential predators of bats, or may compete with bats for roosting or nesting sites (primarily tree hollows), could influence the presence and/or abundance of bats in urban areas (Basham et al. 2011). As part of our broader study on urban fauna, we collected extensive data on the species richness and density of birds in each neighbourhood (see Luck et al. in press) at the same time as surveying bat species. From these data, we extracted information for birds that could be considered predators of bats (e.g. depredate bats when they leave their roost sites at dusk) or compete with bats for tree hollows. We considered that the species richness and density of these bird species may influence the species richness and/or activity levels of bats. We combined data for predatory and competitive birds (hereafter referred to as ‘competitive’ birds) owing to the few records for predatory birds.

The following bird species recorded in our neighbourhoods were considered potential predators of bats: laughing kookaburra (*Dacelo novaeguineae*), pied butcherbird (*Cracticus nigrogularis*), grey butcherbird (*Cracticus torquatus*), pied currawong (*Strepera graculina*), grey currawong (*Strepera versicolor*) and Australian raven (*Corvus coronoides*). The following hollow-nesting bird species were considered potential competitors of bats: little corella (*Cacatua sanguinea*), long-billed corella (*Cacatua tenuirostris*), galah (*Eolophus roseicapillus*), sulphur-crested cockatoo (*Cacatua galerita*), yellow-tailed black cockatoo (*Calyptorhynchus funereus*), gang gang cockatoo (*Callocephalon fimbriatum*), pink cockatoo (*Cacatua leadbeateri*), rainbow lorikeet (*Trichoglossus haematodus*), musk lorikeet (*Glossopsitta concinna*), little lorikeet (*Glossopsitta pusilla*), Australian king parrot (*Alisterus scapularis*), Australian ringneck (*Barnardius zonarius*), crimson rosella (*Platycercus elegans*), eastern rosella (*Platycercus eximius*),

red-rumped parrot (*Psephotus haematonotus*), common starling (*Sturnus vulgaris*) and common myna (*Sturnus tristis*).

Hypotheses, data handling and analysis

The predictor variables included in our analysis (described in ‘Neighbourhood characteristics’ and Table 1) were as follows: vegetation cover, distance to native vegetation, tree density, vegetation complexity, urban intensity, distance to light, species richness of competitive birds and the density of competitive birds.

Based on evidence from the literature and our own ecological knowledge, we established a set of general hypotheses regarding likely variation in bat species richness, total activity level, or the activity level of each functional guild as a factor of various aspects of the urban environment. For species richness and total activity levels, we expected negative relationships with urban intensity and the abundance of competitive birds, and quadratic (hump-shaped) relationships with neighbourhood vegetation cover (because intermediate values should favour both open-adapted species and those more reliant on vegetation; for example, clutter-adapted or edge-high bat species). For open-adapted species, we expected a positive relationship with urban intensity and negative relationships with vegetation complexity and distance to light. For clutter-adapted species, we expected negative relationships with urban intensity and positive relationships with neighbourhood vegetation cover and complexity, whereas for the edge-low and edge-medium guilds we expected quadratic relationships with vegetation cover. As distance to native vegetation increases, we expected to record fewer bat species, lower total activity levels and lower activity of species in the clutter-adapted and edge-high guilds, but we did not expect a relationship with open-adapted species as they are better able to fly in open, less vegetated areas (Norberg and Rayner 1987; Schnitzler and Kalko 2001).

Based on these general hypotheses, we developed a set of competing models as alternative explanations for variation in bat communities (Table 1). These models were representative of the

major characteristics of the urban environment and we were interested in examining key relationships based on our hypotheses rather than testing all possible alternative model combinations, consistent with an information theoretic framework (Burnham and Anderson 2002). We included quadratic variables where we anticipated non-linear relationships. We also included interaction terms between urban intensity and vegetation cover, tree density and distance to native vegetation to account for the fact that, for example, tree density or vegetation cover may be low in some less urbanized neighbourhoods (e.g. those established on previously cleared agricultural land), or high in some of the more urbanized areas (e.g. ‘leafy’ inner-city suburbs). Moreover, some highly urbanized areas can be immediately adjacent to native vegetation patches, whereas some less urbanized areas may be distant from native vegetation.

Owing to the low number of calls for clutter-adapted species, we combined the records for clutter-adapted and edge-high frequency guilds as they are expected to exhibit similar responses to the neighbourhood characteristics (Threlfall et al. 2012). We refer to this combined guild as ‘clutter-adapted’. The following variables were \log_{10} transformed to improve the distribution of the data: total bat activity; activity of each functional guild; distance to native vegetation; and distance to light. Tree density and competitive bird density were square-root transformed and vegetation cover was arcsine(square-root) transformed. Bat species recorded in less than four neighbourhoods were not included in data analysis. We tested for multi-collinearity among the predictor variables using the approach of Zuur et al. (2010) based on variance inflation factors (VIF). Here, one explanatory variable is modelled against all other explanatory variables using linear regression. A high r^2 value and high VIF values suggest collinearity among the predictor variables. To reduce collinearity, we sequentially removed each predictor variable with the highest VIF score and recalculated the r^2 and VIF values for the remaining variables until all VIF values were < 3 . We ensured also that any pairwise correlation among the remaining variables was < 0.6 .

We analysed the relationships between neighbourhood characteristics and bat communities using a hierarchical generalised linear model in a Bayesian framework with uninformative priors

(McCarthy 2007; Link and Barker 2010). Bayesian regression analyses based on uninformative priors will yield similar results (i.e. model coefficients) to likelihood-based frequentist approaches. All analyses were conducted using the software program WinBUGS 3.0.3 (Lunn et al. 2000). We included the categorical variable ‘town’ as a random effect in all models, as this accounted for the hierarchical structure in the data, whereby neighbourhoods were nested within towns.

Using WinBUGS, we generated 100,000 samples from the posterior distribution of each model after discarding an initial burn-in of 10,000 samples. The uninformative priors were drawn from a normal distribution with a mean of zero and a standard deviation of 1000. An uninformative prior with a large variance ensures the posterior is influenced primarily by the data (McCarthy 2007). We recorded the mean and standard deviation (SD) of the model coefficients [parameter estimates], and the 2.5th and 97.5th percentiles of the distribution, which can be interpreted as the 95% Bayesian confidence intervals (referred to as ‘credible intervals’(CIs)). We centred the mean of all explanatory variables to reduce autocorrelation between successive samples. The appropriateness of the models and the convergence of the Monte Carlo Markov Chain was assessed as follows: by examining the shape of the posterior distribution, and auto-correlation, trace and history diagnostics in WinBUGS; by running multiple chains (two or three chains) and assessing the convergence of chains using the Gelman-Rubin convergence statistic (Brooks and Gelman 1998); and by employing the diagnostic tests appropriate for single chains (i.e. the Geweke, Raftery-Lewis and Heidelberger-Welch diagnostics) available in the package CODA (Best et al. 1995) and implemented in R (R Development Core Team 2009). The output of these tests did not indicate a lack of convergence.

The fit of competing models was compared using the deviance information criterion (DIC), which is similar to Akaike’s information criterion (AIC) used in information theoretic approaches. We corrected the DIC value for small sample sizes (referred to as DIC_c from here on; Burnham and Anderson 2002). Smaller values of DIC_c indicate a better fit. The difference in DIC_c values was compared between the best ranked model and model i (Δ_i). Models where $\Delta_i < 2$ are presented in

the main text; the results for all models are included in Table S3. We also calculated DIC_c weights (w_i) for each model (interpreted the same as Akaike weights) and these represent the relative likelihood of the model and can be interpreted as the probability that any given model is the best model based on the data at hand. Model performance was further assessed by comparing the DIC_c values among models that included predictor variables, the constant only, and a model with only the constant plus ‘town’.

RESULTS

Species richness and activity levels

We recorded at least 19 bat species over 340 detector nights. The most widespread species was Gould’s wattled bat (*Chalinolobus gouldii*) occurring in 68 of 72 neighbourhoods (Table S2). This species was also the most commonly recorded, accounting for 46% of all bat passes identified to species ($n = 28,767$). Other widespread species included the white-striped freetail bat (*Tadarida australis*), chocolate wattled bat (*Chalinolobus morio*), little forest bat (*Vespadelus vulturnus*) and *Mormopterus* species 2 and 4, the latter being the second most commonly recorded species (20% of bat passes).

Species richness was remarkably similar across the 18 towns; 16 towns had between 8–10 species (mean 9.2 ± 1 s.e. 0.31). However, mean bat activity per night in each town (averaged across the four neighbourhoods surveyed in each town) varied substantially ranging from 18.8 bat passes per night in Orange to 417.3 passes per night in Griffith, although, only three towns had more than 200 passes per night (Fig. 2). The open-adapted and edge-low guilds contributed most to the overall differences between towns (Fig. 3).

Across neighbourhoods, species richness ranged from 3–11 species (6.9 ± 0.24). The mean number of passes per neighbourhood was 129 (± 20.11); however, these data were skewed (passes/night ranged from 5–834), so the median value of 68 is a better measure of central tendency. Mean activity across functional guilds was highest for the edge-low guild (45 ± 13.50 passes/night);

this is dominated by the activity of Gould's wattled bat. The open-adapted guild was the next most active (28 ± 4.12 passes/night).

Relations with the neighbourhood environment

The highest ranked model explaining variation in bat species richness included distance to native vegetation, urban intensity and the interaction between these variables (Tables 2 and S3). However, three other models had similar support ($\Delta_i < 2$) and these models included only vegetation measures. Among these measures, distance to native vegetation appeared to be the most important as it was included in three of the top four models and its CIs never encompassed zero. In accordance with our expectations, species richness increased closer to native vegetation and decreased with increasing urban intensity. Moreover, the model including a quadratic relationship between species richness and neighbourhood vegetation cover was better supported than any models including linear relationships with vegetation cover (Table S3). Similarly, the best supported model for explaining variation in total activity level was the one containing vegetation cover and its quadratic term (Table 2) and this was the only model among those considered that had substantial support ($\Delta_i < 2$; $w_i = 0.71$).

There was no strong support for any neighbourhood measure explaining variation in the activity of open-adapted species and all variables had CIs that encompassed zero (Table 2). Moreover, the highest ranked model included only the constant and town suggesting that variation in activity levels among towns swamped any neighbourhood effects. Various models had similar support in explaining the variation in the activity levels of clutter-adapted species. The activity of clutter-adapted species increased closer to native vegetation, as expected, but there were only weak relationships with vegetation cover, vegetation complexity and urban intensity (Table S3).

For edge-medium species, the highest ranked model included the quadratic relationship with vegetation cover, but a number of models had similar support ($\Delta_i < 2$; Table 2). For edge-low species, the model containing vegetation cover and its quadratic term had reasonable support ($\Delta_i <$

2; $w_i = 0.30$) and other highly ranked models included primarily vegetation measures (Table 2 and S3).

DISCUSSION

Relations with the neighbourhood environment and the usefulness of functional guilds

Ours is the first comprehensive study of bat use of smaller urban settlements across a broad geographic area. Our results were mostly consistent with findings from large cities, although we recorded greater total bat activity levels. Relatively high bat activity in our study area is surprising given that, unlike most previous studies, we did not survey in remnant vegetation, confining our surveys to residential areas or urban parklands. Our results for the open-adapted and clutter-adapted functional guilds were generally consistent with previous findings, supporting the use of functional guilds in examining the impacts of urbanization more broadly. However, further evaluation of the functional-trait approach is required, as some species within guilds can exhibit differing patterns in relation to urban characteristics.

Bat species richness varied largely as expected. Richness peaked at mid-range values of overall neighbourhood vegetation cover, although this was not the case for tree density (Table S3). The latter relationship depends on the range of tree densities sampled. Not unexpectedly, tree densities in our neighbourhoods were relatively low, peaking at approximately 50 trees/ha. Therefore, we were unlikely to lose bat species that use more open habitats and simply added new species reliant on ‘intermediate’ levels of tree cover. The narrow range of tree densities that we measured also likely explains the lack of a relationship between total bat activity and tree density. For example, Hanspach et al. (2012; see also Lumsden and Bennett 2005) found that the total activity of bats in agricultural areas in south-eastern Australia peaked at around 25–50 trees/ha – the upper bound of our tree densities. If this relationship is consistent across land uses, we might expect a positive relationship in our study also (the parameter estimate was positive, but subject to substantial uncertainty).

There was little support for a negative impact of competitive birds on bat species richness. In our study sites, total bird species richness is positively related to vegetation cover and tree density (Luck et al. in press). Therefore, sites that provide suitable habitat for birds are also suitable for the nocturnal activity of a number of bat species – and as total bird species richness increases, so does the richness of competitive birds. Hence, the positive association between habitat suitability and bat activity appears to outweigh any potential negative effects on activity from bird competition. The minor importance of bird competition is supported by the fact that there was no relationship between the density of competitive birds and any bat measures, contrary to previous findings in the large metropolitan centre of Sydney (Basham et al. 2011).

The activity level of all bats and clutter-adapted and edge-medium species increased further from lights, but these relationships were not strongly supported among alternative competing explanations for variation in bat activity. Moreover, there was no indication that any particular functional guild favoured lights, consistent with some previous studies (e.g. Lesiński et al. 2000; Scanlon and Petit 2008), though contrary to others (Blake et al. 1994; Rydell and Racey 1995). Relationships between bat species and artificial illumination may be decidedly complex and reflect differences in, for example, the type of light source (e.g. mercury vapour vs. sodium vapour lights), bat ecology and landscape context. While certain light sources attract insects and subsequently foraging bats (e.g. Eisenbeis 2006), artificial illumination can disrupt bat foraging behaviour and flight paths. For example, a recent study by Stone et al. (2012) found that LED street lights reduced the activity level of slow-flying bat species (e.g. *Rhinolophus hipposideros*), but did not affect fast-flying species (e.g. *Pipistrellus pipistrellus*).

The results of our study suggest that relationships between particular functional guilds and variation in the urban environment may not be entirely consistent across all urban landscape types, limiting the capacity to make broad generalisations. For example, a number of studies have recorded positive relationships between the presence or activity of open-adapted species and urbanization level (e.g. Duchamp and Swihart 2008; Hourigan et al. 2010; Threlfall et al. 2011)

because the high wing aspect ratios and wing loadings of these species means they are better adapted for flying in open areas. However, we did not record a strong positive relationship between urban intensity and the activity level of open-adapted species. Moreover, there was no relationship between open-adapted activity level and vegetation cover, likely because densely vegetated areas that open-adapted species may avoid (or fly above) were not included in our study sites; although, these species still appear to rely on scattered trees for roost and foraging locations (Lumsden et al. 2002; Lumsden and Bennett 2005). Nevertheless, our results, when combined with those of past studies, suggest that, at the very least, low density urbanization does not have a negative impact on the activity of most open-adapted bat species. Similar conclusions have been made in other cities around the world (Avila-Flores and Fenton 2005). However, at least one open-adapted, south-eastern Australian species appears to avoid urban areas completely. *Mormopterus norfolkensis* occurs along the coast of NSW, yet it was not detected in the two coastal towns we sampled or in recent surveys of the coastal urban centre of Newcastle (McConville and Law unpubl. data).

The relationships we recorded for clutter-adapted species were more consistent with past research. For example, there was a negative relationship between clutter-adapted activity level and urban intensity and distance to native vegetation and this concurs with previous studies showing that clutter-adapted species (with low wing loading and aspect ratio values) mostly avoid highly developed urban areas and concentrate their activity in more densely vegetated sites (e.g. remnant vegetation patches or forests; Gehrt and Chelsvig 2004; Avila-Flores and Fenton 2005; Duchamp and Swihart 2008; Threlfall et al. 2011). Given this association, we expected a positive relationship between the activity of clutter-adapted species and vegetation cover and tree density, but a quadratic relationship was more strongly supported in both cases. In farmland, these species show a linear relationship with tree density when sites with up to 1000 trees/ha are included (Hanspach et al. 2012), and the lack of variation in vegetation measures across our study sites likely explains the somewhat weaker relationships that were recorded for clutter-adapted species.

The relationships we recorded for the activity levels of the edge-low and edge-medium guilds as a factor of urban characteristics varied from past research and our expectations. For example, species in the edge-low guild have been found previously to be associated with both native vegetation and urban areas (e.g. Hourigan et al. 2010), but we found no relationship between the activity of these species and distance to native vegetation or urban intensity. While variability in the results for particular guilds across studies will be influenced by factors such as landscape context and season, we argue that a further contributing factor is an inherent problem with the guild concept as it is currently applied to bats and when the species pool is small.

The problem with the current application of the guild concept to bats relates to the likely differing responses from different species in the same guild, an issue that has been documented in previous studies that found divergent habitat preferences among morphologically similar bat species (Saunders and Barclay 1992; Arlettaz 1999). The patterns associated with a particular guild may be strongly dependent on the activity levels recorded for the various species in the guild. For example, in the edge-medium guild we expected activity to increase closer to street lights because *M. schreibersii*, a member of the guild, has been recorded feeding around lights (B. Law, pers. obs.). However, edge-medium species in the genus *Vespadelus* were recorded at more sites in our study and it is possible these species avoid lights, which would explain why we recorded a positive association between distance to light and edge-medium guild activity. When the species pool is relatively small, and only a few species occur in each functional guild, strong variation in the abundance or activity of any one species can have a substantial impact on guild-level patterns if species-specific patterns vary.

While categorising species based on functional traits and assigning them to guilds is potentially a valuable approach for improving generality in ecology, such approaches should be cautiously applied when knowledge of species behaviour is limited. When the pool of species is small, a focus on species-specific rather than guild-specific patterns may be more appropriate. Moreover, species-specific studies contribute valuable information to aid interpretation of guild-

level patterns, especially for threatened species (Threlfall et al. 2012). Nevertheless, our results show that patterns in the activity of species in the clutter-adapted and to a lesser extent open-adapted guild are broadly consistent across different urban contexts. Variation in the patterns for other guilds between small and large urban settlements appeared to be primarily a factor of site- and landscape-specific differences in the built and natural environment (e.g. the magnitude of the gradient in level of urbanization across study sites).

Comparisons with studies in large cities

Species richness recorded in our study (at least 19 species) was higher than that recorded in recent studies conducted in major (population size > 1 million) Australian cities (Scanlon and Petit 2008, Hourigan et al. 2006; 2010; Basham et al. 2011, Threlfall et al. 2011). Variation in observed species richness is influenced by a number of factors including sampling effort, location of sites, seasons surveyed and the aims of the research. Most previous studies in urban areas included remnant native vegetation in their sampling locations whereas we did not; therefore, our high species count may initially seem surprising. Yet, we believe it is likely a result of the large geographic area that we sampled (much larger than metropolitan-based studies). Indeed, species richness per town was mostly between 8–10 species and turnover in species composition among towns likely yielded the relatively high species richness we recorded overall.

Bat activity levels recorded in our study were generally higher than those recorded in Australia's major cities (Scanlon and Petit 2008, Hourigan et al. 2010; Basham et al. 2011, Threlfall et al. 2011), and were more consistent with results from New South Wales (NSW) forests (Law and Chidel 2002; Lloyd et al. 2006) or native vegetation in agricultural landscapes (Law et al. 1999; Law and Chidel 2006). Our results suggest that relatively small-scale urbanization may have less of a negative impact on bat activity than large-scale urbanization. However, we urge caution in interpreting differences in activity levels across studies because many factors influence variation in

bat activity including landscape and site context, short- and long-term environmental variability, and sampling effort and approach.

Consistent with research in major cities (e.g. Hourigan et al. 2010; Threlfall et al. 2011), we found also that neighbourhoods with moderate tree cover supported the highest bat activity levels, possibly attracting species that forage mostly in open areas and those that forage mostly in denser vegetation. Our results suggest also that the presence of native vegetation close to urban areas increases bat species richness, total activity and the activity of clutter-adapted and edge-medium species. We may have recorded an even stronger relationship with native vegetation if there was a greater range of distances between our neighbourhoods and vegetation patches. Most neighbourhoods were within 2 km of native vegetation with a maximum distance of 6 km. This is within the nightly flight distances of many bat species (Lumsden et al. 2002; Rhodes and Catterall 2008). In summary, the mostly negative relationships we found between bat activity and urban intensity (except for open-adapted species) coupled with simple positive or quadratic relationships with vegetation measures, suggests that ensuring vegetation cover within residential areas (e.g. retaining old-growth native trees, riparian vegetation and vegetation in parks and gardens) is important for supporting bat diversity in urban areas.

Conclusions and study limitations

The results of our study suggest that, at the very least, urban development in smaller towns and cities may not be completely detrimental to bats, and some species (e.g. open-adapted) may readily adapt to urban environments. This depends substantially on the type of land use surrounding urban areas and the degree to which vegetation cover (particularly native vegetation) is retained within settlement boundaries or within nightly flying distances of bat species. For example, Gehrt and Chelsvig (2003) suggested that urban areas embedded within extensively cleared agricultural landscapes dominated by row-crop agriculture may provide habitat components (e.g. roost sites) that are limited in the surrounding landscape. Most of our towns are surrounded by agricultural

land, particularly grazing land and annual or perennial crops (Table S1). Importantly though, these agricultural landscapes still retain remnant native vegetation and native trees scattered among fields. These ‘variegated’ landscapes (McIntyre and Barrett 1992) are the dominant land type in agricultural regions of south-eastern Australia. Remnant native vegetation, including scattered trees, plays a critical role in supporting bat species in these landscapes (Lumsden and Bennett 2005; Hanspach et al. 2012). Hence, urban areas in these regions likely provide supplementary habitat for some bat species rather than offering resources that no longer exist in the surrounding landscape.

Like most large-scale studies in landscape ecology, our results present correlative rather than causal evidence of the impacts of urbanization on bat species. Further work is required that compares key life-history traits of bats (e.g. reproductive rate or survival) in urban vs. non-urban areas (Coleman and Barclay 2011). Moreover, acoustic sampling should be supplemented with population studies (e.g. using marked individuals) where possible to obtain better estimates of population abundance for readily trapped species. Bat use of urban areas may vary seasonally and this variation is not accounted for when pooling samples across seasons or constraining surveys to a single season. Appropriate survey effort is required in each season to adequately determine how bat activity varies seasonally.

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Supplementary material

Supporting Methods and Results.

Table S1. Major land uses surrounding each survey town.

Table S2. Bat species recorded across all neighbourhoods.

Table S3. All models explaining variation in bat communities.

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Table 1. Models tested for each of the response variables.

Model	Variable description (units)
Vegetation cover	Total vegetation cover in each neighbourhood (%)
Distance to vegetation	Distance from neighbourhood to nearest patch of native vegetation (m)
Tree density	Density of all trees (per 2000m ²)
Vegetation complexity	Shannon's diversity index based on understorey–overstorey cover
Urban intensity	Principal component analysis of housing density and impervious surface cover
Distance to light	Distance between Anabat detector and nearest street light (m)
Bird density	Density of potential predators and competitors (per ha)
Bird richness	Richness of potential predators and competitors
Vegetation cover + distance to vegetation	Broad-scale vegetation measures
Tree density + vegetation complexity	Local-scale vegetation measures
Urban intensity + distance to light	Built environment
Bird density + bird richness	Predator/competitor bird community
Vegetation cover + vegetation cover ²	Quadratic relationship
Distance to vegetation + distance to vegetation ²	Quadratic relationship
Tree density + tree density ²	Quadratic relationship
Vegetation complexity + vegetation complexity ²	Quadratic relationship
Vegetation cover + urban intensity + vegetation cover*urban intensity	Interaction between vegetation cover and urban intensity
Distance to vegetation + urban intensity + distance to vegetation*urban intensity	Interaction between distance to vegetation and urban intensity
Tree density + urban intensity + Tree density*urban intensity	Interaction between tree density and urban intensity
Vegetation cover + distance to vegetation + tree density + vegetation complexity	Broad-scale and local-scale vegetation measures

Table 2. The highest ranked models ($\Delta_i < 2$) explaining variation in bat communities. Numbers in brackets are the parameter estimates and their 95% credible intervals.

Model ^a	DIC _c ^b	Δ_i DIC _c	w_i
Species richness			
Distance to vegetation (-1.39, -2.31 – -0.47) + urban intensity (-0.54, -0.98 – -0.10) + distance to vegetation*urban intensity (-0.61, -1.44 – 0.21)	268.9	0.0	0.23
Vegetation cover (3.02, 0.85 – 5.15) + vegetation cover ² (-7.18, -14.29 – -0.11)	269.2	0.3	0.20
Vegetation cover (2.00, -0.22 – 4.21) + distance to vegetation (-1.06, -1.92 – -0.21)	269.4	0.5	0.18
Vegetation cover (0.99, -1.18 – 3.20) + distance to vegetation (-0.95, -1.76 – -0.13) + tree density (1.03, 0.23 – 1.84) + vegetation complexity (1.77, 0.004 – 3.45)	270.0	1.1	0.13
Total activity			
Vegetation cover (0.48, -0.10 – 1.06) + vegetation cover ² (-3.30, -5.51 – -1.14)	104.8	0.0	0.71
Open-adapted activity			
Constant + town	75.5	0.0	0.16
Urban intensity (0.06, -0.06 – 0.17)	75.9	0.4	0.13
Vegetation cover (0.40, -0.28 – 1.08) + urban intensity (0.09, -0.06 – 0.24) + vegetation cover*urban intensity (0.43, -0.17 – 1.03)	76.2	0.7	0.11
Vegetation cover (0.13, -0.41 – 0.67) + vegetation cover ² (-1.73, -3.62 – 0.13)	76.5	1.0	0.10
Vegetation complexity (-0.11, -0.65 – 0.43)	77.1	1.6	0.07
Clutter-adapted activity			
Vegetation cover (0.58, -0.07 – 1.20) + vegetation cover ² (-1.29, -3.29 – 0.74)	86.1	0.0	0.18
Urban intensity (-0.11, -0.23 – 0.02) + distance to light (0.35, -0.01 – 0.70)	86.1	0.0	0.18
Vegetation cover (0.27, -0.37 – 0.92) + distance to vegetation (-0.27, -0.50 – -0.03)	86.9	0.8	0.12
Vegetation cover (0.19, -0.61 – 0.96) + urban intensity (-0.13, -0.30 – 0.02) + vegetation cover*urban intensity (0.49, -0.16 – 1.12)	87.1	1.0	0.11
Vegetation cover (0.53, -0.13 – 1.16)	87.4	1.3	0.09
Distance to vegetation (-0.30, -0.52 – -0.08)	87.7	1.6	0.08
Distance to vegetation (-0.32, -0.57 – -0.06) + urban intensity (-0.09, -0.22 – 0.03) + distance to vegetation*urban intensity (-0.11, -0.34 – 0.12)	87.8	1.7	0.08
Edge-low activity			
Vegetation cover (0.51, -0.18 – 1.21) + vegetation cover ² (-3.12, -5.66 – -0.61)	122.7	0.0	0.30
Edge-medium activity			
Vegetation cover (0.49, -0.14 – 1.12) + vegetation cover ² (-1.98, -4.17 – 0.18)	100.0	0.0	0.15
Bird richness (0.08, 0.02 – 0.14)	100.5	0.4	0.12

Vegetation complexity (0.33, -0.29 – 0.94) + vegetation complexity ² (-2.67, -4.73 – -0.64)	100.8	0.8	0.10
Vegetation cover (0.49, -0.15 – 1.12)	100.9	0.8	0.10
Distance to light (0.45, 0.06 – 0.84)	101.2	1.1	0.09
Bird density (-0.06, -0.24 – 0.13) + bird richness (0.08, 0.02 – 0.14)	101.6	1.6	0.07
Tree density (0.27, 0.04 – 0.51)	102.0	1.9	0.06

^aAll models include the constant + town.

^bDIC_c = deviance information criterion, Δ_i = difference in DIC_c values, w_i = DIC_c weights.

Figure captions

Figure 1. Study area (covering > 250,000 square km) showing the location of the 18 towns surveyed and the major metropolitan cities of Sydney and Melbourne.

Figure 2. Mean total bat activity per night in each town (error bars ± 1 s.e.).

Figure 3. Percentage of bat passes in each town for each functional guild.

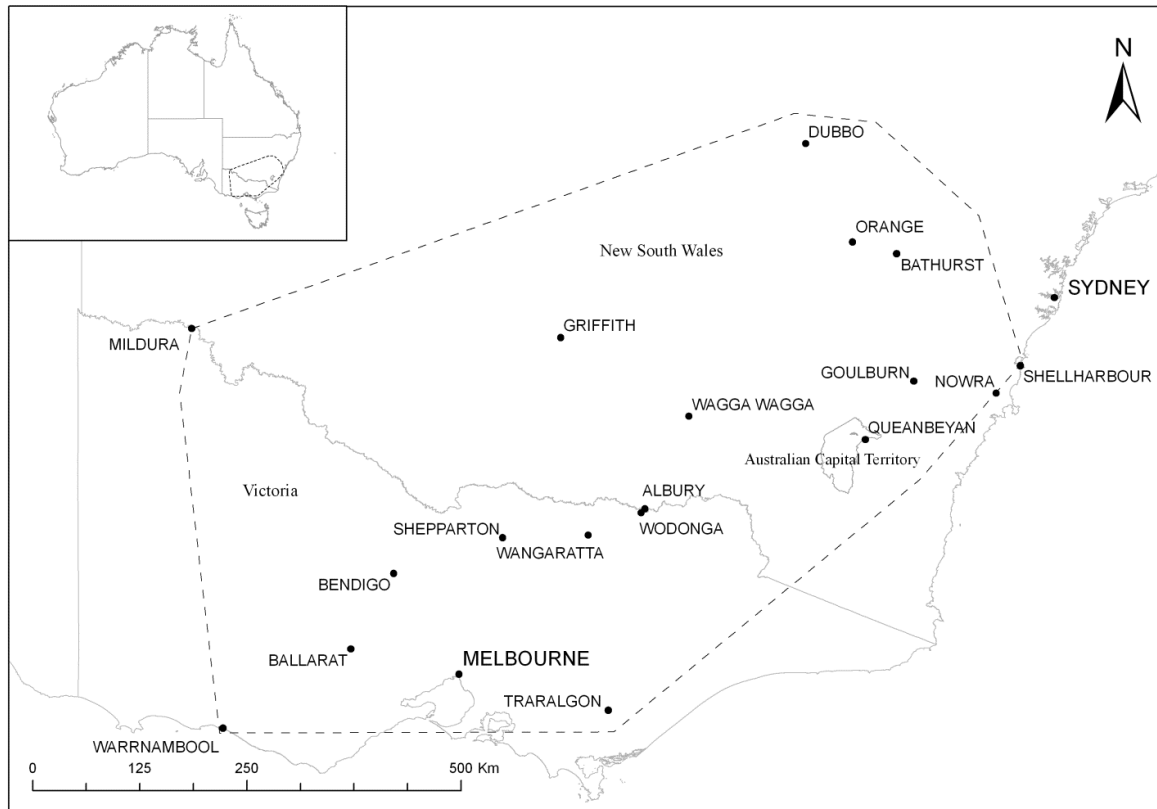


Fig. 2

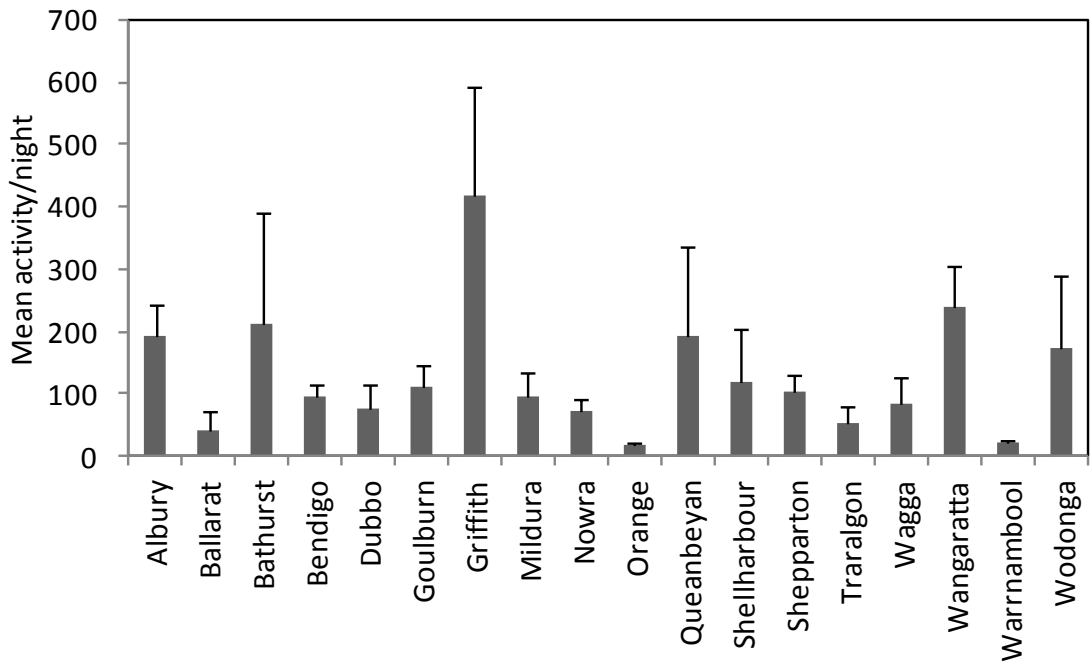


Fig. 3

