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

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27 **ABSTRACT**

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

47
48 **Keywords:** Australia; bat activity; bat diversity; Bayesian analysis; functional traits; guilds;
49 Microchiroptera; urban ecology; urban landscapes

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53 INTRODUCTION

54 The responses of species to landscape change may be dictated by their functional traits (i.e. a
55 morphological, physiological, phenological or behavioural feature of an individual; Violle et al.
56 2007; Luck et al. 2012). Species with similar functional traits (collectively described as ‘guilds’)
57 may be impacted in similar ways by particular landscape changes (Simberloff and Dayan 1991).
58 Therefore, a focus on functional type rather than species identity may enhance the capacity of
59 ecologists to make broader generalisations about the impact of particular land uses on ecological
60 communities regardless of geographic location or differences in taxonomy.

61 Urbanization, one of the most pervasive land-use trends of the 21st century (United Nations
62 2010), creates landscapes with similar structural characteristics and this may result in comparable
63 species assemblages occupying widely separated urban settlements (McKinney 2006). Yet, while
64 research on the ecology of urban landscapes is increasing, knowledge is lacking that enables broad
65 generalisations about the impacts of urbanization on particular taxonomic or functional groups
66 (Gaston 2010). Much of the research on urbanization has focussed on major cities (e.g. Germaine
67 and Wakeling 2001; Niemelä et al. 2002; Crooks et al. 2004; Marzluff 2005) neglecting relations
68 that occur in smaller human settlements. Examination across the full range of settlement types is
69 fundamental to a wider understanding of the impacts of varying levels of urbanization on native
70 ecosystems.

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

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

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

95

96 **METHODS**

97 **Study area**

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

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

108 We recorded bat species richness and activity levels in four neighbourhoods per town (total
109 $n = 72$). Neighbourhood boundaries were defined by census collection districts (≈ 200 houses; mean
110 neighbourhood area: $69 \text{ ha} \pm 1 \text{ s.e. } 9 \text{ ha}$) and neighbourhoods were selected for surveying using
111 stratified random sampling to capture the full range of variation in neighbourhood characteristics
112 such as housing density (see Luck et al. 2009). Across neighbourhoods, housing density ranged
113 from $0.5\text{--}11 \text{ houses ha}^{-1}$, the cover of woody and non-woody vegetation ranged from $1\text{--}78\%$, and
114 the cover of impervious surfaces ranged from $1\text{--}88\%$. All neighbourhoods were at least 20 years of
115 age at the time of sampling and neighbourhoods in the same town were separated by at least 1 km.

116

117 **Bat surveys and call identification**

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

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

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

132 We attempted to sample over two consecutive nights in each season in each neighbourhood
133 (maximum of six sampling nights per neighbourhood across autumn to summer). However, faulty
134 survey equipment resulted in no recording on some nights. Nevertheless, we obtained a minimum of
135 four nights of survey data from 71 of the 72 neighbourhoods, with one neighbourhood sampled only
136 during two nights in summer. Hence, our analyses were based on four to six sampling nights for all
137 but one neighbourhood. The total number of nights we sampled is consistent with the findings of
138 Fischer et al. (2009), who concluded that a minimum of four nights of sampling should be sufficient
139 to account for nightly variability in bat activity in agricultural landscapes in south-eastern Australia.
140 However, the Fischer et al. (2009) study focussed on the sampling effort required to minimise
141 variability across consecutive nights, whereas our samples were pooled across seasons. Pooling
142 samples in this way may mask seasonal variation in bat activity. In our study, bat species richness
143 averaged across neighbourhoods was lowest in autumn (mean 5.1 ± 1 s.e. 0.45) compared to spring
144 (5.4 ± 0.23) and summer (5.5 ± 0.25), but this difference was not significant ($F_{2,173} = 0.53$, $P =$
145 0.59). Similarly, mean bat activity level (bat passes/night) across neighbourhoods was lowest in
146 autumn (94.4 ± 24.4) compared to summer (128.1 ± 20.5) and spring (139.9 ± 26.3), but again the
147 difference was not significant ($F_{2,173} = 1.09$, $P = 0.34$).

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

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

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

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

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

190

191 **Response variables and functional guilds**

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

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

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

213

214 **Neighbourhood characteristics**

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

217

218 *Broad-scale vegetation cover*

219 Overall vegetation cover and/or distance to native vegetation has been shown previously to
220 influence bat species occurrence or activity levels (e.g. Gehrt and Chelsvig 2003; Basham et al.
221 2011). Therefore, we measured broad-scale vegetation cover in each neighbourhood using remote
222 sensing. We developed a land cover classification for each town using Advanced Land Observation
223 Satellite (ALOS) imagery at a 10 m pixel resolution, and measured the proportional cover of woody
224 and non-woody vegetation (‘vegetation cover’) across the entire area of each neighbourhood. We
225 also measured the distance from the centroid of each neighbourhood to the nearest patch of native
226 vegetation > 5 ha using ArcMap 9.3.1 (ESRI 2009).

227

228 *Local-scale vegetation characteristics*

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

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

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

245

246 *Built environment*

247 Bat species richness can be relatively high in low density urban areas, but species richness and total
248 activity levels may decline with increasing urbanization (Hourigan et al. 2006, 2010; Threlfall et al.
249 2011). Therefore, it was important to capture variation in the built environment across
250 neighbourhoods, which we measured using housing density/ha (Australian Bureau of Statistics
251 (ABS) 2006 Australian Census) and the proportional cover of impervious surfaces (data from
252 ALOS satellite imagery as above). Housing density (square-root transformed) and impervious
253 surface cover (arcsine(square-root) transformed) were positively correlated ($r = 0.55$) and we
254 created the composite variable 'urban intensity' from these measures using principal component
255 analysis (see Luck et al. in press).

256 Street lights may favour bats that forage in open areas (Rydell 1992; Rydell and Racey
257 1995; Avila-Flores and Fenton 2005), but artificial illumination has been shown also to negatively
258 influence clutter-adapted species (Stone et al. 2009) and overall bat richness and activity levels

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

261

262 *Predatory and competitive birds*

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

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

284 red-rumped parrot (*Psephotus haematonotus*), common starling (*Sturnus vulgaris*) and common
285 myna (*Sturnus tristis*).
286

287 **Hypotheses, data handling and analysis**

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

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

308 Based on these general hypotheses, we developed a set of competing models as alternative
309 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

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

341 Using WinBUGS, we generated 100,000 samples from the posterior distribution of each
342 model after discarding an initial burn-in of 10,000 samples. The uninformative priors were drawn
343 from a normal distribution with a mean of zero and a standard deviation of 1000. An uninformative
344 prior with a large variance ensures the posterior is influenced primarily by the data (McCarthy
345 2007). We recorded the mean and standard deviation (SD) of the model coefficients [parameter
346 estimates], and the 2.5th and 97.5th percentiles of the distribution, which can be interpreted as the
347 95% Bayesian confidence intervals (referred to as ‘credible intervals’(CIs)). We centred the mean
348 of all explanatory variables to reduce autocorrelation between successive samples. The
349 appropriateness of the models and the convergence of the Monte Carlo Markov Chain was assessed
350 as follows: by examining the shape of the posterior distribution, and auto-correlation, trace and
351 history diagnostics in WinBUGS; by running multiple chains (two or three chains) and assessing
352 the convergence of chains using the Gelman-Rubin convergence statistic (Brooks and Gelman
353 1998); and by employing the diagnostic tests appropriate for single chains (i.e. the Geweke,
354 Raftery-Lewis and Heidelberger-Welch diagnostics) available in the package CODA (Best et al.
355 1995) and implemented in R (R Development Core Team 2009). The output of these tests did not
356 indicate a lack of convergence.

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

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

390

391 **Relations with the neighbourhood environment**

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

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

411 For edge-medium species, the highest ranked model included the quadratic relationship with
412 vegetation cover, but a number of models had similar support ($\Delta_i < 2$; Table 2). For edge-low
413 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).

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

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

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

466 because the high wing aspect ratios and wing loadings of these species means they are better
467 adapted for flying in open areas. However, we did not record a strong positive relationship between
468 urban intensity and the activity level of open-adapted species. Moreover, there was no relationship
469 between open-adapted activity level and vegetation cover, likely because densely vegetated areas
470 that open-adapted species may avoid (or fly above) were not included in our study sites; although,
471 these species still appear to rely on scattered trees for roost and foraging locations (Lumsden et al.
472 2002; Lumsden and Bennett 2005). Nevertheless, our results, when combined with those of past
473 studies, suggest that, at the very least, low density urbanization does not have a negative impact on
474 the activity of most open-adapted bat species. Similar conclusions have been made in other cities
475 around the world (Avila-Flores and Fenton 2005). However, at least one open-adapted, south-
476 eastern Australian species appears to avoid urban areas completely. *Mormopterus norfolkensis*
477 occurs along the coast of NSW, yet it was not detected in the two coastal towns we sampled or in
478 recent surveys of the coastal urban centre of Newcastle (McConville and Law unpubl. data).

479 The relationships we recorded for clutter-adapted species were more consistent with past
480 research. For example, there was a negative relationship between clutter-adapted activity level and
481 urban intensity and distance to native vegetation and this concurs with previous studies showing
482 that clutter-adapted species (with low wing loading and aspect ratio values) mostly avoid highly
483 developed urban areas and concentrate their activity in more densely vegetated sites (e.g. remnant
484 vegetation patches or forests; Gehrt and Chelsvig 2004; Avila-Flores and Fenton 2005; Duchamp
485 and Swihart 2008; Threlfall et al. 2011). Given this association, we expected a positive relationship
486 between the activity of clutter-adapted species and vegetation cover and tree density, but a quadratic
487 relationship was more strongly supported in both cases. In farmland, these species show a linear
488 relationship with tree density when sites with up to 1000 trees/ha are included (Hanspach et al.
489 2012), and the lack of variation in vegetation measures across our study sites likely explains the
490 somewhat weaker relationships that were recorded for clutter-adapted species.

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

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

512 While categorising species based on functional traits and assigning them to guilds is
513 potentially a valuable approach for improving generality in ecology, such approaches should be
514 cautiously applied when knowledge of species behaviour is limited. When the pool of species is
515 small, a focus on species-specific rather than guild-specific patterns may be more appropriate.
516 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).

523

524 **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

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

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

584

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594 **Supplementary material**

595 Supporting Methods and Results.

596 Table S1. Major land uses surrounding each survey town.

597 Table S2. Bat species recorded across all neighbourhoods.

598 Table S3. All models explaining variation in bat communities.

599

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776 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

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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	Δ_i		
	DIC _c ^b	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

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