

Article

Comparative urbanization of birds in China and Europe based on birds associated with trees

Anders Pape MØLLER^{a,b,*}, Canwei XIA^b, Bo ZHOU^c, Xianli CHE^d,
Xingzhi CHU^d, Changzhang FENG^c, Karsten LAURSEN^e, Federico MORELLI^f,
Wangming LI^d, Jianping LIU^c, Qing QUAN^d, Min ZHANG^d, Qiang ZHANG^d,
Qiangwen ZHAN^d, Laikun MA^c, Haitao WANG^g, Fasheng ZOU^d, and
Wei LIANG^c

^aEcologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, Orsay Cedex, France, ^bMinistry of Education Key Laboratory for Biodiversity and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, China, ^cMinistry of Education Key Laboratory for Ecology of Tropical Islands, College of Life Sciences, Hainan Normal University, Haikou, China, ^dGuangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Guangdong Institute of Applied Biological Resources, Guangzhou, China, ^eInstitute of Bioscience, Aarhus University, Denmark, Denmark, ^fFaculty of Environmental Sciences, Department of Applied Geoinformatics and Spatial Planning, Czech University of Life Sciences Prague, Prague, Czech Republic, and ^gJilin Provincial Engineering Laboratory for Avian Ecology and Conservation Genetics, Northeast Normal University, Changchun, China

*Address correspondence to Anders Pape Møller. E-mail: anders.moller@u-psud.fr.

Handling editor: Yanping Wang

Received on 30 November 2018; accepted on 25 February 2019

Abstract

Urbanization effects on living organisms are spatially heterogeneous. Here we quantified the abundance of birds per tree in forested urban and rural habitats for 85,829 trees mainly in China and Europe. A population model was based on the assumption that: 1) birds have a normally distributed habitat preference; 2) an increase in population size linked to the habitat preference; 3) a population size dependent on the habitat preference; and 4) the removal of a certain fraction of individuals giving rise to extinction. We tested for large-scale differences in the impact of urbanization on the frequency distribution of the difference in abundance between urban and rural habitats in China and parts of Europe. The difference in the frequency distribution of urban population density of birds in trees minus rural population density of birds in trees in China and Europe was statistically significant, suggesting that the abundance of birds differed between trees in urban and rural habitats, but more so in China than in Europe. We hypothesize that more pronounced differences in China than in Europe may have arisen due to the Four Pests Campaign in 1958–1962 that resulted in death of hundreds of millions of birds (mainly tree sparrows *Passer montanus*, but also numerous other less common species that were starting to become urbanized around 1960). Species that were less common in 1960 could not sustain reductions in population size in urban areas and hence these species are still rare or absent in urban areas today 60 years later.

Key words: ANOSIM, community composition, distribution, frequency skewness, habitat preference, human-bird interactions, kurtosis, sociality

Urbanization is the biological process that results in the immigration, establishment, and expansion of organisms when expanding their range from rural to urban habitats (e.g., Tomialojc 1970; Gilbert 1989; Klausnitzer 1989; Møller 2015; Møller et al. 2014). This process has been ongoing since humans started living in towns more than 10,000 years ago (Sætre et al. 2012), and numerous recent cases of urbanization either result from birds having “always” been present over immigration to having become urban exploiters. The large number of species that have immigrated from rural habitats during recent centuries are well-known (Gesner 1669; Bonaparte 1828; Møller et al. 2012). Urbanization has increased in pace as a rapidly increasing fraction of humanity has moved from rural to urban habitats. By 2008, more than half of all humans were living in cities (Handwerk 2008; United Nations 2015), and this fraction is predicted to reach 85% by 2050 (Ferenc et al. 2013).

Dramatic changes in land-use have important implications for abundance and species richness of birds (e.g., McKinney 2008; Møller et al. 2012; Aronson et al. 2014). Numerous species have invaded urban habitats whereas others have “always” been present in urban areas (Møller 2008, 2014; Evans et al. 2009a). Such invasions have consequences for homogenization and differential disappearance of rare species from urban environments (Kühn and Klotz 2006; McKinney 2006). Urbanization has also been shown to significantly affect numerous ecological processes like dispersal and migration (Chamberlain et al. 2009; Cheptou et al. 2008; Evans et al. 2009b; Liang et al. 2013; Møller 2009, 2014; Møller et al. 2010; Schneider et al. 2009; Shepherd et al. 2002) with consequences for species richness and composition. Urbanization results in the disappearance of fear reactions to humans in a process that resembles domestication (Darwin 1868; Kohane and Parsons 1988; Møller 2010a, 2010b). Such reductions in behavior may increase species richness (Cooke 1980; Møller 2008; Møller and Ibáñez-Álamo 2012).

Differences between continents may occur due to differences in the initial start and stage of urbanization. For example, urbanization in China has occurred at an increasing speed compared with the situation in Europe (e.g., Chen 2007; Zhou et al. 2004; Hubacek et al. 2009; Kirby 2018). Such differences in rate and extent of urbanization provide opportunities for research.

The Four Pests Campaign in China constituted an official attempt to eradicate 4 pest species that included the killing of hundreds of millions of tree sparrows *Passer montanus*, but as a consequence also large numbers of birds that lived in close proximity of humans. This unique example concerns a dramatic reduction in the abundance of 4 so-called pest species, but also numerous other organisms in China during the 1950s and 1960s. Birds were as recently as 1958–1962 the focus of broad-scale attempts to exterminate these illicit consumers of grain that could otherwise be used as food for humans. The bird eradication program as part of the Four Pests Campaign during 1958–1962 had severe ecological consequences and hence was terminated (e.g., Summers-Smith 1992; Shapiro 2001). Several hundred million birds, mainly tree sparrows, but also numerous other species inhabiting cities were eradicated. Even rare and threatened species were exterminated. However, the consequences of the Four Pests Campaign were never quantified. Here, we first test for a difference in the relative number of individual birds in urban and rural habitats in China, and relative to Europe, where no Four Pests Campaign occurred, in an attempt to identify any effects of this eradication program. Furthermore, we attempt to test whether the frequency distribution of birds in urban and rural habitats differed between China and Europe, whether these different

patterns of abundance could be accounted for by the Four Pests Campaign, and, finally, whether sociality and hence aggregations of birds further increased the probability of successful persecution.

The objectives of this study were to describe heterogeneity in the extent of urbanization and to identify the underlying factors contributing to such heterogeneity in urbanization. Specifically, we had the following objectives: 1) A test of whether species composition differed between rural and urban sites. 2) Whether the frequency distribution of log (abundance of urban birds) minus log (abundance of rural birds) differed between China and Europe, under the expectation that the frequency distribution would be Gaussian in Europe, but deviate from such a distribution in China, where the Four Pests Campaign is likely to have caused a significant deviation in frequency distribution from normality. 3) Finally, whether a theoretical model based on a preference for urban habitats and a frequency-dependent risk of extinction depending on population size could account for the difference in frequency distribution of log urban minus log rural abundance between China and Europe.

Materials and Methods

Study sites

We studied birds in trees in study sites in Southern, Central and Northern China (Figure 1), but also in a number of other countries (Japan as a control site in Asia, Bahrein as a more distant control site in Asia and Denmark and France as control sites in Europe) in order to assess the extent to which estimates of the abundance of birds per tree were consistent across local and global spatial scales. This was done by testing whether differences in the abundance of birds per tree as the sampling unit differed between trees in urban and rural habitats, between the breeding and the non-breeding season, and between China and Europe. Study areas were considered urban when the proportion of built-up surface was >0.50 , whereas areas where the percent of built-up surface was ≤ 0.20 were considered rural areas, as suggested by Marzluff et al. (2001). This categorization of urban and rural habitats has repeatedly been used in a number of different field studies, showing that birds from urban and rural habitats differ in terms of anti-predator response and a number of additional different traits (Møller 2008, 2009; Møller et al. 2012a, 2018; Møller 2010a, 2010b, 2012, 2014, 2015; Møller and Ibáñez-Álamo 2012b). Thus, there are a large number of studies showing that the categorization of urban and rural habitats is consistent across behavioral and other phenotypic characters. A study site was defined as an area where an observer recorded birds on trees. The number of trees sampled per study site was on average 2,452 trees, 95% confidence limits (CL) 1,738–3,165 trees, range 200–10,000, $N = 35$ sites. These trees that were sampled for birds only constituted a small fraction of trees available. We obtained such data on the number of birds observed per tree based on systematic surveys. The study sites, the categorization of study sites as urban or rural and the Geographic Positioning System coordinates are reported in Electronic Supplementary Material Table ESM 1. This table also lists the dates when the studies were conducted.

Data sets

The 15 participants in this study are listed as authors and all are studying or have 1 or more university degrees in biology. Each observer has up to 50 years of field experience in bird surveys. The 15 participants in this project were mainly chosen as part of a 1-week workshop in scientific communication organized by A.P.M. in

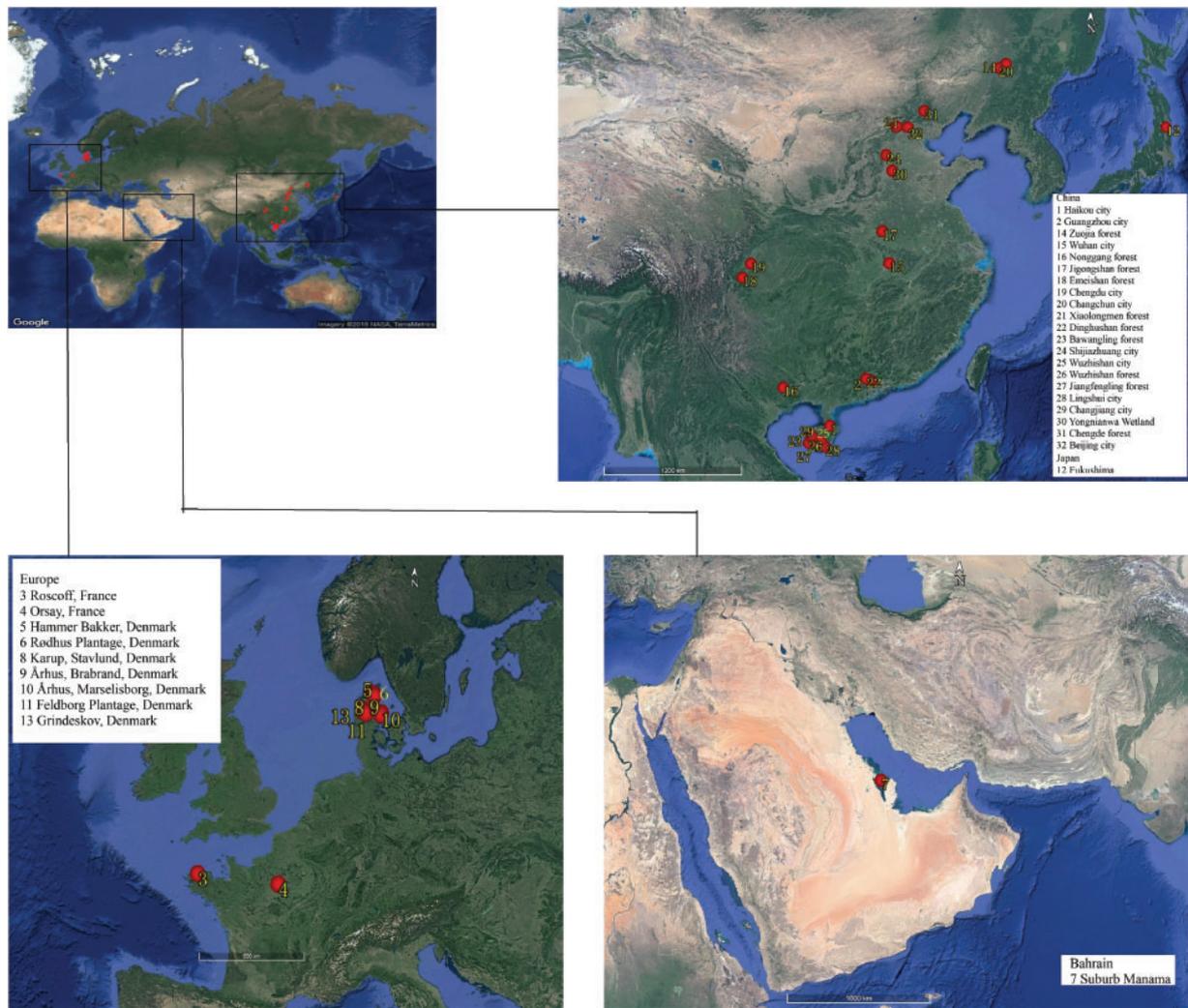


Figure 1. Map of study sites where the number of individual birds and the number of species per tree were recorded.

Guangdong Institute of Applied Biological Resources, Guangzhou, China during November 2017. All study sites were located where the participants were living and hence had a good knowledge of the local avifauna. We collected field data on the number of birds per tree in forests, parks and other habitats with trees. Where possible a pair of forested sites with rural and urban habitats was investigated. We used the definition by [Crowther et al. \(2015\)](#) for a tree as a plant with a woody stem larger than 10 cm diameter at breast height. We chose a random site and recorded all trees along line transects by carefully inspecting each tree with a pair of binoculars recording the number of birds by relying on visual records and calls produced by birds. Calls were used for species identification. All surveys of birds per tree were made during 05:00 to 12:00 h under favorable weather conditions to allow for easy identification. Multiple samples were recorded by each observer on different days to allow for repeatability estimates whenever it was possible to make multiple estimates for logistic reasons. Transects were chosen to ensure that both urban and rural habitats from the same general site within a distance of <50 km were included. We only included sites with at least 1,000 trees to ensure that all sites had the minimum number of trees per site required as a criterion. Three sites had less than 1000 trees surveyed for logistic reasons, but the conclusions of the analyses were qualitatively similar if these three sites were deleted from the

analyses. The same observers were generally responsible for surveys of nearby urban and rural habitats.

Sociality was defined as the occurrence of individuals that moved together as defined in [del Hoyo et al. \(1992–2010\)](#).

We were able to identify almost all species due to the extensive field experience of the participants. We recorded a few unknown calls using mobile phones and took photographs with mobile phones to identify a few additional species. We provide the data in Electronic Supplementary Material Table ESM 1.

Statistical analyses

Two observers made independent surveys of birds without communication while simultaneously surveying 1,000 trees at 2 sites to assess detectability. At Orsay, France and Rødhus, Denmark the number of individual birds per tree recorded by the 2 observers was 0.093 (95% confidence interval (CI) 0.073–0.133 birds per tree) for the first observer and 0.095 for the second observer (95% CI 0.074–0.115 birds per tree). The difference in number of birds per tree for the first site surveyed by 2 observers simultaneously was on average -0.0080 ($SE = 0.0028$). The number of individual birds recorded by the 2 observers was 0.044 birds per tree (95% CI 0.018–0.070 birds per tree) for the first observer and 0.043 (95% CI 0.017–0.060) for the second observer. The difference in number of birds

per tree for the second site surveyed by 2 observers simultaneously was on average 0.0030 ($SE = 0.0017$). Hence, observations showed a high degree of detectability among observers. This was not surprising during the breeding season when birds were generally resident and defended breeding territories and were thus easy to detect visually and acoustically.

Repeatability R is an estimate of consistency in counts ranging from 0 to 1, based on the intra-class correlation (Falconer and Mackay 1996). Repeatability for the number of birds per tree for different survey sites in China was $R = 0.84$ ($SE = 0.08$, $F = 22.81$, $df = 3, 13$, $P < 0.0001$). Repeatability for other countries was for number of birds per tree $R = 0.58$ ($SE = 0.02$, $F = 43.57$, $df = 3, 7$, $P < 0.0001$). The similarity in repeatability estimates and the narrow confidence intervals revealed a high degree of consistency among countries. Likewise, there was significant consistency among observers.

We assessed the reliability of field estimates of the number of birds per tree by relying on multiple estimates from each site, estimating the reliability of estimates from repeatability analyses with site as a factor (Becker 1984; Falconer and Mackay 1996). We used a Generalized Linear Model (GLM) for the number of birds per tree assuming a Poisson distribution of these count data with a log link function. The response variable was the number of birds recorded in different trees whereas the predictors were Julian date, season (breeding or non-breeding), habitat (urban or rural), latitude, longitude, altitude, country (China or not), and island (island or mainland) using backward elimination to reduce this model to a model that only included variables with an associated $P < 0.10$. We calculated mean estimates for the number of birds per tree, and we estimated 95% confidence intervals to provide information on the uncertainty of estimates. See Møller et al. (2018) for further details.

Differences in bird species composition between communities from rural and urban sites were tested by means of analysis of similarities (ANOSIM), a non-parametric technique useful for testing differences in species composition at different environments (Clarke 1993). The ecological distance among sampled sites was based on Jaccard's similarity index (Clarke 1993). The ANOSIM statistic R is based on the difference in mean ranks between groups and within groups (Clarke 1993). The statistical significance of R was calculated by means of 999 permutations. The ANOSIM was performed with the package "vegan" in R (Oksanen et al. 2016).

We used descriptive statistics like mean, variance, skewness and kurtosis for frequency distributions of log (urban abundance) minus log (rural abundance) for bird communities in China and Europe, and we used Welch ANOVA for unequal variances to test for differences in mean values of log (urban abundance) minus log (rural abundance), and Levene's test to test for differences in variances of log (urban abundance) minus log (rural abundance). We used Kolmogorov-Smirnov 2-sample tests to test for differences in frequency distributions of log (urban abundance) minus log (rural abundance).

We modeled heterogeneity in frequency distribution of log (urban abundance) – log (rural abundance) in Appendix 1. In Figure 2A, we assume that: 1) the habitat preference (p) for each bird species was normally distributed (mean = 0, $SD = 1$), with a positive value indicating an urban habitat preference and a negative value a rural habitat preference; 2) total population size (population in urban + population in rural) for each bird species was related to the preference ($N = 100 \cdot \exp(p)$), and thus birds preferring urban habitat had larger population sizes than birds preferring rural habitat; and 3) the population size in urban or rural habitats for each

bird species depended on preference (p), for example, bird species X with a preference value larger than 80% of other birds, 80% of total population size of bird species X live in urban habitat, whereas 20% live in rural habitat. Figure 2A was similar to the situation in Europe. In Figure 3B, besides the assumptions in Figure 2A, we also assumed that a certain ratio (e.g., 80%) of the total population size in urban habitat was removed (this equals the Four Pests Campaign). Therefore, Figure 2B is very similar to Figure 2A. In Figure 2C, besides the assumptions in Figure 2A and 2B, we assumed 1) after removal, species with a population size in urban habitat less than a certain value went extinct in urban habitats (these species can survive in rural habitats), whereas other birds recovered to the population size before removal. Figure 2C reflected this bimodal distribution. In Figure 2D, we only assumed that the habitat preference (p) had a bimodal distribution. This may be due to rapid urbanization, resulting in insufficient time available for adaptation. Most bird species preferred rural habitat, whereas some bird species may have an innate preference for urban habitat (exaptation which implied a predisposition for a preference for urban habitats). Figure 2D shows a bimodal distribution. Both Figure 2C and D were similar to the situation in China.

Results

A Welch ANOVA testing for equal means showed no significant difference (Table 1; $F = 2.14$, $df = 1, 317.81$, $P = 0.14$). However, the variances were much larger in China than in Europe (Levene's test, $F = 29.00$, $df = 1, 316.2$, $P < 0.0001$). A Kolmogorov-Smirnov 2-sample test revealed a significant difference for frequency distribution of log (urban abundance) minus log (rural abundance) between China and Europe (Figure 4; $KS = 0.1119$, $P = 0.0002$).

There was a significant difference in frequency distributions between social and solitary species in Europe with a Welch ANOVA showing a difference in means (Figure 4; $F = 15.53$, $df = 1, 2573$, $P = 0.0006$), but not in variances (Table 1; Levene's test: $F = 1.97$, $df = 1, 152$, $P = 0.16$). Skewness was larger in China, whereas kurtosis was larger in Europe (Table 1).

There was a significant difference in frequency distributions between social and solitary species in China (Figure 5; Kolmogorov-Smirnov 2-sample test: $KS = 0.1776$, $P < 0.0001$). The mean proportion of trees with birds was 0.027 for Fukushima, but 0.036 ($SE = 0.006$, $N = 22$) for China, not differing significantly from each other ($t = 1.44$, $df = 21$, $P = 0.16$).

We obtained data on abundance of birds from 32 sites across China and Europe (Figure 1; Appendix 2). The difference in bird species composition between urban and rural sites was not significant in Europe ($R_{ANOSIM} = 0.07$, $P = 0.544$), whereas it was significant in China ($R_{ANOSIM} = 0.17$, $P = 0.005$) (Figure 6). The large dissimilarities in bird communities were found within rural sites rather than within urban sites or between sites (Figure 6).

When we adopted a theoretical approach and modeled a habitat preference in a normal scenario and linked this preference to population growth, we arrive at a situation resembling the outcomes of the Four Pests Campaign (Figure 2A–C). Given that humans removed a certain fraction of birds, and that this resulted in a certain fraction of extinction (Figure 2B), small differences in population density between urban and rural habitats may result in disproportionately many human induced extinctions (Figure 2C). This simple model can explain the frequency distribution of difference in abundance of birds in Europe and China. The model also accounts for the role of

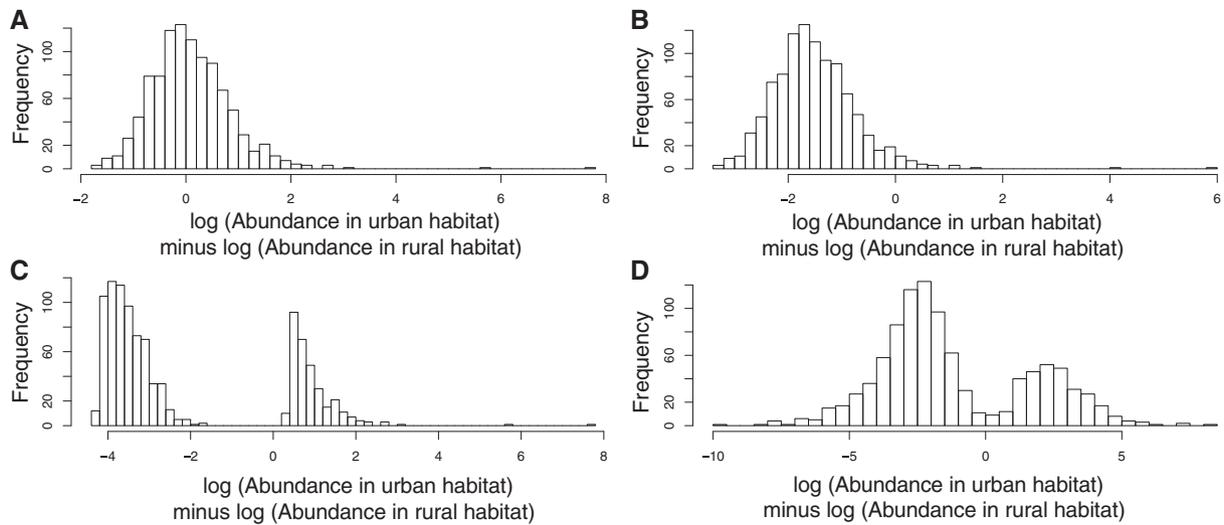


Figure 2. Frequency distribution of log (abundance of a bird species in urban habitat) minus log (abundance of the same bird species in rural habitat) on the x axis. In (A), the normal distribution has a mean of 0 and an SD of 1 and a habitat preference for urban or rural habitats. In (B), a certain proportion of birds in urban habitats is removed, causing the frequency distribution to be displaced from a mean value of 0. In (C), species with a population size in urban habitats less than a certain value goes extinct there, resulting in a bimodal distribution. In (D), the habitat preference is bimodal with most species preferring rural habitat, whereas some have an innate preference for urban habitat, resulting in a bimodal distribution of log (abundance of urban populations) minus log (abundance of rural populations). (C) resembles the outcome after the Four Pests Campaign, while (D) resembles the habitat preference with a bimodal distribution.

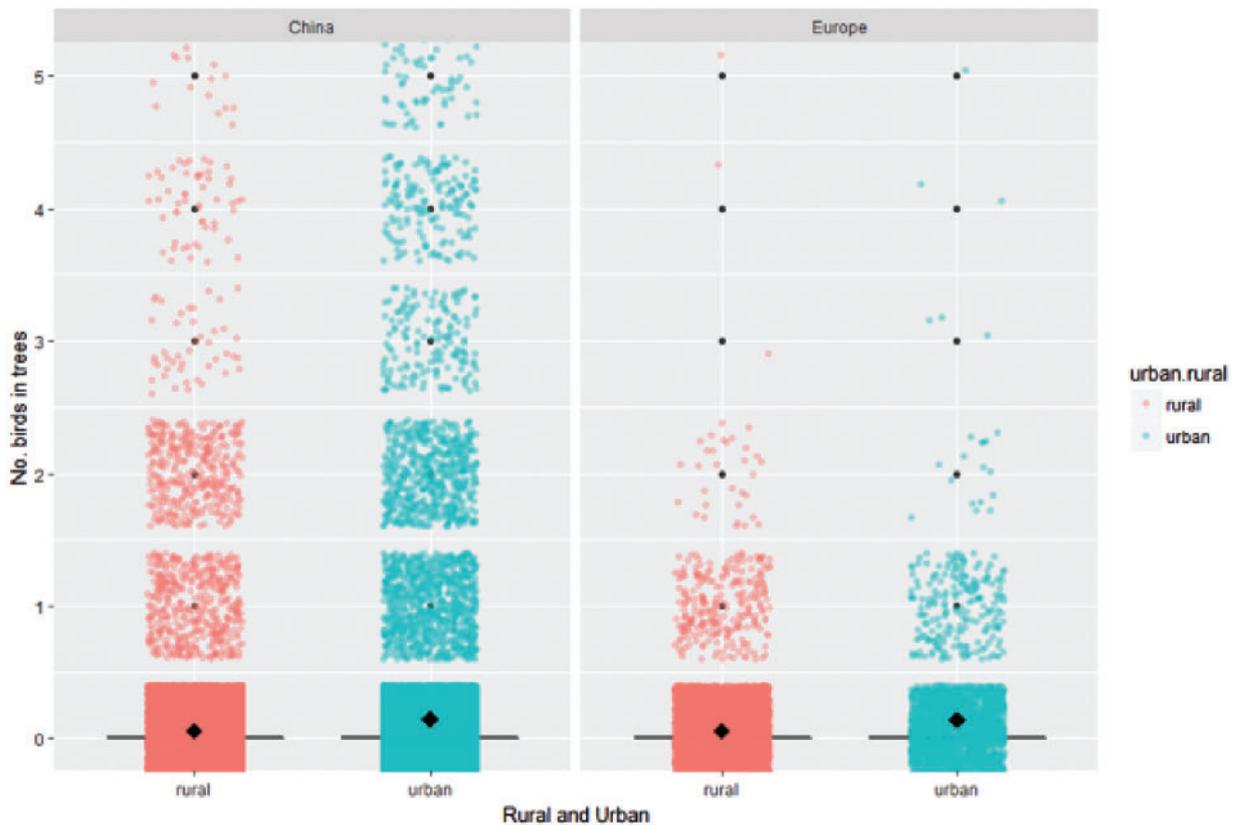


Figure 3. Box plots of the number of birds in trees in rural and urban habitats in China and Europe. Box plots show medians (horizontal lines), means (rhombus), 95-percentiles and extreme values.

habitat preference and differential mortality in the process of urbanization. Two mechanisms may lead to the bimodal distribution shown in Figure 2C–D (the skewed log (urban population density) minus log (rural population density in China): 1) Population size is

related to a habitat preference (species that prefer urban habitat have larger population sizes) and species with fewer individuals than a certain threshold value go extinct in urban habitats after human removal (without recovery of population size). 2) The habitat

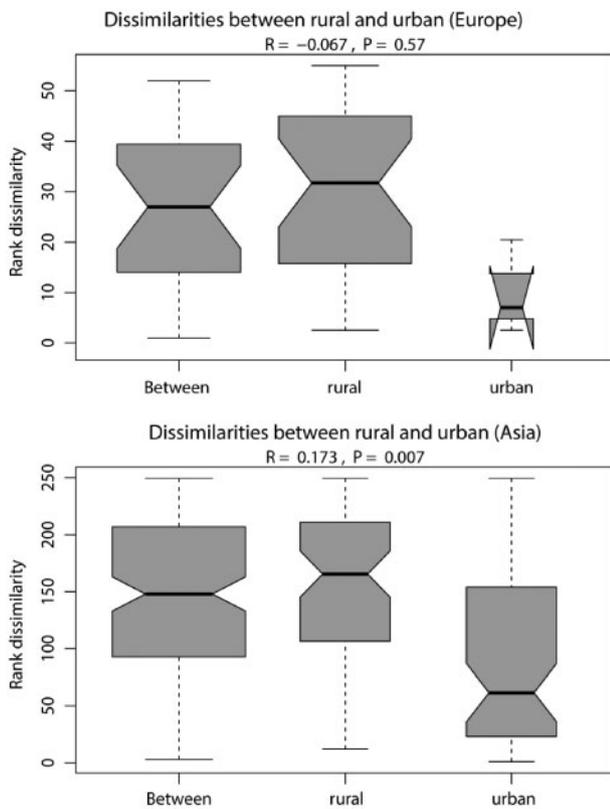


Figure 4. ANOSIM results showing dissimilarity based on bird community composition in sample sites using Jaccard's index for computing the distance (dissimilarity) between rural and urban environments in Europe (top) and Asia (bottom). Notched boxplots indicate the dissimilarity rank distributions for between and within groups presented in plots. Box length indicates interquartile range and medians are indicated as black horizontal bars.

preference (p) has a bimodal distribution (most birds prefer rural habitat, whereas a few birds may have an innate preference for urban habitat).

Discussion

This study contains 4 novel features that make the article unique. 1) The article is novel in terms of the spatial and temporal scale of the study. No other study has ever studied urbanization across so large spatial (Europe and China) and temporal scales (1960–2018) as this study. 2) The study is semi-experimental in its approach by elimination of birds from large urban areas in some study sites, but not in others. We are unaware of any other study adopting experimental approaches at such spatial and temporal scales. 3) The study is unique by development of a novel method for assessment of the abundance of birds based on assessment of the abundance and the species richness of birds based on the number of birds per tree following the unique approach by Crowther et al. (2015) for assessment of the global abundance of trees. 4) Our study is theoretical being unique by merging empirical and modeling approaches. We briefly discuss these novelties that can be expanded to studies of urbanization elsewhere, but also in other taxa than birds such as mammals and invertebrates.

Urbanization is an ongoing process with numerous species having become abundant in urban areas differing from the situation in

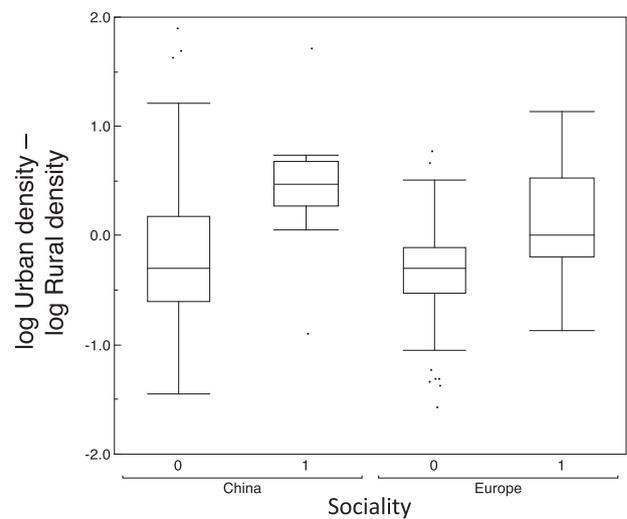


Figure 5. Box plots of log urban population density minus log rural population density in relation to sociality (0 – solitary, 1 – sociality) with means (horizontal lines), quartiles (boxes), 5- and 95-percentiles (error bars), and extreme values (dots).

their ancestral rural populations (Møller et al. 2012). A simple measure of the extent of adaptation to urban habitats is log (abundance of populations in urban areas) minus log (abundance of populations in rural areas; Møller et al. 2012). The frequency distribution of log (abundance of urban populations) minus log (abundance of rural populations) is a normal distribution with a mean value of zero and equally many species with positive and negative values. Indeed, this is the frequency distribution found in Europe in the present study, whereas the frequency distribution for Chinese species shows a clear deviation from a normal distribution among urban species that vary in abundance from rare to common. The non-normal frequency distributions were repeated in different samples from China, as were the normal distributions from Europe. This was shown by a skewed frequency distribution. The cause of these 2 distributions in China and Europe remains unknown. Here we hypothesized that the Four Pests Campaign may be a hitherto unknown contributing factor.

A single event may account for this difference in frequency distributions between Europe and China. During 1958–1962 several hundred million birds, mainly tree sparrows, were killed in an attempt to eradicate grain eating birds from villages and cities across China (Summers-Smith 1992; Shapiro 2001). Birds were killed directly, or chased by as many as 3 million people in Beijing alone (Time 1958), using drums, pots and pans that eventually forced birds to land on the ground, where they were killed. For example, the Polish embassy in Beijing prevented access by humans to its grounds, and after 2 days of constant drumming embassy staff used shovels to clear the grounds for dead birds (China History 1999). That was the case in urban as well as rural habitats. Although tree sparrows were the main target, numerous other species died as well, eliminating any incipient cases of urbanization.

This unique event may be the cause of the clear differences in level of urbanization in China and Europe even today. We cannot exclude the possibility that other factors may have caused this change in pattern of abundance. Urbanization in China is well-known for occurring at an increasing speed compared with the situation in Europe although numerous Chinese cities are also known

Table 1. Summary statistics for the frequency distributions of log urban population density minus log rural population density in birds in China and Europe

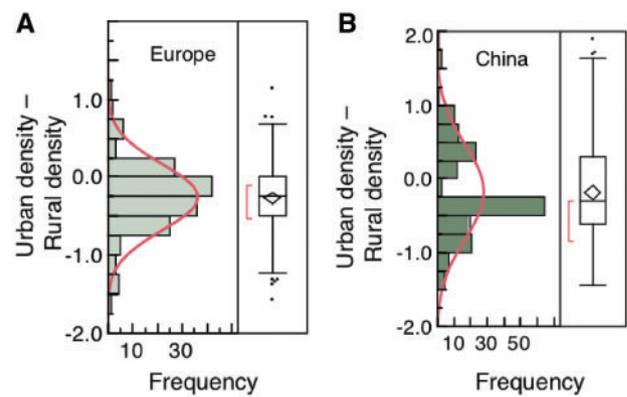
Variable	China	Europe
Mean	-0.1833	-0.2652
SE	0.0476	0.0340
Variance	0.4117 ^a	0.1792 ^a
Upper 95% CL	-0.0895	-0.1981
Lower 95% CL	-0.2772	-0.3324
Skewness	0.6925 (0.1811) ^a	-0.0435 (0.1967) ^a
Kurtosis	0.3821 (0.3621) ^a	1.4587 (0.3935) ^a
N	182	155

^a Values significantly different between China and Europe.

for having an ancient history of urbanization (e.g., Chen 2007; Zhou et al. 2004; Hubacek et al. 2009; Kirby 2018). Three patterns differed between Europe and China. First, the difference in bird species composition between rural and urban sites was not statistically significant in Europe, whereas it was in China. Second, there was a significant difference in frequency distributions of log (abundance of urban populations) minus log (abundance of rural populations) between social and solitary species in China, but not in Europe. Social species would be particularly easy targets for the Four Pests Campaign. Third, there was a significantly greater variance of log (abundance of urban populations) minus log (abundance of rural populations) between China and Europe. This implies that there were many more species with much larger differences in abundance in urban habitats compared with abundance in rural habitats than expected by chance. Such frequent cases of rarity may also be important for conservation priorities. We emphasize that alternative explanations may account for these patterns although the nature of such alternative explanations remain so far unknown. In fact, when we compared the proportion of trees with birds in our Chinese study sites with the situation in an Asian control site (Fukushima), there was no statistically significant difference. Hence, the Chinese and Japanese data constituted a homogeneous sample.

Many other factors than human persecution are associated with environmental change such as changes in land-use or changes in removal of trees, although this equally applies to the Chinese and the European study sites included here. Even if changes in land-use may be particularly prominent in China, it is still difficult to understand how such changes could differentially affect our Chinese study sites and the frequency distributions of the differences in abundance between urban and rural habitats and the variances in the abundance of birds in China, but not in Europe.

The theoretical model analyzing the effect of the Four Pests Campaign was based on simple and verifiable assumptions. First, we assumed that birds have a normally distributed habitat preference, as expected for a quantitative genetic trait in which the character is inherent (i.e., maintained when individuals are hand-reared, but still showing heterogeneity) (Partridge 1978; see also Cody 1985). Second, we assumed an increase in population size linked to the habitat preference so birds preferring urban habitats had larger population sizes, as shown empirically (Møller et al. 2012). Third, we assumed that population size depends on the habitat preference with stronger preferences implying more individuals living in urban habitats. Fourth, we assumed that removal of a certain fraction of individuals would give rise to extinction, whereas more common species would recover from any prosecution or natural cause of death. The model closely fitted the data hence being consistent with the initial expectations. We could not exclude other possibilities

**Figure 6.** Distribution of values of log urban minus log rural population density of birds in Europe and China. Note the high frequency of observations at 0.0 to -0.5. The box plots show means (line), medians (rhombus), quartiles (square), 5- and 95-percentiles (error bars), and extreme values (dots). The normal frequency distribution is also shown.

leading to this bimodal distribution of urban minus rural population density. For example, 1 alternative explanation for the observed patterns was that if the habitat preference was bimodal, this may result in a few species becoming urbanized and subsequently spreading.

In conclusion, we have shown that habitat preferences combined with human persecution may affect the extent and the frequency of urbanization in birds in China, and that human persecution may have broad and long-lasting consequences for populations of free-living animals today 60 years after the Four Pests Campaign. This study had clear limitations preventing us from drawing clear conclusions. Still, we found evidence consistent with a significant role of the Four Pests Campaign as a major determinant of our findings. Finally, this study may also have important implications for our understanding of the mechanisms that result in urbanization.

Funding

This study was supported by the National Natural Science Foundation of China (Nos 31472013 and 31772453 to W.L.). GDAS Special Project of Science and Technology Development (Nos 2017 GDASCX-0107, 2018 GDASCX-0107) to F.S.Z.

References

- Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA et al., 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc R Soc B Biol Sci* 281:20133330.
- Becker WA, 1984. *Manual of quantitative genetics*. Pullman, WA: Academic Enterprises.
- Bonaparte C-L, 1828. *Ornithologie Comparé de Rome et de Philadelphie*. Rome: C-L Bonaparte.
- Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ et al., 2009. Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* 151:1–18.
- Cheptou P-O, Carrue O, Rouifed S, Cantarel A, 2008. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proc Natl Acad Sci USA* 109:3796–3799.
- Chen J, 2007. Rapid urbanization in China: a real challenge to soil protection and food security. *Catena* 69:1–15.
- China H, 1999. *Chiny Historia* June 2nd 1999.
- Clarke KR, 1993. Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* 18:117–143.
- Cody ML, 1985. *Habitat Selection in Birds*. Orlando (FL): Academic Press.
- Cooke AS, 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biol Cons* 18:85–88.

- Crowther TW, Glick HB, Covey KR, Bettigole C, Maynard DS et al., 2015. Mapping tree density at a global scale. *Nature* 525:201–207.
- Darwin C, 1868. *The Variation of Animals and Plants under Domestication*. London: John Murray.
- del Hoyo J, Elliott A, Sargatal J, Christie DA, 1992–2010. *Handbook of the Birds of the World*. Vol. 1–16. Barcelona: Lynx Edicions.
- Evans KL, Gaston KJ, Frantz AC, Simeoni M, Sharp SP et al., 2009a. Independent colonization of multiple urban centres by a formerly forest specialist bird species. *Proc R Soc Lond B* 276:2403–2410.
- Evans KL, Gaston KJ, Sharp SP, McGowan A, Simeoni M et al., 2009b. Effects of urbanization on disease prevalence and age structure in blackbird *Turdus merula* populations. *Oikos* 118:774–782.
- Ferenc M, Sedláček O, Fuchs R, Dinetti M, Fraissinet M et al., 2013. Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. *Glob Ecol Biogeogr* 23:479–489.
- Falconer DS, Mackay TFC, 1996. *Introduction to Quantitative Genetics*. 4th edn. New York: Longman.
- Gesner C, 1669. *Vollkommenes Vogelbuch*. Schlütersche, Hannover, Germany, reprint 1981.
- Gilbert OL, 1989. *The Ecology of Urban Habitats*. London: Chapman and Hall.
- Handwerk D, 2008. Half of humanity will live in cities by year's end. <http://news.nationalgeographic.com/news/2008/03/080313-cities.html> (accessed 1 March 2019).
- Hubacek K, Guan D, Barrett J, Wiedmann T, 2009. Environmental implications of urbanization and lifestyle change in China: ecological and water footprints. *J. Cleaner Production* 17:1241–1248.
- Kirby RJR, 2018. *Urbanization in China*. London: Routledge.
- Klausnitzer B, 1989. *Verstädterung Von Tieren*. Wittenberg-Lutherstadt: Neue Brehm-Bücherei.
- Kohane MJ, Parsons PA, 1988. Domestication: evolutionary change under stress. *Evol Biol* 23:30–48.
- Kühn I, Klotz S, 2006. Urbanization and homogenization: comparing the floras of urban and rural areas in Germany. *Biol Conserv* 127:292–300.
- Liang W, Yang C, Wang L, Møller AP, 2013. Avoiding parasitism by breeding indoors: cuckoo parasitism of hirundines and rejection of eggs. *Behav Ecol Sociobiol* 67:913–918.
- Marzluff JM, Bowman R, Donnelly R, 2001. *Avian Ecology and Conservation in an Urbanizing World*. Dordrecht: Kluwer Academic Press.
- McKinney ML, 2006. Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260.
- McKinney ML, 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst* 11:161–176.
- Møller AP, 2008. Flight distance of urban birds, predation and selection for urban life. *Behav Ecol Sociobiol* 63:63–75.
- Møller AP, 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* 159:849–858.
- Møller AP, 2010a. Interspecific variation in fear responses predicts urbanization in birds. *Behav Ecol* 21:365–371.
- Møller AP, 2010b. The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behav Ecol* 21:913–918.
- Møller AP, 2014. Behavioural and ecological predictors of urbanization. In: Gil D, Brumm H editors. *Avian Urban Ecology Behavioural and Physiological Adaptations*. Oxford: Oxford University Press, 54–68.
- Møller AP, 2015. Environmental indicators of biological urbanization. In: Armon R, Hänninen O editors. *Environmental Indicators*. Dordrecht: Springer. 421–432.
- Møller AP, Erritzøe J, Nielsen JT, 2010. Causes of interspecific variation in susceptibility to cat predation on birds. *Chinese Birds* 1:97–111.
- Møller AP, 2012. Urban areas as refuges from predators and flight distance of prey. *Behav Ecol* 23:1030–1035.
- Møller AP, Diaz M, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD et al., 2012a. High urban population density of birds reflects their timing of urbanization. *Oecologia* 170:867–875.
- Møller AP, Ibáñez-Álamo JD, 2012b. Escape behavior of birds provides evidence of predation being involved in urbanization. *Anim Behav* 84:341–348.
- Møller AP, 2014. Life history, predation and flight initiation distance in a migratory bird. *J Evol Biol* 27:1105–1113.
- Møller AP, Jokimäki J, Skorka P, Tryjanowski P, 2014. Loss of migration and urbanization in birds: a case study of the blackbird *Turdus merula*. *Oecologia* 175:1019–1027.
- Møller AP, Zhou B, Xianli C, Chu X, Feng C et al., 2018. How many birds are there in China? *Sci Rep* (submitted).
- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, et al., 2016. *vegan: Community Ecology Package*. R package version 2.3-4. 291.
- Partridge L, 1978. Habitat selection in titmice. *Nature* 247:573–574.
- Schneider A, Friedl MA, Potere D, 2009. A new map of global urban extent from MODIS satellite data. *Environ Res Lett* 4
- Shapiro JR, 2001. *Mao's War against Nature: Politics and the Environment in Revolutionary China*. Cambridge: Cambridge University Press.
- Shepherd JM, Pierce H, Negri AJ, 2002. Rainfall modification by major urban areas: observations from spaceborne rain radar on the TRMM satellite. *J Appl Meteorol* 41:869–701.
- Sætre G-P, Ruyahi S, Aliabadian M et al. 2012. Single origin of human commensalism in the house sparrow. *J Evol Biol* 35:788–796.
- Summers-Smith JD, 1992. *In Search of Sparrows*. London: Poyser.
- Time, 1958. *Red-China: Death to Sparrows*. Time May 5, 1958.
- Tomialojc L, 1970. Quantitative studies on the synanthropic avifauna of Legnica town and its environs. *Acta Ornithol* 12:293–392.
- United Nations, Department of Economic and Social Affairs, Population Division, 2015. *World Urbanization Prospects: The 2014 Revision (ST/ESA/SER.A/366)*.
- Zhou L, Dickinson RE, Tian Y, Fang J, Li Q et al., 2004. Evidence for a significant urbanization effect on climate in China. *Proc Natl Acad Sci USA* 101:9540–9544.

Appendix 1. R script for the model on the distribution of log (urban) – log (rural) abundance of birds

```
par (mfrow=c(2, 2))
```

```
p<-rnorm(1000, mean = 0, SD = 1) #habitat preference (p) of 1,000 species is normal distribution (mean = 0, SD = 1), with positive value indicating urban habitat preference and negative value indicating rural habitat preference. Main result keeps steady if uniform distribution used here. Main result keeps steady if number of species be changed (e.g., 100).
```

```
n<-100*exp(p) #This is the key point for the bimodal distribution in result. Total population size (population in urban + population in rural) for each bird is related to preference (n = 100*exp(p)), thus birds prefer urban habitat have larger population size than birds prefer rural habitat. Main result keep steady if base number (100) be changed (e.g., 1000).
```

```
r_n1<-(max(p)-p)/(max(p)-min(p))*n + 1; u_n1<-(p-min(p))/(max(p)-min(p))*n + 1 #population size in urban (u_n1) or rural (r_n1) for each species is depended on preference (p), for example, bird X with the preference value larger than 80% of other birds, 80% total population size of bird X live in urban habitat, whereas 20% total population size of bird X live in rural habitat. There is somewhat strange: as the total population size is larger in species which prefer urban habitat, species, which prefer urban habitat, may have larger population size in rural than species which prefer rural habitat.
```

```
hist(log(u_n1)-log(r_n1), breaks = 50, main = "Figure a") #this result is unimodal distribution, similar to the situation in Europe.
```

```
u_n2<-u_n1*0.2; r_n2<-r_n1 #a certain ratio (e.g., 80%) population size in urban is removed; whereas population size in rural is not changed.
```

hist(log(u_n2)-log(r_n2), breaks = 50, main="Figure b") #this result is also unimodal distribution.

r_n3<-r_n1

u_n3<-u_n1; u_n3[u_n2 < 20]<-0 #Species with the population size in urban habitat less than a certain value (here is 20) is extinct in urban, but the population size for these species in rural habitat is not changed. Species with the population size in urban habitat larger than a certain value (here is 20) recover to the population size before removing (this assumption is not obligatory. if this assumption is deleted, main result keep steady). Main result keep steady if the value (20) be changed (e.g., 60).

hist(log(u_n3 + 1)-log(r_n3), breaks = 50, main="Figure c") #this result is bimodal distribution.

#in the following model, I only assume habitat preference (p) is bimodal distribution (two exponential distribution). More species (here is 700) prefer rural habitat, whereas some species (here is 300) may innate prefer urban habitat (exaptation).

p<-c(rexp(700), 10-rexp(300))

n<-100*exp(p)

r_n4<-(max(p)-p)/(max(p)-min(p))*n

u_n4<-(p-min(p))/(max(p)-min(p))*n

hist(log(u_n4)-log(r_n4), breaks = 50, main="Figure d") #this result is bimodal distribution.

Appendix 2. Survey localities of the number of birds in trees for different localities, cities, seasons (breeding or non-breeding), and number of trees

Country	No birds	Prop with birds	Latitude	Longitude	Urban or rural	Breeding	Mean	95% Upper CI	5% Lower CI	No. of trees
Denmark	336	0.0845	56.27	10.35	Rural	Non-breeding	0.109	0.1531	0.0649	367
Denmark	195	0.0201	56.2	10.33	Urban	Non-breeding	0.0201	0.0398	0.0004	199
China	1980	0.0100	19.08	109.08	Rural	Breeding	0.027	0.0425	0.0115	2,000
China	1962	0.0832	39.93	116.38	Urban	Breeding	0.1687	0.1985	0.1388	2,140
China	3572	0.0359	43.83	125.28	Urban	Breeding	0.0877	0.1191	0.0563	3,705
China	1651	0.0288	19.28	109.05	Urban	Breeding	0.06062	0.0922	0.029	1,700
China	3275	0.0452	42.42	117	Rural	Breeding	0.0898	0.1041	0.0754	3,430
China	4871	0.0258	30.65	104.08	Urban	Breeding	0.1288	0.1663	0.0913	5,000
China	3825	0.0438	23.17	112.53	Rural	Breeding	0.1225	0.1457	0.0993	4,000
China	3921	0.0198	29.53	103.33	Rural	Breeding	0.058	0.0773	0.0387	4,000
Denmark	976	0.0240	56.37	8.95	Rural	Breeding	0.024	0.0335	0.0145	1,000
Japan	973	0.0270	37.75	140.47	Rural	Breeding	0.028	0.0386	0.0174	1,000
Denmark	980	0.0200	56.34	8.99	Rural	Breeding	0.02	0.0287	0.0113	1,000
China	4857	0.0286	23.17	113.46	Urban	Breeding	0.076	0.0911	0.0609	5,000
China	5099	0.1255	23.08	113.3	Urban	Non-breeding	0.278	0.3097	0.2463	5,831
China	1117	0.0692	19.98	110.52	Urban	Non-breeding	0.3633	0.4856	0.2411	1,200
Denmark	962	0.0380	57.15	10.02	Rural	Breeding	0.039	0.0513	0.0267	1,000
China	1973	0.0135	19.27	109.05	Rural	Breeding	0.0395	0.0614	0.0176	2,000
China	3929	0.0178	31.82	114.07	Rural	Breeding	0.0305	0.0416	0.0194	4,000
Denmark	198	0.0704	56.28	9.12	Rural	Non-breeding	0.0986	0.1518	0.0454	213
China	1984	0.0080	19.27	109.05	Urban	Breeding	0.0265	0.0451	0.0079	2,000
China	3925	0.0188	22.48	106.97	Rural	Breeding	0.0495	0.0643	0.0347	4,000
France	927	0.0730	48.7	2.18	Rural	Breeding	0.101	0.1292	0.0728	1,000
France	888	0.1429	48.7	2.18	Urban	Breeding	0.1544	0.179	0.1299	1,036
France	914	0.0860	48.7	2.18	Rural	Breeding	0.094	0.1137	0.0743	1,000
Denmark	971	0.0290	57.2	9.55	Rural	Breeding	0.044	0.0705	0.0175	1,000
France	943	0.0570	48.72	-3.98	Urban	Non-breeding	0.146	0.218	0.074	1,000
China	957	0.0430	38.25	114.68	Urban	Breeding	0.249	0.3413	0.1567	1,000
Bahrein	262	0.1813	26.2	50.6	Urban	Non-breeding	0.3969	0.5368	0.2569	320
China	9661	0.0339	30.53	114.37	Urban	Breeding	0.1206	0.1386	0.1025	10,000
China	954	0.0460	19.28	109.05	Urban	Breeding	0.191	0.2715	0.1105	1,000
China	1977	0.0115	19.28	109.05	Rural	Breeding	0.02	0.0298	0.0102	2,000
China	4918	0.0164	39.97	115.43	Rural	Breeding	0.0292	0.0365	0.0219	5,000
China	3076	0.0388	36.68	114.72	Rural	Breeding	0.1081	0.1447	0.0716	3,200
China	3414	0.0178	44.05	126.08	Rural	Breeding	0.0235	0.0299	0.0173	3,476