Urban tolerance of birds changes throughout the full annual cycle

Running title: Bird urban tolerance through time and space

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NOTE: This is a pre-print, and the final published version of this manuscript can be found here: https://doi.org/10.1111/jbi.14093

ACKNOWLEDGMENTS
We thank the countless citizen scientists who are contributing data that is continuously increasing our collective knowledge of biodiversity. We also thank the eBird team and the Cornell Lab of Ornithology who are dedicated to further bird conservation with their commitment to open-access data. Two anonymous reviewers and the associated editor provided comments that improved our manuscript. F.M. and Y.B. were financially supported by the Czech Science Foundation GAČR (Project Number 18-16738S).

SIGNIFICANCE STATEMENT

Urban tolerance in birds is a function of both species and season, and it is therefore important to consider the dynamic nature of birds' use of urban ecosystems throughout the full annual cycle.

ABSTRACT

Aim: Our objective was to quantify urban tolerance for North American birds across the full annual cycle. We tested (1) whether intra-annual variability of urban tolerance differed between migrants and residents and (2) whether intra-annual variability of urban tolerance was phylogenetically conserved. We then assessed how the relationship between ecological and life history traits and urban tolerance differed both across the year and between migrants and residents.

Location: North America.

Taxon: Birds.

Methods: We integrated a large citizen science dataset of observations for 237 bird species, remotely-sensed VIIRS night-time lights data, and trait data on each species. We estimate, for each species and each month of the year, a continuous measure of urban tolerance (i.e. the median of their distribution of observations across an urbanization gradient). We then use phylogenetic linear models to assess the relationship between this measure of urban tolerance and various life history and ecological traits.

Results: There was a distinct drop in the overall urban tolerance scores corresponding with the breeding period; this pattern was more pronounced for migrants compared to residents. Migrants also had greater intra-annual variability than resident species. We also found that the strength of the relationships between ecological and life history traits and urban tolerance was highly seasonal for most traits considered, and some divergent patterns were noted between migrants and residents.

Main conclusions: The urban tolerance of birds greatly changed throughout the annual cycle, with different patterns for migrants and residents. Compared to residents, migrants showed more intra-annual variability of urban tolerance with a drop in the average urban tolerance score during the breeding season. Together, our results suggest that urban tolerance is a function of both species and season, and they highlight the importance of considering the dynamic nature of birds' use of urban ecosystems throughout the full annual cycle.

Keywords: birds; big data; biodiversity; citizen science; phylogenetic models; urban tolerance; full annual cycle; migration

INTRODUCTION

The process of urbanization leads to habitat loss, degradation, and fragmentation — all of which can combine to negatively impact biodiversity (McKinney & Lockwood, 1999; La Sorte et al., 2018a; Piano et al., 2020, Schneiberg et al., 2020). Globally, urban areas are expected to expand by 1.2—1.8 million km^2 between 2000 and 2030 (Seto et al., 2012; Güneralp & Seto, 2013), making such urban expansion a major threat to biodiversity (Czech et al., 2000, Parnell et al., 2013). But urban expansion differentially affects biodiversity: some species are more at-risk than others (Rodewald & Gehrt, 2014; Lintott et al., 2016; Aronson et al., 2016; Sol et al., 2018). This is because each species has a unique set of life history, behavioural, and physiological attributes (Rodewald & Gehrt, 2014; Narango & Rodewald, 2018), as well as interactions with other species (Bonier & Martin, 2018), that lead to differential responses to urban environments (Lintott et al., 2016). As a result, some species are negatively impacted by urban expansion, but others can adapt, persist, and even thrive in novel urban environments (Chace & Walsh, 2006; Evans et al., 2009; Sol et al., 2014; Marzluff, 2017; Alberti et al., 2017; Sol et al., 2017). Traditionally, species have often been categorically classified as urban avoiders, utilizers, adapters, or exploiters (Blair 1996; Croci et al., 2008; Fischer et al., 2015); or even simply as urban or non-urban based on their presence in urban environments (Møller, 2009). Wildlife responses to urbanization are complex (Fischer et al., 2015), and it is now apparent that species do not fall neatly into two or three categories. Rather each species falls at a particular place along an urbanization-response continuum reflecting the differences in urban tolerance among species. As such, species' level of risk with increasing urbanization is more accurately classified using continuous, data-driven metrics compared to broad categories (Lepczyk et al., 2008; Evans et al., 2011; Sol et al., 2013; Marzluff, 2017).

An important challenge in quantifying a species' urban tolerance is accounting for the dynamic changes in the urban tolerance of a species through time. For example, species urban tolerance may change over long time periods showing adaptation and expansion into urban areas (e.g. Evans et al., 2009), species may become increasingly urban-tolerant in response to extreme climatic events such as droughts or bushfires (e.g. Davis et al., 2011), or species may alter their degree of urban tolerance based on their developmental stages (e.g. Whittaker & Marzluff, 2009; La Sorte et al., 2017). The most predictable example of a species changing their urban tolerance through time may be intra-annual changes, especially important for highly mobile species such as birds (La Sorte et al., 2014; 2017).

In the effort of quantifying the dynamic changes in a species' urban tolerance, migration is an important complication. This is reflected by the relatively high turnover throughout the year in urban areas with associated peaks of biodiversity during migration (La Sorte et al., 2014). Some individual birds may choose not to migrate but instead rely on the resources in urban ecosystems throughout the full annual cycle (Bonnet-Lebrun et al., 2020). The three-way interaction between migratory behavior (i.e. migrants vs residents), species' usage of urban areas, and life history strategy is crucial to fully dissect (Marra et al., 2015). One way to do this is to assess a species' variability of urban tolerance throughout the year, where species that show high intra-annual variability equate to species which use urban areas differentially throughout the year, and conversely, species with low intra-annual variability are rather consistent in their usage of urban areas throughout the year — whether tolerant or intolerant. However, the majority of previous studies which have assessed the urban tolerance of birds have mostly focused on the breeding season (e.g. Møller, 2009; Kark et al., 2007; Evans et al., 2011; Clergeau et al., 2006; Croci et al., 2008) or less commonly, the non-breeding season (e.g. Clergeau et al., 1998; Murthy et al., 2016). There are relatively few studies which quantify urban tolerance of birds across the full annual cycle (Marra et al., 2015), likely limiting our understanding of which species are most threatened by the negative impacts of urbanization and when these threats are greatest.

One mechanism to better understand which species are most susceptible to urbanization is a trait-based approach — i.e. understanding the relationship between urban tolerance and the ecological and life history traits that promote urban tolerance. However, life history traits are only one potential mechanism to dictate if, and to what extent, a species is found in urban areas: climatic factors, human facilitation, urban form, cultural factors, and species interactions can also influence species distributions in cities (Aronson et al., 2016; Lepczyk et al., 2017). Nevertheless, many ecological and life history traits are associated with urban bird species: migratory status (Friesen et al., 1995; Kark et al., 2007), residual brain size (Maklakov et al., 2011), degree of sociality (Kark et al., 2007; Jokimäki & Suhonen, 1998), diet (Fuller et al., 2008; Major & Parsons, 2010), fecundity (Møller, 2009), and niche breadth or width (Kark et al., 2007; Evans et al., 2011; Callaghan et al., 2019b) are among these traits. Despite the prevalence of this research question, the results are frequently inconclusive. Residual brain size, for example, is sometimes positively associated with urbanization (Maklakov et al., 2011, Møller & Erritzøe, 2015) and sometimes it is not an important trait

(Kark et al., 2007; Evans et al., 2011). Results have also been mixed for annual fecundity (cf. Croci et al., 2008; Møller, 2009; Evans et al., 2011) and niche breadth (cf. Kark et al., 2007; Evans et al., 2011). Despite the contradictory results, there appears to be a somewhat consistent pattern in the relationship between ecological and life history traits and urban tolerance: generalist species — species with relatively wide niche breadths — are less vulnerable to urban environments than specialist species (Evans et al., 2011; Callaghan et al., 2019b; Bonier et al., 2007; Pagani-Núñez et al., 2019). A better understanding of the relationship between ecological and life history traits and urban tolerance continues to be important (see Table 1 for our predictions).

In addition to traits, species may have a phylogenetic predisposition to being urban tolerant or intolerant, where certain subsets of species remain tolerant of, and therefore persist in, urban environments. And this relationship is non-independent with some traits (e.g. body size) being highly phylogenetically conserved. This line of thinking is evidenced by consistent findings of reduced phylogenetic diversity in urban areas (e.g. Sol et al., 2017; La Sorte et al., 2018a). While previous studies have tested for phylogenetic relatedness in urban tolerance responses (e.g. Evans et al.. 2011; Callaghan et al., 2019b), these have focused on static measures of urban tolerance, neglecting potential intra-annual changes. Testing whether there is phylogenetic relatedness in the intra-annual variability of urban tolerance will better help us understand the ecological and evolutionary consequences that promote urban tolerance among different species.

Our aim here was to quantify urban tolerance for North American birds across the full annual cycle — at a monthly resolution. We predicted that intra-annual variability of urban tolerance would be greater for migrants than residents because of their increased usage of urban areas during spring and fall migration (La Sorte et al., 2014; La Sorte et al., 2017), compared with their usage of mostly natural areas for breeding and wintering. Because of this predicted difference in migratory vs resident behavior, we also predicted that this would lead to strong phylogenetic relationships of intra-annual variability of urban tolerance. We then quantified the relationship between ecological and life history traits (see predictions in Table 1) and a species' urban tolerance throughout the full annual cycle — i.e. at a monthly temporal resolution. With this analysis, we tested (1) whether the relationship between life history traits and urban tolerance changes throughout the full annual cycle, and (2) whether there were differences in these relationships between migrants and residents. We predicted that there would be seasonal changes in the relationship between life history traits and urban tolerance, corresponding with the breeding season because some traits are likely most important during the breeding season when birds are focused on reproductive output than during other parts of their full annual cycle. We also predicted that the importance of traits would differ between migrants and residents as a result of these diverging life histories leading to different usage of urban areas throughout the full annual cycle.

METHODS

eBird citizen science data

We used eBird data as the basis of our bird observations. eBird (Sullivan et al., 2009; Sullivan et al., 2014; Sullivan et al., 2017), launched in 2002, is a successful citizen science project with >800 million global observations. The project collects data from volunteer birdwatchers who submit their observations via a mobile phone app or online portal. eBird is semi-structured, and collects data in the form of checklists, allowing a user to submit a complete or incomplete list of birds seen and/or heard while birdwatching. Filters are set by regional volunteers (Gilfedder et al., 2019) which provide expected species and abundances of species based on associated spatiotemporal coordinates of a checklist, and when an observation exceeds these filters, it undergoes rigorous review before being added to the eBird dataset.

We used the eBird basic dataset (version ebd_relMay-2019) and filtered the data between January 1st, 2014 and May 31st, 2019. We additionally further filtered the suite of potential eBird checklists, minimizing the influence of outliers on our analyses (Callaghan et al., 2017). The following criteria were employed: (1) only complete checklists were included in analyses; (2) only checklists which recorded birds for > 5 minutes and < 240 minutes were included in analyses; (3) only checklists which travelled < 5 km were included in analyses. Although we included only complete checklists, it is possible that some birders may not include some typical urban birds (e.g. Rock Pigeon, House Sparrow, European Starling) on eBird lists in urban settings, but possibly would include such species in rural settings. However, this remains to be formally tested.

Species-specific urban tolerance

After filtering by the above criteria, we only considered terrestrial species for inclusion in analyses: traditional seabird species (e.g. Procellariidae, Alcidae) were excluded from potential inclusion. For a species to be considered for inclusion, the species had to have a minimum of 250 observations per month — the temporal resolution of our analysis. The cut-off of 250 observations has previously been shown to correspond with the ability of continental-scale data to predict local-scale responses to urbanization (Callaghan et al., 2020). We then used the American Birding Association’s checklist of birds (a maintained list of regularly occurring North American birds as well as rare, casual, and accidental species) to only include regularly occurring North American avifauna by eliminating code 3 (i.e. rare), 4 (i.e. casual), and 5 (i.e. accidental) species (see http://listing.aba.org/checklist-codes/ for more details). We only considered species found in the contiguous continents and excluded species found on oceanic islands, as well as Alaska. Because our analysis was focused on year-round urban tolerance of a species, we used all observations from North and South America to incorporate the full range of urban tolerance throughout the year for those species which are not year-round residents in North America (e.g. neotropical migrants). Each species was treated individually, and because we used a minimum value of 250 observations in each month, we ensured that the species was relatively well-sampled, thus minimizing the effects of the sampling bias in eBird with North America more thoroughly sampled compared to South America. We were then left with a total of 490 species which met the above criteria (Table S1).

Each observation for a species (i.e. the underlying checklist species are observed on) was assigned a measure of continuous urbanization — VIIRS night-time lights (Elvidge et al., 2017). VIIRS night-time lights is a proxy for a continuous measure of urbanization (Pandey et al., 2013; Zhang & Seto, 2013; Stathakis et al., 2015), as measured from space. This definition is focused on a macro-ecological scale, measuring very urban areas (i.e. central business districts) to very non-urban areas (i.e. protected areas far from human habitation). Importantly, our analysis does not account for fine-scale measures of urbanization such as the amount of greenspace a bird uses, or the quality of a given habitat patch. Previous work has demonstrated that the urban scores assigned to birds behave similarly when assigned using underlying VIIRS night-time lights and human population density (Callaghan et al., 2019a) — two disparate measures of urbanization. These urban scores have also been demonstrated to highly correspond with local-scale urbanization responses (Callaghan et al., 2020). We used Google Earth Engine (Gorelick et al., 2017) to assign each eBird checklist its associated level of urbanization (i.e. VIIRS night-time lights). The VIIRS product is available from NOAA and already archived in Google Earth Engine, where we used it. The native resolution of the product is at 15-arc-seconds (approximately 500 meters) and was used in the default projection of Google Earth Engine of WGS84. Because of computational restrictions, we used a reduction technique to aggregate the measure of VIIRS night-time lights. Monthly scenes of average radiance (nW cm^{-2} sr^{-1}) between January 1st, 2014 and January 1st, 2019 were used, and the temporal median radiance was calculated per 15-arc-second pixel. These values were then reprojected to a pixel size of 5 km, using a composite stack of the 2014-2019 VIIRS night-time light layers. This 5 km scale was used to account for any spatial mismatches between the eBird data and underlying urbanization level, and because eBird checklists are able to travel (up to 5 km based on our aforementioned criteria), making the precise location of where a specific species was seen uncertain. The relative ranking of urban scores among species is robust based on the buffer size used to assign VIIRS night-time lights (Callaghan et al., 2019a).

Every bird species was accordingly left with a distributional response to urbanization, representing the number of that species' observations as it relates to urbanization, stratified by month (e.g. Figure 1). The median of each monthly distribution (Figure 1) was defined as the urban tolerance for a species in that particular month (Callaghan et al., 2019b; 2019a; 2020). Previous work has shown that these urban scores are robust, despite the biases (e.g. a differential effort among checklists) associated on different eBird checklists (Callaghan et al., 2020; Callaghan et al. 2019a). To account for potential intra-specific variation in the urban tolerance of a species throughout a species' geographic range we resampled the urban tolerance measure to calculate a mean urban score for each species per month by using the mean of 1000 medians drawn from 100 observations each (see details in Figure S1), which also provided us with a measure of variance (i.e. standard deviation) for each species' urban score.

Ecological and life history traits

We used eight published ecological and life history traits extracted from a variety of sources (see Table 1) which have previously been used to describe a species relationship with urbanization. We used a discrete classification of migrants and residents, and continuous classifications of diet breadth, habitat generalism, clutch size, brain residual, range size, mean flock size, and body size. All continuous variables were tested for collinearity before modelling and minimal correlation was found between any variables (Figure S2). Table 1 provides details on each trait and an associated prediction. Of our 490 original species possible for analyses, a total of 237 had complete trait data and we used these 237 species for further analyses (Table S1).

Quantifying intra-annual variability of urban tolerance within and among bird species

We defined the intra-annual variability in urban tolerance as the standard deviation of the 12 monthly urban scores and tested whether the intra-annual variability measures were phylogenetically related. A consensus tree was obtained using 1,000 backbone trees from Jetz et al. (2012) for the 237 species in our analysis and applying the 50% majority rule. We then tested for phylogenetic signal (Losos, 2008) as a measure of the extent of phylogenetic relatedness in the intra-annual variability of urban tolerance, using 5 different indices: C-mean, I, K, K*, and Lambda (Keck et al., 2016). To test whether migrants had greater intra-annual variability of urban tolerance than residents, we ran a phylogenetic linear model where migration status was the predictor variable and the response variable was log-transformed intra-annual variability of urban tolerance of a species. Significance was concluded when p-value < 0.05.

Quantifying the relationship between a species' urban tolerance and ecological and life history traits across the full annual cycle

We again first tested for phylogenetic relatedness, by testing for a phylogenetic signal, using 5 different indices: C-mean, I, K, K*, and Lambda (Keck et al., 2016). The resampled monthly urban scores were the response variable, and this test was performed separately for each month since our aim was to explore how species-specific urban tolerance measures varied monthly. We found a strong phylogenetic signal in species-specific urban tolerance measures for all months of the year (Table S2) and therefore used phylogenetic linear models where the response variable was log-transformed species-specific urban tolerance. First, we fitted a model where migratory status was included as a categorical variable, assessing the overall relationships among all 237 species. However, because there was a clear difference in migrants and residents, we then stratified models to these two discrete classifications. We ran a total of 24 phylogenetic linear models (i.e. 12 monthly models for migrants and 12 monthly models for residents). For each model we included all predictor terms in a single model. The response variable for each model was log-transformed species-specific urban tolerance, and the predictor variables were continuous classifications of diet breadth, habitat generalism, clutch size, log-transformed body size, log-transformed flock size, and log-transformed range size (Table 1). Because our analysis was focused on investigating the relationship between ecological and life history traits (i.e. predictor variables) and urban tolerance (i.e. response variable) throughout the year, we conducted 12 separate models (one for each month) stratified to residents and migrants (24 total models). In each model, we used the inverse of the standard deviation of the urban tolerance measure as weights, providing more weighting to those species whose urban tolerance did not vary due to potential intra-specific variability in urban tolerance (see details in Figure S1). By stratifying our models to a monthly resolution, we minimized the undue leverage of seasonal differences in data submitted to eBird because the relative urban tolerance scores among species are specific to each month, independent of the amount of data submitted in other months. We did not conduct model selection and were not focused on significance of the model fits, but rather the patterns shown of the intra-annual relationships. We then extracted the parameter estimates from each of these 24 models for each predictor variable. All predictor variables were scaled and centered to ensure standardized parameter estimates (Gelman, 2008). We present the results from the global phylogenetic models, but also corroborated these results with a model averaging approach, finding similar patterns.

Data analyses and availability

All data were processed in the R environment (R Core Team, 2020) and relied heavily on the tidyverse workflow (https://workflows.tidymodels.org) which helps for data manipulation and visualization (Wickham et al., 2019). For phylogenetic analyses, we relied on the following packages: ‘ape’ (Paradis et al., 2004) for reading, writing, and manipulating phylogenetic trees; ‘phangorn’ (Schliep, 2010) for visualizing phylogenetic trees; and ‘Rphylip’ (Revell and Chamberlain, 2014) for various phylogenetic methods. All eBird data are freely available for download (https://ebird.org/data/download) and the phylogenetic tree can be downloaded for free (https://birdtree.org/). The summarized portions of the eBird data and the predictor variables necessary for our analyses, along with code to reproduce our analyses are available at: https://zenodo.org/record/4448909.

RESULTS

A total of 171,114,243 observations were used to derive monthly species-specific urban scores for 237 species throughout North America (Table S1). Species-specific urban scores were generally log-normally distributed for each month (Figure 2a). Urban tolerance, among all species, was greatest during the winter months (highest mean of all urban scores) and lowest during the summer months (lowest mean of all urban scores) demonstrating that during the winter, birds were more likely to be found in urban ecosystems. There was a distinct drop in the mean urban scores corresponding with the breeding period (Figure 2b); but this pattern was more pronounced for migrant species compared with resident species (Figure 2c), and the variability was greater for migrants than residents.

There was large variation among species' intra-annual variability of urban tolerance (i.e. the standard deviation of all monthly urban scores), ranging from 0.002 to 5.266, with a mean of 0.835 ± 0.744 (Figure S3). The species with the lowest intra-annual variability in urban scores were Mexican Jay (0.002), Canada Jay (0.033), Painted Redstart (0.037), and Pinyon Jay (0.045). Conversely, the species with the highest intra-annual variability in urban scores were Red-crowned Parrot (5.266), White-throated Swift (4.688), Rufous Hummingbird (3.501), and Yellow-crowned Night-Heron (2.946). Across all species, intra-annual variability of urban tolerance tended to be clustered around the phylogenetic tree, as we found a strong phylogenetic signal in the intra-annual variability of urban tolerance ($K=0.1719$, p-value=0.0001; Figure 3; Table S3). Migrants had greater intra-annual variability (0.925 ± 0.716) than resident species (0.557 ± 0.768), but this was not statistically significant when accounting for phylogeny (Figure S4; Table S4).

When considering a model with all 237 species (i.e. migrants and residents) we found that for a number of traits, the relationship between urban tolerance and that trait varied in time

(Figure 4). The relationship between clutch size, mean flock size, habitat generalism, and diet breadth with urban tolerance varied throughout the year. There was positive association between urban tolerance with clutch size and mean flock size, and this relationship showed a strong increase during the breeding months. Similarly, the relationship between urban tolerance and habitat generalism showed a strong positive correlation during the breeding months, while the same relationship was negative during all months besides April, May, and June. Diet breadth showed a strong negative association during the breeding months. Conversely to these traits, range size, brain residuals, and body size did not show any apparent differences in the strength of the relationship throughout the year. Urban tolerance was negatively associated with body size and range size across all months and was positively associated with brain residual across all months. And lastly, urban tolerance had a more positive relationship with resident species than with migrant species across all months, but this was most pronounced in June (Figure 4).

When we further stratified our models to migrants and residents (i.e. a model fit for each discrete category for each month; 24 unique models), we found similar patterns to a model including all species (Figure 5, Figure S5). The relationship between urban tolerance and clutch size, diet breadth, and brain residuals all varied seasonally, whereas the relationship between urban tolerance and habitat generalism and flock size showed weaker seasonal changes. For both migrants and residents, clutch size was strongly associated with urban tolerance and this peaked during the breeding months. For migrants, brain residual was strongly associated with urban tolerance during the breeding months, but for residents, brain residual was negatively associated with urban tolerance during the breeding months. For both migrants and residents, diet breadth was negatively associated with urban tolerance during June, but generally positively related with urban tolerance throughout other months. While the relationship between urban tolerance and habitat generalism and flock size showed little variation throughout the year, there were contrasting patterns for migrants and residents. Habitat generalism was positively associated with urban tolerance for residents but not for migrants, and flock size was positively associated with urban tolerance for migrants but not for residents. The relationship between urban tolerance and body size and range size did not show any noticeable changes throughout the year, but both showed diverging patterns for migrants and residents. Body size was negatively related to urban tolerance for migrants and neither positively nor negatively related to urban tolerance for residents, and conversely range size was negatively related to urban tolerance for residents but neither positively nor negatively related to urban tolerance for migrants.

DISCUSSION

By quantifying urban tolerance of North American birds (N=237 species) across the full annual cycle, we demonstrated that on average, the urban tolerance of birds decreases during the breeding season (Figure 2b). Our results suggest that birds — across species — use urban areas more during the non-breeding season than the breeding season, confirming previous studies (e.g. La Sorte et al., 2014) but extending these studies by providing species-specific measures of urban tolerance. Importantly, this breeding season drop in the use of urban environments was much stronger for migrants compared to residents (Figure 2c). This result aligns with greater intra-annual variability of urban tolerance for migrants. Shifts in the extent to which birds use urban areas throughout the year (e.g. La Sorte et al., 2014; La Sorte et al., 2017; La Sorte & Graham 2020) are important in the context of expanding urban areas and suggests that simple classifications of urban tolerance based on one season or yearly averages may exclude important information.

We extended the longstanding relationship between life history traits and urban tolerance (e.g. Beissinger & Osborne, 1982; Kark et al., 2007; Croci et al., 2008; Fuller et al. 2008) to a monthly resolution, made possible by our dynamic continuous measure of urban tolerance. We showed clear intra-annual patterns in the relationship between life history traits and urban tolerance (Figure 4; Figure 5): almost all traits investigated, with the exception of body size, showed some differential responses corresponding roughly with the breeding season. For example, clutch size, habitat generalism, and flock size showed the strongest positive association with urban tolerance during the breeding season, whereas diet breadth showed the opposite pattern (Figure 4). These results generally confirm previous studies which have found — during the breeding season — the importance of clutch size (Croci et al., 2008, Møller, 2009), gregariousness (Coleman & Mellgren, 1994, Jokimäki & Suhonen, 1998), and habitat generalism (DeVictor et al., 2008), indicating the relevant importance of such traits for urban birds during the breeding season. Conversely, we found that diet breadth was least associated with urban tolerance during the breeding season, contradicting the importance of diet found in previous studies (Beissinger & Osborne, 1982; Major & Parson, 2010; Evans et al., 2011). We note, however, that our measure of diet breadth — as well as our measure of urban tolerance — differs to that of previous research (Fischer et al., 2015). The contradictory result of diet breadth could be due to these methodological differences, as well as contrasting sample sizes. Or, it could be a result of a biological difference that is shown by looking at the relationship of diet breadth throughout the year. Species can change their diet throughout the course of the year with increased diet breadth during the non-breeding season compared with the breeding season, for example nectarivores can sometimes heavily rely on insects during certain parts of their full annual cycle. Our measure of diet breadth, however, does not account for these potential species-specific differences throughout the year. Ultimately, more research of the relationship between urban tolerance and life history traits throughout the full annual cycle will help understand how the importance of species traits (e.g. diet breadth) changes throughout the year.

By separating resident and migrants we found a number of diverging patterns between these two life history strategies: (1) habitat generalism was always positively associated with urban tolerance for residents but generally showed little association for migrant species; (2) flock size was positively associated with urban tolerance for migrant species but negatively associated for resident species; and (3) brain residuals were positively associated with urban tolerance for migrants but negatively associated for resident species. Migrants clearly had greater intra-annual variability than resident species (Figure S4), suggesting that migrants encounter urban areas to a greater extent than residents throughout their annual life cycle. While this pattern may be unsurprising — as migrant species likely use a greater range of habitat throughout their full-annual cycle — this is the first time this pattern has ever been clearly delineated with such a broad taxonomic and geographic coverage. This is best explained by the fact that migrant species will use urban areas during their migrations (La Sorte et al., 2014; La Sorte et al., 2017; Amaya-Espinel & Hostetler, 2019; Cohen et al., 2021) and some migrants may even over-winter in urban areas (Bonnet-Lebrun et al., 2020). Yet, migratory species face many threats in urban environments throughout their migration, including night-time light pollution in urban environments (Horton et al., 2019), window collisions (Santiago-Alarcon & Delgado-V, 2017), and an increased predation risk in urban environments (Frey et al., 2018). Such threats are probably more detrimental to species with a migratory life history, explaining why we found that resident species had higher urban tolerance scores than migrant species for every month of the year, and this pattern was pronounced during the breeding season (Figure 5).

When considering migrants compared with residents across a large geographic range, such as in this study, it is important to consider the different migration strategies and differences in breeding seasons that species will undergo at different latitudes. Different groups of birds will migrate at different times of the year throughout North America (cf. waterfowl and neotropical migrants) and this pattern can change throughout different parts of North America (cf. western and eastern North America). Further, we categorically treated residents and migrants as two distinct groups. We acknowledge that migration strategies are complex (e.g. Phillips 1951) including species with fully-migratory populations, species with partially-migratory populations, and species which show both migrant and sedentary populations. These different migration timings can lead to different breeding periods in different parts of North America (e.g. some species can start breeding in Florida in April before other species even reach their breeding grounds in New York in May). Some of these differences are evidenced by the variance surrounding our average urban tolerance scores (Figure 2). More refined spatial-temporal analyses in the future (e.g. by repeating our analysis at different latitudes) will help to understand the extent to which birds change their urban tolerance throughout the year. Another important issue is intra-specific variability of a species' urban tolerance (i.e. a given species could have a population that is highly urban tolerant in one region but a population intolerant to urban environments in another). This is represented as the within month spread of values in Figure 1. We accounted for this by resampling the mean urban tolerance for every species (see Figure S1). North America is unique given their large migratory signal whereby many migrants are long-distance neotropical migrants, and this process leads to intra-annual temporal turnover (Hurlbert & Liang, 2012; La Sorte et al., 2014). Our finding that migrants have greater intra-annual variability of urban tolerance than resident is likely to generalize to other regions with similar signals in migratory activity (e.g.

Europe), but less likely to generalize to regions with little or no migratory behavior (e.g. the tropics, Australia); yet this remains to be formally tested.

We capitalized on the big data revolution in ornithology (La Sorte et al., 2018b) — relying on > 200 million citizen science observations submitted to eBird — to disentangle the relationships between patterns of urban tolerance throughout the full annual cycle. Our methodological approach is easily repeatable in other parts of the world, relying predominantly on trait-data, citizen science data, and an open-access remotely sensed measure of urbanization. Further development of continuous metrics of urban tolerance will help enhance our understanding of the dynamic temporal changes in species-specific responses to urbanization. This approach should be leveraged for other taxa, other regions of the world, and at both local and macroecological scales.

Currently, our results are restricted to a macro-ecological scale, incorporating a broad measure of urbanization. Our methods were aimed at incorporating a broad geographic and taxonomic coverage in our analysis, and therefore we are unable to determine differences in how a species uses the urban matrix. For example, because we used a 5 km buffer to minimize biases in spatial mismatch with eBird citizen science data, our analysis does not incorporate the heterogeneity of urban areas (Shwartz et al., 2008). Urban areas can have high- or low-quality greenspaces, which would influence the likelihood a species using that urban area (Sandström et al., 2006; Aronson et al., 2017). During the breeding season, birds breeding in urban areas are likely restricted to urban green spaces (Ferenc et al., 2013), and there may be requirements in the greenspace size necessary for breeding (La Sorte et al., 2020). Future research should therefore look to build upon our research to investigate local-scale analyses of how different species use urban areas, and how ecological and life history traits influence the extent of this usage. Further exploration will likely require more fine-scale measures of urbanization (see Moll et al., 2019), below the 500 m native resolution of VIIRS night-time lights that we use here. We also average intra-annual changes throughout the study period (2014-2019), but some changes in urbanization are possible throughout this time frame. Understanding intra-annual changes in urban tolerance coupled with changes in urban tolerance among years, will be an important area of future research. There is a difference between a species using urban areas, and successfully thriving in urban areas (Fischer et al., 2015), that we did not incorporate here. A potential avenue to extend our research would be to move beyond presence/absence and incorporate relative abundance of birds (e.g. Fink et al., 2020) along the urbanization gradient.

Given the anticipated increase in urban expansion throughout the world (Seto et al., 2012; Güneralp & Seto, 2013), it is increasingly important to understand the winners and losers as land use shifts all across the world. Our results suggest that migrant species are less urban-tolerant than resident species on average and especially during the breeding season. In addition, migrants with small relative brain size and large body size are at the greatest significant risk from increased urbanization. These effects add to a more complete understanding of bird urban tolerance, especially as the need for a full annual cycle conservation plan is increasingly recognized (Schuster et al., 2019; Aronson et al., 2017). Habitat within urban centers may be important for migrants, even if it does not support high level of breeding diversity, and thus at a given latitude urban greenspaces may be crucial for species migrating towards distant breeding grounds, but may not be sufficient for locally breeding birds (e.g. Carbó-Ramírez & Zuria, 2011). The spatial and temporal changes of a species urban tolerance should be accounted for in future research and future conservation planning.

TABLES

Table 1. The ecological and life history traits used in this analysis, with a brief description, a summary of our hypothesis, and a reference for the data source. The complete references for each source are provided in the references.

Trait	Description	Predictions	Source of data
Clutch size	Continuous measure of fecundity (mean clutch size)	We predicted that increased clutch size would be positively associated with urban tolerance.	Lislevand et al. 2007
Migrant status	Categorical measure of either resident or migrant	We predicted that residents would be more urban tolerant than migrants.	Sayol et al. 2018
Habitat generalism	Continuous measure of the generalism for a species in their habitat choice taken as the sum of IUCN habitats they occupy	We predicted that increased habitat generalism would be positively associated with urban tolerance.	Langham et al. 2015
Body size	Continuous measure of body size (mass in grams)	We predicted that large body size would be positively associated with urban tolerance.	Myhrvold et al. 2015
Flock size	Continuous measure of mean flock size across all eBird observations submitted for a species	We predicted that large flock size would be positively associated with urban tolerance.	eBird 2019
Diet breadth	Continuous measure of niche expansion	We predicted that increased diet breadth would be positively associated with urban tolerance.	Sayol et al. 2018
Brain residual	Continuous variable of residuals from a log-log phylogenetic Generalized Least Square regression of absolute brain size against body mass	We predicted that larger residual brain size would be positively associated with urban tolerance.	Sayol et al. 2018
Range size (km^2)	Continuous variable of total range size in km^2	We predicted that increased range size would be positively associated with urban tolerance.	BirdLife International 2019

FIGURES

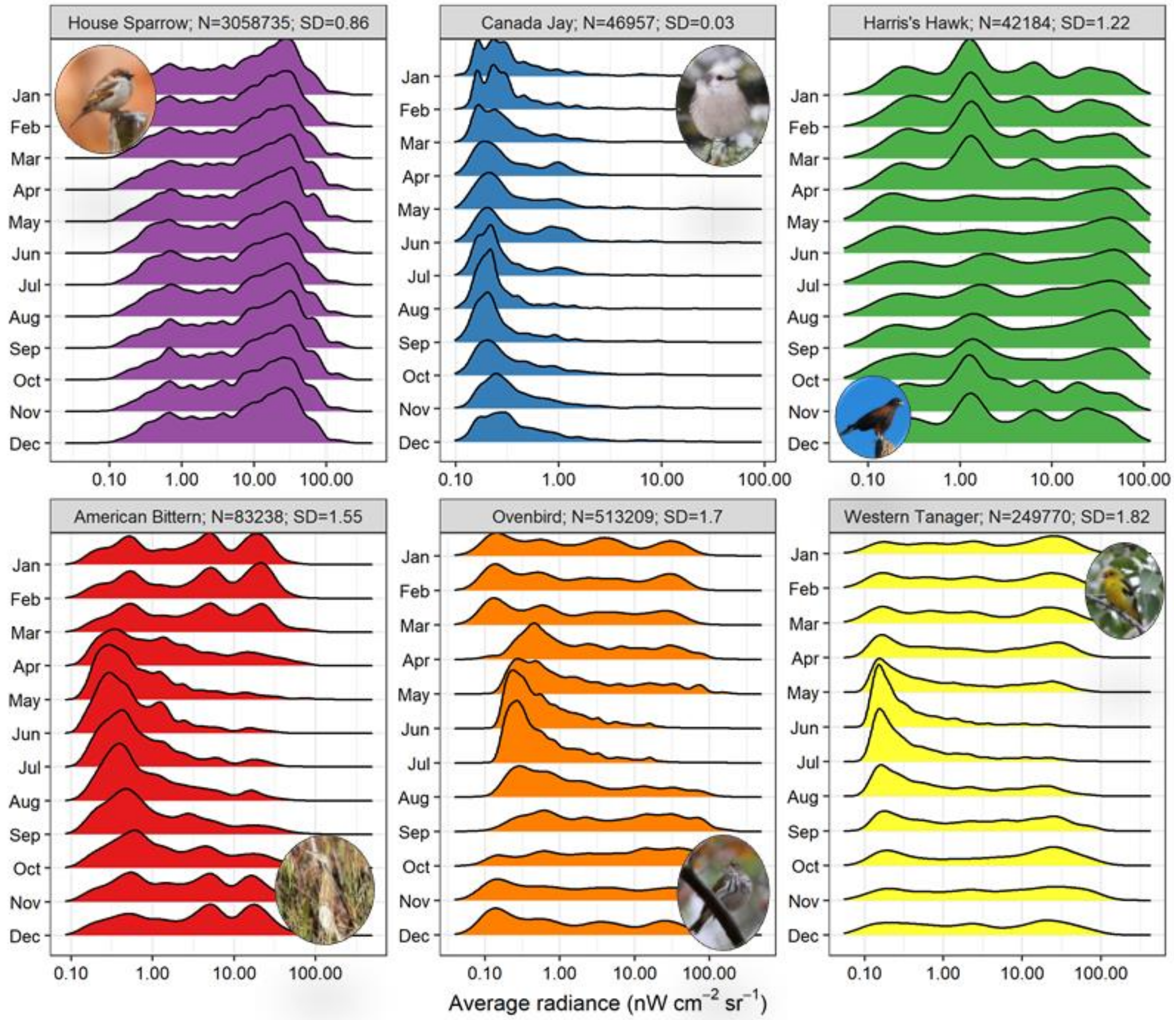


Figure 1. Six example species (House Sparrow [photo by Paul Reeves], Canada Jay [photo by Dakota Duff], Harris's Hawk [photo by Jerry Oldenettel], American Bittern [photo by Corey Callaghan], Ovenbird [photo by Mark Dennis], and Western Tanager [photo by Osiel]) examined in our analyses, showing their monthly distribution of observations in response to VIIRS night-time lights. The House Sparrow represents an example of a bird with high urban tolerance with little change through the year; Canada Jay's urban tolerance is relatively static and low; and Harris's Hawk are more generalist with minimal changes throughout the year. In contrast, the American Bittern, Ovenbird, and Western Tanager all show seasonal shifts in urban tolerance. For each species, the plot title shows both the total number of observations for that species and the standard deviation of the monthly mean urban tolerance scores (i.e. the species-specific intra-annual variability of urban tolerance); note the contrasting SD values for Western Tanager versus Canada Jay.

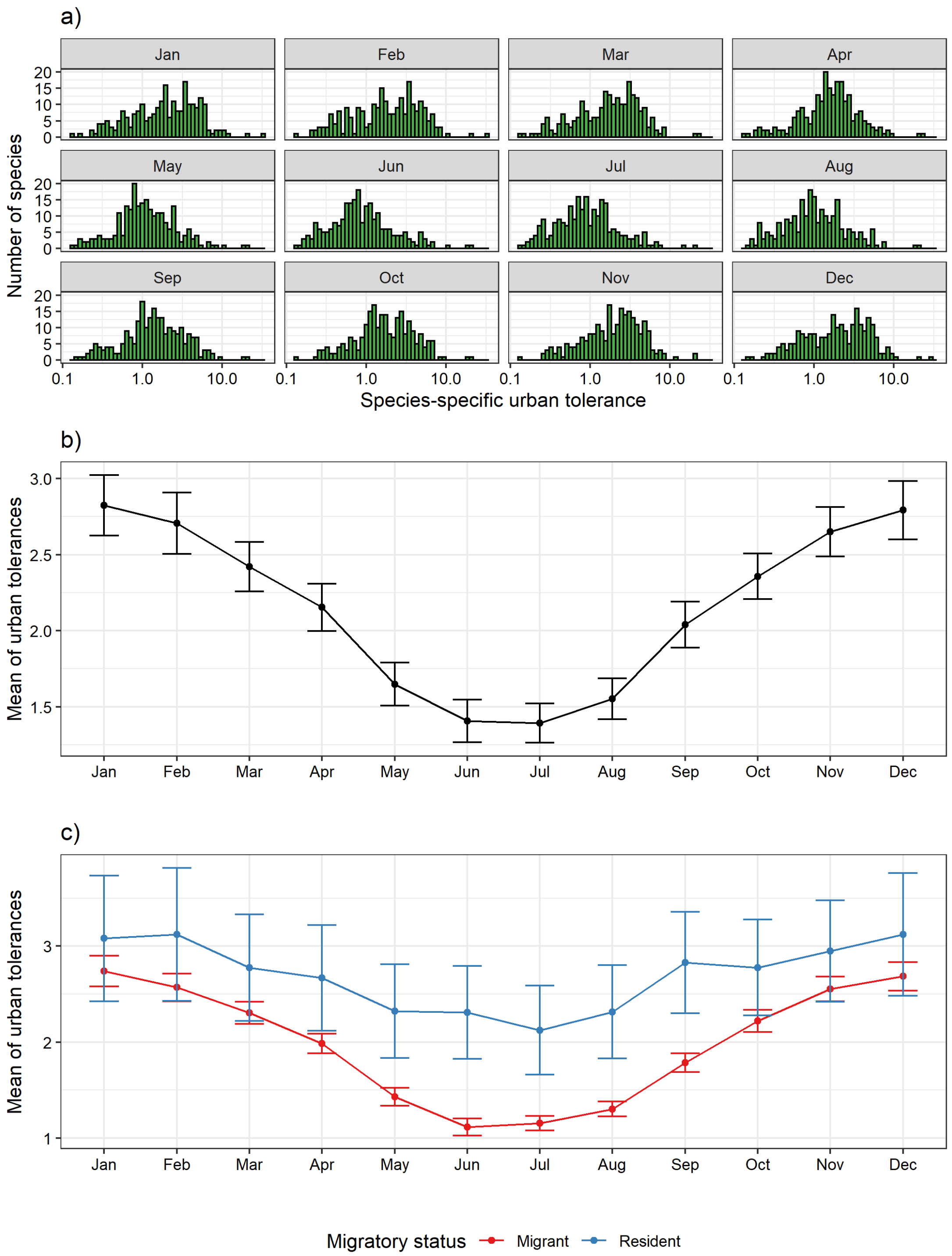


Figure 2. a) Monthly distributions of species-specific urban scores, showing a generally log-normal distribution across months; b) The mean (and standard error) of all species-specific urban scores plotted for each month showing a distinct drop during the breeding months, and c) The mean (and standard error) of all species-specific urban scores plotted for each month, stratified for migrants and residents, showing a more pronounced drop in urban scores during the breeding months for migrants compared with residents.

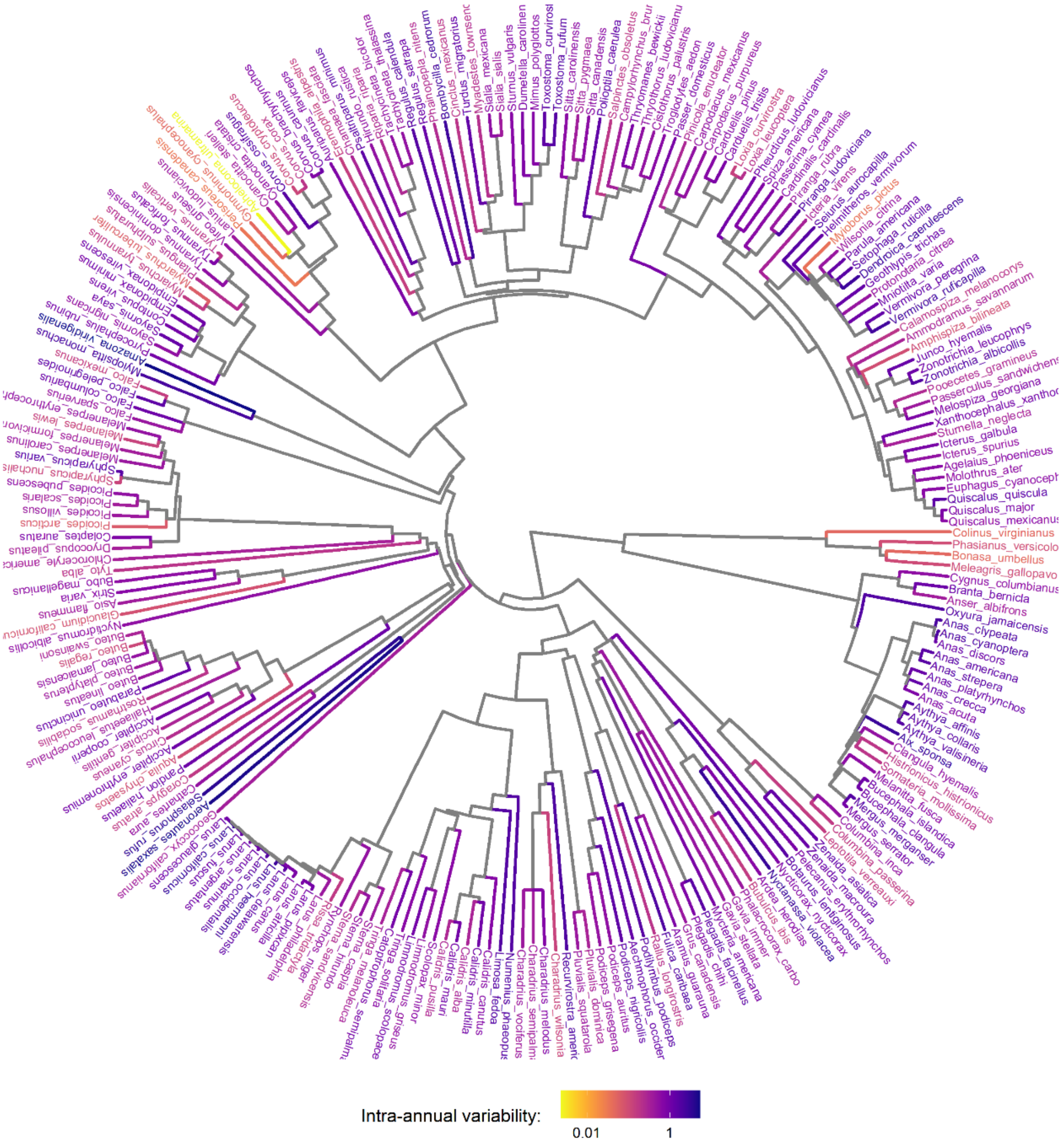


Figure 3. Phylogenetic tree for 237 species, from Jetz et al. (2012), mapped with a species-specific measure of intra-annual variability (i.e. the standard deviation of the monthly urban tolerance scores of a species). We found a strong phylogenetic signal in this response variable (Table S3).

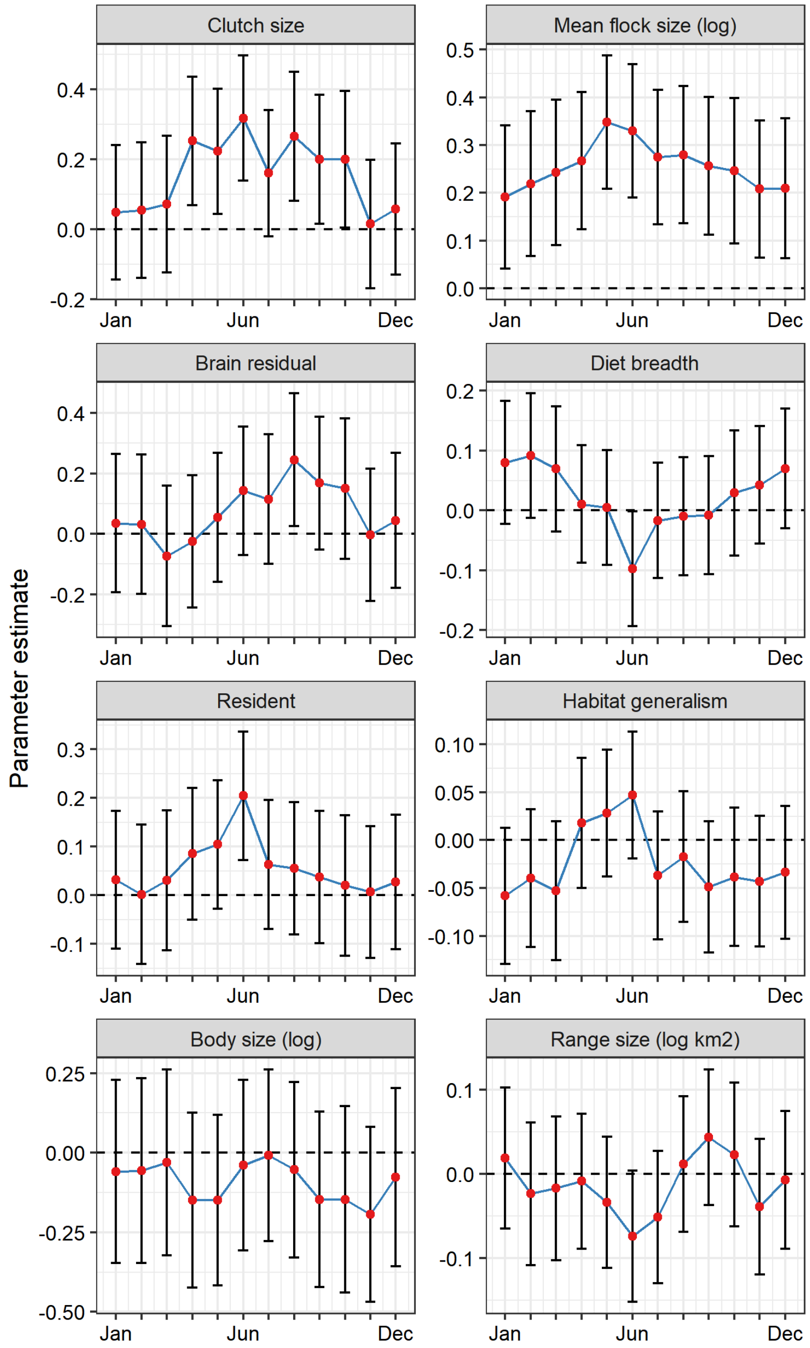


Figure 4. Standardized parameter estimates for phylogenetically controlled models where the response variable was log-transformed species-specific urban tolerance, and models were repeated for each month. Resident is a categorical variable compared with migrants (the intercept – not shown here), with a positive parameter indicating a resident species have a higher urban tolerance value compared to migrant species for a given month. The error bar represents 95% confidence intervals of the parameter estimate. The dashed line represents zero, and any parameter estimates above this can be interpreted as positively interacting with urban tolerance, and vice versa for any parameter estimates below this dashed line. Clutch size, flock size, brain residual, and diet breadth all showed clear seasonal patterns, whereas habitat generalism, body size, and range size showed less clear seasonal patterns. Residents were always more associated with urban tolerance compared to migrants, and this was pronounced during June.

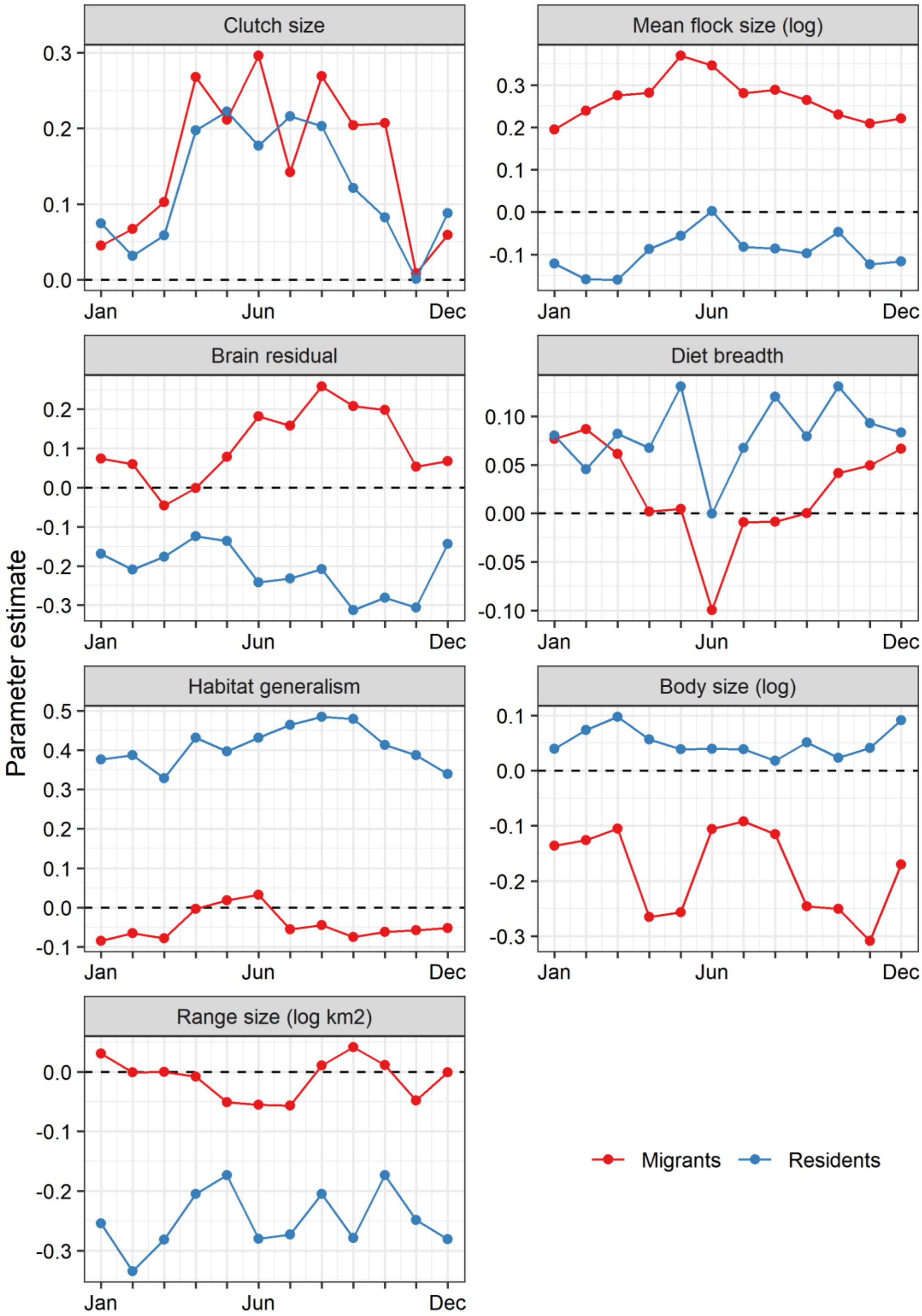


Figure 5. Standardized parameter estimates for phylogenetically controlled models where the response variable was log-transformed species-specific urban tolerance, and models were repeated for each month, stratified to migratory status. The dashed line represents zero, and any parameter estimates above this can be interpreted as positively affecting urban-tolerance, and vice versa for any parameter estimates below this dashed line. For parameter estimates with 95% confidence intervals see Figure S5.

DATA AVAILABILITY

All eBird data are freely available for download (https://ebird.org/data/download) and the phylogenetic tree can be downloaded for free (https://birdtree.org/). The summarized portions of the eBird data and the predictor variables necessary for our analyses, along with code to reproduce our analyses are available at: https://zenodo.org/record/4448909.

REFERENCES

Alberti, M., Correa, C., Marzluff, J. M., Hendry, A. P., Palkovacs, E. P., Gotanda, K. M., Hunt, V. M., Apgar, T. M., & Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proceedings of the National Academy of Sciences*, **114**, 8951–8956.

Amaya-Espinel, J. D., & Hostetler, M. E. (2019). The value of small forest fragments and urban tree canopy for Neotropical migrant birds during winter and migration seasons in Latin American countries: A systematic review. *Landscape and Urban Planning*, **190**, 103592.

Aronson, M. F. J., Nilon, C. H., Lepczyk, C., Parker, T. S., Warren, P. S., Cilliers, S. S., Goddard, M. A., Hahs, A. K., Herzog, C., Katti, M., La Sorte, F. A., Williams, N. S. G., & Zipperer, W. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology*, **97**, 2952–2963.

Aronson, M. F. J., Lepczyk, C., Evans, K. L., Goddard, M. A., Lerman, S. B., Maclvor, J. S., Nilon, C. H., & Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, **15**, 189–196.

Beissinger, S. R., & Osborne, D. R. (1982). Effects of urbanization on avian community organization. *The Condor*, **84**, 75–83.

BirdLife International. (2019). BirdLife DataZone. Available here: http://datazone.birdlife.org/.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506–519.

Bonier, F., Martin, P. R., & Wingfield, J. C. (2007). Urban birds have broader environmental tolerance. *Biology Letters*, **3**, 670–673.

Bonnet-Lebrun, A., Manica, A., & Rodrigues, A. S. L. (2020). Effects of urbanization on bird migration. *Biological Conservation*, **244**, 108423.

Callaghan, C., Lyons, M., Martin, J., Major, R., & Kingsford, R. (2017). Assessing the reliability of avian biodiversity measures of urban greenspaces using eBird citizen science data. *Avian Conservation and Ecology*, **12**(2), 12.

Callaghan, C., Major, R. E., Cornwell, W. K., Poore, A. G., Wilshire, J. H., & Lyons, M. (2020). A continental measure of urbanness predicts avian response to local urbanization. *Ecography*, **43**, 528–538.

Callaghan, C. T., Major, R. E., Lyons, M. B., M, M. J., Wilshire, J. H., Kingsford, R. T., & Cornwell, W. K. (2019a). Using citizen science data to define and track restoration targets in urban areas. *Journal of Applied Ecology*, **56**, 1998–2006.

Callaghan, C. T., Major, R. E., Wilshire, J. H., Martin, J. M., Kingsford, R. T., & Cornwell, W. K. (2019b). 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. *Oikos*, **128**, 845–858.

Carbó-Ramírez, P., & Zuria, I. (2011). The value of small urban greenspaces for birds in a Mexican city. *Landscape and Urban Planning*, **100**, 213–222.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, **74**, 46–69.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., & Dinetti, M. (2006). Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation*, **127**, 336–344.

Clergeau, P., Savard, J.L., Mennechez, G., & Falardeau, G. (1998). Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. *The Condor*, **100**, 413–425.

Cohen, E. B., Horton, K. G., Marra, P. P., Clipp, H. L., Farnsworth, A., Smolinsky, J. A., Sheldon, D., & Buler, J. J. (2021). A place to land: spatiotemporal drivers of stopover habitat use by migrating birds. *Ecology Letters*, **24**, 38–49.

Coleman, S. L., & Mellgren, R. 1994. Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, , 903–907.

Croci, S., Butet, A., & Clergeau, P. (2008). Does urbanization filter birds on the basis of their biological traits? *The Condor*, **110**, 223–240.

Czech, B., Krausman, P. R., & Devers, P. K. (2000). Economic associations among causes of species endangerment in the united states: associations among causes of species endangerment in the united states reflect the integration of economic sectors, supporting the theory and evidence that economic growth proceeds at the competitive exclusion of nonhuman species in the aggregate. *BioScience,* **50**, 593–601.

Davis, A., Taylor, C. E., & Major, R. E. (2011). Do fire and rainfall drive spatial and temporal population shifts in parrots? A case study using urban parrot populations. *Landscape and Urban Planning*, **100**, 295–301.

Dearborn, D. C. & Kark, S. (2010). Motivations for conserving urban biodiversity. *Conservation Biology*, **24**, 432–440.

Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**, 507–514.

Elvidge, C. D., Baugh, K., Zhizhin, M., Hsu, F. C., & Ghosh, T. (2017). VIIRS night-time lights. *International Journal of Remote Sensing*, **38**, 5860–5879.

Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D., & Gaston, K. J. (2011). What makes an urban bird? *Global Change Biology*, **17**, 32–44.

Evans, K. L., Gaston, K. J., Frantz, A. C., Simeoni, M., Sharp, S. P., McGowan, A., Dawson, D. A., Walasz, K., Partecke, J., Burke, T., & Hatchwell, B. J. (2009). Independent colonization of multiple urban centres by a formerly forest specialist bird species. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2403–2410.

Fink, D., Auer, T., Johnston A., Ruiz-Gutierrez, V., Hochachka, W. M., & Kelling S. (2020). Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications*, **30**, e02056.

Fischer, J. D., Schneider, S. C., Ahlers, A. A., & Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, **29**, 1246–1248.

Ferenc, M., Sedláček, O., & Fuchs, R. (2014). How to improve urban greenspace for woodland birds: site and local-scale determinants of bird species richness. *Urban Ecosystems*, **17**, 625–540.

Frey, D., Vega, K., Zellweger, F., Ghazoul, J., Hansen, D., & Moretti, M. (2018). Predation risk shaped by habitat and landscape complexity in urban environments. *Journal of Applied Ecology*, **55**, 2343–2353.

Friesen, L. E., Eagles, P. F., & Mackay, R. (1995). Effects of residential development on forest-dwelling neotropical migrant songbirds. *Conservation Biology*, **9**, 1408–1414.

Fuller, R. A., Warren, P. H., Armsworth, P. R., Barbosa, O., & Gaston, K. J. (2008). Garden bird feeding predicts the structure of urban avian assemblages. *Diversity and Distributions*, **14**, 131–137.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistical Methods*, **27**, 2865–2873.

Gilfedder, M., Robinson, C. J., Watson, J. E., Campbell, T. G., Sullivan, B. L., & Possingham, H. P. (2019). Brokering trust in citizen science. *Society & Natural Resources*, **32**, 292–302.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google earth engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, **202**, 18–27.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global chance and the ecology of cities. *Science*, **319**, 756–760.

Güneralp, B. & Seto, K. (2013). Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environmental Research Letters,* **8**, 014025.

Horton, K. G., Nilsson, C., Van Doren, B. M., La Sorte, F. A., Dokter, A. M., & Farnsworth, A. (2019). Bright lights in the big cities: migratory birds' exposure to artificial light. *Frontiers in Ecology and the Environment*, **17**, 209–214.

Hurlbert, A. H., & Liang, Z. (2012). Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PLoS One*, **7**, e31662.

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., Bekessy, S. A., Fuller, R. A., Mumaw, L., Rayner, L., …. Kendall, D. (2016). Cities are hotspots for threatened species. *Global Ecology and Biogeography*, **25**, 117–126.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature,* **491**, 444–448.

Jokimäki, J. & Suhonen, J. (1998). Distribution and habitat selection of wintering birds in urban environments. *Landscape and Urban Planning*, **39**, 253–263.

Kark, S., Iwaniuk, A., Schalimtzek, A., & Banker, E. (2007). Living in the city: can anyone become an 'urban exploiter'? *Journal of Biogeography*, **34**, 638–651.

Keck, F., Rimet, F., Bouchez, A., & Franc, A. (2016). phylosignal: An R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, **6**, 2774–2780.

Langham, G. M., Schuetz, J. G., Distler, T., Soykan, C. U., & Wilsey, C. (2015). Conservation status of North American birds in the face of future climate change. *PLoS One*, **10**, e0135350.

La Sorte, F. A., Tingley, M. W., & Hurlbert, A. H. (2014). The role of urban and agricultural areas during avian migration: an assessment of within- year temporal turnover. *Global Ecology and Biogeography*, **23**, 1225–1234.

La Sorte, F. A., Fink, D., Buler, J. J., Farnsworth, A., & Cabrera-Cruz, S. A. (2017). Seasonal associations with urban light pollution for nocturnally migrating bird populations. *Global Change Biology*, **23**, 4609–4619.

La Sorte, F. A., Lepczyk, C. A., Aronson, M. F. J., Goddard, M. A., Hedblom, M., Katti, M., … Yang, J. (2018a). The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constricted through urbanization. *Diversity and Distributions*, **24**, 928–938.

La Sorte, F. A., Lepczyk, C., Burnett, J. L., Hurlbert, A. H., Tingley, M. W., & Zuckerberg, B. (2018b). Opportunities and challenges for big data in ornithology. *The Condor*, **120**, 414–426.

La Sorte, F. A., Aronson, M. F. J., Lepczyk, C. A., & Horton, K. G. (2020). Area is the primary correlate of annual and seasonal patterns of avian species richness in urban green spaces. *Landscape and Urban Planning*, **203**, 103892.

La Sorte, F. A., & Graham, C. H. (2020). Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. *Journal of Animal Ecology*, early view: https://doi.org/10.1111/1365-2656.13345

Lepczyk, C. A., La Sorte, F. A., Aronson, M. F. J., Goddard, M. A., MacGregor-Fors, I., Nilon, C. H., & Warren, P. S. (2017). In Ecology and Conservation of Birds in Urban Environments (Ed. Murgui, E., and Hedblom, M.), pp 13-33.

Lepczyk, C. A., Flather, C. H., Radeloff, V. C., Pidgeon, A. M., Hammer, R. B., & Liu, J. (2008). Human impacts on regional avian diversity and abundance. *Conservation Biology*, **22**, 405–416.

Lintott, P. R., Barlow, K., Bunnefeld, N., Briggs, P., Roig, C. G., & Park. K. J. (2016). Differential responses of cryptic bat species to the urban landscape. *Ecology and Evolution*, **6**, 2044–2052.

Lislevand, T., Figuerola, J., & Székely, T. (2007). Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology*, **88**, 1605–1605.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1003.

Major, R. E. & Parsons, H. (2010). What do museum specimens tell us about the impact of urbanisation? a comparison of the recent and historical bird communities of Sydney. *Emu - Austral Ornithology*, **110**, 92–103.

Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Rönn, J., & Kolm, N. (2011). Brains and the city: big-brained passerine birds succeed in urban environments. *Biology Letters*, **7**, 730–732.

Marra, P. P., Cohen, E. B., Loss, S. R., Rutter, J. E., & Tonra, C. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, **11**, 20150552.

Martin, P. R., & Bonier, F. (2018). Species interactions limit the occurrence of urban-adapted birds in cities. *Proceedings of the National Academy of Sciences*, **49**, E11495–E11504.

Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis*, **159**, 1–13.

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*, **52**, 883–890.

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453.

Møller, A. P. (2009). Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the western palearctic. *Oecologia*, **159**, 849–858.

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Tans, E., Robison, T., Millspaugh, J. J., & Montgomery, R. A. (2019). What does urbanization actually mean? A framework for urban metrics in wildlife research. *Journal of Applied Ecology*, **56**, 1289–1300.

Murthy, A. C., Fristoe, T. S., & Burger, J. R. (2016). Homogenizing effects of cities on North American winter bird diversity. *Ecosphere*, **7**, e01216.

Myhrvold, N., Baldridge, E., Chan, B., Sivam, D., Freeman, D. L., & Ernest, M. S. K. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, **96**, 3109–3110.

Narango, D. L., & Rodewald, A. D. (2018). Signal information of bird song changes in human-dominated landscapes. *Urban Ecosystems*, **21**, 41–50.

Pagani-Núñez, E., Liang, D., He, C., Zhou, X., Luo, X., Liu, Y., & Goodale, E. (2019). Niches in the Anthropocene: passerine assemblages show niche expansion from natural to urban habitats. *Ecography*, **42**, 1360–1369.

Pandey, B., Joshi, P., & Seto, K. C. (2013). Monitoring urbanization dynamics in india using dmsp/ols night time lights and spot-vgt data. International *Journal of Applied Earth Observation and Geoinformation*, **23**, 49–61.

Paradis, E., Claude, J., & Strimmer, K. (2004). Ape: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.

Parnell, S., Schewenius, M., Sendstad, M., Seto, K. C., & Wilkinson, C. (2013). *Urbanization, biodiversity and ecosystem services: Challenges and opportunities*. Springer, Dordrecht.

Phillips, A. R. (1951). Complexities of migration: A review. *The Wilson Bulletin*, **63**, 129–136.

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., … Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, **26**, 1196–1211.

R Core Team. (2019). R: A language and environment for statistical computing.

Revell, L. J. & Chamberlain, S. A. (2014). Rphylip: an R interface for phylip. Methods in *Ecology and Evolution*, **5**, 976–981.

Sandström, U. G., Angelstam, P., & Mikusiński, G. (2006). Ecological diversity of birds in relation to the structure of urban green space. *Landscape and Urban Planning*, **77**, 39–53.

Sayol, F., Downing, P. A., Iwaniuk, A. N., Maspons, J., & Sol, D. (2018). Predictable evolution towards larger brains in birds colonizing oceanic islands. *Nature Communications*, **9**, 2820.

Schliep, K. P. 2010. phangorn: phylogenetic analysis in R. *Bioinformatics,* **27**, 592–593.

Schneiberg, I., Boscolo, D., Devoto, M., Macilio-Silva, V., Dalmaso, C. A., Ribeiro, J. W., …Varassin, I. G. (2020). Urbanization homogenized the interactions of plant-frugivore bird networks. *Urban Ecosystems*, **23**, 457–470.

Schuster, R., Wilson, S., Rodewald, A. D., Arcese, P., Fink, D., Auer, T., & Bennet, J. R. (2019). Optimizing the conservation of migratory species over their full annual cycle. *Nature Communications*, **10**, 1754.

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, **109**, 16083–16088.

Shwartz, A., Shirley, S., & Kark, S. (2008). How do habitat variability and management regime shape the spatial heterogeneity of birds within a large Mediterranean urban park? *Landscape and Urban Planning*, **84**, 219–229.

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, **85**, 1101–1112.

Sol, D., Maspons, J., Gonzalez-Voyer, A., Morales-Castilla, I., Garamszegi, L. Z., & Moller, A. P. (2018). Risk-taking behavior, urbanization and the pace of life in birds. *Behavioral Ecology and Sociobiology*, **72**, 59.

Sol, D., Bartomeus, I., González-Lagos, C., & Pavoine, S. (2017). Urbanisation tolerance and the loss of phylogenetic diversity in birds. *Ecology Letters*, **20**, 721–729.

Stathakis, D., Tselios, V., & Faraslis, I. (2015). Urbanization in European regions based on night lights. *Remote Sensing Applications: Society and Environment*, **2**, 26–34.

Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., Damoulas, T., Dhondt, A. A., Dietterich, T., Farnsworth, A., … Kelling, S. (2014). The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation*, **169**, 31–40.

Sullivan, B. L., Phillips, T., Dayer, A. A., Wood, C. L., Farnsworth, A., Iliff, M. J., Davies, I. J., Wiggins, A., Fink, D., Hochachka, W. M., …. Kelling, S. (2017). Using open access observational data for conservation action: A case study for birds. *Biological Conservation*, **208**, 5–14.

Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, **142**, 2282–2292.

Tratalos, J., Fuller, R. A., Evans, K. L., Davies, R. G., Newson, S. E., Greenwood, J. J., & Gaston, K. J. (2007). Bird densities are associated with household densities. *Global Change Biology*, **13**, 1685–1695.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. … Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, **4**, 1686.

Whittaker, K. A., & Marzluff, J. M. (2009). Species-specific survival and relative habitat use in an urban landscape during the postfledging period. *The Auk*, **126**, 288–299.

Zhang, Q. & Seto, K. (2013). Can night-time light data identify typologies of urbanization? A global assessment of successes and failures. *Remote Sensing*, **5**, 3476–3494.

BIOSKETCH

Corey T. Callaghan is broadly interested in the use of broad-scale citizen science data to understand organismal responses to urbanization, and understanding the patterns of biodiversity responses to urbanization in space and time.

Editor: Jon Sadler

AUTHOR CONTRIBUTIONS

CTC conceived the study with input from YB and FM. CTC, WKC performed the analyses with input from AGBP, YB, and FM. All authors contributed to drafting and writing the manuscript.

SUPPLEMENTARY FIGURES

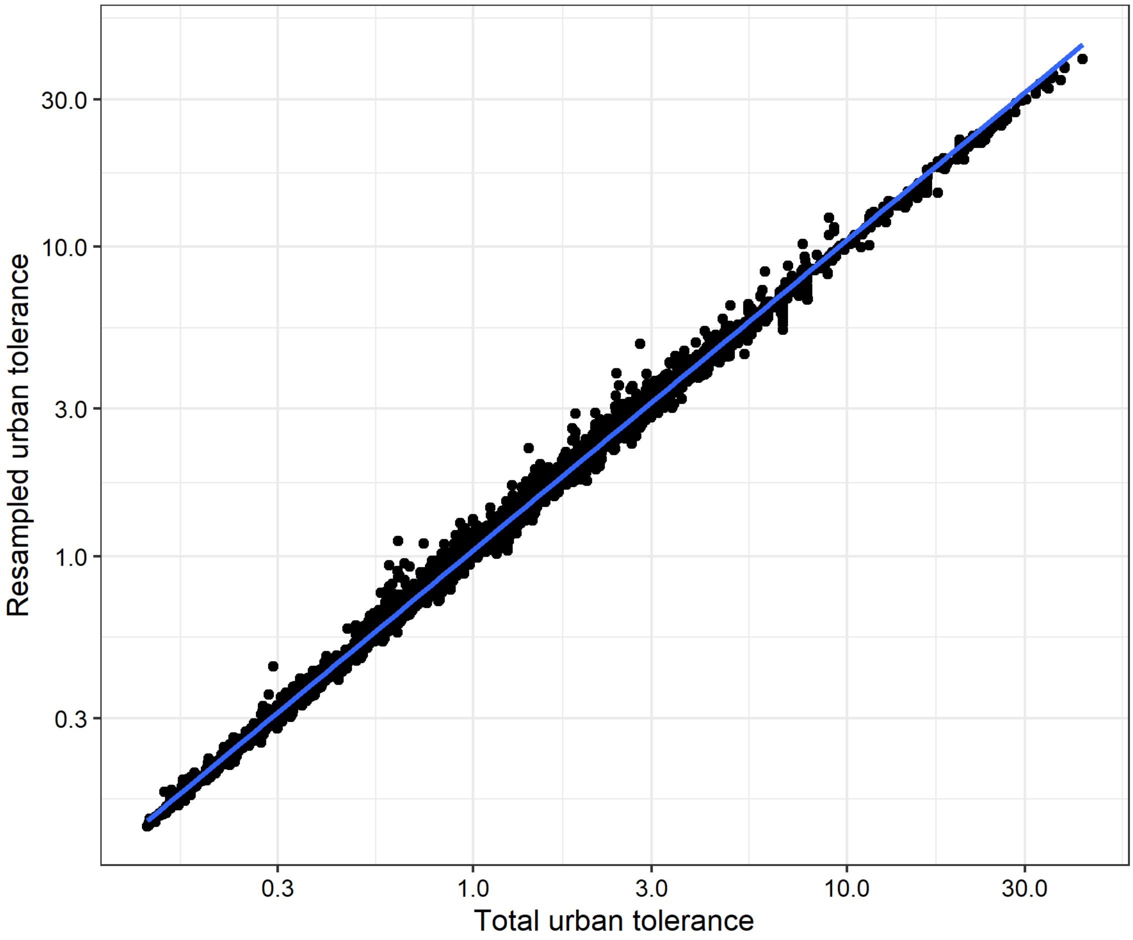
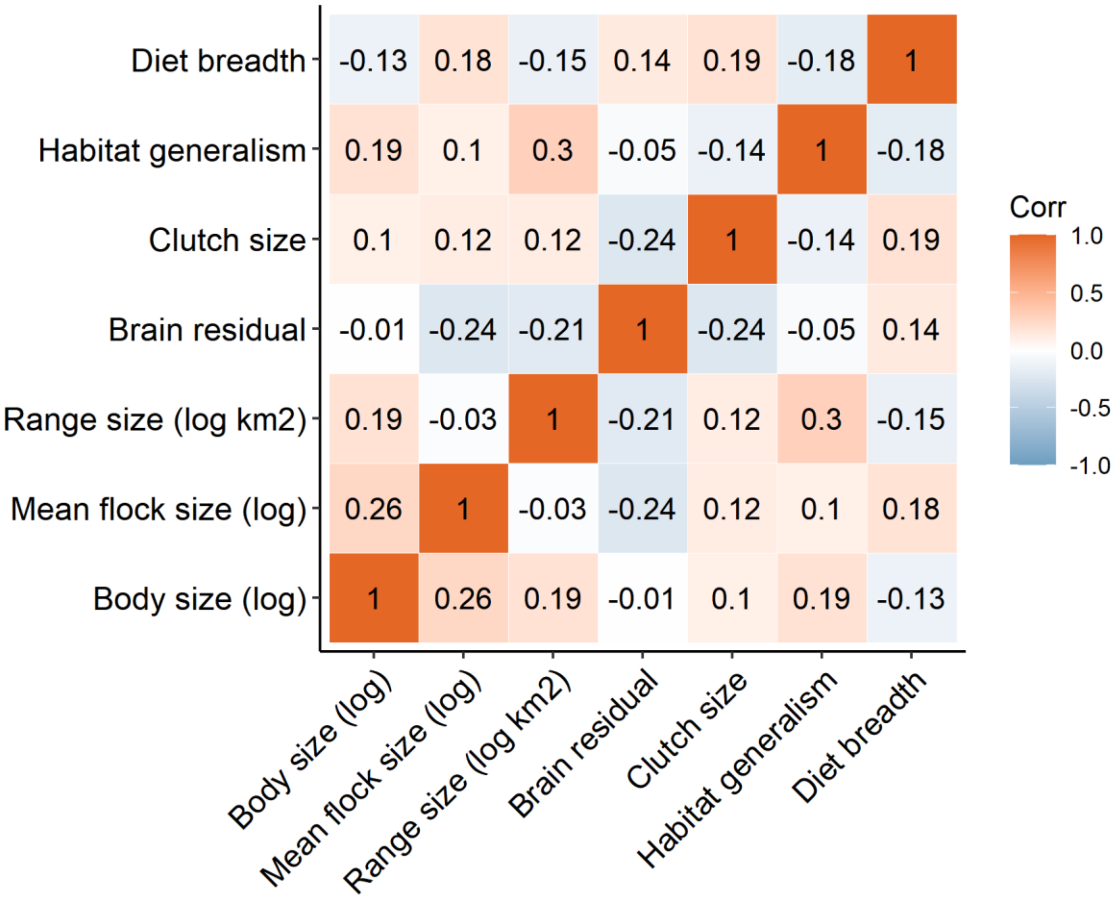


Figure S1. The relationship between the resampled urban score (i.e., the mean of 1000 medians drawn from 100 observations each) and the total urban score (i.e., the median of all observations) for all 490 possible species considered for analysis. This was done by randomly sampling 100 eBird observation for each species (Callaghan et al. 2019b; Callaghan et al. 2019a), with replacement, 1000 times and taking the median of the VIIRS night-time lights from each random sample. Accordingly, we were left with a mean urbanness and associated standard deviation for each month, for each species (Table S1). There was strong agreement between the overall urbanness in a month (i.e., the median of all observations) and the mean urbanness in a month (i.e., the resampled measure of urbanness), but we used the resampled measure of urbanness to account for variability in this measure in models by using weights in the models, where a species was weighted as the inverse of its standard deviation, capped at 50.



	Body size (log)	Mean flock size (log)	Range size (log km2)	Brain residual	Clutch size	Habitat generalism	Diet breadth
Diet breadth	-0.13	0.18	-0.15	0.14	0.19	-0.18	1
Habitat generalism	0.19	0.1	0.3	-0.05	-0.14	1	-0.18
Clutch size	0.1	0.12	0.12	-0.24	1	-0.14	0.19
Brain residual	-0.01	-0.24	-0.21	1	-0.24	-0.05	0.14
Range size (log km2)	0.19	-0.03	1	-0.21	0.12	0.3	-0.15
Mean flock size (log)	0.26	1	-0.03	-0.24	0.12	0.1	0.18
Body size (log)	1	0.26	0.19	-0.01	0.1	0.19	-0.13

Figure S2. The collinearity between continuous variables investigated in our analyses. All variables were correlated <0.7 and thus all variables were included in analyses.

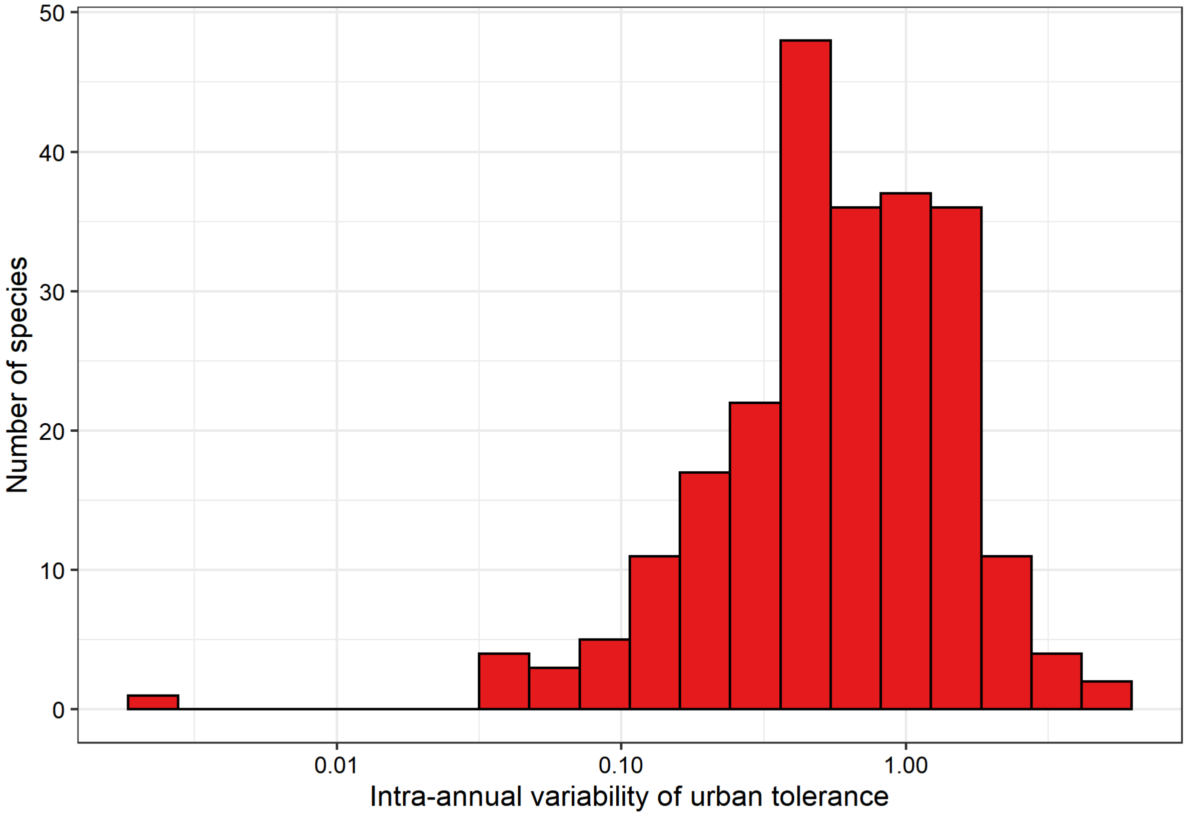


Figure S3. Histogram showing the intra-annual variability of urban-tolerance among 237 species included in our analyses, where the y-axis shows the number of species corresponding with a specific bin of intra-annual variability.

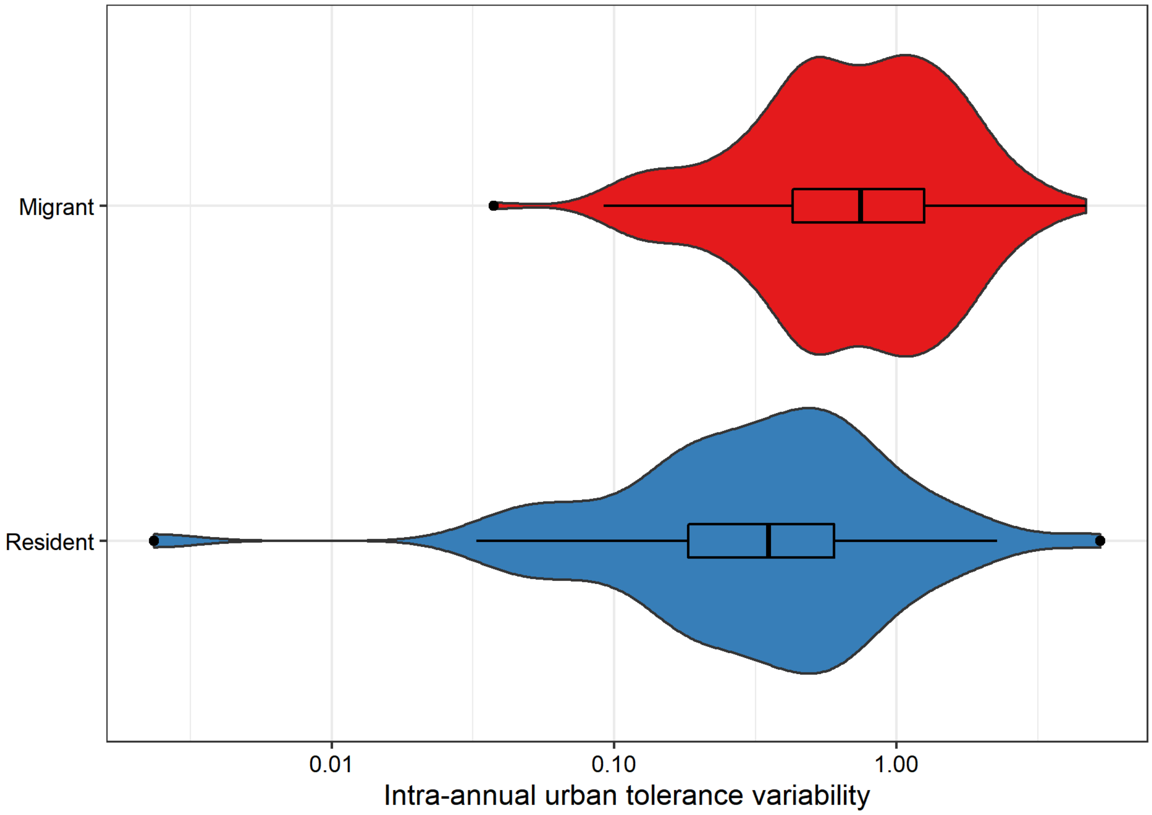


Figure S4. Violin plots (and boxplots) of the intra-annual urbanness variability of urban tolerance on a logarithmic scale. There was a statistically significant relationship for non-phylogenetic models but not for phylogenetic models (Table S4).

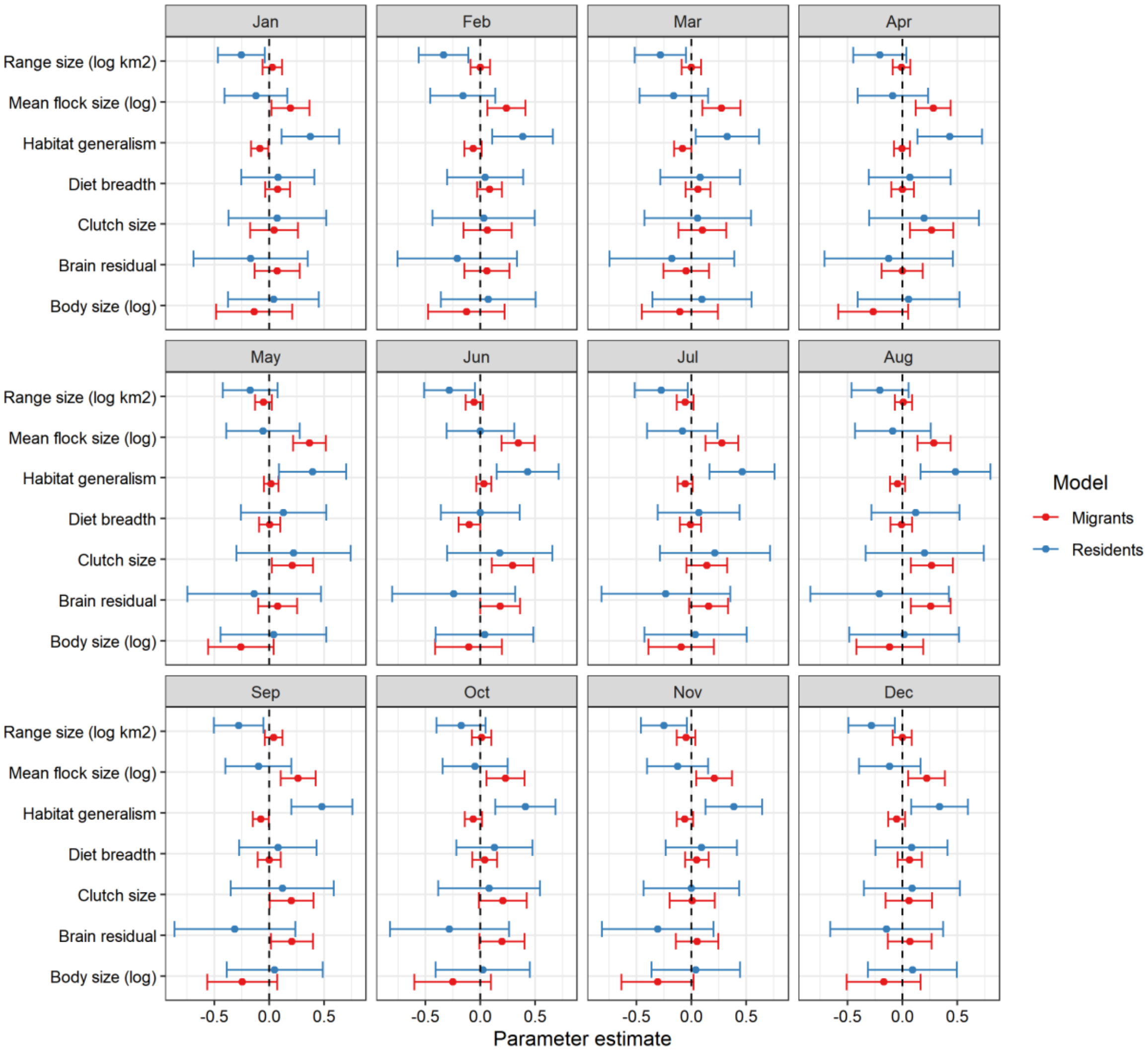


Figure S5. Standardized parameter estimates for phylogenetically controlled models where the response variable was log-transformed species-specific urbanness, and models were repeated for each month, stratified to migratory status. The dashed line represents zero, and any parameter estimates to the right of this can be interpreted as positively interacting with urban-tolerance, and vice versa for any parameter estimates to the left of this dashed line. To better see the temporal patterns in the parameter estimates, see Figure 5.

SUPPLEMENTARY TABLES

Table S1. The 237 species included in the analyses, and their respective monthly mean urbanness scores derived from the resampling approach, as well as their intra-annual variability (i.e., the standard deviation of the monthly urbanness scores), and the species traits used in the analysis. The taxonomy follows the eBird Clements taxonomy (version 2019), and TipLabel presents the taxonomy which matches the Jetz et al. (2012) phylogenetic tree.

*this table is uploaded separately

Table S2. Phylogenetic signal for species-specific urbanness for each month of the year, as the species-specific urbanness was calculated monthly.

Month		C-mean	I	K	K*	Lambda
Jan	Statistic	0.2584	0.0735	0.1652	0.1848	0.3915
	p-value	0.0001	0.0001	0.0001	0.0001	0.0001
Feb	Statistic	0.2512	0.0663	0.1659	0.1856	0.3899
	p-value	0.0001	0.0001	0.0001	0.0001	0.0001
Mar	Statistic	0.2057	0.0454	0.1437	0.1599	0.2871
	p-value	0.0001	0.0002	0.0001	0.0001	0.0002
Apr	Statistic	0.1170	0.0119	0.1390	0.1492	0.0838
	p-value	0.0044	0.0454	0.0003	0.0001	0.4599
May	Statistic	0.1227	0.0117	0.1404	0.1531	0.0000
	p-value	0.0040	0.0535	0.0002	0.0005	1.0000
Jun	Statistic	0.1888	0.0268	0.1389	0.1554	0.4292
	p-value	0.0001	0.0033	0.0002	0.0002	0.0053
Jul	Statistic	0.1895	0.0222	0.1507	0.1684	0.4002
	p-value	0.0001	0.0092	0.0001	0.0001	0.0300
Aug	Statistic	0.1370	0.0070	0.1495	0.1651	0.0001
	p-value	0.0016	0.1128	0.0001	0.0001	1.0000
Sep	Statistic	0.1907	0.0146	0.1554	0.1684	0.3635
	p-value	0.0002	0.0323	0.0001	0.0001	0.1212
Oct	Statistic	0.1521	0.0086	0.1263	0.1363	0.0603
	p-value	0.0005	0.0831	0.0008	0.0014	0.3948
Nov	Statistic	0.1997	0.0320	0.1388	0.1552	0.2321
	p-value	0.0001	0.0016	0.0002	0.0003	0.0169
Dec	Statistic	0.2614	0.0656	0.1658	0.1855	0.3947
	p-value	0.0001	0.0001	0.0001	0.0001	0.0001

Table S3. Results of the phylogenetic analysis of the intra-annual variability measure for 245 species. Phylogenetic signal analysis was performed on a consensus tree for 1000 trees.

	C-mean	I	K	K*	Lambda
Statistic	0.2806	0.0542	0.1610	0.1719	0.5214
p-value	0.0001	0.0002	0.0002	0.0001	0.0001

Table S4. Results of a phylogenetic and model between intra-annual variability and migration status.

Term	Estimate	Standard Error	t-value	p-value
Intercept (migrants)	-0.320	0.483	-0.663	0.508
Resident	-0.053	0.072	-0.737	0.462