

# How do birds with different traits respond to Urbanization? A phylogenetically controlled analysis based on citizen science data and a diverse urbanization measurement

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## HIGHLIGHTS

- Chinese birds with larger clutch sizes and more generalist diets were the most tolerant of urban environments.
- Omnivores nesting on architectural buildings or cliffs showed higher urban tolerance within clades.
- We provide novel evidence in Chinese birds and highlight challenges in identifying consistent trait-urban tolerance patterns.
- We recommend compensating habitat and food resources for ground-nesters and summer migrants.

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## ABSTRACT

The acceleration of urbanization has globally threatened bird diversity. Understanding how birds respond to the urban environment, and what, if any, traits predict this response to urban environments, is crucial in mitigating these declines. However, existing research often focuses on local or regional scales, utilizes restricted measures of urban tolerance, and does not always consider the interaction between evolutionary relatedness and traits, resulting in an unsettled relationship between some traits and urban tolerance. Our analyses aimed to test whether there is generalizability in previous results with that of the results in China, integrating 947,030 citizen science observations of birds with continuous measure of urbanization. We synthesized an urbanization index for 874 species, representing their tolerance to urbanization by accounting for stressors such as built-up land, population density, and night-light intensity. First, we aimed to quantify which traits were positively and negatively associated with urban tolerance in Chinese birds, when considering all possible ecological and life history traits. Second, we tested specific hypotheses, based on a priori literature. Third, we tested whether the results from above change when phylogenetic relatedness is included in the models. The findings reveal that passage migrants or species with multiple main migration types with larger clutch sizes and more generalist diets are the most common in urban environments. Moreover, the evolutionary relationship between species conceals the expression of several traits in urban tolerance that omnivorous species that nest on architectural buildings or cliffs showed higher urban tolerance within clades. Our findings highlight the challenges in identifying consistent patterns in the relationships between species traits and their tolerance of urban environments. To optimize urban design and reduce the negative influence on birds from rapid urbanization, protecting existing trees and buildings where birds nest, increasing the proportion of shrubs to compensate for sources of ground-dwelling birds, and controlling the predation risk of the ground nests are beneficial.

## 1. Introduction

Bird diversity is globally threatened (Chace and Walsh, 2006;

McKinney, 2002) — hundreds of species are expected to experience a dramatic decline in range, and potentially become listed as endangered by 2100 (Jetz et al., 2007; Sekercioglu et al., 2004). Urbanization is a

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driving force for the loss of bird diversity (Beissinger and Osborne, 1982; Bonnet-Lebrun et al., 2020; Chace and Walsh, 2006). Natural habitats of birds in cities are replaced by impervious surface due to high-density urban expansion, thereby facing the dilemma of substantial reduction and fragmentation (Haaland and van Den Bosch, 2015; Pauleit and Breuste, 2011). At the same time, high-density human activities, such as noise (Slabbekoorn and Ripmeester, 2008), light (Cabrera-Cruz et al., 2019), air and water pollution (Grimm et al., 2008), and high risk of collisions with man-made objects (Rebolo-Ifrán et al., 2019), pose a threat to birds. These factors highlight the importance of bird diversity conservation in urban environments (McKinney, 2002).

Importantly, urbanization does not entirely pose threats to all bird species equally (Chace and Walsh, 2006; Lowry and Lill, 2007; Máthé & Batáry, 2015). Some species have high urban tolerance, where they can successfully settle, and thrive in urban environments (Aronson et al., 2016; Croci et al., 2008; Evans et al., 2011). Urban constraints seem to act as filters that select species based on their biological traits (Patankar et al., 2021). Birds with different clutch size (Callaghan et al., 2019), body size (Maklakov et al., 2011), egg mass (Partecke et al., 2020), feather color (Leveau, 2019), nesting substrate (Croci et al., 2008), diet (Evans et al., 2011), foraging (Croci et al., 2008), or migration preferences (Lakatos et al., 2022) are likely to show differentiated tolerance to the urban environment. A study in the Midwestern United States suggested that body mass, nesting preference, incubation, and fledging times predicted species that had a relationship with human influence (Lepczyk et al., 2008). In contrast, a study that focused on the city of Jerusalem observed clear trends for dietary preference and migratory status along a gradient of increasing urbanization (Kark et al., 2007). Likewise, a study in France and Switzerland showed that nesting, diet, and migratory preference are associated with urban tolerance in birds (Croci et al., 2008). More generally, several studies have indicated that species with wider niches (i.e., generalists) have a higher tolerance to urban environments than those with narrower niches (specialists) (Bonier et al. 2007, Callaghan et al., 2019; Davies et al., 2004). Species with a wide ecological niche utilize a wide range of resources, enhancing their tolerance to urbanization (McKinney & Lockwood, 1999; Patankar et al., 2021). Identifying which traits are associated with high urban tolerance could increase our understanding of biodiversity responses to increasing urbanization, highlighting those species which are predicted to be most susceptible to ongoing urbanization.

Despite numerous studies that focused on bird traits in urban environments (Amaya-Espinel et al., 2019; Croci et al., 2008; Máthé & Batáry, 2015), the results are mixed. The relationship between some traits and urban tolerance remains unsettled. In terms of life history traits, a study in central Argentina found that highly urbanized areas were dominated by species with small and medium sizes (Leveau, 2019). However, a study in Australia showed the opposite trend — species with the largest body size were most tolerant of urban environments within clades (Callaghan et al., 2019). Similarly, a study in the midwestern United States found that body mass was a good predictor of species well associated with human influence, but the direction of the effect could not be determined (Lepczyk et al., 2008). The same contradiction also appears in diets. Research conducted in Brazil showed a positive correlation between the number of houses and the richness of plant specialists and granivores (Souza et al., 2019), but in contrast, in Australia specialized feeding strategies (i.e., insectivores and granivores) were negatively associated with urbanization (Callaghan et al., 2019). In terms of nesting and foraging preference, high-nesters seem favored in UK cities (Evans et al., 2011), but a meta-analysis showed that there was no general pattern of nest failure either across species or within species (Chamberlain et al., 2009). In terms of residence type, migrant species are able to avoid harsh conditions by migrating to obtain more resources (Somveille et al., 2015). However, several studies suggested that compared with residents, migrants seem to be more susceptible to tall buildings and elevated temperatures (Cotton, 2003; Loss et al., 2014), making them potentially less urban tolerant than resident species.

Contrasting relationships found in previous studies could be due to several reasons. First, data may be spatiotemporally limited (Croci et al., 2008; Kark et al., 2007; Souza et al., 2019), restricting the generalizability of the results. Several studies have compared bird traits across multiple regions among continents, but most explorations of the association of bird traits with urban tolerance have focused on local or regional scales (Blair, 1996; Clergeau et al., 1998; Kark et al., 2007). Second, there are few studies at national scales in most of the southern hemisphere, leaving a gap in knowledge. Third, assigning species to categorical groups according to urban tolerance may constrain the sensitivity and accuracy of a model. Specifically, some researchers strictly divide birds' as present or absent within urban environments (Bonier et al., 2007; Möller, 2009), whereas others assign species to a priori groups, such as urban avoider, utilizer, or dweller species (Amaya-Espinel et al., 2019; Kark et al., 2007; McKinney, 2002). This classification subjectively assumes that the same group of birds responds to urbanization similarly (Conole & Kirkpatrick, 2011), leading to difficulty in the interpretation of the results. More refined continuous measures of urbanization are required (*sensu* Lepczyk et al., 2008; Evans et al., 2011), where species are assessed in terms of their entire distribution in response to urban environments.

Considering phylogenetic constraints may also reveal different results among studies. Numerous studies have shown that birds in urban areas are more phylogenetically concentrated than in surrounding natural areas (Blair, 2001; La Sorte et al., 2018). The homogenization mainly stems from the reduction of species in certain clades (Sol et al., 2017). The reduction of species in certain clades may conceal the expression of several traits in urban tolerance (Losos, 2011). The use of a statistical method that assumes independence may cause overstatement of the significance in hypothesis tests (Felsenstein, 1985). Thus, several studies have controlled for the effect of evolutionary history (Callaghan et al., 2019), highlighting the influence of specific traits (Kellermann et al., 2012). Given the inconsistent evolutionary clades of birds involved in previous studies, it is important to further our understanding of the phylogenetic relatedness in bird traits and response to urbanization.

We identify the traits associated with high urban tolerance for bird species at a national scale. We focus our analysis on China, a country with diverse natural environments and rich biodiversity, but underrepresented in the literature on species' traits and urban tolerance. The country has about 1371 species of birds (Zheng, 2011). And most areas in China are in a stage of rapid development, with the urban population expected to increase to 292 million people by 2050 (Chen & Wang, 2017), highlighting the importance of quantifying the effect of urbanization on birds. To improve the comprehensiveness and generalizability of the results, we attempt to 1) include a wide range of traits, 2) cover a large spatial scale, 3) adopt a continuous measure of urban tolerance, and 4) consider phylogenetic constraints. Broadly, our analyses aimed to test whether there is generalizability in previous results with that of the results in China. First, we aimed to quantify which traits were positively and negatively associated with urban tolerance in Chinese birds, when considering all possible ecological and life history traits (Table 1). Second, we tested specific hypotheses, based on a priori literature (Table 2). Third, we tested whether the results from above change when phylogenetic relatedness is included in the models.

## 2. Data

### 2.1. Bird observation data

The birds' location in China were obtained from the Bird Report database (<https://www.birdreport.cn>). The Bird Report, launched in 2002, is the first nongovernmental organization in China focused on collecting bird data. Participants submit recordings of one or more bird species through a web-portal that collects date, time, location metadata, and number of individuals observed. After downloading the data, we

**Table 1**

Description of bird traits and urban tolerance. A) Diet and foraging data were adopted from the database EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammal (Wilman et al., 2014), which details the estimated percent use of each diet category and foraging preference category for each bird species. The categories sum to 100%. Diet and forage preference are divided into 10 and 7 categories, respectively. For each species, we count the categories of diet and foraging preference with a proportion >0, as the diet generalism and feeding habitat generalism. B) Species with different migration preferences due to their geographical distribution were classified as "Migration-others".

Variable	Definition	Mean	Std.	Reference
<i>Response to urbanization</i>				
Urban tolerance	PC1 of multiple measurements of response to urbanization			
<i>Life history traits</i>				
Clutch size	Number of eggs in the nest	4.13	1.81	(Myhrvold et al., 2015)
Egg mass	Average egg weight (g)	17.75	37.17	(Myhrvold et al., 2015)
Body mass	Average body weight (g)	331.18	972.08	(Myhrvold et al., 2015)
Body size	Average body length (mm)	287.67	362.33	Birds of the world
<i>Niche breadth<sup>A</sup></i>				
Feeding habitat generalism	Number of habitat types	2.17	0.95	( Wilman et al., 2014)
Diet generalism	Number of diet types	2.48	1.22	
<i>Ecological preference</i>				
Nesting type				
Nest - canopy	Nesting in upper-middle layer vegetation such as tree crowns or branches			( Wilman et al., 2014)
Nest - ground	Nesting on the ground or in lower-middle layer vegetation such as shrubs			
Nest - waterside	Nesting on waterfronts, wetlands, tidal flats or other areas close to water			
Nest - building	Nesting on building walls, air-conditioning cases, or soil walls			
Nest - others	More than one main nesting site			
Diet type				
Diet - herbivores	Foraging leaves, seeds, or fruits mainly			( Wilman et al., 2014)
Diet - carnivores	Foraging fish, mollusks, amphibians, small mammals, or other birds mainly			
Diet - omnivores	Corrosive or with more than one main diet			
Diet - insectivores	Foraging insects mainly			
Forage type				
Forage - canopy	Foraging in upper-middle layer vegetation such as tree crowns or branches			Birds of the world
Forage - ground	Foraging on the ground or in lower-middle layer vegetation such as shrubs			

**Table 1 (continued)**

Variable	Definition	Mean	Std.	Reference
Forage - waterside	Foraging on waterfronts, wetlands, tidal flats or other areas close to water			
Forage - flight	Foraging flight			
Forage - others	More than one main foraging area			
<i>Migration type</i>				
Migration - resident	Live in China all year round			Birds of the world
Migration - summer	Breeding in China			
Migration - winter	Overwintering in China			
Migration - passing	Passing through China during the spring and autumn			
Migration - others <sup>B</sup>	More than one residence in China			

corrected any potentially incorrect coordinates. For example, observations that evidently fell into the sea or did not align with the stated province (i.e., fell outside the reported province) were manually excluded. We used data from January 2012 to December 2020 (Fig. 1) as this temporal scale corresponded to the most abundant period of bird observations, minimizing the mismatch between the bird collection and the change of urbanization index. Only species with 50 or more observations were analyzed, and 874 species of birds (>60% of all Chinese birds) were included. We analyzed a total of 947,030 bird records, including multiple observations of 874 bird species at 12,307 locations. The count of observations and the total number of individuals varied among bird species (Supplement A).

## 2.2. Urbanization indicators

Urbanization was measured from three perspectives: urban and built-up lands (reflecting the amount of impervious surface), population density (reflecting interference from human activities), and night lights (reflecting the intensity of night lighting). With the classification method of International Earth Biosphere Project (IGBP) of the MODIS annual land cover type MCD12Q1 from 2012 to 2020 with a resolution of 500 m (Friedl & Sulla-Menashe, 2019), urban and built-up lands in China (proportion of impervious surface greater or equal to 30%) were extracted. The population density came from the WORLDPOP annual population density product at a resolution of 1 km from 2012 to 2020 (<https://www.worldpop.org/>) (Tatem, 2017). The population density was missing in some boundary in which the bird records were excluded. The monthly night light data of VIIRS were synthesized according to year, and the annual night light intensity data from 2012 to 2020 at a resolution of 1 km were obtained. VIIRS night lights filtered out background noise (such as fire and other light pollution), which ensured the effective connection with the human community (<https://eogdata.mines.edu/products/vnl/>) (Elvidge et al., 2021). All spatial data and maps were handled and drawn using the Albers projection, datum WGS84.

We used an approach to continuously rank each species in its 'urban tolerance', defined as a relative measure of where a species is found in relation to the urban environment (Callaghan et al., 2019, 2021). To match bird observations and minimize potential deviations caused by scale errors, the proportion of urban and built-up lands, the average population density, and the average intensity of night lights within a 5 km buffer of each observation location were calculated. For each species, mean, and median of its entire distribution in response to an urbanization measurement were calculated, reflecting the species' responses to urban habitats. In addition, to account for uncertainty and differences in sampling, we calculated the weighted average by the

**Table 2**

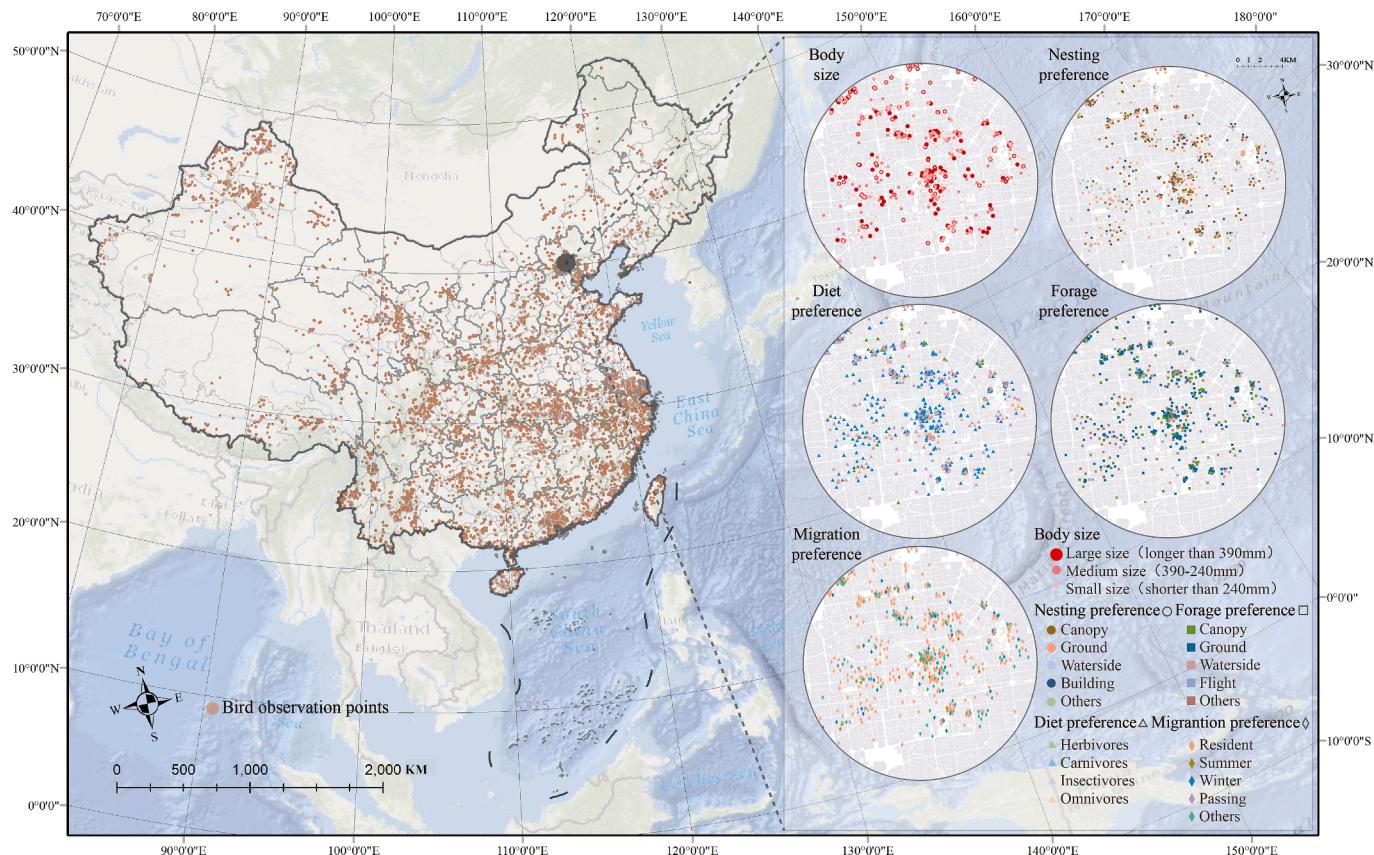
An overview of previous literature that has investigated the relationship between species' traits and urban tolerance. This list is intended as an overview and not meant to be exhaustive.

Tested trait	Specific hypothesis	Reference
Life history traits (Clutch size)	* Bird species which are generalists, with large clutch size, and large residual brain size are among the most urban-tolerant bird species.	(Callaghan et al., 2019)
	* With increasing urbanization, differential food resources and predatory pressure results in changes in life history traits, including prolonged breeding duration, and increases in clutch and brood size to compensate for lower survival.	(Patankar et al., 2021)
Life history traits (Body mass)	* Birds correlated with human influence were significantly smaller in body mass.	(Lepczyk et al., 2008)
	* The body mass shows significantly negative effect in urban environments.	(Maklakov et al., 2011)
Life history traits (Body size)	* Highly urbanized areas were dominated by grey color, plumage dimorphism, polymorphism and small and medium sizes.	(Leveau, 2019)
	* Species with largest body size were most tolerant of urban environments within clades.	(Callaghan et al., 2019)
Niche breadth	* Urban adapters have large wingspans.	(Croci et al., 2008)
	* Human tolerance for predators generally declines with increases in the predators' body size, which leads to removals of large species from cities.	(Fischer et al., 2012)
Nesting preference	* Urban adapters are widely distributed.	(Croci et al., 2008)
	* Generalist species are better adapted to urban areas than specialists.	(Evans et al., 2011)
Forage preference	* Urbanization has stronger negative effects on more specialized traits.	(Máthé & Batáry, 2015)
	* Small-ranged specialist species will be impacted more than larger-ranged generalists as urbanization continues.	(Bonier et al., 2007)
Diet preference	* Bird species which are generalists, with large clutch size, and large residual brain size are among the most urban-tolerant bird species.	(Callaghan et al., 2019)
	* Urban bird community being dominated by generalist species, while specialist species show decline.	(Patankar et al., 2021)
Migration preference	* Urban adapters prefer forest, cliffs, and mountains environment rather than shrub habitats, aquatic or open landscapes.	(Croci et al., 2008)
	* Ground-nesting species are at a disadvantage, whereas high-nesters are at an advantage.	(Evans et al., 2011)
Diet preference	* Species that did not nest on or close to the ground tended to have higher urban to rural densities than ground-nesting species.	(Lakatos et al., 2022)
	* Ground nesting birds were negatively affected by urbanization.	(Lepczyk et al., 2008)
Forage preference	* Species responding to human influences had minimum nest heights closer to the ground than species exhibiting no relationship.	(Máthé & Batáry, 2015)
	* Open-cup nesting species were most abundant in suburban areas.	(Chamberlain et al., 2009)
Diet preference	* Species richness of cavity nesters increased with urbanization gradient in winter, but decreased in the breeding season.	(Lakatos et al., 2022)
	* There was no general pattern of nest failure either across species or within species.	(Croci et al., 2008)

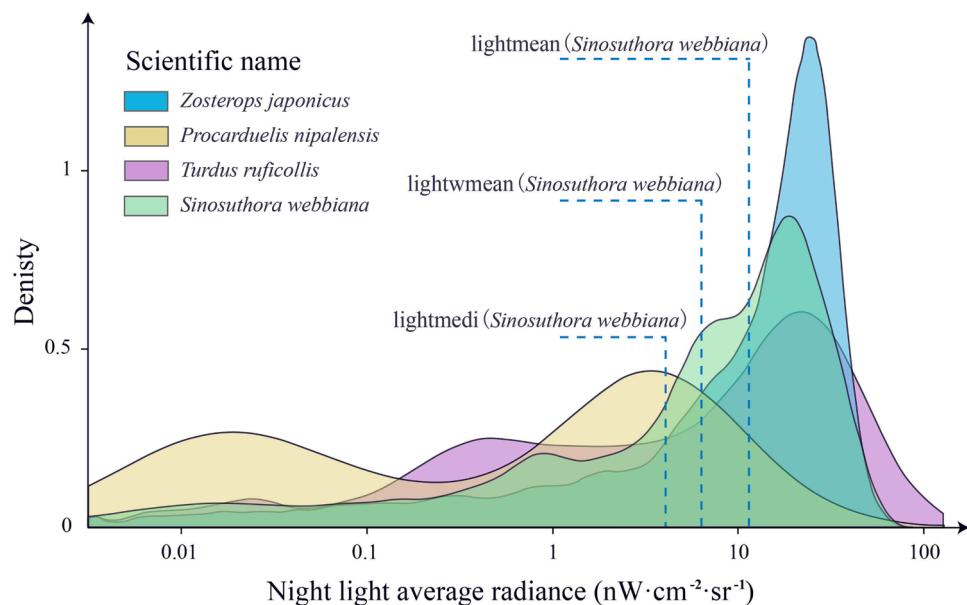
**Table 2 (continued)**

Tested trait	Specific hypothesis	Reference
	* As the matrix around a small urban park had increased building densities, bird richness and abundance of insectivorous species decreased and omnivorous species increased.	(Amaya-Espinel et al., 2019)
	* Specialized feeding strategies (i.e., insectivores and granivores) were negatively associated with urbanization.	(Callaghan et al., 2019)
	* A greater proportion of terrestrial foragers (i.e., birds feeding on land for one or several food types, such as granivores and frugivores) had a negative response to human influence.	(Lepczyk et al., 2008)
	* There was no evidence that insectivores were the most impacted groups for diet traits.	(Lakatos et al., 2022)
	* Granivores were the most negatively impacted groups.	
	* No evidence suggests that species which included invertebrates in diet had lower urban densities.	(Evans et al., 2011)
	* Species that included plant material in diets have higher urban densities than species which did not.	
	* With increasing urbanization, the proportion of granivorous species increased whereas the proportion of species feeding on invertebrates declined.	(Kark et al., 2007)
	* The number of houses and the landscape heterogeneity have a positive effect on plant specialists and granivores.	
	* Insectivorous species were most abundant in suburban areas.	(Souza et al., 2019)
	* Omnivorous species richness was not related to urbanization gradient.	(Máthé & Batáry, 2015)
Migration preference	* Sedentary species are at an advantage.	(Croci et al., 2008)
	* The species were significantly more social and sedentary with increasing urbanization.	(Kark et al., 2007)
	* Only limited evidence that long distance migrants have lower urban densities, and migratory status has a negligible influence on the ratio of urban and rural densities.	(Evans et al., 2011)
	* There was no evidence that long-distance migrants were the most impacted groups for the migration.	
	* Short-distance/partial migrants were the most negatively impacted groups.	(Lakatos et al., 2022)

number of individuals in each location (Fig. 2, Supplement B). Species with high values indicated that most of the species' observations were found in urban areas, whereas species with low values indicated the species predominantly use more natural habitats, with low levels of urbanization. This approach uses the data from Bird Report, similar to other work that has used presence-only data to quantify urban tolerance for multi-taxa assessments (Callaghan et al., 2020), butterflies (Callaghan et al., 2021), and frogs (Liu et al., 2021). The urbanization index using the different measurements of urbanization, including urban and built-up lands, population density, and night lights, were all correlated (see Supplement C). To account for the potential differential responses to different measures of urbanization (Moll et al. 2019) we derived a synthetic urbanization index by performing a principal components analysis (PCA) using the package "psych" (Revelle & Revelle, 2015) on 9 urbanization indices listed in Supplement C. The first principal components (PC1) was considered as a synthetic urban index to represent the response to urban habitats for each species. High values represent a species with high 'urban tolerance' whereas species with low values represent 'urban intolerant'. Importantly, these are relative measures of urban tolerance and thus these values are only comparable among species considered in this analysis.



**Fig. 1.** The study area of our analysis, China. We used data from January 2012 to December 2020, including 947,030 bird records of 874 bird species at 12,307 locations. The enlarged circles on the right panel showed the central area of Beijing. We have marked the bird observations by categorizing them based on their body size (large ( $>390$  mm), medium (390–240 mm), and small sizes ( $<240$  mm)), nesting preference ('canopy', 'ground', 'waterside', 'building', and 'others'), forage preference ('canopy', 'ground', 'waterside', 'flight', and 'others'), diet preference ('herbivores', 'carnivores', 'insectivores', and 'omnivores'), and migratory preference ('resident', 'summer', 'winter', 'passing' and 'others').



**Fig. 2.** Night light average radiance-density distributions of *Zosterops japonicus*, *Procarduelis nipalensis*, *Turdus ruficollis*, and *Sinosuthora webbiana* are shown. The x-axis is log10-transformed. The blue dotted line marks the weighted average (lightwmean), average (lightmean) and median (lightmedi) distribution of *Sinosuthora webbiana* on night light average radiance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

### 2.3. Morphological and life history traits

Based on the open-source dataset Ecological Archives E096-269 (Myhrcold et al., 2015), E095-178 (Wilman et al., 2014), and Birds of the World (<https://birdsoftheworld.org>), 10 morphological and life history traits were collated for each species (Table 1, Supplement A), including: clutch size, egg mass, body mass, body size, feeding habitat generalism, diet generalism, nesting type, diet type, foraging type, and migration type. For some missing information, a comprehensive evaluation was made with reference to similar species of the same genus. In addition, phylogenetic trees containing the 874 bird species observed in this study were established, which were pruned from the global bird phylogeny tree with the option of “Hackett All Species: a set of 10,000 trees with 9993 OTUS each” (<https://birdtree.org/>) (Jetz et al., 2012) (Fig. 3). We sampled 5000 pseudo-posterior distributions and constructed the Maximum Clade Credibility tree using mean heights by TreeAnnotator (version 1.10.4) of the BEAST package (Drummond & Rambaut, 2007).

### 3. Statistical analysis

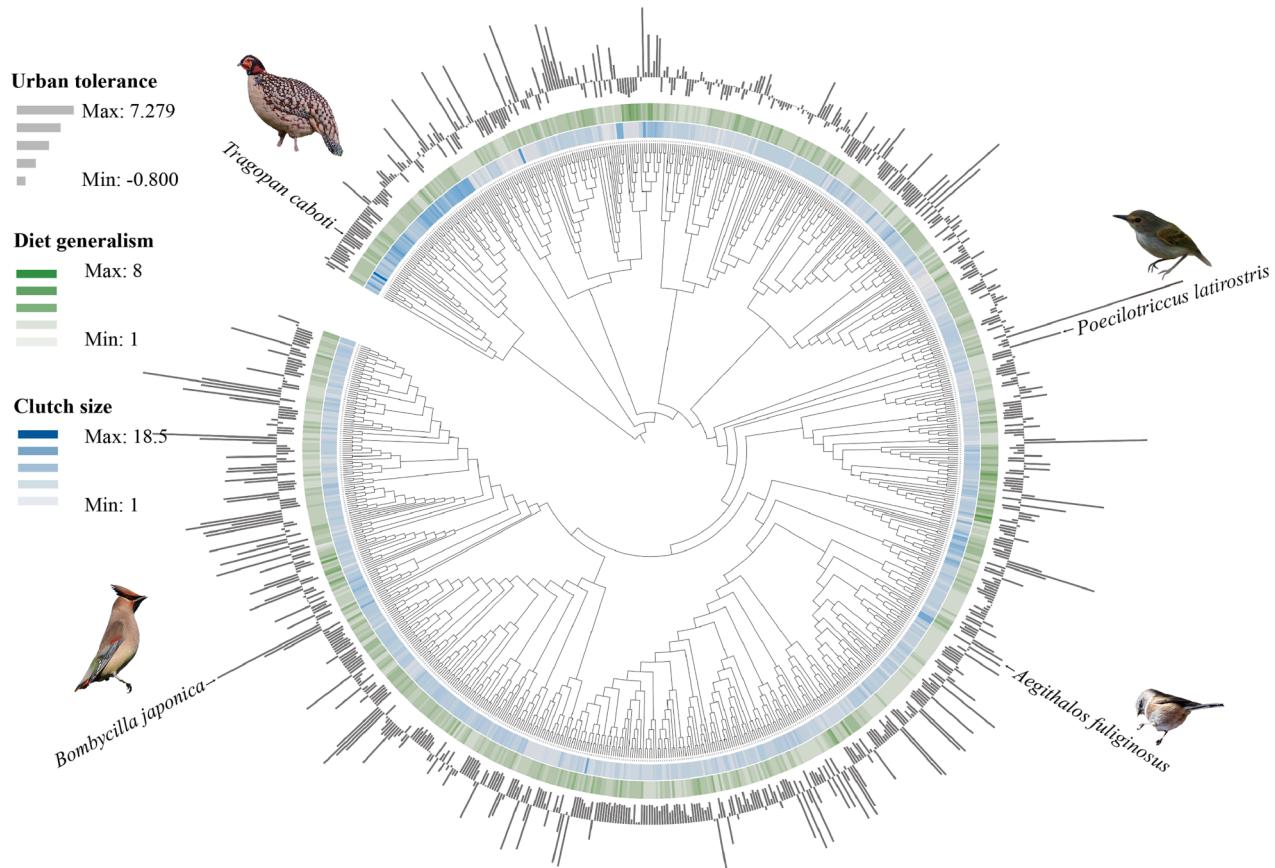
Throughout our analyses, we used  $\alpha < 0.05$  as a measure to infer statistical significance of a species' trait and the relationship with urban tolerance.

#### 3.1. Multiple regression model

First, we tested which traits were most associated with urban tolerance (response variable) in Chinese birds, considering all possible ecological and life history traits (predictor variables; Table 1), using a

multiple linear regression model. Prior to model building, the variables were evaluated for collinearity using the package “corplot” (Wei et al., 2017) in R 4.0.2. A highly positive correlation between egg mass (EM) and body mass (BM) existed (Supplement D) and thus we excluded body mass from subsequent analysis and also because additionally body mass was relatively strongly correlated with body size (BS). We then were left with a total of 9 potential predictor variables (see Table 1). To comply with the linear model assumption, clutch size (CS), egg mass (EM), and body size (BS) were transformed logarithmically. Model estimates were standardized to represent relative effect sizes using the “arm” package (Gelman et al., 2016). The model was weighted with the proportion of the counts of observations (C) divided by the number of observation sites (NS). The practice made the model better suitable for the species that were more observational in the unit site, whose responses to urbanization were more reliable. Collinearity in the model was also checked by variance inflation factor (VIF) using the “car” package of R 4.0.2 (Fox et al., 2012) (VIF values < 5).

Considering the lack of consistent results previously reported in the literature, we used a model-averaging approach. Model averaging accounts for model selection uncertainty, and provides a robust means of obtaining parameter estimates by averaging the top model set (Burnham & Anderson, 2002; Grueber et al., 2011). All possible sub-models ( $N = 512$ ) from a global model of 9 predictor variables were fitted with the function “dredge” in the “MuMin” package (Barton, 2009), and any possible combination of traits was allowed to be the dominant predictor variable to avoid over-fitting. We then determined weighted average parameter estimates across the top sub-models ( $\Delta AIC_c < 4$ ;  $N = 4$ ), using the conditional average, as we wanted to evaluate all potentially important traits and expected some to have relatively weak effects (Grueber et al., 2011).



**Fig. 3.** Reproduced phylogenetic tree of our 874 species showing urban tolerance, diet generalism, and clutch size. Clutch size and diet generalism were illustrate due to their importance in our results. Four species with high (*Bombycilla japonica*), medium (*Poecilotriccus latirostris*), and low urban tolerance (*Tragopan caboti*, *Aegithalos fuliginosus*) are illustrated.

### 3.2. Single regression models

In addition to above, and to test individual hypotheses where each trait was treated separately (see Table 2), we ran multiple individual linear models of the relationships between each trait and urban tolerance. We placed each ecological and life history trait into models separately to verify their performance. Clutch size, egg mass, and body size were logarithmically transformed as previously described. Additionally, the model estimates were standardized, and the models were weighted by the proportion of observation counts to the number of observation sites, as outlined above.

### 3.3. Phylogenetic models

To determine whether the relationship between bird traits and responses to urbanization is influenced by coevolutionary history, phylogenetic analysis was used. We calculated four phylogenetic signals for urbanization measurements and each continuous predictor variable using the packages “AdePhylo” (Jombart et al., 2017) and “Phytools” (Revell & Revell, 2020). As the indices differed in their assessment of the importance of phylogeny on species’ responses to the urban environment (see results), we constructed phylogenetically controlled linear regression models, using the “Phylolm” package (Ho et al., 2016), based on the same approach above (including multiple and single regression models). Phylogenetic models were fitted based on the same basic model as the nonphylogenetic ones. The former was a linear-time algorithm that simulates Brownian motion on the tree to study the evolutionary association of traits. It can effectively perform likelihood calculation and parameter inference on large phylogenetic trees (Tung Ho, si, & Ané, 2014).

## 4. Results

### 4.1. Descriptive analysis

Our study included a total of 947,030 observations of 874 bird species, averaging  $1084 \pm 2317$  ( $\pm SD$ ) observations per species (Supplement A). *Carpodacus rhodochlamys* was the least frequently observed species (count = 50), whereas the species with the highest observations was *Pycnonotus sinensis* (count = 21105). The range of urban index varied depending on the distribution of the species (Fig. 3). The highest indices were recorded in *Psittacula eupatria* (PC1 = 7.279), *Ficedula albicollis* (5.492), and *Luscinia cyane* (4.889), indicating high urban tolerance. *Tragopan caboti* (-0.800), *Phylloscopus hainanus* (-0.799), *Xiphirhynchus superciliaris* (-0.797) recorded the lowest indices, indicating they are the species with the least urban tolerance in our study.

### 4.2. The relationship between traits and urban tolerance

When assessing traits using non-phylogenetically controlled multiple linear regression (Table 3), the most important predictors of urban tolerance (i.e., standardized parameter estimates, p - value) in the averaged model were clutch size (0.13,  $<0.001$ ), diet generalism (0.08, 0.019), canopy nesting (0.13, 0.001), passage migrants (0.54,  $<0.001$ ), summer migrants (0.39,  $<0.001$ ), winter migrants (0.24,  $<0.001$ ), and species with more than one migration types (0.41,  $<0.001$ ), which were positively associated with urban tolerance in Chinese birds, whereas egg mass (-0.14, 0.005) was negatively associated with the urban tolerance.

When traits were assessed independently for specific hypotheses (Table 3), clutch size (0.18,  $<0.001$ , Fig. 4.a), canopy nesting (0.11, 0.009, Fig. 4.b), passage migrants (0.51,  $<0.001$ , Fig. 4.e), summer migrants (0.40,  $<0.001$ , Fig. 4.e), winter migrants (0.23,  $<0.001$ , Fig. 4.e), and species with more than one migration type (0.39,  $<0.001$ , Fig. 4.e) remained strongly positively associated with urban tolerance, indicating that they are stable predictors of urban tolerance. Conversely, egg mass and diet generalism did not show a significant relationship with

urban tolerance. Besides, waterside nesters (0.21,  $<0.001$ , Fig. 4.b) and species with more than one main nesting site (0.16, 0.010, Fig. 4.b) were more tolerant of urbanization than ground-nesters. In terms of diet type, carnivores (0.12, 0.039, Fig. 4.c) performed better than omnivores in the urban environment. As for forage preference, canopy foragers (0.09, 0.041, Fig. 4.d), and waterside forages (0.19,  $<0.001$ , Fig. 4.d) showed more tolerance to urbanization than ground foragers.

### 4.3. Phylogenetic analysis

There was a distinct relationship between the phylogenetic signal and urban tolerance (Supplement E), significantly different from random for I, Cmean, and Lambda, indicating that urban tolerance of bird species was nonrandomly distributed on the phylogenetic tree. Further, life history traits such as clutch size, egg mass, and body size showed a strong correlation in phylogeny (Supplement E). Niche breadths such as feeding, habitat, and diet generalism had slightly lower phylogenetic correlation than the aforementioned life history traits.

After controlling for the potential effects of phylogeny (Table 3), clutch size (0.19,  $<0.001$ ), diet generalism (0.09, 0.008), passage migrants (0.32,  $<0.001$ ), and species with more than one migration types (0.36,  $<0.001$ ) kept the strong positive association with urban tolerance in the multiple linear regression averaged-model. In contrast, egg mass, summer migrants, and winter migrants were no longer significant. In terms of nesting preference, the difference shown in the non-phylogenetic multiple linear regression is no longer significant. Instead, birds that nest on architectural buildings or cliffs performed better in the urban environment compared with ground-nesters (0.21, 0.001). Additionally, herbivorous species showed a significant negative association with urban tolerance compared to omnivores (-0.12, 0.011).

When testing specific hypotheses, the phylogenetic analysis also showed inconsistent results with the non-phylogenetic ones (Table 3), clutch size was still an important predictor of urban tolerance (0.35,  $<0.001$ ). In addition, a significant positive correlation between urban tolerance and species with wider feeding habitat generalism (0.14,  $<0.001$ ) and diet generalism (0.22,  $<0.001$ ). In terms of nesting preference, waterside nesters (0.12, 0.028), and species with more than one main nesting type (0.11, 0.038) kept a positive association with the urban tolerance. Instead, canopy-nesters showed no significance, and birds that nest on architectural buildings or cliffs performed better in urban environments compared with ground-nesters (0.26,  $<0.001$ ). As for diet type, carnivores showed no difference anymore, while herbivores showed a significant negative association with urban tolerance compared with omnivores (-0.44,  $<0.001$ ). Canopy foragers did not show the difference with ground-nesters anymore. It is worth noting that waterside nesters showed a strong negative association with urban tolerance (-0.41,  $<0.001$ ). Compared to non-phylogenetic analyses, summer birds were not significant anymore.

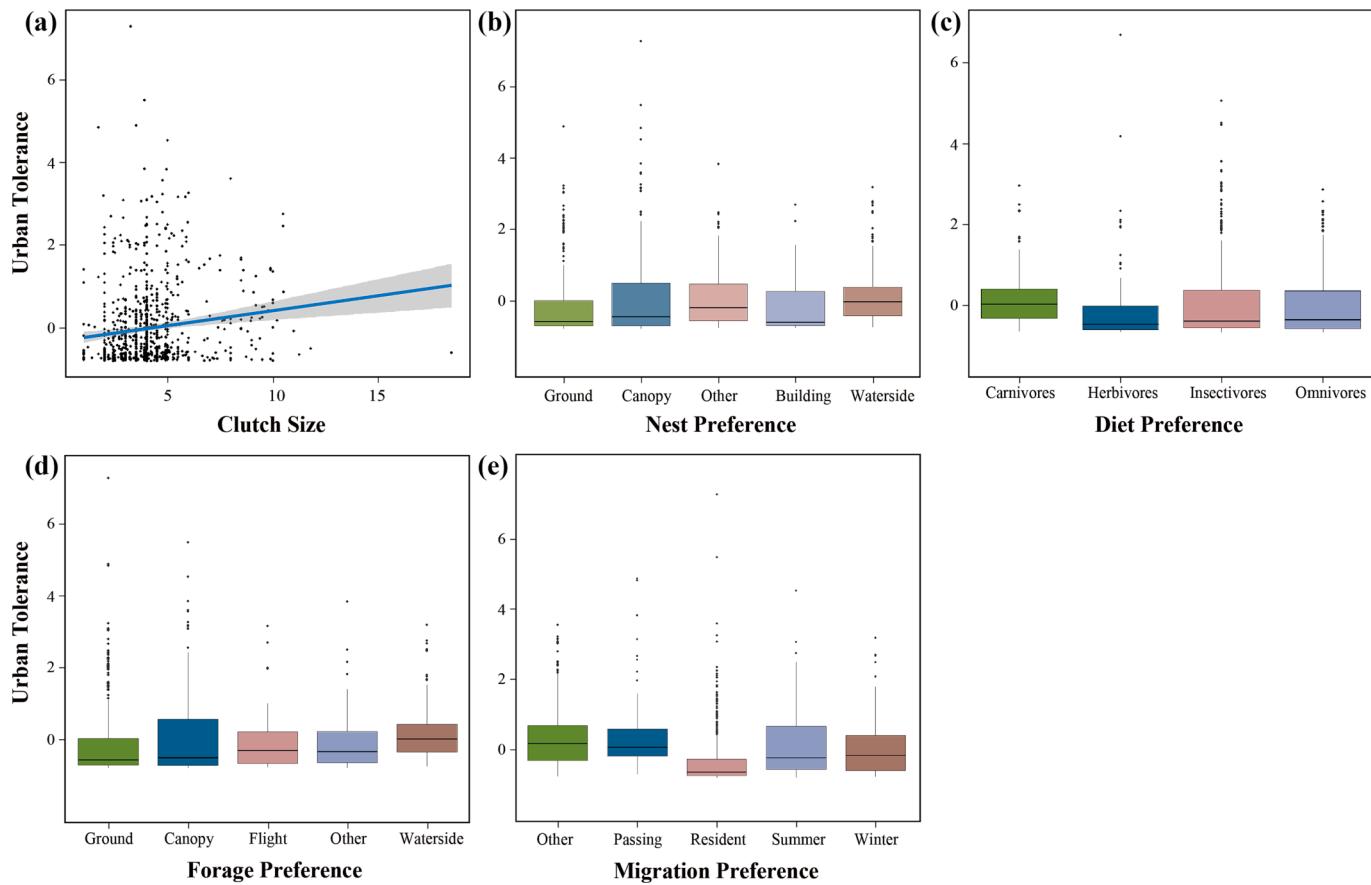
## 5. Discussion

We used non-phylogenetic and phylogenetic analyses to explore the relationship between traits and urban tolerance in Chinese birds. The results of the above two analyses are inconsistent, indicating that the evolutionary relationship between species conceals the expression of several traits in urban tolerance to some extent. Across both phylogenetically and non-phylogenetically controlled models, the most robust and most consistent relationships were for larger clutch size, more generalist diets, and passage birds or species with more than one migration types, related to a high urban tolerance. The phylogenetic analysis also showed some unique trends. With the control of the phylogenetic effect, both multiple and single linear regression models showed that the positive association between canopy-nesters and urban tolerance was not significant anymore. In contrast, birds that nest on architectural buildings or cliffs showed higher urban tolerance

**Table 3**

Summaries of relationships between species' traits and urban tolerance for the four different modelling approaches employed in our analysis: non-phylogenetically controlled (lm) or phylogenetically controlled (phylolm) multiple linear regression with model averaging, or single regressions for each trait. For linear regressions contains categorical variables, the intercept was the reference level for categorical traits (e.g. nest type; diet type; forage type; migration type). Bolded indicate significance at the level of 95%. The sum of model weights (sw) and adjusted R-squared(adjR2) were showed in the table.

	Multiple regression (lm)					Multiple regression (phylolm)					Single regression (lm)					Single regression (phylolm)				
	Estimate	SE	z	p-value	sw	Estimate	SE	z	p-value	sw	Estimate	SE	t	p-value	adjR2	Estimate	SE	t	p-value	adjR2
(Intercept)	-0.24	0.03	8.36	<0.001		-0.12	0.59	0.21	0.833											
<i>Life history traits</i>																				
lg(clutch size)	0.13	0.03	4.07	<0.001	1	0.19	0.04	4.35	<0.001	1	0.18	0.03	5.51	<0.001	0.03	0.35	0.05	7.65	<0.001	0.06
lg(egg mass)	-0.14	0.05	2.84	0.005	1	-0.14	0.09	1.58	0.115	0.56	0.00	0.04	0.12	0.901	0	-0.13	0.09	-1.38	0.169	0
lg(body size)	0.01	0.07	0.17	0.869	0.23	0.03	0.08	0.39	0.698	0.29	-0.01	0.03	-0.18	0.856	0	0.02	0.08	0.26	0.792	0
<i>Niche breadth</i>																				
Feeding.habitat. generalism	0.03	0.03	0.91	0.361	0.37	-0.04	0.03	1.26	0.208	0.44	0.05	0.03	1.52	0.129	0	0.14	0.03	4.10	<0.001	0.02
Diet.generalism	0.08	0.03	2.34	0.019	0.87	0.09	0.03	2.64	0.008	1	0.07	0.03	2.03	0.043	0	0.22	0.03	7.47	<0.001	0.06
<i>Nesting type</i>															0.02					0.02
Nest - ground																				
Nest - canopy	0.13	0.04	3.39	0.001	1	-0.03	0.04	0.60	0.553	1	0.11	0.04	2.62	0.009		-0.02	0.05	-0.43	0.665	
Nest - others	0.06	0.06	0.94	0.348	1	0.08	0.05	1.79	0.074	1	0.16	0.06	2.58	0.010		0.11	0.05	2.08	0.038	
Nest - building	0.04	0.07	0.59	0.557	1	0.21	0.07	3.23	0.001	1	0.04	0.08	0.54	0.586		0.26	0.07	3.53	<0.001	
Nest - waterside	0.05	0.05	0.87	0.386	1	0.07	0.05	1.41	0.157	1	0.21	0.05	4.19	<0.001		0.12	0.05	2.20	0.028	
<i>Diet type</i>															0.01					0.11
Diet - omnivores																				
Diet - herbivores						-0.12	0.05	2.56	0.011	1	-0.06	0.05	-1.14	0.256		-0.44	0.04	-10.54	<0.001	
Diet - insectivores						0.05	0.04	1.13	0.260	1	0.02	0.04	0.37	0.714		-0.07	0.05	-1.62	0.107	
Diet - carnivores						0.07	0.06	1.2	0.228	1	0.12	0.06	2.07	0.039		-0.01	0.06	-0.15	0.883	
<i>Forage type</i>															0.02					0.09
Forage - ground																				
Forage - canopy																				
Forage - flight																				
Forage - others																				
Forage - waterside																				
<i>Migration type</i>																0.14				0.19
Migration - resident																				
Migration - passing	0.54	0.08	7.20	<0.001	1	0.32	0.07	4.85	<0.001	1	0.51	0.07	6.85	<0.001		0.34	0.06	5.51	<0.001	
Migration - other	0.41	0.04	9.33	<0.001	1	0.36	0.04	9.76	<0.001	1	0.39	0.04	9.63	<0.001		0.43	0.03	13.78	<0.001	
Migration - summer	0.39	0.07	5.41	<0.001	1	0.07	0.05	1.41	0.159	1	0.40	0.07	5.64	<0.001		-0.01	0.04	-0.28	0.783	
Migration - winter	0.24	0.06	4.09	<0.001	1	0.08	0.06	1.39	0.165	1	0.23	0.06	3.90	<0.001		0.11	0.06	2.02	0.044	



**Fig. 4.** Relationships between birds' traits and urban tolerance. Boxplots of categorical variables (b–e) depict medians, interquartile ranges and full ranges: (a) clutch size (number of eggs in the nest); (b) nest preference; (c) diet preference; (d) forage preference, and (e) migration preference.

compared with ground-nesters. Meanwhile, herbivores showed worse performance than omnivores within clades.

In terms of life history and niche breadth traits, we found that species with larger clutch sizes and more generalist diets showed higher urban tolerance. This conforms with previous literature that has shown birds living in drastically changing environments have larger clutch sizes (Jetz et al., 2008), which are often associated with a faster reproduction rate and richer food resources (Ashmole, 1963), likely allowing the increased reproduction to overcome the potential hazards of living in urban environments. Moreover, birds with more generalist diets are more tolerant toward environmental changes (Callaghan et al., 2019) because they can improve performance to human disturbances through varied food choices (Bonier et al., 2007). The views above support a general explanation, namely, birds that reproduce quickly and use resources extensively are more tolerant to urbanization (Davies et al., 2004; Webb et al., 2010), whereas those that reproduce slowly and with specific resource requirements may require special protection strategies in urban areas (Bonier et al., 2007). As for nesting preference, the urban tolerance of ground-nesters is significantly lower than canopy-nesters in the nonphylogenetic analysis. However, with the control of the phylogenetic effect, the difference above is no longer significant. Instead, birds that nest on architectural buildings or cliffs or have multiple nesting preferences were more urban tolerant compared with canopy-nesters. Several studies explained that the predation risk of nesting on the ground is much higher than that at high altitudes in an urban environment (P. Li & Martin, 1991; Shochat et al., 2005). Research on 579 bird nests indicated that the probability of successful reproduction in high-altitude nests is nearly 80% higher than that on the ground (Xie et al., 2016). For species in the same clade that nesting heights are similar, whether artificial buildings can be fully utilized and whether nesting

preference can be generalized have become the main factors of urban tolerance among birds. For example, *Hirundo rustica* and *Hirundo daurica* are able to make full use of artificial buildings for nesting, showing higher urban tolerance than some species in the same clades like *Hirundo smithii* and *Hirundo rupestris* who nests on areas close to water. Based on the results, existing trees and buildings where birds nest should be protected. The ratio of shrubs should be appropriately increased to compensate for habitat and food sources of birds that live on the ground or in lower-middle layer vegetation (Ilkin et al., 2013), and the predation risk of the ground nest should be controlled (Smith et al., 2011).

Some mixed results were also found compared with previous studies. Although body size is an important predictor of urban response based on previous literature (Fischer et al., 2012; Leveau, 2019), body size did not show a significant association in our study. It might be due to the need for further detailed considerations of brain size or wingspans, correlates of body size. In terms of diet preference, we found that omnivorous species showed lower urban tolerance than granivores within clades in China, similar to Croci et al., (2008), and Clergeau et al. (1998). Omnivores eat a wide range of food, which might be an advantage in cities, where human activities mass produce novel resources such as garbage (Clergeau et al. 1998). Forage type did not show significance when considering all possible variables, whereas, in single regression models, it was a non-negligible predictor variable. Ground-foraging species are at a disadvantage compared with waterside or canopy foragers in our non-phylogenetic analysis, similar to Jokimäki & Huhta (2000), and Lakatos et al. (2022), following the same argument that human disturbance will be greatest at ground level. Unexpectedly, waterside foragers showed less urban tolerance than ground-foragers within clades. While it is unclear how this result emerged, it may be due to an increased human presence near water bodies in cities due to recreation activities of

local residents.

Our initial prediction that urbanization would benefit residents was not supported – rather, migrants were shown to be more urban tolerant. It might be due to factors which have not been specifically examined. For example, migrants are able to avoid particularly harsh conditions in urban environments (e.g., winter time) by migrating to obtain more resources compared with residents (Somveille et al., 2015). Changes in the migratory status of species are also a possible influencing factor. The highly altered urban habitats, the heat island effect, and year-round resource availability together may increase the propensity of birds to remain in cities rather than migrate (Bonnet-Lebrun et al., 2020). After considering the potential effects of phylogeny, the advantage of summer migrants was less obvious. The high-density impervious surface restricts the development of small greenspaces such as parks and street greening (Dallimer et al., 2011), potentially limiting the amount of available habitat for summer resident species to persist in the cities. Strengthening small green spaces and providing suitable space for summer migrants to stay and forage may be necessary (De Groot et al., 2021; Tryjanowski et al., 2017). Our findings highlight the challenges in identifying consistent patterns in the relationship between species traits and their tolerance for urban environments.

The current study also has several limitations. First, the research adopted a synthetic index to explore the overlap among different urbanization measurements of urban and built-up lands, population density, and night lights. However, the non-overlapping parts among indicators, which may be due to the difference in how species respond to the effect of habitat loss, human disturbance, and night light, require further distinction. Future analysis could consider exploring interactions or non-linear models in addition to the linear regression approach used in our study for a more comprehensive understanding. Moreover, our urban tolerance index was less combined with population trends for each species, especially for threatened or rarely observed species. This may be a bias, as the records may come primarily from targeted surveys conducted for the species. To improve our understanding of the rarest species in China, it is recommended to encourage citizen birdwatching across diverse habitat types, and promote sensitive recording methods where possible, such as using recording and video equipment, to obtain comprehensive and reliable data on the distribution and abundance of endangered or rare species.

## 6. Conclusion

Advancing urbanization is an important driving force of bird diversity loss. Mitigating these declines relies on understanding how birds respond to the urban environment. We integrated continuous measurements of urbanization response with citizen science data to derive the most taxonomically comprehensive analysis of urban tolerance among Chinese birds to date. Our findings reveal that passage migrants or species with more than one main migration type with larger clutch sizes and varied diets are the most well-suited for urban living. Moreover, the evolutionary relationship between species conceals the expression of several traits in urban tolerance: omnivorous birds that nest on architectural buildings or cliffs showed higher urban tolerance within clades. Responses to urbanization varied among species with different nesting, diet, foraging, and migration preference, highlighting the importance of diverse protection strategies (Croci et al., 2008). To optimize urban design and reduce the negative influence on birds from rapid urbanization, protecting existing trees and buildings where birds nest, increasing the proportion of shrubs to compensate for sources of ground birds (Conole & Kirkpatrick, 2011; Ikin et al., 2013), and controlling the predation risk of the ground nests are beneficial (Smith et al., 2011). Strengthening small green spaces and providing suitable space for summer migration is necessary (De Groot et al., 2021; Tryjanowski et al., 2017). Ultimately, our analyses highlight the difficulties and potential in explaining how species' traits influence urban tolerance, while adding knowledge for this question from an under-represented part of

the world.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.landurbplan.2023.104801>.

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