

## Research

### Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization

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Identifying which ecological and life history traits influence a species' tolerance to urbanization is critical to understanding the trajectory of biodiversity in an increasingly urbanizing world. There is evidence for a wide array of contrasting patterns for single trait associations with urbanization. In a continental-scale analysis, incorporating 477 species and >5 000 000 bird observations, we developed a novel and scalable methodology that evaluated the ecological and life history traits which most influence a species' adaptability to persist in urban environments. Specifically, we assigned species-specific scores based on continuous measures of response to urbanization, using VIIRS night-time light values (i.e. radiance) as a proxy for urbanization. We identified generalized, phylogenetically controlled patterns: bird species which are generalists (i.e. large niche breadth), with large clutch size, and large residual brain size are among the most urban-tolerant bird species. Conversely, specialized feeding strategies (i.e. insectivores and granivores) were negatively associated with urbanization. Enhancement and persistence of avian biodiversity in urban environments probably relies on protecting, maintaining and restoring diverse habitats serving a range of life history strategies.

Keywords: brain size, citizen science, eBird, life history traits, phylogenetics, urban ecology

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#### Introduction

Species' specialization, based on a suite of biological traits, can dictate population-level response to changing environments. Generally, species with limited niche breadth experience higher extinction risk than those with wider niche breadth (McKinney and Lockwood 1999, Davies et al. 2004, Munday 2004, Boulangeat et al. 2012). Further, some organisms have traits that allow for adaptation of their niches with changing environments, leading to potential ecological inheritance (Odling-Smee et al. 2013)

through the environmental filtering of trait distributions (Webb et al. 2010). Urbanization drastically changes natural habitats through destruction, fragmentation and isolation (Marzluff and Ewing 2001, Melles et al. 2003, Loram et al. 2007), often providing ecologically novel landscapes for species, including invasive species, anthropogenic food sources and increased pollution. Some species successfully adapt, colonize and thrive in urban environments (McKinney 2002, Chace and Walsh 2006, Evans et al. 2009, Lowry et al. 2013, McDonnell and Hahs 2015), while others, common in surrounding natural habitats, rarely occur in urban environments (Tratalos et al. 2007, Evans et al. 2011, Gatesire et al. 2014). Urbanization selects for specific sets of species, based on the regional pool (Aronson et al. 2016), globally threatening biodiversity through processes such as biotic (McKinney 2006, 2008), functional (Devictor et al. 2007), and phylogenetic homogenization (Ibáñez-Álamo et al. 2017, Sol et al. 2017), a major concern for conservation (Czech et al. 2000, Dearborn and Kark 2010). It is important to identify which ecological and life history traits most associate with successful or unsuccessful species in urban environments (McClure 1989, Bonier et al. 2007, Møller 2009, McDonnell and Hahs 2015). Identifying these traits can improve understanding of relationships between biodiversity and urbanization, and guide protection of the species most at-risk of extinction, through habitat protection, management and restoration.

Many ecological and life history traits are associated with bird species in urban environments, including degree of sociality (McClure 1989, Coleman and Mellgren 1994, Jokimäki and Suhonen 1998); nesting substrate (Kark et al. 2007, Croci et al. 2008, Conole and Kirkpatrick 2011); diet (Beissinger and Osborne 1982, Fuller et al. 2008, Major and Parsons 2010, Evans et al. 2011); range size (Jokimäki and Huhta 2000, Chace and Walsh 2006, Croci et al. 2008); migratory status (Friesen et al. 1995); niche breadth (Clergeau et al. 2006, Kark et al. 2007, Evans et al. 2011); and fecundity (Croci et al. 2008, Møller 2009, Vaugoyeau et al. 2016) (Supplementary material Appendix 1 Table A1). In Jerusalem, urban bird species were best predicted by diet, degree of sociality, sedentarity and preferred nesting sites (Kark et al. 2007), while, throughout France and Switzerland, urban bird species were positively associated with forested habitats, sedentary, omnivorous, high-elevation nesters and had large range sizes (Croci et al. 2008). Despite the breadth of research which has focused on ecological and life history traits associated with urbanization in birds, the results are severely mixed and frequently contradictory. For example, residual brain size in birds is sometimes positively associated with urbanization (Maklakov et al. 2011, Møller and Erritzøe 2015) and sometimes not (Kark et al. 2007, Evans et al. 2011). Similarly, contrasting results have been reported for annual fecundity (Croci et al. 2008, Møller 2009, Evans et al. 2011) and niche breadth (Kark et al. 2007, Evans et al. 2011). As a consequence, a more comprehensive and generalized understanding of ecological and life history traits associated with urban-tolerant birds is necessary.

A possible explanation of the frequently contrasting results that have previously been reported in this research area are methodological constraints. One example of a methodological constraint is the assignment of species to discrete a priori groups such as urban avoiders, adapters, or exploiters (McKinney 2002, 2006, Kark et al. 2007, McDonnell and Hahs 2015) or strictly presence/absence within urban environments (Bonier et al. 2007, Møller 2009). These approaches severely limit the capacity to generalize, as it assumes grouped species respond equally to urbanization (Lepczyk et al. 2008, Evans et al. 2011). Terminology (i.e. differentiating among avoiders, adapters, or exploiters) also varies among studies (Kark et al. 2007, Croci et al. 2008, Geschke et al. 2018), affecting interpretation (Fischer et al. 2015, McDonnell and Hahs 2015). There is clearly a need for continuous measures of urbanization (Evans et al. 2011), where a species is assessed over its entire distribution in response to urban environments. Further, temporally limited data (Blair 1996, Kark et al. 2007, Croci et al. 2008) can additionally restrict the generalizability of the results. Broad-scale empirical data allow hypotheses to be tested at large spatiotemporal scales. Citizen science can provide such data (reviewed by Devictor et al. 2010, Tulloch et al. 2013, Bonney et al. 2014, Kobori et al. 2016), and can be used to describe patterns of abundance, distribution and functional composition of birds in urban ecosystems (McCaffrey 2005, La Sorte et al. 2014, Morelli et al. 2016, Lepczyk et al. 2017, Callaghan et al. 2017).

We aimed to determine what suite of life history traits predicted avian tolerance to urbanization at a continental scale. Our study represented a large sample size and large spatial scale, with regards to ecological and life history traits and urban-tolerance in birds. We predicted that different traits would positively and negatively associate with urbanization. For generality, our analyses had to 1) be comprehensive in faunal coverage, 2) account for phylogenetic constraints, 3) include a broad-range of traits, and 4) employ a continuous measure of urbanization. We integrated a series of large datasets to establish a novel continuous measure of response to urbanization to test associations with ecological and life history traits influencing species' responses to urbanization. We first investigated whether our urbanization measure was statistically independent in relation to phylogeny (i.e. phylogenetic signal – Revell et al. 2008, Evans et al. 2011), given our comprehensive sample size. We then developed models, including and excluding phylogenetic effects, to test for associations between our urbanization measure and a suite of continuous and categorical predictor variables representing species' traits.

## Methods

### Bird observation data

We collated bird observations throughout mainland Australia from eBird (Sullivan et al. 2009, 2014), a large-scale empirical dataset contributed by citizen scientists. Volunteer

birdwatchers submit lists of species seen or heard at a given location, over a user-determined duration and survey area (Wood et al. 2011), often comparable to trained observers (Callaghan and Gawlik 2015). We downloaded the eBird basic dataset (ver. ebd\_rel Feb-2018; available at: <<https://ebird.org/data/download>>), and used all observations between 1 January 2010 and 28 February 2018. This temporal scale corresponded to the richest period of eBird data, minimizing undue leverage of mismatch between changes in response variables over which bird observations were collected.

We filtered bird observations (La Sorte et al. 2014, Callaghan et al. 2017), only including observations on ‘complete’ checklists – defined as checklists where the observer submitted all birds seen and/or heard – and which were either travelling, random, stationary, area, or followed BirdLife Australia protocols (Barrett et al. 2003) (for more information: <<http://help.ebird.org/customer/portal/articles/1006209-understanding-observation-types>>). We then filtered the checklists to those which travelled <5 km or covered <500 ha, to ensure the highest quality data were used. Any checklists shared among multiple observers were subsampled, including only one checklist to avoid duplication. We were left with 637 482 eligible checklists throughout Australia. Seabirds (e.g. gannets, petrels, shearwaters) were omitted from analyses as we did not expect any correlation with seabirds using urban areas. Further, only species with >100 observations were analyzed. We selected 100 observations as a cut-off based on visual interpretation of the data, and the number of observations relative to other species. Our analysis encapsulated a potential 580 species, most (~80%) of Australia’s bird species, suggesting that 100 observations was a reasonable cut-off for species to include. It is likely that those species with <100 observations are those that are generally uncommon birds in Australia (e.g. night parrot *Pezoporus occidentalis*). We used differing taxonomic authorities (Supplementary material Appendix 1 Table A2).

### A continuous measure of urbanization

A number of measures of urbanization have previously been used (Sanderson et al. 2002, Hahs and McDonnell 2006), but we focused on a continuous measure that is globally applicable (i.e. applicable and easily downloaded for anywhere in the world). As such, we used VIIRS night-time lights (Elvidge et al. 2017) as a continuous measure for urban habitat, measuring the electric lighting associated with human settlement (Supplementary material Appendix 1 Fig. A1). This has filtered out background noise (e.g. fires, degraded data and other light source contamination) to ensure validity of the data and its association with human settlement (Elvidge et al. 2017). There is a strong positive relationship between VIIRS night-time lights and human population density (Supplementary material Appendix 1 Fig. A2), another commonly used proxy for level of urbanization. For our checklists and their associated species, we used the spatial coordinates and Google Earth Engine (Gorelick et al. 2017), to assign the average radiance value, calculated from

the VIIRS layer. For each checklist, the average radiance was calculated within a 5 km buffer, to match the spatial scale of the checklists included and to minimize any potential bias in eBird sampling protocols. Any negative radiance values were forced to 0.00001 (sensu Ou et al. 2015). Every bird species subsequently had a distribution of average radiance values (Fig. 1), with the median of each species’ distribution becoming the response variable. There was no definitive range for the response variable, dependent on a species’ distribution of observations.

### Ecological and life history traits

Ecological and life history traits were chosen on the basis of existing support (McClure 1989, Kark et al. 2007, Evans et al. 2011) (Table 1, Supplementary material Appendix 1 Table A1, Derivation A1), including a wide array of potential traits for all of Australia’s birds (Garnett et al. 2015). A total of 22 traits, grouped into seven categories, were included (Table 1): life history traits (n=3), measures of niche breadth (n=4), specific habitat preferences (n=3), specific nesting preferences (n=2), specific diet preferences (n=4), movement and range size (n=3), and degree of sociality (n=3). For any missing trait in the dataset (Garnett et al. 2015) for a species, we assumed it did not exist. For example, if a species had no data for a specific habitat, it was deemed not to occur in that habitat. Our preliminary analyses, which included IUCN status, showed that exotic birds strongly associated with urbanization; these were omitted from the final analyses to avoid bias, given the preferential selection by acclimatization societies for their proven synanthropy (Blackburn et al. 2009). We also excluded IUCN status because most (96%) of our candidate species were of Least Concern. In total, 477 species

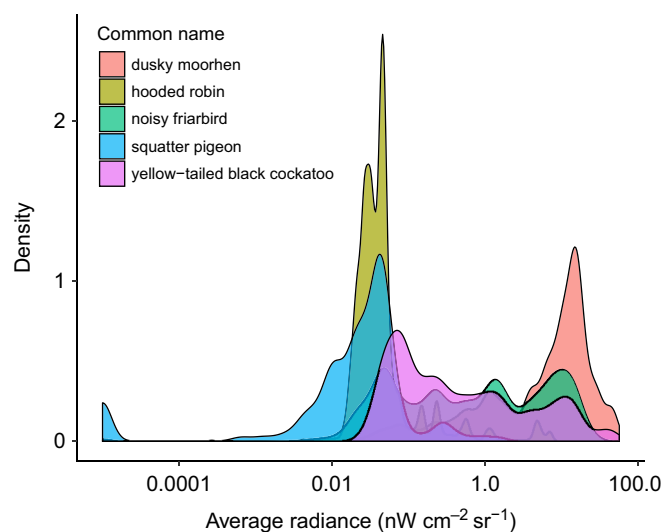


Figure 1. Average radiance density distributions, on a logarithmic scale, across the range of five species with different distributional responses. The measure of response to urbanization, used as the response variable in our analyses, was taken as the median for a given species’ distribution.

Table 1. Description of the 22 ecological and life history traits used in our analysis, grouped by broad categories. Traits were extracted from Garnett et al. (2015), except range size. Supplementary material Appendix 1 Table A1, Derivation A1 for a full description of each trait, how each trait was calculated, and relevant references.

Category	Trait	Description
Life history traits	clutch size	average clutch size
	body size	mass (kg)
Niche breadth	brain residual	brain size adjusted for body size – a general measure of behavioural flexibility
	nest generalism	number of nesting types
	feeding habitat generalism	number of feeding habitats
	breeding habitat generalism	number of breeding habitats
Habitat preferences	diet generalism	number of major diet types
	habitat – agricultural	feeding and/or breeding association with agricultural habitats
	habitat – tree/forest	feeding and/or breeding association with forested habitats
Nesting preferences	habitat – grass/shrubland	feeding and/or breeding association with grassland/shrubland habitats
	hollow-nesting	nests in hollows
Diet preferences	ground-nesting	nests on the ground
	plant eater	eats plants
Movement and range size	granivore	granivorous
	insectivore	insectivorous
	carrion eater	eats carrion
	movement – nomadic/irruptive	nomadic and/or irruptive
Degree of sociality	movement – migratory	a partial or full migratory species
	range size (1000s km <sup>2</sup> )	measured as modelled climate space (Supplementary material Appendix 1 Table A1, Derivation A1)
Degree of sociality	nest aggregation	nests solitary or colonial
	feeding aggregation	feeds in flocks, solitary, or pairs
	cooperative breeding	cooperatively breeding species

had complete data for all candidate traits and were included in analyses. Importantly, given the mixed results of previous research assessing this question and thus competing a priori hypotheses, we found it important to include a broad range of predictor variables in the models.

### Statistical analysis

Before modelling of predictor variables (Table 1), we investigated multi-collinearity among continuous variables (Supplementary material Appendix 1 Fig. A3), using the ‘corrplot’ package (Wei and Simko 2017). We used generalized variance inflation factors (Fox and Monette 1992), from the ‘car’ package (Fox and Weisberg 2011), which accounts for the degrees of freedom for a particular term, providing the minimal correlation compared with other traits; all traits <2 suggested negligible correlation (Supplementary material Appendix 1 Table A3). We used two independent linear modelling approaches: one without and one with phylogenetic effects. Phylogenetic effects are defined as the tendency of closely related organisms to have similar life history components due to their shared evolutionary history (Derrickson and Ricklefs 1988, McKittrick 1993). Both approaches were used because of shortcomings (Cadotte et al. 2017) and importance (Losos 2008, Graham et al. 2018) of incorporating evolutionary distinctness in ecological research.

We performed linear regression models with the response variable being the species-specific measure of response to urbanization, log-transformed to meet model assumptions, and the predictor variables the 22 ecological and life history

traits. This was done without and with controlling for phylogenetic effects. All linear regression models were weighted (Solon et al. 2015), using a source of error associated with the species’ responses to urbanization. This error was the proportion of the number of total observations for a species, divided by the number of its unique localities (Supplementary material Appendix 1 Fig. A3 shows the correlation between the two). This weighted the model-fitting to those species with more observations in more unique locations, likely to be the most reliable species’ responses. All models and analyses were conducted in R ver. 3.5 (<www.r-project.org>), relying on the tidyverse workflow (Wickham 2017). Statistical significance was concluded at  $\alpha < 0.05$ . Variability of means is reported as SD.

We first ran a global model, including all 22 predictor traits, standardizing model estimates to represent relative effect sizes, using the standardize function from the ‘arm’ package (Gelman 2008, Gelman and Su 2016). To corroborate our global model results, we employed a model-averaging approach (Grueber et al. 2011), ‘dredging’ all possible subsets of the global model with the dredge function in the ‘MuMIn’ package (Barton 2016). Because of the contradictory results reported across the various studies which assess the relationship between species’ traits and urbanization, we chose a model-averaging approach to allow any possible combination of traits to be the dominant predictor variable, and then only model-averaged across the top model set. We fitted 11 candidate traits at any one time to avoid over-fitting, assessing 784 626 models. Model-averaged parameter estimates were calculated from the subsequent top

models, with  $\Delta\text{AIC} < 4$ , where standardized estimates represented relative effect sizes of respective traits.

As associations between traits and urbanization may be influenced by shared evolutionary history of a species (Felsenstein 1985), we also modelled these relationships phylogenetically. We tested for a phylogenetic signal (Revell et al. 2008, Münkemüller et al. 2012) associated with our urbanization measure and for each of the continuous predictor traits (Table 1), using published phylogenetic trees (Jetz et al. 2012). This was defined as the statistical nonindependence among species' traits, due to their phylogenetic relatedness (Revell et al. 2008), assessing relative contribution of phylogeny on a given trait. There are different indices used to assess phylogenetic signal, each with strengths and weaknesses (Keck et al. 2016); we assessed all available indices (Blomberg's  $K$  and  $K^*$ , Abouheif's  $C_{\text{mean}}$ , Moran's  $I$  and Pagel's  $\Lambda$ ), using the *phylo*signal package (Keck et al. 2016) in R.

We then used phylogenetically informed models to test for repeated evolutionary associations between traits of interest (Felsenstein 1985). Phylogenetic models were fitted based on the same global model as the non-phylogenetic models, but using the 'phylolm' function (Ho and Ane 2014), which fits a linear regression model where the likelihood is linear in the number of tips in the tree. We similarly model-averaged the global phylogenetic model. To account for phylogenetic uncertainty, we fitted the same model to 1000 highly probable trees from Jetz et al. (2012), examining the distribution of putatively important traits across the distribution of trees.

## Data deposition

This work relied heavily on open-source, fully accessible datasets. The necessary portions of those datasets, along with code to reproduce the analyses are available at zenodo repository <<https://zenodo.org/record/2542948>>. The supporting data used for modelling has been included in the article's supplementary material (Supplementary material Dataset 1).

## Results

We analyzed 316 306 checklists (subsampled from the candidate set after filtering for the best possible checklists), including 5 944 819 observations of our 477 different species (subsampled from the candidate set, restricted by incorporation of the ecological and life history information). The least recorded species was *Turnix melanogaster* (black-breasted buttonquail;  $n = 104$ ), while the most recorded species was *Cracticus tibicen* (Australian magpie;  $n = 158\ 615$ ). The mean number of observations for a species was  $10\ 930 \pm 19\ 498$ . Distributions of measured VIIRS average radiance values (shown for each species in Supplementary material Appendix 1 Fig. A4), traits, number

of observations and urbanization indices for the 477 species varied considerably (Supplementary material Dataset 1). The mean urbanization measure was  $0.91 \pm 1.76$ , ranging from 0.008 (*Cracticus mentalis* black-backed butcherbird) to 11.85 (*Ninox strenua* powerful owl; Fig. 2).

## Non-phylogenetic models

The most important predictors of urbanization (i.e. the largest model-derived, standardized parameter estimates – shown in parentheses with 95% confidence intervals) in the non-phylogenetic global model (Fig. 4, Supplementary material Appendix 1 Table A4) were feeding habitat generalism (0.79: 0.33, 1.25), breeding habitat generalism (0.76: 0.30, 1.21), and clutch size (0.73: 0.41, 1.04). Further, feeding habitat generalism ( $t = 3.40$ ,  $p = 0.001$ ), breeding habitat generalism ( $t = 3.27$ ,  $p = 0.001$ ), clutch size ( $t = 4.52$ ,  $p < 0.001$ ), and diet generalism ( $t = 2.74$ ,  $p = 0.006$ ) were significant. Urban-tolerant birds were also significantly positively associated with agricultural habitats ( $t = 2.88$ ,  $p = 0.004$ ) and more likely to be migratory ( $t = 2.15$ ,  $p = 0.032$ ), but had smaller effect sizes than previous traits. Conversely, urban-tolerant birds were significantly negatively associated with solitary nesting ( $t = -2.06$ ,  $p = 0.040$ ), group foraging ( $t = -2.24$ ,  $p = 0.025$ ), granivorous diet ( $t = -3.40$ ,  $p = 0.001$ ), using forested habitats ( $t = -2.94$ ,  $p = 0.003$ ), and grass/shrubland habitats ( $t = -4.26$ ,  $p < 0.001$ ), with insectivorous diet ( $t = -3.96$ ,  $p < 0.001$ ) and solitary feeding ( $t = -2.90$ ,  $p = 0.004$ ). The strongest negative associations with the urbanization measure were solitary feeding ( $-0.92$ ,  $-1.56$ ,  $-0.30$ ), insectivorous diet ( $-0.85$ :  $-1.28$ ,  $-0.43$ ), grass/shrubland habitat association ( $-0.73$ :  $-1.07$ ,  $-0.40$ ), and tree/forest habitat association ( $-0.63$ :  $-1.04$ ,  $-0.21$ ).

With model-averaging, patterns remained similar (Fig. 4, Supplementary material Appendix 1 Table A4). However, the most strongly associated trait was clutch size (0.75, 0.44–1.05), followed by birds associated with agricultural habitats (0.58: 0.25, 0.92), and then diet generalism (0.28: 0.14, 0.43). Breeding habitat (0.15: 0.05, 0.24) and feeding habitat (0.12: 0.05, 0.19) generalism parameter estimates were substantially smaller than in the non model-averaged approach. Clutch size ( $z = 4.83$ ,  $p < 0.001$ ), diet generalism ( $z = 3.84$ ,  $p < 0.001$ ), breeding habitat generalism ( $z = 3.09$ ,  $p = 0.002$ ), and feeding habitat generalism ( $z = 3.27$ ,  $p = 0.001$ ) were all significantly associated with our urbanization measure. Additionally, species associated with agricultural habitats were significantly associated with urbanization ( $z = 3.40$ ,  $p = 0.001$ ). Urban-tolerant birds remained significantly negatively associated with solitary feeding ( $z = 3.39$ ,  $p = 0.001$ ), insectivorous diet ( $z = 5.42$ ,  $p < 0.001$ ), using grassland/shrubland habitats ( $z = 4.05$ ,  $p < 0.001$ ), group foraging ( $z = 3.16$ ,  $p = 0.002$ ), granivorous diet ( $z = 3.91$ ,  $p < 0.001$ ), and using forested habitats ( $z = 3.30$ ,  $p = 0.001$ ). Solitary feeding ( $-1.00$ :  $-1.58$ ,  $-0.42$ ) was the strongest negatively associated trait with urbanization, followed by insectivorous diet ( $-0.98$ :  $-1.33$ ,  $-0.62$ ).

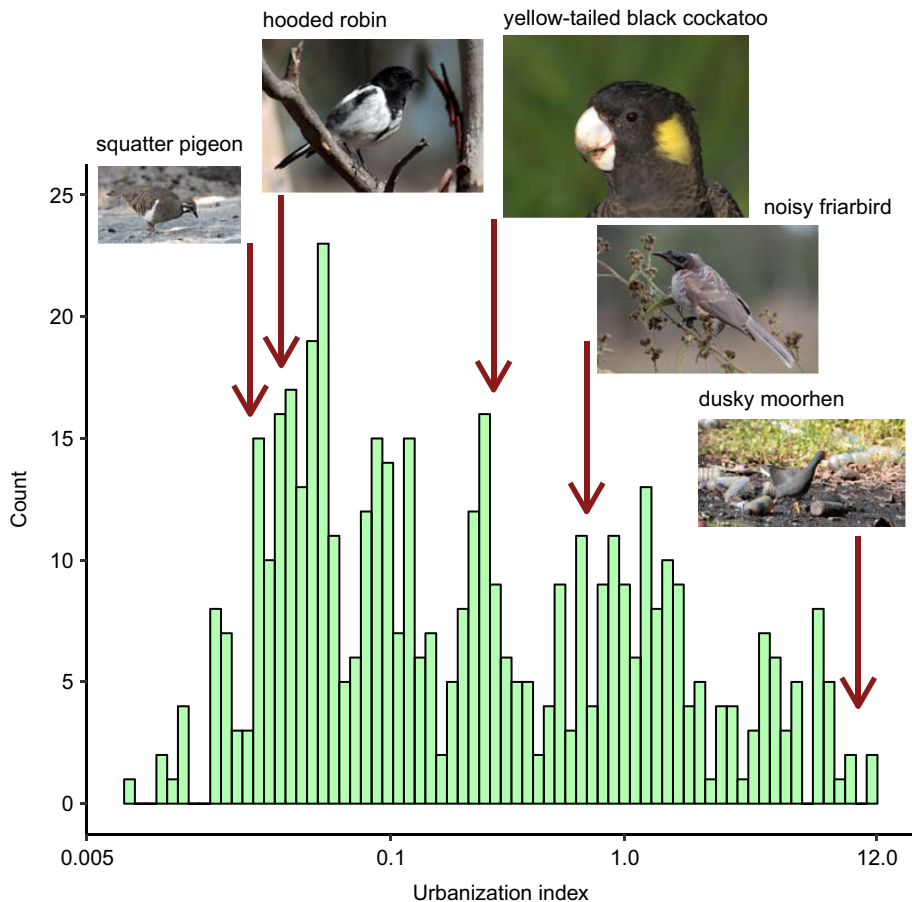


Figure 2. Histogram showing the count of the 477 species, relative to the urbanization measure, on a logarithmic scale, highlighting the five species in Fig. 1. (Supplementary material Appendix 1 Fig. A1 for randomly chosen indices for a given point to help orient the urbanization measure.)

## Phylogenetic analyses

### Phylogenetic signal

There was a distinct relationship between the phylogenetic signal and our measure of urbanization response (Fig. 3, Table 2), significantly different from random for 4 out of 5 indices (Cmean, I, K\* and Lambda). For example, the urbanization measure was disproportionately important with respect to the phylogenetic tree (Fig. 3), evidenced by the highest urbanization indices clustered throughout the water-bird clade. Further, within a specific clade, there were some species with substantially higher urbanization indices (e.g. *Manorina melanocephala*, noisy miner, cf. honeyeaters). We generally found weaker signals for behavioral, compared with morphological traits. For behavioural traits, the estimates of phylogenetic signal were weaker than Brownian motion, but usually significant (Table 2). Additionally, there was a strong phylogenetic signal for body size and brain residual size (Table 2).

### Phylogenetically controlled models

Residual brain size (1.25: 0.57, 1.93) had the largest standardized parameter estimate for the phylogenetically

controlled global model (Fig. 4, Supplementary material Appendix 1 Table A4), followed by feeding habitat generalism (1.18: 0.68, 1.68), clutch size (0.91: 0.32, 1.50), and body size (0.82: -0.11, 1.76). The most significantly positive traits associated with urbanization were brain residual size ( $t = 3.58$ ,  $p < 0.001$ ), feeding habitat generalism ( $t = 4.63$ ,  $p < 0.001$ ), clutch size ( $t = 3.04$ ,  $p = 0.002$ ), diet generalism ( $t = 2.07$ ,  $p = 0.039$ ), and breeding habitat generalism ( $t = 2.80$ ,  $p = 0.005$ ). Conversely, nest generalism ( $t = -2.06$ ,  $p = 0.040$ ), range size, ( $t = -4.38$ ,  $p < 0.001$ ), cooperative breeding ( $t = -3.25$ ,  $p = 0.001$ ), and species without any known nest aggregation ( $t = -3.28$ ,  $p = 0.001$ ) were significantly negatively associated with urbanization.

With model-averaging (Fig. 4, Supplementary material Appendix 1 Table A4), feeding habitat generalism (1.30: 0.96, 1.63), clutch size (1.15: 0.84, 1.45), body size (0.66: 0.33, 0.98), and residual brain size (0.32: 0.02, 0.63) were most strongly associated with our urbanization measure, while species with no known nest aggregation (-1.22: -1.78, -0.65) and species associated with grass/shrubland (-1.16: -1.46, -0.87) showed the strongest negative response. Feeding habitat generalism ( $z = 7.54$ ,  $p < 0.001$ ), clutch size ( $z = 7.31$ ,

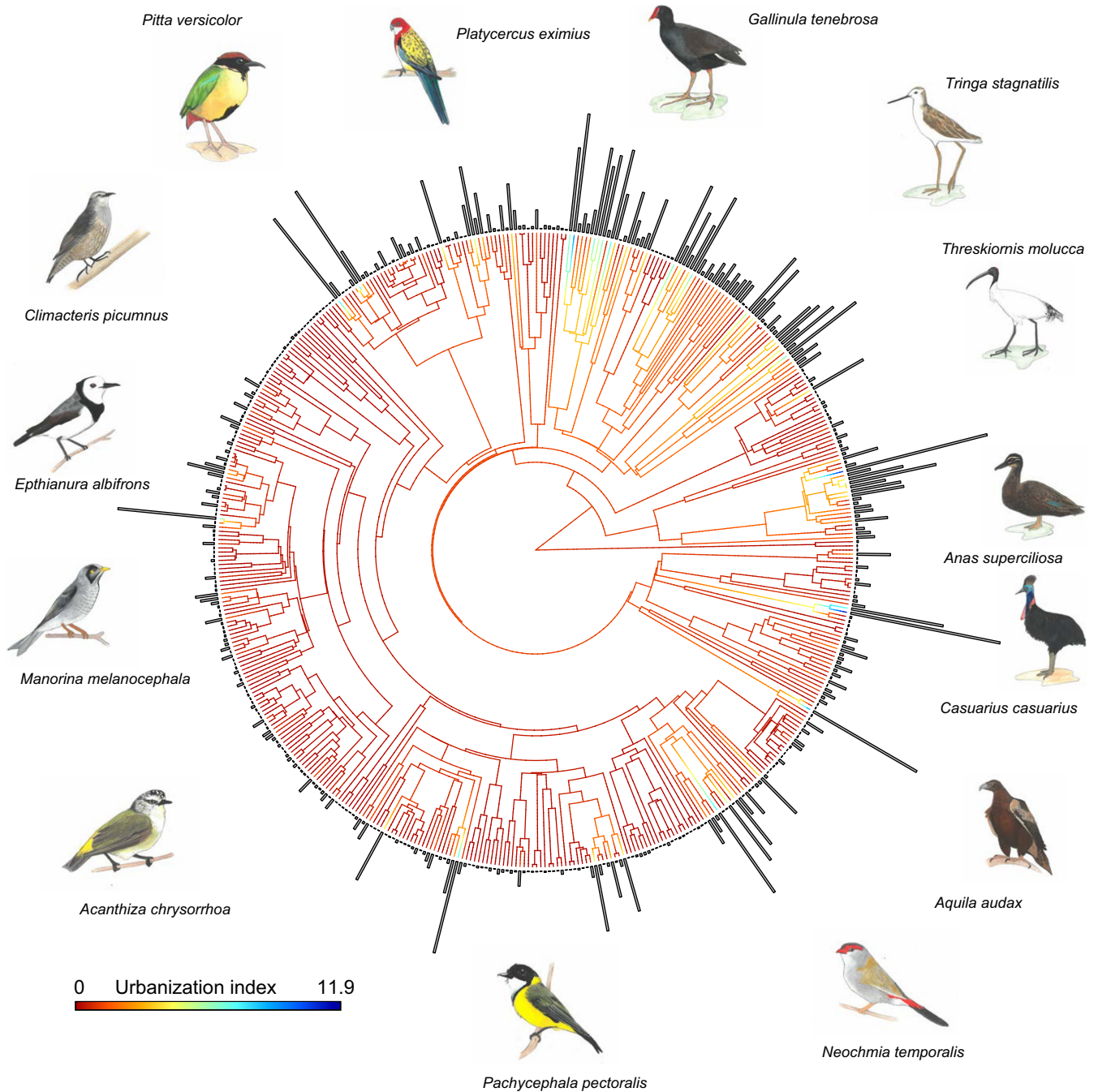


Figure 3. Reproduced phylogenetic tree (Jetz et al. 2012) of our 477 species (Supplementary material Dataset 1 for a full list of species with their urbanization indices), demonstrating clustering of species' associations with the urbanization measure relative to phylogeny. There are two representations of the urbanization measure for each species: 1) coloring ranges from a low urbanization measure (dark red) to a high urbanization measure (dark blue), with 2) magnitude of the urbanization measure (barplot). The urbanization measure was the median of the distribution for a species' average radiance values, as shown in Fig. 1. For reference, Supplementary material Appendix 1 Fig. A3 is a phylogenetic tree with the names of each tip displayed.

$p < 0.001$ ), body size ( $z = 3.93$ ,  $p < 0.001$ ), and brain residual size ( $z = 2.10$ ,  $p = 0.036$ ), were significantly positively associated, while species which were cooperative breeders

( $z = 2.53$ ,  $p = 0.011$ ), used grass/shrubland habitats ( $z = 7.64$ ,  $p < 0.001$ ), and had no known nest aggregation pattern ( $z = 4.20$ ,  $p < 0.001$ ) were statistically negatively associated.

Table 2. Summary of results showing an assessment of a phylogenetic signal for our response variable (urbanization measure) and the continuous predictor traits. We show all available indices (Keck et al. 2016), each of which represents the statistical non-independence of a trait's value due to its phylogenetic relatedness (Revell et al. 2008).

Variable	Value	Abouheif's Cmean	Moran's I	Blomberg's K	K*	Pagel's Lambda
Urbanization index	statistic	0.282	0.038	0.083	0.107	0.381
	p-value	0.000	0.000	0.059	0.043	0.000
log(clutch size)	statistic	0.711	0.105	0.559	0.477	0.931
	p-value	0.000	0.000	0.000	0.000	0.000
log(body size)	statistic	0.829	0.126	3.277	1.169	0.988
	p-value	0.000	0.000	0.000	0.000	0.000
Brain residual	statistic	0.805	0.113	0.802	0.473	0.949
	p-value	0.000	0.000	0.000	0.000	0.000
Nest generalism	statistic	0.323	0.036	0.121	0.152	0.686
	p-value	0.000	0.003	0.025	0.014	0.000
Feeding habitat generalism	statistic	0.327	0.030	0.117	0.139	0.645
	p-value	0.000	0.001	0.002	0.001	0.000
Breeding habitat generalism	statistic	0.153	0.015	0.083	0.101	0.382
	p-value	0.000	0.007	0.067	0.082	0.000
Diet generalism	statistic	0.475	0.043	0.209	0.249	0.817
	p-value	0.000	0.000	0.000	0.000	0.000
Range size (1000s km <sup>2</sup> )	statistic	0.180	0.017	0.017	0.020	0.390
	p-value	0.000	0.003	0.804	0.812	0.000

## Discussion

Understanding the connection between traits, bird performance and the environment is key to a generalized predictive understanding (Webb et al. 2010) of how birds respond to their environment. It is especially important to understand how birds' traits influence responses to urban environments, given the increasing trend towards global urbanization, as well as the fact that urban environments are relatively new in relation to the evolutionary history of birds. This is the first study to comprehensively assess the urban-tolerance of the majority of Australian bird species (~80%), and the largest study that we know of to assess this question, broadly. The most urban-tolerant species in our analyses, defined based on their urbanization indices, had large niche breadths (i.e. generalists). Specialist species were the least urban-tolerant: specialized feeding strategies (i.e. granivorous and insectivorous diets) seldom occurred in urban environments. These results were robust across separate non-phylogenetic and phylogenetic models, model-averaging approaches and across phylogenetic uncertainty (Supplementary material Appendix 1 Fig. A5), indicating that urbanization is generally excluding specialist species (Sorace and Gustin 2009, Concepción et al. 2015). These results support a general understanding that environmental tolerance is a critical component of a bird's life history (Bonier et al. 2007): species with broad environmental tolerance (generalists) can rely on their catholic life history choices to succeed under multiple environmental, physiological and ecological scenarios common in urban ecosystems. Conversely, it is predicted (Webb et al. 2010) that species with low environmental tolerance (specialists) are less likely to find their specific environmental, physiological or ecological conditions necessary in disturbed urban ecosystems (Bonier et al. 2007).

The non-random distribution of the urbanization measure across the phylogeny (Fig. 3, Table 2) is consistent with reduced phylogenetic diversity in urban areas (La Sorte et al. 2018). Particular phylogenetic effects (Derrickson and Ricklefs 1988, McKittrick 1993) probably allow specific subsets of species to remain tolerant of urban environments (Morelli et al. 2016, Ibáñez-Álamo et al. 2017, Sol et al. 2017). This strong phylogenetic signal contradicts other studies (Evans et al. 2011), but was unsurprising given our large sample size of 477 species compared to the next highest of 55 species (Evans et al. 2011). We also demonstrated the importance of treating species as non-independent, by considering phylogeny in the context of the linear models, highlighting the importance of investigating trait-urbanization relationships in a phylogenetically informed manner. Although non-phylogenetic and phylogenetic models had similar relative ranks of standardized trait estimates and statistical significance (Fig. 4, Supplementary material Appendix 1 Table A4), there were some important and significant differences between the two approaches. For example, residual brain size was not significant in either of the non-phylogenetic model approaches (Fig. 4) but was significantly associated with urbanization in the phylogenetic modelling, showing the strongest relative response in the phylogenetic global model (Fig. 4, 5). Further, diet generalism, feeding habitat generalism and breeding habitat generalism were relatively more important in the phylogenetic models, compared with the non-phylogenetic models (Fig. 5, Supplementary material Appendix 1 Table A4). Lastly, body size was minimally important for the non-phylogenetic models, but substantially more important for the phylogenetically controlled models (Fig. 4, 5). This indicates that within clades, species with the largest residual brain size (Maklakov et al. 2011) and largest body size (Major and Parsons 2010) were most tolerant of



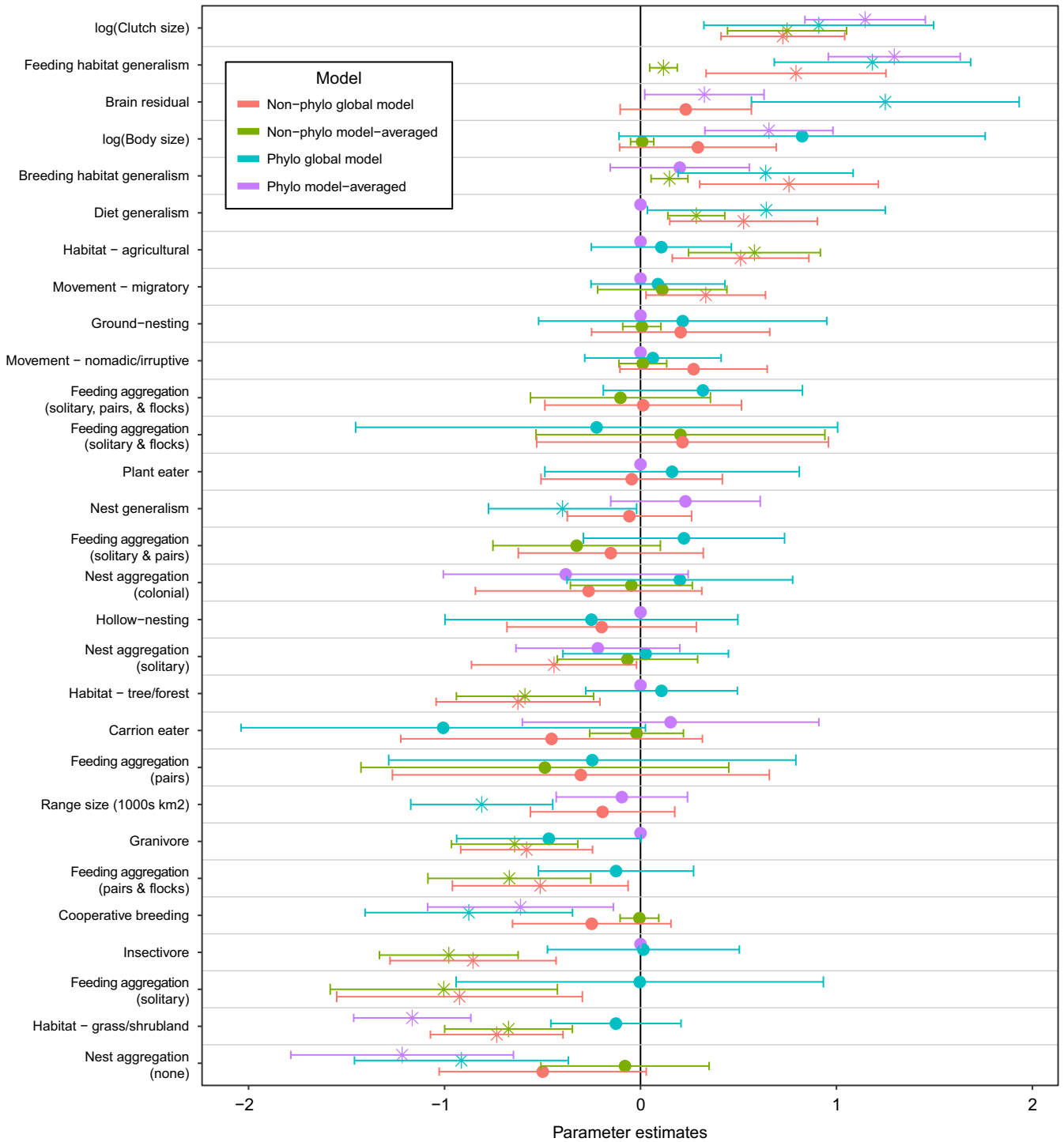


Figure 4. Standardized parameter estimates for each of the four modelling approaches employed (see Supplementary material Appendix 1 Table A4 for full model results), where a star represents significant effects. Model-averaged results did not contain every possible trait variable, in the instance that the specific trait did not occur in the top model set.

urban environments. Some other studies have shown little evidence that urban-tolerant species have large residual brain size (Kark et al. 2007, Evans et al. 2011), but we found it was highly correlated with urban-tolerance (Fig. 4, 5; Møller 2009, Maklakov et al. 2011, Møller and Erritzøe 2015). Some

studies have found little evidence that urban-tolerant species have large residual brain size (Kark et al. 2007, Evans et al. 2011), but we found it was highly correlated with urban-tolerance (Fig. 4, 5; Møller 2009, Maklakov et al. 2011, Møller and Erritzøe 2015), reflecting a species' adaptability

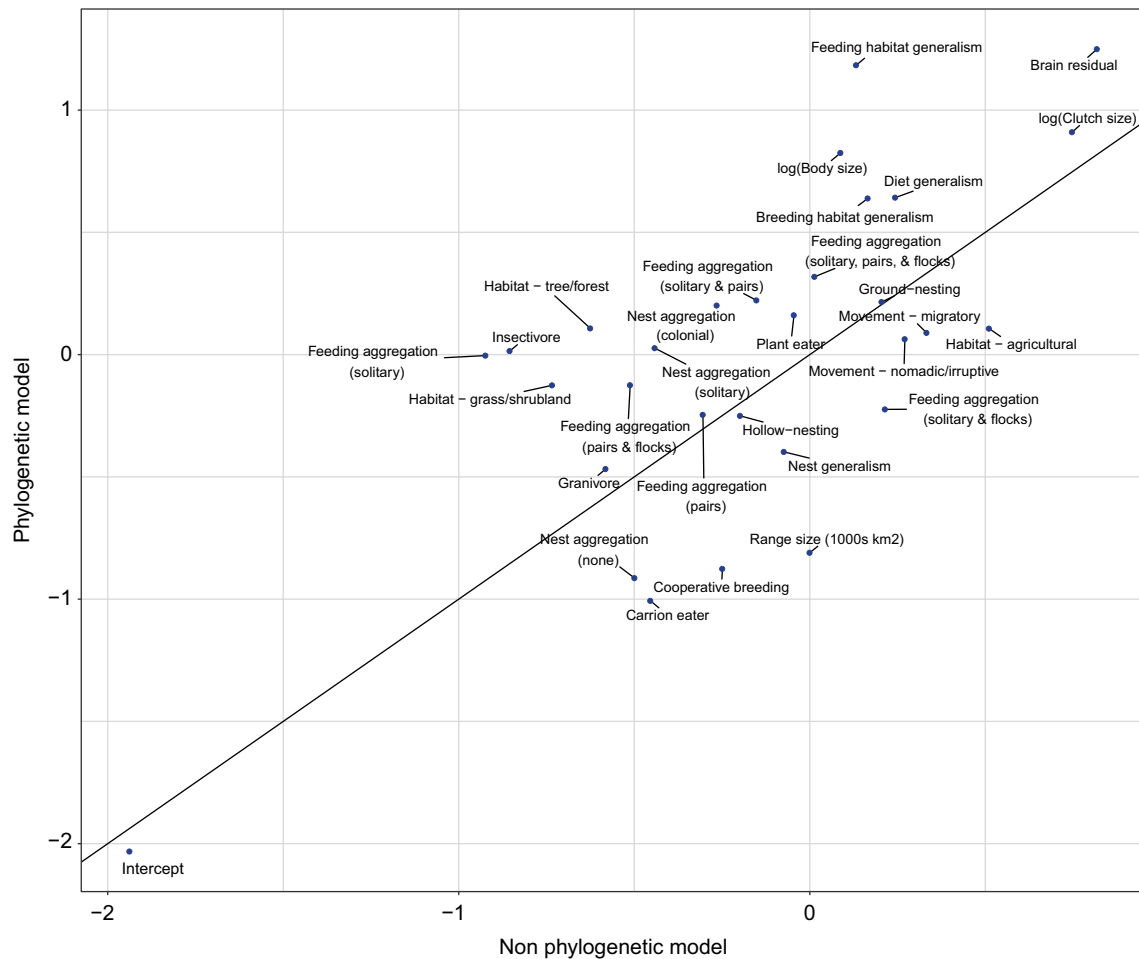


Figure 5. Proportional differences for each of the 22 traits' (Table 1) standardized parameter estimates, for the 477 species. Proportional differences represented the difference between a given trait's parameter estimate for the non-phylogenetically controlled and phylogenetically controlled global models.

to increasingly novel ecosystems. For example, Australia has a large number of parrots which are relatively successful in urban areas (Fig. 3; Burgin and Saunders 2007, Major and Parsons 2010), and generally have larger residual brain size than species in many other orders (Sol et al. 2007).

Although many traits can identify a species' adaptability to urban environments, the published evidence to this point has been equivocal. Previously, much of the current focus was on discrete classifications of species, based on their responses to urbanization (McKinney 2002, Kark et al. 2007, Møller 2009, McDonnell and Hahs 2015, Geschke et al. 2018). Contrastingly, we assessed the applicability of traits relative to one another; we did not run separate models or statistical tests for each specific trait (Kark et al. 2007), allowing comparable effect sizes. There appear to be some consistent and generalizable trends within the trait–urbanization complex across the globe. For instance, our identification of the relative importance of annual fecundity was consistent with work from Europe (Crocì et al. 2008, Møller 2009), suggesting that species which have the ability to maximize breeding output (Farnsworth and Simons 2001) are more likely to be

successful in urban ecosystems. Urbanization also appears to select against insectivorous species (Chace and Walsh 2006, Evans et al. 2011). The degree of sociality was also generally positively associated with urbanization, as found elsewhere (Coleman and Mellgren 1994, Jokimäki and Suhonen 1998, Kark et al. 2007), likely a result of cooperative breeding being a successful life history strategy in variable environments (Griesser et al. 2017). However, our study also highlighted differences with global norms. For our data, urbanization selected against granivorous species, not previously identified (Chace and Walsh 2006, Kark et al. 2007, Evans et al. 2011); this could be an artefact of relatively little supplementary feeding in Australian cities (Jones 2018) compared to European cities (Fuller et al. 2008).

The large scale of our analysis was only possible following successful integration of broad-scale empirical datasets (i.e. citizen science data (Silvertown 2009) and remote sensing technology (Gorelick et al. 2017)), which aid our understanding of the impacts of urbanization on birds (Aronson et al. 2014, 2016, Gutiérrez-Tapia et al. 2018). We acknowledge that there are biases associated with citizen

science data (Uychiaoco et al. 2005, Belt and Krausman 2012, Boakes et al. 2010), and indeed some of these were applicable to our study. One potential bias is that of varying detectability among species (Hochachka et al. 2012), relative to different habitats. For instance, Powerful Owl (and other nocturnal birds) was the ‘most urban’ based on their urbanization scores, but this is likely a result of the increased detectability of nocturnal species in urban areas, partially a result of known roosting individuals (Callaghan et al. 2018). Further, sampling is disproportionately skewed towards urban areas (Kelling et al. 2015). However, this systematic sampling bias is likely the same for all species, particularly for those within the same phylogenetic clade (i.e. similar species detected by similar methods experience similar biases; Phillips et al. 2009), suggesting that comparisons made among species with systematic biases (as done in this study) are valid (Andrew and Mapstone 1987). Our approach of weighting the models accounts for some of these biases by allowing the species with the greatest number of observations the greatest weight in the models. We did not explicitly incorporate temporal changes in relation to the life cycle for different species’ (La Sorte et al. 2014, Lepczyk et al. 2017, Katuwal et al. 2018), but migratory status was considered. In future, especially within migrant-dominated systems (e.g. Europe, North America), temporal changes in association with our urbanization measure would add considerable value (Hostetler et al. 2015, Marra et al. 2015). Australia has only a recent history of rapid urbanization (Coffee et al. 2016) and our results may differ for parts of the world with long histories of development, and at different spatial scales (Suárez-Castro et al. 2018). This relatively recent era of urbanization (cf. European cities) likely results in a particular scale and mix of built and greenspace habitats, with remnant urban bushland a feature of Australian cities. Moreover, gardens in Australian cities incorporate a mix of both native and European species (French et al. 2005), resulting in a substantial and year-round nectar supply (Sewell and Catterall 1998), providing a resource for generalist and/or large-brained species (e.g. Lorikeets, Rosellas) that have the necessary traits to exploit them. Despite minor differences, there is an opportunity to test our model predictions in urban environments in other parts of the world, potentially allowing prediction of which species face the greatest risk of impending urbanization.

Understanding which traits promote urban-tolerance or intolerance can inform actions to maintain avian biodiversity in urban environments (Evans et al. 2011). Our results found that specialist species are least urban-tolerant, suggesting that focusing on managing habitat for those species with life history traits that make them less likely to be found in urban environments could help maintain biodiversity. As one example, focus could be on protecting intact native vegetation (Sushinsky et al. 2013) connected by corridors (Litteral and Shochat 2017), heavily utilized by granivores, advantaging granivorous species detrimentally affected by landscape fragmentation and disturbance (Devictor et al. 2008). Further, increasing insect abundance and diversity in urban environments is

potentially important (Baldock et al. 2015), given collapsing insect populations around the world (Hallmann et al. 2017). A species-specific approach helps to enhance urban biodiversity, which assesses foraging (Shochat et al. 2004) or nesting (Fernandez-Juricic and Jokimäki 2001) requirements of each species, for example, used to guide protection, mitigation and restoration of necessary habitats in cities. Our urbanization measure could provide quantifiable targets for local restoration projects, where a project aims to reduce the mean urbanization measure for their local avifauna, especially if combined with other urban ecological theories, such as land sharing and land sparing (Geschke et al. 2018).

In conclusion, implementation of a trait-based approach to understand the impacts of urbanization on bird species requires a general understanding of the role of traits with respect to the urban environment. This requires accurate measures of species’ response to the environment (Webb et al. 2010), in this case urbanization, with our novel continuous measure providing greater accuracy compared to discrete classifications (Evans et al. 2011). Our results are also generalizable and comprehensive, given the large sample size and spatial scale used to address this question. Further, the methodology used is globally applicable, dependent only on observational data and trait data, combined with remotely-sensed products. Improving understanding of the temporal nature of these relationships will be important, as is the relationship with phylogeny. It is the generalist species (Shochat et al. 2006), with large clutch sizes and large residual brain sizes that have been successful (Webb et al. 2010) based on their ability to survive in the ecologically novel aspects of urban environments. Importantly, those urban-intolerant species and their life history requirements (e.g. insectivores and granivores) need to be carefully managed for with increasing urbanization.

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*Author contributions* – CTC, WKC and JHW conceived and designed the methodology of the study. CTC, WKC performed the statistical analyses. JMM, REM and RTK contributed in drafting the manuscript. All authors provided editorial advice, approved the final version of the manuscript, and agree to be accountable for all aspects of the work.

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Supplementary material (available online as Appendix oik-06158 at <[www.oikosjournal.org/appendix/oik-06158](http://www.oikosjournal.org/appendix/oik-06158)>). Appendix 1, Dataset 1.