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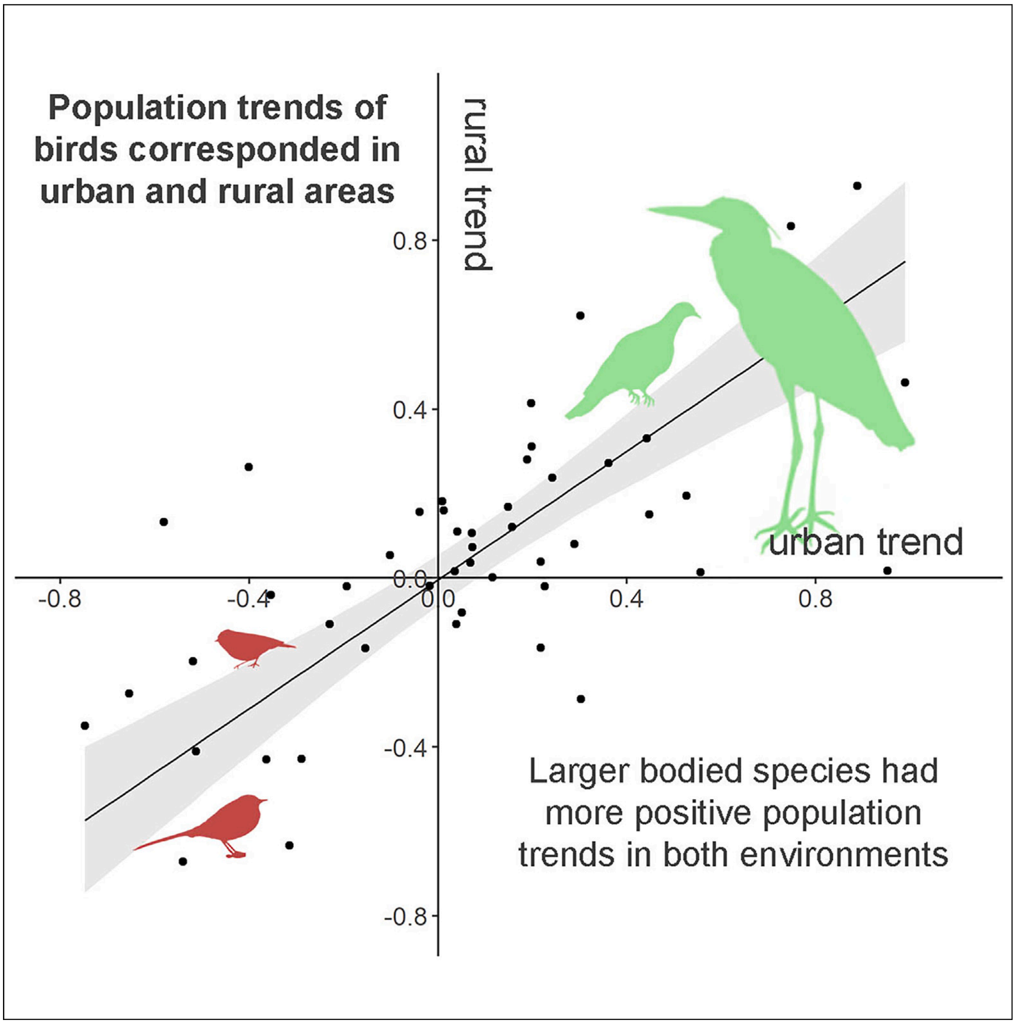

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Highlights

We computed urban and rural long-term population trends in 48 bird species

Urban and rural trends corresponded in most species implying connected populations

More species had positive than negative trends suggesting wildlife-friendly cities

Larger-bodied species had more positive trends in both urban and rural habitats

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Long-term population trends of 48 urban bird species correspond between urban and rural areas

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SUMMARY

Colonization of urban areas by wild species is a widespread phenomenon investigated from various ecological and evolutionary perspectives, yet long-term population trends of organisms in urban areas remain understudied. To fill this knowledge gap, we used data from a large-scale breeding bird monitoring scheme and computed population trends in 48 urban bird species in urban and rural areas of a central European country, Czechia. In most species, trends were similar in both environments, indicating common drivers and/or connections between urban and rural populations. In species with significant trends, the positive trends prevailed, suggesting good performance of urbanized species. This may result from wildlife-friendly environmental changes in cities, such as the expansion of green areas and the maturing of woody vegetation. In respect to species traits, more positive trends were found in larger species than in smaller species in both habitats, likely due to the recovery of previously depleted populations.

INTRODUCTION

Urbanization is one of the most conspicuous processes in the world nowadays, and the majority of the human population inhabits urban areas.[1] The transformation of the landscape toward human settlements affects the ecological communities and properties of the organisms occupying these novel habitats.[2–4] Despite most organisms respond negatively to urbanization,[5] some species thrive in urban habitats.[6–8] These species are often referred to as "urban winners" or "urban exploiters."[6,9] Thus, urbanization works as an ecological filter leading to a similar composition of ecological communities not only in particular regions but also globally.[9] In addition, urban areas are typically an originating harbor for non-indigenous organisms[10] introduced both deliberately by people (e.g., as ornamental vegetation)[11,12] or accidentally (e.g., as a byproduct of international transportation or escaped pets).[13] Also, the pressures of human disturbance, pollution, and other aspects of civilization create characteristic environmental challenges for urban wildlife.[14]

Birds are considered relevant ecological indicators since they are widely distributed, are easy to observe, and respond rapidly to changes in their environment.[15] This also holds true in cities where birds are among the most frequently studied wildlife taxa[16] and may serve as high-quality indicators of urban environments.[17] Cities comprise a mosaic of different habitats, such as woody landscapes (city parks), open habitats (brownfields), rocky areas (buildings), or freshwater habitats (sewage ponds, recreational ponds, etc.), which represent fragments of semi-natural habitats occurring outside urban areas and providing breeding and feeding opportunities for birds specialized for many different habitats.[18] The extensive knowledge of birds' urban ecology enables us to test advanced hypotheses on avian urban ecology, especially in Europe, North America, and Australia, where most research took place in the last decades.[19] Urban birds were therefore studied from many perspectives, such as community composition,[20] colonization processes,[21] or behavioral and physical adaptations.[22,23] Nevertheless, the population trends of urban birds were rarely investigated (but see Murgui[24] and Petrenko et al.[25]).

At the same time, population trends are informative in terms of tracking birds' responses to environmental changes. If an environmental change has relevant population consequences, it is reflected in a long-term population trend.[26–28] In the case of population trends of urban birds, we suggest that this is particularly the case as cities change quickly to meet changes in human needs.[29] Buildings are being modernized, green areas are extending or disappearing, new waterbodies are being created, or existing waterbodies are being revitalized. All these processes affect the possibilities for birds to breed and find food. These changes have their own trends, causing a fast gradual transformation of the urban surface.[30] Such changes in urban areas might be more suitable for certain groups of birds than for others. This can result in different performance of species, depending on their ecological traits.[31]

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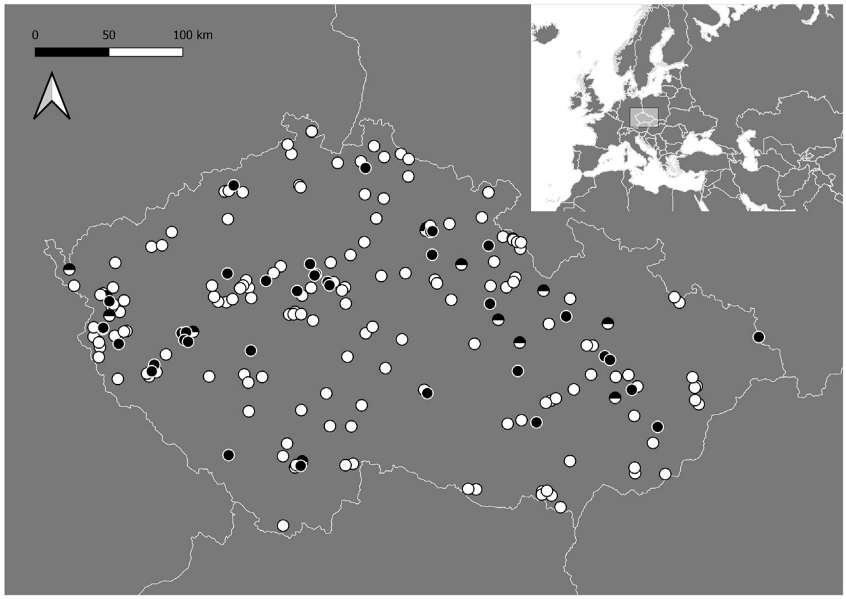

Figure 1. Location of study sites in Czechia

The study sites are represented by monitoring transects (n = 209) containing survey points used for bird counts. Transects containing only urban points are shown by black dots (n = 37), transects containing only rural points by the white dots (n = 158), and transects where both urban and rural points are present by split black and white dots (n = 14).

In respect to birds in urban areas, we can hypothesize about three such traits: association with woodland habitat, association with wetland, and body mass. In some European cities, urban woody vegetation is supported to mitigate climate change impacts, resulting in an increasing cover of urban green areas.[32,33] This effort should be mirrored in increasing populations of species associated with woodlands, while populations of open-habitat species should decline. Restoration and creation of urban wetlands[34] should result in a similar pattern, i.e., increasing populations of species associated with wet habitats in contrast to other species. Body mass is a trait that informs about a species' life history strategy: larger-bodied species are typically those with a slow pace of life and long generation time, laying smaller clutches of larger eggs and having long parental care in contrast to smaller-bodied species.[35] Recent studies show that urban areas support slow pace-of-life traits, such as smaller clutches and higher adult survival.[36,37] This might be caused by lower predation pressure and better food availability in cities as well as by a lower prevalence of macroparasites in urban areas.[36] Therefore, we expect larger-bodied species to have more positive urban population trends than the smaller-bodied species.

Here, we investigate urban and rural population trends using country-wide, long-term standardized monitoring data on bird populations in Czechia, a central European country. We test (i) whether the urban and rural population trends correspond to each other and (ii) whether these trends are linked to species' ecological traits. In accordance with the theoretical background outlined earlier, we predict that species associated with woodlands, wetlands, and larger-bodied species will have more positive trends than open-habitat, non-wetland, and smaller-bodied species, respectively.

RESULTS

Over a 42-year time series, we calculated population trends of 48 bird species separately for urban and rural environments based on data from a national breeding bird monitoring scheme covering the entire country of Czechia (Figure 1). In the urban environment, the population trends were significantly different from zero in 22 species: 14 were positive, indicating a population increase, and 8 were negative, indicating a population decrease (Figure 2). In the rural environment, the trends were significant in 29 species: 18 positive and 11 negative (Figure 2). We recorded the most positive trends in the urban environment in the common wood pigeon (*Columba palumbus*), common firecrest (*Regulus ignicapilla*), gray heron (*Ardea cinerea*), and green woodpecker (*Picus viridis*). On the other hand, we recorded the most negative urban population trend in the gray wagtail (*Motacilla cinerea*), dunnock (*Prunella modularis*), mute swan (*Cygnus olor*), and goldcrest (*Regulus regulus*) (Figure 2). In the rural environment, the most positive trends were recorded in the gray heron, green woodpecker, common redstart (*Phoenicurus phoenicurus*), and common wood pigeon. The most negative trends were recorded in the goldcrest, European serin (*Serinus serinus*), garden warbler (*Sylvia borin*), and European greenfinch (*Chloris chloris*) (Figure 2). The trend values and accompanying statistics are shown in Table S1.

Across all 48 species, their population trends were closely positively related between urban and rural environments (Figure 3), meaning that the trend of urban population largely corresponded to the trend of the rural population of the same species. The slope of the regression line was 0.76 (95% credible interval from 0.55 to 0.96), and the intercept was −0.004 (−0.06, 0.05). However, plotting the trends in a 1:1 plot

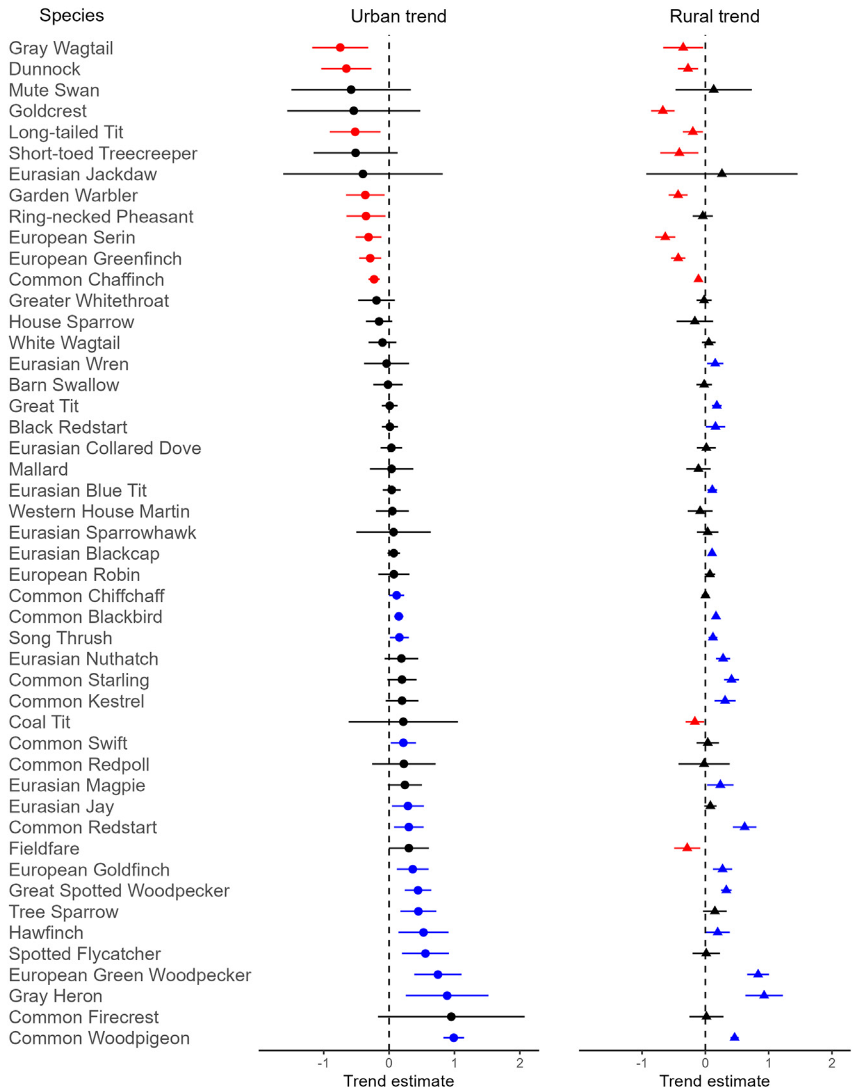

Figure 2. Urban and rural population trends of 48 urban bird species in Czechia

Trend estimates are regression slopes (with 95% confidence intervals) depicting the mean change in abundance of a given species between years, calculated on a log scale. The species are ordered in ascending order by urban population trends. Significant results are marked with red (indicating a significantly negative trend) and blue (indicating a positive trend).

showed that some species deviated from this general pattern (Figure 3). While the trends in most species (n = 38) corresponded between the urban and rural environment, trends in 10 species did not support this general pattern (Figure 3). In this respect, the most conspicuous deviations were represented by the Eurasian jackdaw (*Corvus monedula*), mute swan, and fieldfare (*Turdus pilaris*) (Figure 3).

Sixteen out of 48 species had their population trends significantly different from zero in both urban and rural environments (Figure 2). In all these species, their trends had the same direction in both environments (Figure 2). Nine of these species were increasing: gray heron, common wood pigeon, great spotted woodpecker (*Dendrocopos major*), European green woodpecker, hawfinch (*Coccothraustes coccothraustes*), European goldfinch (*Carduelis carduelis*), common redstart, common blackbird (*Turdus merula*), and song thrush (*Turdus philomelos*). Seven were decreasing: long-tailed tit (*Aegithalos caudatus*), common chaffinch (*Fringilla coelebs*), European greenfinch, gray wagtail, dunnock, European serin, and garden warbler (Figure 2).

Regarding the relationships to species traits, urban and rural trends showed similar patterns (Table 1). In both environments, we found a positive relationship with body mass: larger-bodied species had more positive trends than the smaller ones, and the pattern received more statistical evidence for urban population trends (Table 1). We did not find any convincing evidence for the relationships with the association with woodland habitat for urban or rural trends (Table 1). We found good statistical evidence that, in the urban environment, species not associated with wetland habitats (WetN) had positive population trends (Table 1). We found a similar pattern in the rural environment, but the statistical support for this effect was weak (Table 1).

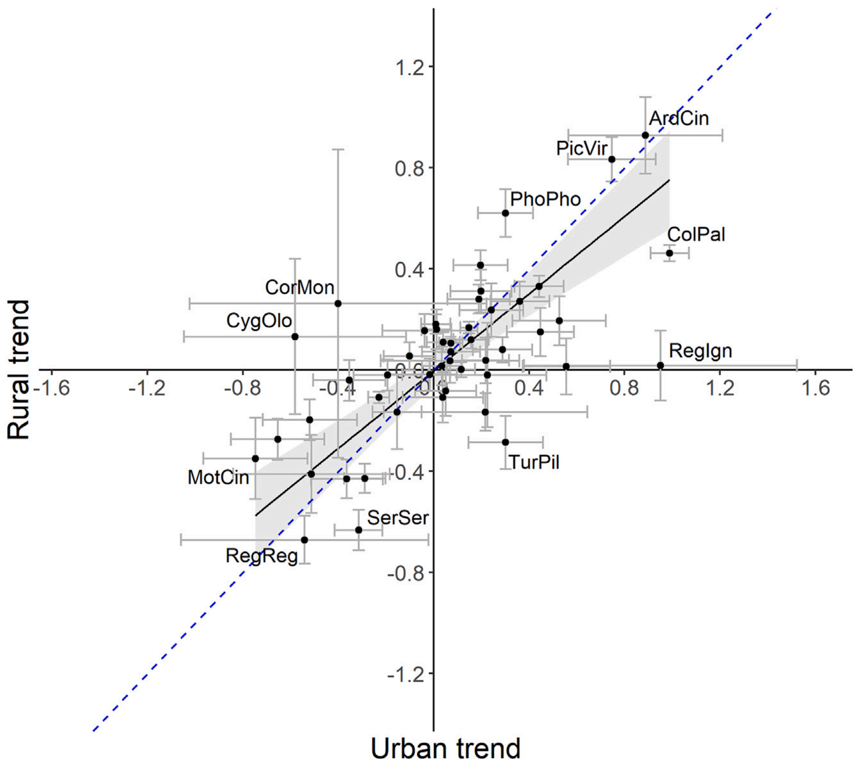

Figure 3. Relationship between urban (x axis) and rural (y axis) population trends in 48 urban bird species in Czechia, as fitted by a Bayesian linear model (black regression line with a 95% credible interval)

Trend estimates (dots) represent regression slopes with ± 1 SE displayed as error bars, depicting the mean change in abundance of a given species between years, calculated on a log scale. Species with the greatest trend magnitude (ArdCin – gray heron, ColPal – common wood pigeon, MotCin – gray wagtail, PhoPho – common redstart, PicVir – European green woodpecker, RegReg – goldcrest, SerSer – European serin) and the greatest incongruence between urban and rural trends (CorMon – Eurasian jackdaw, CygOlo – mute swan, TurPil – fieldfare, RegIgn – common firecrest) are highlighted. The blue dashed line represents the 1:1 line.

DISCUSSION

By analyzing a large-scale dataset collected by citizen scientists, we estimated long-term population trends of 48 species of urban birds, separately for urban and rural areas in Czechia. We found that, in most species, the urban and rural trends corresponded, suggesting that the species performed similarly in both environments. This correspondence provides support for the findings of recent studies, which indicate that regional trends have a significant impact on the performance of species in urban areas.[24,38,39] In addition, the prevalence of positive trends over negative trends indicated the overall good performance of urban birds in Czechia. In both urban and rural environments, more positive trends were associated with larger species.

Similar long-term population trends in urban and rural environments can be underpinned by common drivers, such as climate change, which act over large regions containing both urban and rural areas.[40] In addition, there might be some similar aspects of land use that result in common trends in land cover changes in urban and rural areas. This concerns, for instance, land abandonment creating brownfields in urban areas and abandoned farmland in rural areas, both encroached by woody plants, often of non-native origin.[41] Another possible explanation is that, in species with corresponding trends, the urban populations are connected with the rural ones.[42,43] As a consequence, any population changes outside cities will inevitably result in changes in populations within city borders. We suggest that the connectivity between urban and rural populations will be particularly strong in the case of recently urbanized species such as the gray heron or common redstart.[44]

Many species showed statistically non-significant trends, and this was particularly true in urban habitat. Such trends may indicate long-term population stability, and the prevalence of non-significant trends among species in urban habitat suggests that cities may be a more stable environment than expected. Such environmental stability can be underpinned by the persistence of housing areas—once they are built, the attempts for their removal and replacement by other land cover types are rare. However, cities are typically considered as highly dynamic environments where the mosaic of different land uses evolves rapidly, especially at small spatial scales.[45] Therefore, it is also possible that trends not differing from zero signify more complex population dynamics.[46] As our time series is relatively long (42 years), it may be the case for some species that underwent multiple phases of population decline and recovery.[44]

More species increased than decreased in urban areas over the examined period according to our data. This pattern is in striking contrast with the situation in the UK, where urban bird populations are decreasing on average and urban birds are dominated by declining species.[47,48]

Table 1. Mean marginal effects of bird traits related to population trends in urban and rural environments as obtained from Bayesian linear models

Urban	Estimate	95% HDI	PD	% ROPE
Log(body mass)	0.187	0.077; 0.309	0.998	0.007
Habitat position	−0.087	−0.198; 0.025	0.937	0.196
WetN	0.110	0.019; 0.200	0.992	0.070
WetY	−0.250	−0.712; 0.160	0.871	0.073
Wetdiff	0.359	−0.075; 0.820	0.943	0.041
Rural				
Log(body mass)	0.164	0.052; 0.276	0.998	0.009
Habitat position	−0.010	−0.106; 0.096	0.584	0.464
WetN	0.066	−0.026; 0.157	0.925	0.207
WetY	−0.100	−0.473; 0.275	0.700	0.117
Wetdiff	0.166	−0.233; 0.550	0.794	0.095

The range of the highest density interval (95% HDI), the probability of direction (PD) of an effect, and the percentage of the posterior distributions of the effects in ROPE (% ROPE; the region of practical equivalence) are shown. WetN represents species not associated with wetland habitats, WetY represents species occupying wetland habitats, and Wetdiff represents the difference between trends in WetN and WetY.

The authors explain these negative changes as a result of the filling of green spaces within city borders with houses.[49] It seems that this is not the case in Czechia, where urban green areas are expanding.[50] Even though we did not find a significant effect of woodland habitat association on urban bird trends in the interspecific analysis, Czech urban birds may have also benefited from the increasing availability of brownfields, which became widespread in urban areas after the closure of numerous factories with heavy industry that lost their competitive ability in the early 1990s.[51] In the UK, such socioeconomic changes took place before launching the bird monitoring scheme that provided data for the studies cited earlier,[52] and the British urban birds indeed suffer from brownfield loss, being subject to subsequent housing development.[48]

Another factor underlying positive urban bird trends might be the maturing of vegetation in urban parks and higher biodiversity awareness on private properties (gardens), benefiting especially species linked to woody plants such as the Eurasian jay (*Garrulus glandarius*) or the great spotted woodpecker.[20,29] Another simple mechanism of how urbanization might increase trends in birds breeding in cities is the expansion of urban areas.[53] If increasingly more space is available for urbanized birds to inhabit, more positive trends are expected in these species. This may be the case for well-established urban dwellers such as the common blackbird or the common swift (*Apus apus*), whereas species intolerant to urban habitats suffer from this process.[54] Finally, the positive trends of some species in our dataset that frequently occur in urban areas but still have abundant rural populations might be a reflection of the favorable status of these rural populations. This could be the case for some forest birds or waterbirds that have increased in numbers in the past decades due to suitable forest management and wetland protection, respectively.[55–57]

On the other hand, some species did not perform well according to our data. This might be, once again, explained by environmental changes in cities. Growing and maturing vegetation in urban areas might disfavor open-landscape species of birds, as manifested in our data by declines in the ring-necked pheasant (*Phasianus colchicus*). As humans prefer a clean and "nice-looking" environment, the cities are becoming more "sterile" from a wildlife point of view, with insufficient breeding and feeding opportunities.[58,59] This might lead to weaker performance in species nesting in dense shrubs (e.g., dunnock, long-tailed tit, garden warbler) and generalist species that feed on organic waste in the streets or trash bins (e.g., house sparrow).[60] Finally, since many of the species have only a limited portion of their total populations in cities, it is possible that their negative trends are influenced by phenomena in the rural environment, such as agricultural intensification.[61] For some species, the increase in the population of corvid species (especially Eurasian jay and Eurasian magpie) might also be a threat, as they often prey on their nests.[62] Another phenomenon contributing to negative population trends in urban areas may be modernization of buildings.[63,64] This modernization causes problems for species that place their nests either on building surfaces (swallows and martins) or inside cavities on buildings, such as Eurasian jackdaw, which has decreased more in urban areas compared to rural areas in our data.[65]

Among the traits tested for potential relationships to population trends, we found that body mass was linked to these trends. The results showed greater population increases of larger species in both urban and rural areas. Finding similar patterns in both urban and rural trends is not surprising, given their clear correspondence suggesting a connection of populations, as discussed earlier. This pattern was previously documented in different studies where slower pace-of-life traits were found to be linked to the urban areas.[36,37] One reason for the good performance of large-bodied species may be population recovery after reducing hunting pressure upon their populations. Our long time series, starting in the early 1980s, covers the times when larger species, such as raptors or corvids, were hunted in Czechia. The regulation was first set in the early 1990s[66] and reinforced in the mid-2000s.[67] So, the observed increases may indeed signify the recovery of populations from initial low levels. The smaller population increases in urban habitat may be explained by urban areas acting as refuges from hunting,[68] so the baseline population level might be higher in these areas resulting in a smaller increase.

Limitations of the study

We examined the long-term population trends of birds by analyzing data collected at survey points located in both urban and rural areas that were occasionally only a few kilometers apart. This kind of data calls for addressing potential non-independence of data points in both temporal and spatial aspects. To fix potential issues in the temporal aspect, we included the temporal autocorrelation structure into the models when needed, ensuring that data from adjacent years linked by species population dynamics (e.g., density-dependent population growth) can be considered for inference. In the case of potential spatial autocorrelation, it should ideally be addressed by including a spatial autocorrelation structure into the models, which would, however, be very complex and extremely computationally intensive. Therefore, we addressed the issue of spatial autocorrelation by including specific random effects. Although this solution is not perfect from a statistical point of view, it is fully appropriate from a biological perspective. Birds are territorial in their breeding season (occupying home ranges of a few hectares at maximum),[69] and the minimum distance of 3 km between urban and rural points assures their independence in a given year. However, advanced modeling of spatiotemporal patterns in bird populations may be an interesting subject for future studies. By that means, it would be possible to identify spatial (in)congruence in trends across urban and rural sites, as well as determine the potential factors influencing these trends.

Conclusions

Our analysis of long-term population trends of 48 species breeding in urban and rural areas in Czechia showed that the trends were strikingly congruent between environments. This congruence implies the existence of connections between urban and rural populations, possibly as a result of colonization of urban areas from prospering rural populations. Although the observed population changes were likely generated by numerous species-specific drivers discussed earlier, our analysis relating population trends to several ecological traits uncovered that populations of larger-bodied species increased more than populations of smaller species in both urban and rural areas. We suggest that this general pattern may result from population recovery after a hunting ban came into effect at the start of our time series. Even though there are good reasons to consider the expansion of urban habitat as a threat to biodiversity, including birds,[70] our long-term data report stable or positive population trends in most species. This suggests that wildlife-friendly management approaches are being adopted in Czech cities. Nevertheless, this conclusion should be tested by future studies focusing on a deeper investigation of the temporal trajectories of urban bird species.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
  - Bird data
  - Species and site selection
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Calculation of long-term population trends

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109717.

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AUTHOR CONTRIBUTIONS

Conceptualization, J.R. and J.G.; methodology, J.G., J.R., and J.H.; formal analysis, J.G. and J.H.; resources, J.R. and P.V.; writing – original draft, J.G. and J.R.; writing – review and editing, J.H. and P.V.; visualization, J.H. and J.G.; funding acquisition, J.G. and J.H.; supervision, J.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data for this study	This study	https://doi.org/10.5281/zenodo.10562873
Habitat position and association with wetlands	Hanzelka et al.[71]	https://doi.org/10.1111/ddi.12945
Body mass	Storchová and Hořák[72]	https://doi.org/10.1111/geb.12709
Software and algorithms		
All code for this study	This study	https://doi.org/10.5281/zenodo.10573789
R software version 4.2.2	R Core Team[73]	https://www.r-project.org/
glmmTMB package for R	Magnusson et al.[74]	https://CRAN.R-project.org/package=glmmTMB
DHARMa package for R	Hartig[75]	https://CRAN.R-project.org/package=DHARMa
Performance package for R	Lüdecke et al.[76]	https://cran.r-project.org/web/packages/performance/readme/README.html
Emmeans package for R	Lenth et al.[77]	https://cran.r-project.org/web/packages/emmeans/
Brms package for R	Bürkner[78]	https://cran.r-project.org/web/packages/brms/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Jiří Reif (e-mail: jirireif@natur.cuni.cz).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

This is an observational study; any experimental model organisms were used.

METHOD DETAILS

Bird data

We obtained the data on bird populations in Czechia from the Breeding Bird Monitoring Programme (Jednotný program sčítání ptáků – JPSP), a long-term common bird monitoring project launched in 1982. JPSP is based on fieldwork by experienced volunteers, who are members of the Czech Society for Ornithology and are qualified to recognize all bird species regularly breeding in Czechia by voice and plumage. Volunteers count the birds annually along monitoring transects, each consisting of 20 survey points. Each point is visited 1–3 times (mostly twice) per breeding season for 5 minutes, and all heard and seen birds are recorded. The points are at least 300 m apart, so the transects extend for 5-6 km. Since the transect locations are chosen by the observer, they are distributed non-randomly but sample all main habitats in Czechia in proportions broadly corresponding to their cover at the country level, with urban areas being slightly overrepresented.[79] The participants in the monitoring scheme are instructed that the aim of the scheme is to produce high-quality data on national populations of common bird species, and not to observe as many birds as possible or watch the rare species.[80] Therefore, the observers should establish their transects in habitats typical for the region where they conduct the fieldwork, and not in sites that are attractive to birdwatchers. This approach of the participants enables this program to be a reliable source for estimating the long-term population trends of birds in Czechia.[81–83] See Reif et al.[84] for more details on JPSP data. The data from 1982–2023 were used in this study.

Species and site selection

We focused on 48 species that commonly breed in urban areas in Czechia, based on information from national literature.[44] Most of these species were passerines (Table S1), and these species are easily detectable using the monitoring technique applied in JPSP.

To calculate the urban long-term population trends, we selected data from urban points included in JPSP. We considered a point to be urban if it was located within a human settlement with more than 1500 inhabitants in 2021[85] and completely surrounded by built-up areas. Although the national literature defines urban settlements as those with more than 2000 inhabitants,[86,87] we used the 1500 inhabitant limit because the settlements with 1500-2000 inhabitants sampled by the JPSP data clearly exhibited urban characteristics (i.e., towns with a central square surrounded by densely packed multistorey buildings) as confirmed by visual inspection. The population size of the human settlements sampled for our urban points ranged from 1667 to 1335084 inhabitants (median = 10353 inhabitants). We also included points located in urban parks among urban points, provided they were enclosed within the city (parks on the city borders were excluded). We only considered points that were monitored for at least two consecutive years. As a result, we selected 246 points distributed across 51 transects (Figure 1).

For the long-term population trends in rural areas, we used points that avoided urban areas, i.e., human settlements with more than 1500 inhabitants, and were located at least 3 km away from the nearest urban point to ensure independence of bird counts. Some transects contained both urban and rural points (Figure 1), but they were positioned on opposite ends of these transects and always adhered to the rule of a 3 km distance between urban and rural points. Additionally, our sample of rural points represented all major land cover types in proportions broadly corresponding to their distribution in the Czech landscape, including agricultural lands, aquatic ecosystems, rocks, forests, grasslands, small villages, and wetlands (Table S2). To adequately cover these land cover types, the number of rural points used for the analysis was larger than the number of urban points, totalling 2111 rural points distributed across 172 transects (Figure 1). Similar to the urban population trend data, each rural point had to be monitored for at least two consecutive years. Land cover type data was obtained from the Consolidated Layer of Ecosystems of the Czech Republic,[88] updated for the year 2022.[89] See Table S3 for the numbers of urban and rural points occupied by respective species.

Following the approach applied in similar studies,[82,90] we considered the maximum count of a species at a specific point in a given year as the abundance of that species. These maximum counts of focal species were used for further analysis.[91]

For each species, we retrieved information from the literature regarding their habitat preferences and body mass (Table S3). To determine the association with woodland vs. open habitat (referred to as habitat position), we used the position of each species along the gradient from forest interior (value = 1) to open treeless landscape (value = 7) as defined by Hanzelka et al.[71] For the association with wetlands, we used the classification by Hanzelka et al.,[71] which identified whether a species was associated (value = WetY) or not associated (value = WetN) with wetlands. As for body mass, we considered the mean body weight of each species provided by Storchová and Hořák.[72]

QUANTIFICATION AND STATISTICAL ANALYSIS

Calculation of long-term population trends

We computed the long-term population trends using generalized linear mixed models (GLMM) with Poisson or negative binomial structure of errors (see below) from the 'glmmTMB' package in R.[74] We ran a separate model for each species.[92] The dependent variable was the abundance of a species on the individual points, the explanatory variables were *year* and *type of environment,* where *year* is the year of the census and *type of environment* is a categorical variable with two levels (urban and rural), and their interaction, i.e., *year* × *type of environment.* By that means, we quantified the effect of the *year* in respective environments, obtaining the values of urban and rural trends, respectively, for each species. The random intercept was point nested in the monitoring transect, and the random slope was *year*, but some of these respective effects might be omitted in some species provided that the effect showed zero variance. The models could further include a temporal autocorrelation structure AR(1), to account for time dependencies in bird counts between years, if a Durbin-Watson test on simulated model residuals performed using the 'DHARMa' package[75] was significant ($p < 0.05$). An observation-level random effect (OLRE) accounting for model overdispersion was included if the model dispersion parameter was significantly ($p < 0.05$) different from 1, which we tested using the 'performance' package.[76] The choice of Poisson or negative binomial structure of errors, as well as the assessment of the contribution of AR(1) structure and random effects were made based on model comparison via the Akaike Information Criterion (AIC), and the best model (ΔAIC < 2) was selected (see Table S4 for notation of the best models used for inference in respective species). We obtained the urban and rural population trends using the function 'emtrends' in the R-package 'emmeans'.[77] The significance of the trend (i.e., difference from zero) was tested using a z-test.

Having the urban and rural population trends for every species, we related these trends to each other across species using a Bayesian linear model from the 'brms' R package.[78] In this analysis, rural population trends with their standard errors (SE) were the response variable, and urban population trends with their SE were the predictor. The model was run with 1000 warmup iterations and 2000 total iterations per each of four Markov chains, and the thinning rate was set to one. Priors were set to a normal(0, 0.5) distribution for the effect of urban trends and for the intercepts, and the default student_t(3, 0, 2.5) distribution prior was set for sigma parameters. Relationships of trends to species traits were tested by two Bayesian linear models run separately for urban and rural trends as respective response variables with standard errors (SE) of the trends as measurement errors. Habitat position, association with wetland (a categorical variable with two levels: WetY and WetN), and log-transformed body mass were explanatory variables in both models. Continuous trait predictors were standardized to zero mean and unit variance. These two models were run with 1000 warmup iterations and 2000 total iterations per each of four Markov chains, and the thinning rate was set to one. Priors were left as the default, i.e., flat priors for the distributions of predictors, a student_t(3, 0.1, 2.5) distribution for the intercept, and a student_t(3, 0, 2.5) distribution for sigma parameter. Statistical evidence for an effect was assessed by the 95% highest density interval (HDI) of the posterior distribution, probability of direction (PD), and the percentage of the full posterior distribution in a region of practical equivalence (% ROPE), which was calculated as ± 0.1*SD(response variable).[93] Model convergence was checked using R-hat statistics (R-hat <1.01 at convergence) and visually by posterior predictive distributions plotted via the 'pp_check' function.

All statistical analyses were performed in R version 4.2.2.[73]