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WILDLIFE RESEARCH

# More trees and fewer roads: the importance of local and landscape features for insectivorous bats in open urban green spaces

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## ABSTRACT

**Context.** Urbanisation poses new challenges for wildlife worldwide, and recent research suggests that urban parks, although highly modified, may act as important refuges. Insectivorous bats can persist in urban landscapes and play an important role in keeping insect populations in balance. Previous research on use of urban landscapes by these bats has often focused on patches of remnant bushland within cities, but their use of highly modified open spaces is not well understood. **Aims.** We aimed to determine the use of open green spaces (e.g. open parks, sports ovals) by insectivorous bats in Melbourne, Australia and to identify landscape factors that influence their presence and activity level. **Methods.** We conducted passive acoustic surveys at 35 sites across greater Melbourne. Once species were identified from the echolocation call data, we modelled species richness, total activity and activity of individual species against landscape and weather variables, using Generalised Linear Mixed Models and Generalised Additive Mixed Models. **Key results.** Across 557 detector nights, we identified at least 11 of the 17 species recorded to occur in Melbourne. Both species richness and activity were greater in areas with more nearby trees and lesser in areas with more roads. There were weaker species-specific relationships between bat activity and both distance to the nearest water source and Normalised Difference Vegetation Index. Species richness and activity levels were lower on nights with a lower temperature at dusk, higher rainfall and stronger wind. **Conclusions.** Our results show that multiple bat species consistently use Melbourne's open green spaces, highlighting the potential habitat value of these areas, especially those surrounded by high tree densities and fewer roads. **Implications.** Insectivorous bats play important roles within ecosystems and bring benefits to human society. To encourage the diversity and activity of insectivorous bats in urban landscapes, we recommend retaining and increasing indigenous vegetation surrounding open areas in urban parks, as well as more strategic planning of new urban parks that further increases tree density in cities.

**Keywords:** insectivorous bats, local councils, microbats, open green space, sports ovals, urban ecology, urban parks, urbanisation.

## Introduction

The rate of urbanisation is increasing around the world, bringing with it a suite of challenges for wildlife. Australia is quickly becoming one of the world's most urbanised countries; by 2050, it is projected that over 90% of Australians will live in an urban area (United Nations Department of Economic and Social Affairs Population Division (UNDESA) 2019). This increasingly urbanised landscape often incorporates patches of remnant vegetation that are highly modified and fragmented. Wildlife persisting in these landscapes often need to rely on highly modified parks and artificial green spaces for the resources they require. These areas are typically designed for human use rather than ecological functionality, but recent research is beginning to uncover previously unknown importance of these areas as refuges for biodiversity in our cities (Fernandez-Juricic and Jokimaki 1998; Lowry *et al.* 2013; Koh and Sodhi 2017). Although the factors enabling these species to survive in the urban environment are not fully understood, a wide variety of taxa, including some threatened species, have been observed utilising and even thriving in modified urban green spaces (e.g. Angold *et al.* 2006; Carbó-Ramírez and Zuria 2011; Van Helden *et al.* 2020).

Small, insectivorous bats (hereafter called 'bats') are one group of wildlife known to persist in urban landscapes worldwide. Australia is home to a diverse range of insectivorous bats, with 70 species across eight families (Armstrong *et al.* 2020). Seventeen of these species have been recorded in the greater Melbourne area (Australasian Bat Society 2021), making them the most diverse group of native mammals that inhabit the city. Due to their small size, large surface area and specialised mode of movement (flying), bats have high energy requirements, which they satisfy by consuming large quantities of insects. This makes them important ecosystem service providers keeping insect populations in balance, including many agricultural pest species (Suarez-Rubio *et al.* 2018); in the USA alone, the economic value of these services is estimated to be at least $3.7 billion USD per year (Boyles *et al.* 2011).

Urbanisation, including increased housing and road density, habitat fragmentation and noise and light pollution, has been linked by previous studies to decreased activity of bats in Australian cities (Threlfall *et al.* 2012; Bonsen *et al.* 2015; Caryl *et al.* 2016; Haddock *et al.* 2019*a*). The availability of water and watercourses is also important for bats because these features can act as corridors between patches of suitable habitat and support flying invertebrates, the main prey items of most species (Ober and Hayes 2008; Jones *et al.* 2009; Threlfall *et al.* 2012; Altringham and Kerth 2016; Straka *et al.* 2016). Riparian habitat along waterways also provides trees for roosting for many bat species (Gaisler *et al.* 1998; Threlfall *et al.* 2012). Vegetation structure can have species-specific impacts on bats, linked to differences in flight pattern and wing morphology between species. Fast-flying species with long, narrow wings, like white-striped free-tailed bat (*Austronomus australis*) are considered better adapted to open spaces, whereas slow-flying species with shorter, broader wings, such as the long-eared bats (*Nyctophilus* spp.), are more manoeuvrable and able to forage in dense vegetation (Norberg and Rayner 1987; Adams *et al.* 2009; Threlfall *et al.* 2011).

The impacts of landscape factors on bat activity have been widely explored, yet little research has considered whether these patterns are also applicable to open urban green spaces, including parks, sporting ovals and tennis courts. Existing literature on urban bats has largely focused on remnant vegetation patches, with little investigation of openness as a feature of urban parks (Basham *et al.* 2011; Caryl *et al.* 2016; Linley 2017; Haddock *et al.* 2019*a*; Moretto *et al.* 2019). Additionally, existing studies that have investigated bat activity in open areas have largely been conducted in rural–agricultural areas, which are much larger than the typical urban park or oval (Lumsden and Bennett 2005; Crisol-Martínez *et al.* 2017). Urban parks may have a low perceived conservation value, but these highly modified areas are often far more common features of the urban landscape than remnant bushland patches. It is therefore important that we understand the value of these areas to bat communities, to inform future urban park design and contribute to better management outcomes for these species.

Bats' high energy requirements and insectivorous diet also mean that weather factors such as ambient temperature, rainfall, relative humidity and wind speed can influence their activity levels (e.g. Richards 1989; Scanlon and Petit 2008). For example, during colder months in southern Australia, bats enter torpor as ambient temperature and prey availability become low (Turbill 2008). Therefore, studies investigating activity patterns need to consider the potential influence of weather variables.

This study aims to investigate patterns of bat activity in open urban green spaces in greater Melbourne to determine the importance and suitability of these areas as habitat for bats. We specifically examine landscape factors that may influence activity patterns and species richness. The influence of prevailing weather conditions is also modelled to account for its possible confounding influence, with an expectation that the bat activity will be lower in colder, wetter and/or windier nights in general.

## Materials and methods

### Study area

This study was conducted in the greater metropolitan area of Melbourne (37°48′50.4″S, 144°57′47.95″E), Victoria, Australia (Fig. 1). Melbourne is expected to become the most populous city in Australia in the 2030s, with the current estimated population of approximately five million people (Australian Bureau of Statistics (ABS) 2023). The area continues to experience one of the highest population growth rates of all Australian capital cities, at 1.1–2.3 percent per annum (Australian Bureau of Statistics (ABS) 2023). The area has a temperate oceanic climate, with warm to hot summers and mild winters, and a mean annual rainfall of 648.3 mm (Bureau of Meteorology 2020).

### Experimental design

Sites were selected across three local government areas in Melbourne (City of Whitehorse, City of Monash and City of Frankston), with sites situated in either an open area within an urban park, or at an outdoor sporting venue with comparable size of areas with no tree cover (Supplementary Fig. S1). In total, we surveyed for bats at 36 locations within 18 urban parks and sporting venues across the study area, with the mean distance between sites of 221 m (range: 100–14,000 m). Sites were carefully selected so that there was no permanent light source nearby, and during our survey period, there was no temporary lighting used at the sporting venues.

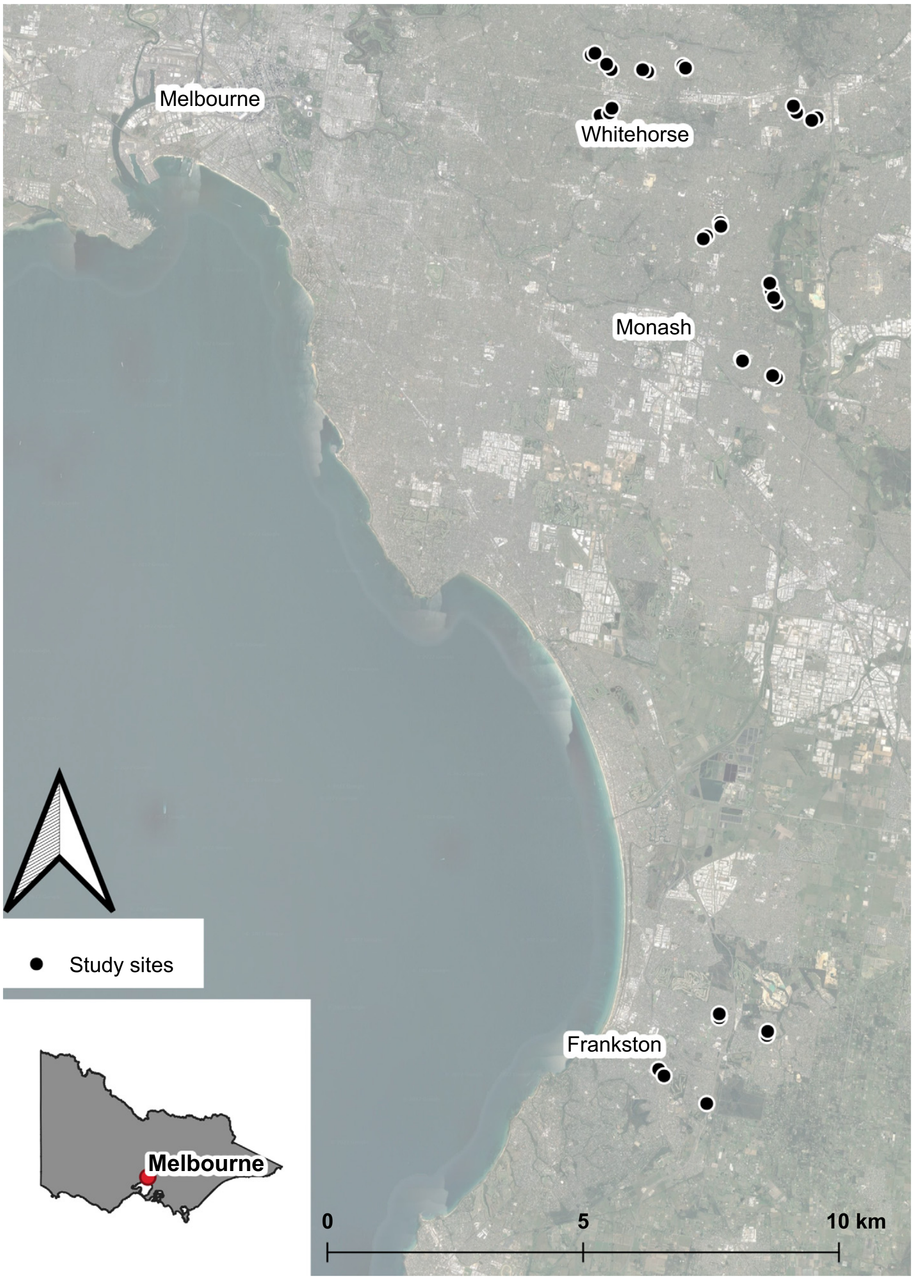

**Fig. 1.** Locations of the 36 survey points acoustically monitored for bats within urban Melbourne, Australia, within the local council areas of Whitehorse, Monash and Frankston (Google Earth v.7.3.1 2019).

## Bat surveys

At each site we deployed an ultrasonic bat detector to record bat echolocation calls at night. Acoustic bat surveys were conducted between January and March 2020, with three deployments conducted sequentially. We selected this survey period because it sits in the middle of warmer months in Melbourne when the bats are most active, and their activity level is less likely to be impacted by seasonal behavioural changes within these months, compared with earlier or later parts in the warmer months (e.g. November or April). Each deployment consisted of eight Anabat SD2 detectors (Titley Scientific, Brendale, Australia) and four Anabat Swift detectors (Titley Scientific, Brendale, Australia), for a total of 12 detectors per deployment ($n = 36$). Detectors were secured within a nest-box to protect them from severe weather and possible theft. The microphones were set to point horizontally, with the SD2 detector microphones sheathed in a small plastic pipe for additional protection from the weather. Each nest-box was mounted to a tree at 2–3 m off the ground.

All nest-boxes were placed so that their microphones were directed out into an open area without obstruction from tree branches or foliage. The location of each detector was recorded on a handheld GPS (Garmin Ltd, Kansas, USA).

Before their first deployment, a controlled pilot study was conducted to ensure that the sensitivity and detection range of the Anabat Swift and SD2 models were comparable. First, we used a handheld ultrasonic signal source at different distances to determine the range of each detector and calibrate its sensitivity. Once calibrated, these detectors were deployed together at the same location for 1 week, in a setup identical to the field survey (i.e. including nest boxes and pipes). We then confirmed that the number of bat calls recorded was comparable across detector types, and that the quality was similar and resulted in equivalent identification rates.

After the pilot study, detectors were deployed for 23 days in January and February and 12 days in March, with a mean of 15.9 survey nights per site (range: 9–23 nights). All detectors recorded bat echolocation calls from 1900 to 0700 hours (1 h before sunset to 1 h after sunrise at the time of sampling). The dates of surveys were chosen to avoid the two nights either side of a full moon as previous surveys have shown that the activity of some bat species may be impacted by the increased lunar illumination on these nights (Basham *et al.* 2011; Threlfall *et al.* 2011; Caryl *et al.* 2016; Linley 2017). One detector experienced technical issues and did not record any data; we therefore include data from just 35 survey sites in the analyses.

## Call identification

Bat call data were recorded in Zero Crossing format. The calls were initially viewed using AnalookW software (Titley Scientific, Brendale, Australia) to remove any obvious noise files that were large in size because these can cause the species identification program to crash. Files containing bat echolocation calls were then analysed using AnaScheme (Lumsden and Bennett 2005; Adams *et al.* 2010), via an identification key developed for this region, based on an extensive reference library of calls. Call sequences were identified to species by analysing a range of call parameters such as frequency and slope measures, time between pulses and duration of pulses. Species identification was only attempted for files that contained five or more valid pulses (i.e. those with a minimum of six data points and model quality greater than 0.9), and these were defined as a 'pass'. A pass was included in our activity count for a certain species if more than 50% of its pulses were identified to that species (*sensu* Threlfall *et al.* 2011; Caryl *et al.* 2016; Haddock *et al.* 2019*a*). Automated identifications were manually checked when the software identified a species that was rare or outside of its known distribution within the Melbourne region. A genus complex was used to combine *Nyctophilus* species and *Myotis macropus* because these species could not be confidently distinguished acoustically. Passes that could not be identified to a species or this genus complex were grouped into 'unknown' calls (i.e. ≤50% of pulses within the pass were identified to a single species); these unknown calls were included in the calculation of total bat activity but excluded from analyses of species-specific activity patterns.

Our dataset therefore consisted of the number of passes per night per site for each species and a count of the number of passes per night per site for all species combined, including 'unknown' calls. Because it cannot be determined how many individual bats made the passes, this measure was used as an index of activity, not a measure of abundance. Species richness per site per night was also calculated.

## Landscape and weather variables

We assessed the influence of both landscape and weather variables on species richness and activity levels. Landscape variables included the number of trees (any woody plants above 2 m height) recorded within a 25-m radius of each site (hereafter 'Trees') and variables that were spatially generated using QGIS (QGIS Development Team 2020): mean annual Normalised Difference Vegetation Index (NDVI) for the calendar year preceding surveys (mean value within 500 m of the site); distance to the closest waterbody (m); and the total length of watercourses and roads within a 500-m radius of the site (see Table 1 for full details). We estimated weather variables for each survey night based on hourly data between 1900 and 0700 hours, taken at the Scoresby Research Institute weather station by the Bureau of Meteorology (Table 1).

## Statistical analyses

We used Generalised Linear Mixed Models (GLMMs) with a negative binomial distribution to examine the effects of landscape and weather variables against species richness, total bat activity and activity (i.e. the number of recorded passes) of individual species. Site was included as a random factor to account for repeated sampling at each site and therefore controlled for inherent site-level variability. Individual species modelling was conducted for all species that recorded over 1000 passes during our survey period. Where evidence of non-linear relationships existed, Generalised Additive Mixed Models (GAMMs) with a negative binomial distribution were used instead. The white-striped free-tailed bat, eastern bent-winged bat (*Miniopterus orianae oceanensis*), and the long-eared bats (*Nyctophilus*) and *Myotis* genus complex were all recorded at relatively low numbers; we therefore reduced these data to presence or absence and used a binomial distribution. Landscape models were not constructed for these three species and genus complex because they were present at 90–100% of sites. GLMMs were run in 'lme4' (Bates *et al.* 2015) and GAMMs in 'gamm4' (Wood and Scheipl 2020), using R statistical software (R Core Team 2020). Models were validated by comparing

**Table 1.** Variables used in analysis for this study, data sources and rationale for their inclusion.

| Variable | Unit | Source | Rationale | Observed range |
|---|---|---|---|---|
| Road length | m within 500-m radius of survey point | Vicmap Transport DELWP Spatial Datamart | Used as a measure of urbanisation around each site. Roads may also have direct impacts on bats by causing mortality and creating barriers to movement (McGregor *et al.* 2017; Medinas *et al.* 2019). | 5116–12,005 |
| Watercourse length | m within 500-m radius of survey point | Vicmap Hydro DELWP Spatial Datamart | Watercourses provide corridors for movement throughout the landscape and support riparian habitat for roosting and foraging (Threlfall *et al.* 2012; Altringham and Kerth 2016). | 0–1637 |
| Distance to water | m | Vicmap Hydro DELWP Spatial Datamart | Water sources support flying invertebrate populations (Gili *et al.* 2020), on which bats feed. The distance from a site to the nearest water source may influence occupancy and species richness (Straka *et al.* 2016). | 13–1485 |
| NDVI | Mean annual NDVI from all 2019 images within 500-m radius | Sentinel 2A satellite data | Normalised Difference Vegetation Index: used as a measure of greenness around each survey point to investigate the impact of varying vegetation availability and productivity on bat activity (Pettorelli *et al.* 2011). | 0.20–0.31 |
| Total trees | Number within 25 m of survey point | Data collected on site | Trees are important resources for foraging, roosting and shelter for bats (Verboom and Spoelstra 1999; Threlfall *et al.* 2012; Straka *et al.* 2016). This variable was chosen for modelling over the number of trees with DBH of >20 cm because the results were the same for both variables. | 8–61 |
| Rainfall | Total nightly rainfall in mm | Bureau of Meteorology | Nights of heavy rainfall result in lower total bat activity, possibly due to changes in insect activity and the increased energy requirements of flying in rain (Voigt *et al.* 2011). | 0–23.2 |
| Dusk temperature | °C | Bureau of Meteorology | Temperature can impact insect activity and bat activity (O'Donnell 2000). We used dusk temperature as bat activity peaks around dusk (Maier 1992; Rydell *et al.* 1996). | 13–29 |
| Wind speed | Mean of hourly speed at night in km/h | Bureau of Meteorology | High wind speeds may reduce insect activity and impact bat flight ability, reducing their activity (Rydell 1989; Adam *et al.* 1994; Verboom and Spoelstra 1999). | 1.5–13.0 |
| Humidity | Mean of hourly measurements at night in % | Bureau of Meteorology | High humidity positively impacts activity of some species, possibly due to increased insect abundance (Pasek 1988; Haddock *et al.* 2019*b*). | 44.7–97.7 |

residual values with fitted values and comparing residual values with each variable included in the model. Cook's distance was used to identify influential values. Where outliers were identified, models were run with and without the outlier to determine its influence – no outliers influenced our results. All independent variables were scaled and centred prior to modelling, and no variable having a correlation coefficient of >0.4 with any other variable was included in the same model.

We developed global models for landscape and weather variables and used a backward model selection approach. Model selection was performed in the package 'AICcmodavg' (Mazerolle 2020), using Akaike's Information Criterion corrected for small sample sizes (AICc) to determine the most parsimonious model. Models were considered to have support if they had a delta AICc score of <2 (Burnham and Anderson 1998). A null model was generated and included in all model selection. *R*-squared values were calculated using the MuMin package (Barton 2020) to determine the amount of variation explained by each model. For GLMMs, both marginal and conditional $R^2$ values are reported to distinguish between the explanatory power of fixed and random effects. For GAMMs, only adjusted $R^2$ values are reported, because marginal and conditional values cannot be obtained.

This research was approved by Deakin University Animal Ethics Committee (WECW-B) under the project number B33-2019.

## Results

In the three months of survey, we recorded 92,665 bat passes from a total of 557 detector nights across 35 sites (mean detector nights per site = 16, median = 19). These passes were identified to ten species and one genus complex (*Nyctophilus–Myotis* genus complex) (Table 2), with each site recording 6–11 species/genus complex. Sufficient data were available for four species to enable species-level activity modelling: Gould's wattled bat (*Chalinolobus gouldii*); chocolate wattled bat (*Chalinolobus morio*); little forest bat (*Vespadelus vulturnus*); and the southern free-tailed bat (*Ozimops planiceps*). Additionally, when examining weather variables, *A. australis*, *M. o. oceanensis* and the *Nyctophilus–Myotis*

**Table 2.** Total recorded passes of bat species during 557 detector nights across 35 sites in the greater Melbourne region, with the percentage of sites at which each species was present and percentage of nights on which the species was detected.

| Scientific name | Common name | Total recorded passes | % sites present | % detector nights recorded | Functional guild |
|---|---|---|---|---|---|
| *Chalinolobus gouldii*[A] | Gould's wattled bat | 13,550 | 100% | 93.2% | Edge |
| *Vespadelus vulturnus*[A] | Little forest bat | 12,748 | 100% | 79.4% | Edge |
| *Ozimops planiceps*[A] | Southern free-tailed bat | 5117 | 100% | 89.1% | Open |
| *Chalinolobus morio*[A] | Chocolate wattled bat | 4695 | 100% | 64.6% | Edge |
| *Miniopterus orianae oceanensis*[B] | Eastern bent-winged bat | 1964 | 91.4% | 47.8% | Edge |
| *Nyctophilus* and *Myotis* genera[B] | Long-eared bats and mouse-eared bats | 1564 | 91.4% | 51.5% | Clutter |
| *Austronomus australis*[B] | White-striped free-tailed bat | 1534 | 100% | 58.2% | Open |
| *Vespadelus darlingtoni* | Large forest bat | 266 | 42.9% | 14.5% | Edge |
| *Vespadelus regulus* | Southern forest bat | 45 | 45.7% | 5.9% | Edge |
| *Ozimops ridei* | Ride's free-tailed bat | 13 | 11.4% | 0.9% | Edge |
| *Scotorepens orion* | Eastern broad-nosed bat | 2 | 5.7% | 0.4% | Edge |

Functional guilds are classified according to Adams *et al.* (2009) and Threlfall *et al.* (2011). They describe the typical foraging environment of the species, based on proximity to vegetation clutter.

[A] Signifies species that were modelled using activity data.

[B] Signifies species that were modelled using presence/absence data.

genus complex were modelled using a binomial presence–absence model due to their smaller sample size. The remaining species were excluded from individual modelling due to insufficient data; however, their data were included in the total bat activity and species richness models.

## Landscape models

Road length, used as a measure of urbanisation, was in the best supported model for species richness, total activity and the activity of all modelled species (Table 3). Greater road lengths resulted in lower species richness and activity for all species, with confidence intervals overlapping zero for *V. vulturnus* (Fig. 2).

The number of trees within a 25-m radius was present in the best models for species richness, total activity and activity levels of *C. morio*, *V. vulturnus* and *O. planiceps* (Table 3). Support also existed for *C. gouldii* (ΔAIC = 0.58, AICωi = 0.24). More trees were associated with higher species richness, overall bat activity and activity of *C. morio* and *O. planiceps*, and trended towards increased activity levels for *C. gouldii* and *V. vulturnus* (Fig. 2).

Distance to the nearest water source was in the best supported model for *C. gouldii* and *C. morio* (Table 3). There was also support in models for total activity (ΔAIC = 0.71) and *O. planiceps* (ΔAIC = 1.35; Table 3). Higher activity levels were associated with greater distances from water sources for all modelled species, although the confidence intervals overlapped zero for total activity, *C. gouldii, V. vulturnus* and *O. planiceps*, indicating uncertainty (Fig. 2). There was no support for an influence of distance to the nearest water source on species richness.

NDVI was in the best supported model for *C. morio*, with support also given for its influence on total activity (ΔAIC = 0.71; Table 3). More green areas in the landscape were associated with higher activity levels of *C. morio*, with a similar trend observed for total activity (Fig. 2). There was no support for an influence of NDVI on species richness or the activity of *C. gouldii*, *V. vulturnus* and *O. planiceps*.

The length of watercourse within a 500-m radius of a site was not a variable in the best model for any species or group; however, support existed for species richness (ΔAIC = 1.16), *C. morio* (ΔAIC = 1.62) and *O. planiceps* (ΔAIC = 1.35). In each case, areas with higher water course length trended towards having higher activity and richness levels; however, confidence intervals strongly overlapped zero, suggesting considerable uncertainty (Fig. 2). There was no support for total activity or the activity of *C. gouldii* and *V. vulturnus*.

## Weather models

Dusk temperature was included in the best model for all species and groups modelled (Table 4). Higher dusk temperatures were associated with increased species richness and activity of *A. australis*, *O. planiceps* and the *Nyctophilus–Myotis* genus complex (Fig. 3). There was a non-linear relationship between dusk temperature and total activity: activity levels of *C. gouldii*, *C. morio*, *V. vulturnus*, *O. planiceps* and *M. o. oceanensis* increased with dusk temperature up to approximately 20–25°C, at which point activity levels appear to plateau (Fig. 4). However, large variations in activity levels of *C. morio* and *V. vulturnus* were recorded across survey nights, especially in higher temperatures, reducing these models' explanatory power.

**Table 3.** Top-ranking models for total bat activity, species richness and activity of individual bat species, based on model selection for landscape variables.

| Response variable/species | Model | $K$ | LL | AICc | ΔAICc | AICcωi | $R^2$m | $R^2$c |
|---|---|---|---|---|---|---|---|---|
| Total activity | RD + Tr | 5 | −3261.36 | 6532.80 | 0.00 | 0.36 | 0.134 | 0.500 |
| | Dwater + NDVI + RD + Tr | 7 | −3259.67 | 6533.50 | 0.71 | 0.25 | 0.171 | 0.500 |
| | Dwater + RD + Tr | 6 | −3260.78 | 6533.70 | 0.89 | 0.23 | 0.152 | 0.503 |
| | Null | 8 | −3266.73 | 6539.50 | 6.68 | 0.01 | 0.000 | 0.504 |
| Species richness | RD + Tr | 5 | −1154.31 | 2318.70 | 0.00 | 0.48 | 0.156 | 0.482 |
| | RD + WL + Tr | 6 | −1153.87 | 2319.90 | 1.16 | 0.27 | 0.164 | 0.481 |
| | Null | 3 | −1160.99 | 2328.00 | 9.30 | 0.00 | 0.000 | 0.488 |
| *Chalinolobus gouldii* | Dwater + RD | 5 | −2232.12 | 4474.36 | 0.00 | 0.32 | 0.069 | 0.360 |
| | Dwater + RD + Tr | 6 | −2231.39 | 4474.94 | 0.58 | 0.24 | 0.085 | 0.361 |
| | RD | 4 | −2233.53 | 4475.12 | 0.77 | 0.22 | 0.039 | 0.357 |
| | Null | 3 | −2231.18 | 4478.62 | 4.27 | 0.04 | 0.000 | 0.358 |
| *Chalinolobus morio* | Dwater + NDVI + RD + Tr | 7 | −1332.19 | 2678.59 | 0.00 | 0.54 | 0.283 | 0.693 |
| | Dwater + NDVI + WL + RD + Tr | 8 | −1331.97 | 2680.21 | 1.62 | 0.24 | 0.290 | 0.693 |
| | Dwater + RD + Tr | 6 | −1334.13 | 2680.41 | 1.82 | 0.22 | 0.247 | 0.702 |
| | Null | 3 | −1351.33 | 2708.71 | 30.12 | 0.00 | 0.000 | 0.697 |
| *Vespadelus vulturnus* | RD + Tr | 5 | −1930.27 | 3870.64 | 0.00 | 0.24 | 0.084 | 0.703 |
| | RD | 4 | −1931.43 | 3870.94 | 0.30 | 0.21 | 0.043 | 0.703 |
| | Null | 3 | −1932.55 | 3871.14 | 0.50 | 0.19 | 0.000 | 0.703 |
| | Dwater + RD + Tr | 6 | −1929.53 | 3871.21 | 0.57 | 0.18 | 0.118 | 0.706 |
| *Ozimops planiceps* | RD + Tr | 5 | −1700.36 | 3410.84 | 0.00 | 0.36 | 0.087 | 0.405 |
| | WL + RD + Tr | 6 | −1699.74 | 3411.64 | 0.80 | 0.24 | 0.098 | 0.403 |
| | Dwater + WL + RD + Tr | 7 | −1698.99 | 3412.18 | 1.35 | 0.18 | 0.117 | 0.406 |
| | Null | 3 | −1704.36 | 3414.76 | 3.92 | 0.05 | 0.000 | 0.408 |

Models are ranked using Akaike's Information Criterion corrected (AICc). Included are the number of parameters within each model (K): log-likelihood of each model (LL); AICc scores of each model (AICc); differences between ranked models (ΔAICc); AICc weights (AICcωi); and *R*-squared values for each model (adjusted = Adj. $R^2$; marginal = $R^2$m; conditional = $R^2$c). Model parameters include distance to water (Dwater), Normalised Difference Vegetation Index (NDVI), road density (RD), watercourse length (WL) and surrounding trees (Tr). Only models with ΔAICc <2 were considered supported and thus included in this table; null models are reported for comparison.

Rainfall was included in the best supported model for species richness, total activity and all species modelled (Table 4). Nights with more rainfall were associated with lower species richness and activity levels in all cases (Fig. 3).

Wind speed was included in the best supported models for species richness, total activity and activity levels of *C. gouldii*, *O. planiceps*, *A. australis* and *M. o. oceanensis* (Table 4). Support also existed in the *Nyctophilus–Myotis* genus complex (ΔAIC = 1.28, AICωi = 0.29; Table 4). Greater wind speeds were associated with higher total activity and activity levels of *C. gouldii* and *A. australis*. Conversely, greater wind speeds were associated with lower activity levels of *M. o. oceanensis*, and a similar trend was observed for the *Nyctophilus–Myotis* genus complex (Fig. 3). A non-linear relationship existed between wind speed and *O. planiceps*, with activity levels remaining constant at low wind speeds before increasing when wind speeds were >10 km/h (Fig. 5). The effect on species richness was weak ($\beta$ = 0.022), and confidence intervals overlapped zero (Fig. 3).

Humidity was in the best supported model for species richness and activity levels of *C. gouldii*, *C. morio*, *V. vulturnus*, *O. planiceps*, *A. australis* and *M. o. oceanensis* (Table 4). Support also existed for total activity (ΔAIC = 1.70, AICωi = 0.30). Higher humidity was associated with greater activity of *C. gouldii*, *O. planiceps* and *A. australis*. As humidity increased, there was a trend for greater species richness ($\beta$ = 0.0029; 95%CI: −0.0066 to 0.0125) but lower activity level for *M. o. oceanensis* (Fig. 3).

## Discussion

Our results highlight the value of Melbourne's open urban green spaces as habitat for insectivorous bats. We detected at least 11 of the 17 species known from Melbourne, a value slightly lower but similar to earlier studies on bats in the greater Melbourne region (Caryl *et al.* 2016; Straka *et al.* 2016), despite these earlier studies sampling areas with

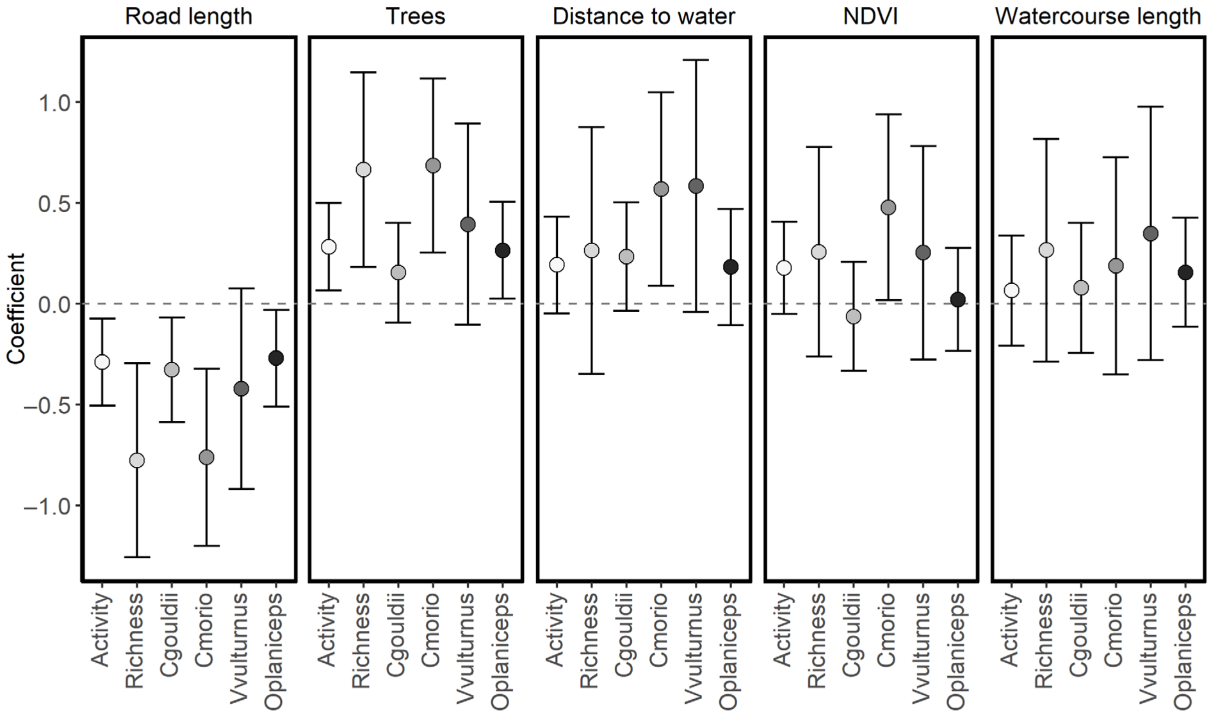

**Fig. 2.** Coefficients of landscape variables ($\beta \pm$ 95%CI) on total bat activity (Activity), species richness (Richness) and the activity of individual species: Gould's wattled bat (*Chalinolobus gouldii*) [Cgouldii]; chocolate wattled bat (*Chalinolobus morio*) [Cmorio]; little forest bat (*Vespadelus vulturnus*) [Vvulturnus]; and southern free-tailed bat (*Ozimops planiceps*) [Oplaniceps].

higher densities of trees than our study. Average activity levels were also comparable between studies for most species, except for the species that typically forage in cluttered environments (e.g. *Nyctophilus*–*Myotis* genus complex) showing slightly lower activity levels in our study (Caryl *et al.* 2016). These slight differences confirm our current understanding that reserves with patches of remnant vegetation can support a wider range of bat species compared with open green spaces; however, it also highlights that open green spaces still hold habitat value for multiple bat species.

Species richness and activity levels in our study were influenced by landscape features such as the presence of nearby trees, road density and water courses in the surrounding area. We found that greater levels of urbanisation (based on road length) were associated with lower bat species richness and activity levels, and greater number of trees was associated with higher species richness and activity levels. Limited trends were observed with NDVI, a result likely attributed to the influence of open green spaces (i.e. grass) contributing to overall 'greenness' at sites – supporting the relatively narrow variability in sites observed. As such, this metric likely reflects habitat and non-habitat for microbats. Such findings suggest that even small-scale tree planting efforts in urban green spaces could benefit bats within the urban matrix and potentially mitigate some impacts of urbanisation. Our results also add support for the importance of urban landscape as habitat for wildlife (Fernandez-Juricic and Jokimaki 1998; Angold *et al.* 2006; Carbó-Ramírez and Zuria 2011; Koh and Sodhi 2017; Van Helden *et al.* 2020).

We found that road density was negatively associated with species richness and activity levels in open urban parks. This is consistent with previous findings, which have similarly recorded lower bat activity with increasing urbanisation (Threlfall *et al.* 2012; Luck *et al.* 2013; Caryl *et al.* 2016). Highly urbanised areas may have smaller property sizes with less yard space, higher building density and fewer trees available for roosting and foraging. In addition to being a surrogate for urbanisation, roads may directly impact bat activity by fragmenting areas of potential habitat, creating a barrier to movement or causing mortality through vehicle collisions (Altringham and Kerth 2016; Fensome and Mathews 2016). Bats could also be indirectly impacted by roads, with these environments experiencing higher levels of anthropogenic noise and artificial light – factors that have been identified to impact activity levels (Bennett and Zurcher 2013; Song *et al.* 2020). These combined impacts of roads have previously been thought to be species-specific, with low-and slow-flying species considered to be most at risk (Stone *et al.* 2015; Fensome and Mathews 2016). We could not directly examine the impacts of road density on clutter-adapted species (e.g. *Nyctophilus*–*Myotis* genus complex) due to their lower activity levels in our open study areas in general; however, the lower species richness and consistent negative relationship between activity levels and road density among modelled

**Table 4.** Top-ranking models for total bat activity, species richness and activity or presence of individual species, based on model selection for weather variables.

| Response variable/species | Model | *K* | LL | AICc | ΔAICc | AICcωi | Adj. $R^2$ | $R^2$m | $R^2$c |
|---|---|---|---|---|---|---|---|---|---|
| Total activity | Rain + s(Temp) + Wind | 7 | −3185.84 | 6385.89 | 0.00 | 0.70 | 0.108 | | |
| | Rain + s(Temp) + Wind + Humidity | 8 | −3185.66 | 6387.59 | 1.70 | 0.30 | 0.113 | | |
| | Null | 3 | −3268.25 | 6542.54 | 156.65 | 0.00 | 0.000 | | |
| Species richness | Rain + Temp + Humidity | 6 | −1085.67 | 2183.49 | 0.00 | 0.48 | | 0.126 | 0.602 |
| | Rain + Temp | 5 | −1087.01 | 2184.13 | 0.64 | 0.35 | | 0.122 | 0.605 |
| | Rain + Temp + Wind + Humidity | 7 | −1085.63 | 2185.47 | 1.98 | 0.18 | | 0.127 | 0.602 |
| | Null | 3 | −1160.99 | 2328.02 | 144.53 | 0.00 | | 0.000 | 0.488 |
| *Chalinolobus gouldii* | Rain + s(Temp) + Wind + Humidity | 8 | −2134.88 | 4286.03 | 0.00 | 1.00 | 0.141 | | |
| | Null | 3 | −2251.66 | 4509.36 | 223.33 | 0.00 | 0.000 | | |
| *Chalinolobus morio* | Rain + s(Temp) + Humidity | 7 | −1320.47 | 2655.15 | 0.00 | 0.73 | −0.006 | | |
| | Null | 3 | −1356.27 | 2718.58 | 61.39 | 0.00 | 0.000 | | |
| *Vespadelus vulturnus* | Rain + s(Temp) + Humidity | 7 | −1890.38 | 3794.97 | 0.00 | 0.53 | −0.002 | | |
| | Rain + s(Temp) | 6 | −1892.05 | 3796.26 | 1.29 | 0.28 | 0.004 | | |
| | Null | 3 | −1942.23 | 3890.50 | 95.53 | 0.00 | 0.000 | | |
| *Ozimops planiceps* | Rain + Temp + s(Wind) + Humidity | 8 | −1627.02 | 3270.30 | 0.00 | 0.90 | 0.102 | | |
| | Null | 3 | −1709.20 | 3424.45 | 154.15 | 0.00 | 0.000 | | |
| **Austronomus australis* | Rain + Temp + Wind + Humidity | 6 | −354.77 | 721.70 | 0.00 | 0.70 | | 0.069 | 0.141 |
| | Temp + Wind + Humidity | 5 | −356.66 | 723.43 | 1.74 | 0.30 | | 0.059 | 0.132 |
| | Null | 2 | −371.94 | 747.91 | 26.21 | 0.00 | | 0.000 | 0.090 |
| * *Nyctophilus–Myotis* genera | Rain + Temp | 4 | −295.99 | 600.04 | 0.00 | 0.56 | | 0.054 | 0.480 |
| | Rain + Temp + Wind | 5 | −295.60 | 601.32 | 1.28 | 0.29 | | 0.055 | 0.480 |
| | Null | 2 | −312.29 | 628.60 | 28.56 | 0.00 | | 0.000 | 0.472 |
| **Miniopterus orianae oceanensis* | Rain + s(Temp) + Wind + Humidity | 7 | −267.54 | 549.29 | 0.00 | 1.00 | 0.052 | | |
| | Null | 2 | −294.26 | 592.55 | 43.26 | 0.00 | 0.000 | | |

Models are ranked using Akaike's Information Criterion corrected (AICc). Species that were run using a binomial (presence–absence) model are denoted with an asterisk (*). Included are the number of parameters within each model (K): AICc scores of each model (AICc); differences between ranked models (ΔAICc); AICc weights (AICcωi); *R*-squared values for each model (adjusted = Adj. $R^2$; marginal = $R^2$m; conditional = $R^2$c); and log-likelihood of each model (LL). Model parameters include total overnight rainfall (Rain), temperature at dusk (Temp), median overnight wind speed (Wind) and median overnight humidity (Humidity). Non-linear smoothers are denoted by *s*(*x*). Only models with ΔAICc <2 were considered supported and thus included in this table; null models are reported for comparison.

species highlight the negative impacts of roads and urbanisation on the insectivorous bat community in general.

Species richness and activity were greater in open urban green spaces with more trees in the surrounding area. This is consistent with existing knowledge of bat activity; trees offer roosting opportunities, shelter from illumination (and thus predation) and support flying insect populations (Lumsden and Bennett 2005; Basham *et al.* 2011; Threlfall *et al.* 2012; Straka *et al.* 2016; Crisol-Martínez *et al.* 2017; Haddock *et al.* 2019*a*). All modelled species in this study showed positive responses to tree density; however, previous studies have recorded different responses to vegetation structure across functional guilds (Norberg and Rayner 1987; Ober and Hayes 2008; Threlfall *et al.* 2012). There are two possible explanations for this disparity between studies: (1) we only modelled the activity of four species that are all edge- (*C. gouldii*, *C. morio*, and *V. vulturnus*) or open-adapted (*O. planiceps*) species (Threlfall *et al.* 2011); or (2) previous research on bat activity in open areas have focused on rural–agricultural landscapes and open farmland (Lumsden and Bennett 2005; Crisol-Martínez *et al.* 2017) – areas that are typically much larger (and thus may exhibit different species trends) than smaller-scale urban parks and sporting fields. Our results suggest that even in highly modified open urban parks, increasing tree availability is beneficial for bats, leading to greater species richness and activity.

Within our urban environment, proximity to a water source did not appear to be associated with the activity of most species, but unexpectedly was associated with lower activity levels of *C. morio*. Previous research identified watercourses as important flyways and corridors for bats (Law *et al.* 1998); waterways are considered particularly important in highly urbanised areas, where they may be the only available corridors that remain relatively dark (Barré *et al.* 2020) and

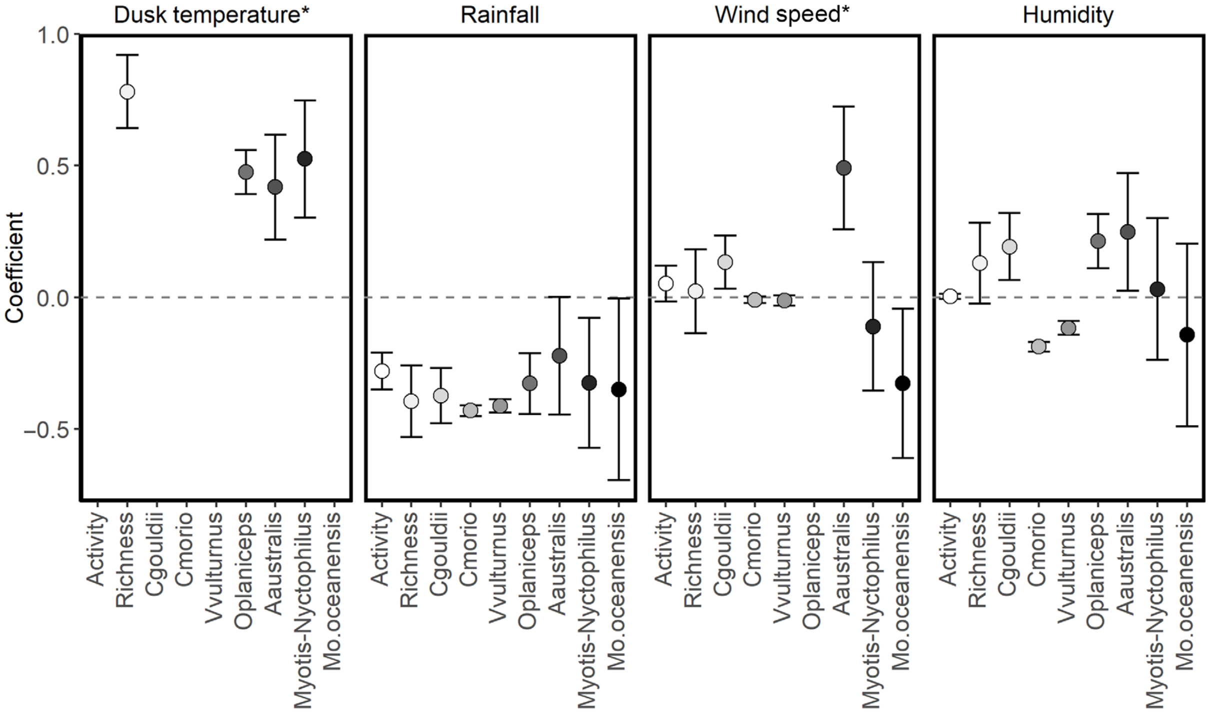

**Fig. 3.** Coefficients of temporal variables ($\beta \pm 95\%$CI) on total bat activity (Activity), species richness (Richness) and the activity of individual species: Gould's wattled bat (*Chalinolobus gouldii*) [Cgouldii]; chocolate wattled bat (*Chalinolobus morio*) [Cmorio]; little forest bat (*Vespadelus vulturnus*) [Vvulturnus]; and southern free-tailed bat (*Ozimops planiceps*) [Oplaniceps]. *only linear effects are reported here, with non-linear relationships shown in Figs 4 and 5.

support increased invertebrate abundances (Ober and Hayes 2008; Threlfall *et al.* 2012). Our results, however, indicated a weak or no relationship with distance to waterbodies, and this is likely linked to the distribution of waterbodies in our study area. The local government areas we surveyed contained multiple water bodies and watercourses, with the maximum distance to a water source from our survey sites being approximately 1.5 km. Given that the species modelled in this study can fly greater distances than this each night (e.g. Lumsden *et al.* 2002), distance to water was likely not a major driver of bats' activity. Therefore, our results here are likely a reflection of the high availability of water in the landscape, rather than *C. morio* showing active avoidance of watercourses.

Weather factors were found to strongly influence bat species richness and activity levels. Higher dusk temperatures were associated with greater species richness and activity levels, whereas higher night-time rainfall figures were associated with lower species richness and activity levels of all species and the genus complex group, which is consistent with previous research (O'Donnell 2000; Straka *et al.* 2016). During each deployment period, sites across multiple landscape contexts were deployed simultaneously; we therefore consider detectability across different landscape types comparable throughout our landscape models. Higher temperatures likely increase invertebrate activity and thus increase foraging opportunities, although this effect seemed to plateau or decline at higher temperatures for some species, which could be attributed to seasonality, prey availability and/or satiation of bats given the higher abundance of insects on warmer nights (Richards 1989; O'Donnell 2000). Greater uncertainty was observed at higher temperatures, especially for *C. morio* and *V. vulturnus*, probably because only 6% of our survey nights experienced dusk temperature of above 25°C. The consistent negative association with rainfall could be linked to a range of factors, including: (1) a reduced detection probability due to ambient rain noise, as has been suggested for some mammals (Whisson *et al.* 2021); (2) an increased energetic cost of flight (Voigt *et al.* 2011); and/or (3) rainfall interfering with echolocation and reducing the ability of bats to forage (Griffin 1971; Voigt *et al.* 2011). These impacts could also have been exacerbated in our study due to the open nature of our survey sites, leading to bats being more exposed to rain during poor weather.

Wind speed and humidity had species-specific associations with bat activity levels, supporting the conflicting results of previous studies (Rydell 1989; Maier 1992; Adam *et al.* 1994; Hecker and Brigham 1999; Verboom and Spoelstra 1999). This diversity of associations could be attributed to interspecies variations in wing morphology and flight patterns. *Chalinolobus gouldii*, *O. planiceps* and *A. australis* all had increased activity levels on nights with higher wind speeds; these species are edge- or open-adapted species, which

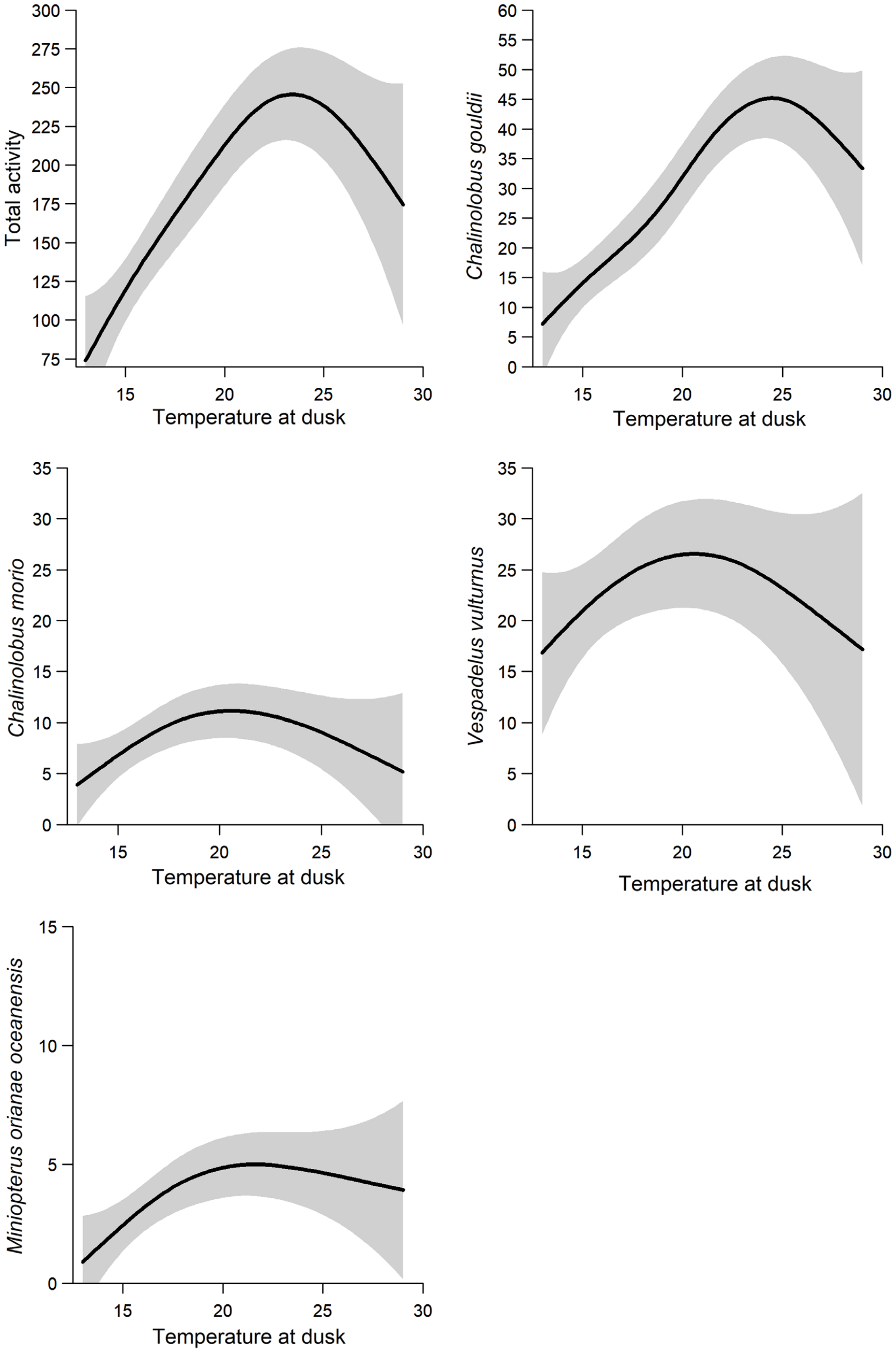

**Fig. 4.** Non-linear relationship between bat activity levels and temperature at dusk (line of best fit ± 95%CI), including for total bat activity (top left), *Chalinolobus gouldii* (top right), *C. morio* (middle left), *Vespadelus vulturnus* (middle right) and *Miniopterus orianae oceanensis* (bottom left).

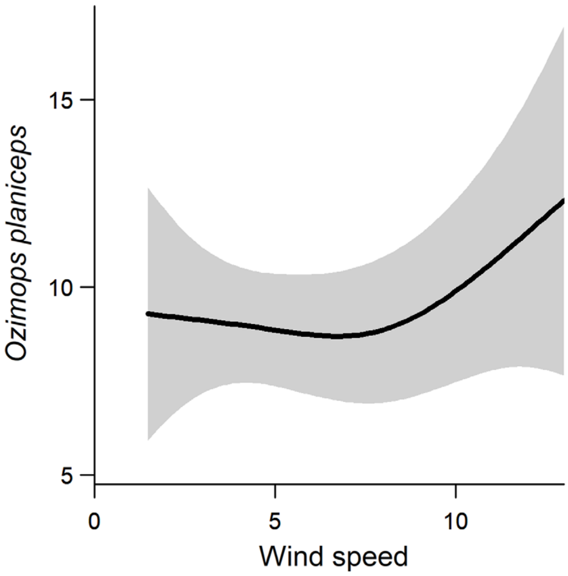

**Fig. 5.** Non-linear relationship between *Ozimops planiceps* and wind speed (line of best fit ± 95% CI).

typically display faster flight and lower manoeuvrability (Threlfall *et al.* 2011). In contrast, the clutter-adapted *Nyctophilus–Myotis* genus complex, which includes the slow-flying *Nyctophilus* species, was recorded less on windy nights. Presence of *M. o. oceanensis*, which is generally considered an edge-adapted species, showed a negative association with wind speed. This species is considered a strong flyer; however, previous research found that they may forage in more sheltered areas in a coastal healthy strip in absence of large trees, and that their activity lowered on nights with strong wind (White 2011). A similar trend to this was also found in the open areas we surveyed. Open-adapted species with a greater speed capability are likely better equipped to continue foraging during strong winds when compared wth clutter-adapted species, leading to species-specific response to wind speed. The effect of humidity may, however, relate more to increased flying invertebrate activity when humidity increases (Pasek 1988). Previous research has suggested increased humidity may reduce the effectiveness of echolocation and thus reduce activity levels (Griffin 1971). Our inferences may be limited, however, by the narrow range of wind speeds (min = 1.5 km/h, max = 13 km/h) and humidity levels (45% to 98% median) recorded during this study.

## Management implications

Our results show that a diverse range of insectivorous bat species are using open green spaces in urban environments. This highlights the value of these spaces as habitat for bats persisting in the urban landscape, which can provide valuable ecosystem services in surrounding areas. Our findings can inform future urban park design and management to make these spaces more hospitable to insectivorous bats, and likely other wildlife. We make two key recommendations to local councils or land managers managing open urban green spaces:

1. *Increase tree availability and connectivity in existing open urban green spaces*. Increasing the number of trees near open areas can increase both the species richness and activity levels of bats. Land managers should aim to protect existing vegetation while also planting more, preferably indigenous, trees around open spaces such as parks, ovals and tennis courts. These management options should be strategic to improve connectivity, particularly linking these areas to remnant vegetation patches such as along waterways and riparian corridors.
2. *Planning of new urban parks and outdoor sporting facilities*. Councils and urban planners should carefully consider the development of new parks and ovals, selecting areas in which remnant trees can be retained and revegetation can provide good connectivity to nearby remnant patches. Construction of a new park should occur in existing cleared patches so that removal of trees is avoided. The new park should, with strategic revegetation, increase connectivity among existing remnant patches in the landscape.

## Supplementary material

Supplementary material is available online.

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**Data availability.** The data that support this research will be shared upon reasonable request to the corresponding author.

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