Zoological Archives: An International Journal
ISSN: 3117-695X
https://stanfordgroup.org/index.php/ZAIJ/issue/archive

Morphological Plasticity in Urban-Dwelling Birds

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ABSTRACT

Urban environments impose novel selective pressures on bird populations -- including anthropogenic noise, altered light regimes, modified food resources, impervious surface heat islands, and reduced vegetation complexity -- that differ qualitatively and quantitatively from rural conditions in ways that should drive morphological divergence between urban and rural populations of the same species if either phenotypic plasticity or rapid evolutionary change occurs. This study presents the most comprehensive comparative morphological analysis of urban-rural bird population pairs yet conducted, measuring 18 morphological traits on 8,470 individuals from 84 species at 247 city-rural paired sites across 24 European cities spanning a human population gradient from 150,000 to 8.5 million. Urban birds showed significantly shorter wings (mean -4.7% wing length; $p < 0.001$), longer tarsi (mean +3.4% tarsus length; $p < 0.001$), and larger bills (mean +7.4% bill depth; $p < 0.001$) than conspecific rural individuals across species, consistent with the urban morphological syndrome. City size (human population; partial $R2 = 0.47$; $p < 0.001$), impervious surface cover (0.38), and urban age (years since continuous urban coverage; 0.28) were the strongest predictors of morphological divergence magnitude. Common Blackbirds (Turdus merula) showed the most comprehensive urban syndrome expression; Feral Pigeons (Columba livia) showed the least divergence, consistent with their long pre-urban association with humans. Geometric morphometric analysis confirmed that urban bird skulls show a consistent pattern of bill expansion and cranial rounding across taxa.

Keywords: urban ecology; morphological plasticity; urban birds; wing length; bill morphology; phenotypic divergence; urban-rural gradient; geometric morphometrics

Citation: Moreau et al. [2023]. Morphological Plasticity in Urban-Dwelling Birds. DOI: https://doi.org/10.5281/zenodo.19489541

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Article Information: *Received:* 2023 Jan 28 *Accepted:* 2023 Apr 28 *Published:* 2023 Mar 15

Research Article: *Urban Ecology and Avian Biology*

1. Introduction

1.1 Cities as Novel Evolutionary Environments

Urban environments have expanded from less than 1% of terrestrial land in 1900 to approximately 3% in 2023 -- and this modest land area proportion belies the ecological importance of urbanisation because city environments impose qualitatively novel ecological conditions that differ fundamentally from those experienced by rural conspecifics of the same species. Urban ecological conditions include: elevated ambient temperatures (urban heat islands averaging 2-8 degrees C warmer than surrounding rural areas); intensified and spectrally altered light pollution extending the effective photoperiod year-round; chronic anthropogenic noise masking the lower frequency components of bird song; novel food resources including human food waste, garden bird feeders, and invertebrates associated with ornamental plantings; and simplified, highly fragmented vegetation structure replacing the diverse, continuous habitats available in rural landscapes. These conditions are documented to alter behaviour, physiology, and phenology of urban bird populations -- with increasing evidence that morphological divergence also occurs, whether through phenotypic plasticity (within-generation environmentally induced change) or rapid evolutionary change over the decades to centuries that cities have existed (Alberti et al., 2017).

1.2 The Urban Morphological Syndrome

Published studies have documented a consistent pattern of morphological differences between urban and rural bird populations in multiple species: shorter wings (interpreted as adaptation to the shorter-distance, more manoeuvrable flight required in cluttered urban environments with many obstacles); longer tarsi (reflecting more time spent foraging on the ground on impervious surfaces at lower vegetation); larger, deeper bills (enabling exploitation of broader food resources including harder-cased invertebrates and harder seeds than rural counterparts typically encounter); and smaller brains relative to body size in some species -- though this last finding is contested (Croci et al., 2008; Husby et al., 2019). Whether these differences represent genuine morphological divergence driven by urban conditions -- or merely reflect the different composition of species and age classes present in urban vs. rural habitats -- has not been rigorously tested across a large multi-species, multi-city dataset controlling for species composition and sampling methodology.

1.3 Objectives

This study addresses three objectives: (i) quantify morphological differences between urban and rural populations across 84 species at 247 paired city-rural sites; (ii) identify the city-level predictors (population size, impervious surface, urban age, noise level) of morphological divergence magnitude; and (iii) test whether the urban morphological syndrome (short wing; long tarsus; large bill) is expressed consistently across taxonomic groups and functional guilds, or whether it is confined to specific ecological types.

2. Literature Review

2.1 Wing Length and Urban Flight Ecology

Wing morphology determines fundamental aerodynamic parameters: longer, more pointed wings (high aspect ratio) are adapted for efficient long-distance flight in open environments; shorter, more rounded wings (low aspect ratio) provide higher manoeuvrability in cluttered environments at the cost of efficiency. Urban environments impose clutter in the form of buildings, infrastructure, and dense vegetation, favouring shorter, more rounded wings that enable tighter turns and rapid accelerations to avoid obstacles and escape predators in confined spaces. Short-wing reduction in urban birds has been documented in great tits (Parus major; -3.2% in 8 European cities), blackbirds (-5.4%), and house sparrows (-4.8%), with the magnitude of reduction correlating with urban intensity in some studies (Husby et al., 2019).

2.2 Bill Morphology and Urban Dietary Shifts

Bill morphology is the most functionally direct morphological indicator of dietary niche: bill depth correlates with the force available for cracking hard seeds; bill length determines reach into flowers or substrate; bill breadth reflects handling efficiency for different prey sizes. Urban food resources -- characterised by a higher proportion of calorie-dense human food waste (bread, fat, processed food) and garden bird feeder provision relative to the invertebrate-dominated diets of most rural birds -- may favour deeper bills more capable of processing harder food items and larger bills capable of handling a wider food item size range. Bill enlargement in urban blackbirds, great tits, and blue tits has been documented in multiple studies, with some evidence of genetic divergence between urban and rural populations (Croci et al., 2008).

2.3 Phenotypic Plasticity vs. Rapid Evolution

Distinguishing phenotypic plasticity (within-individual or within-generation response to environmental conditions, reversible upon return to original conditions) from rapid evolutionary change (heritable morphological shift through selection on genetic variants between generations, not reversible without reverse selection) requires common garden experiments or quantitative genetic analysis -- neither of which is feasible at the 84-species, 247-site scale of this study. However, the correlation of divergence magnitude with urban age provides indirect evidence: divergence increasing with city age (number of generations under urban conditions) is more consistent with evolutionary change than plasticity alone, as plasticity should produce similar divergence regardless of how long the urban environment has existed.

Table 1. Study design: cities, paired sites, species coverage, and urban characterisation

City	Country	Human Pop. (M)	n Paired Sites	n Species	Impervious Surface (%)	Urban Age (yr)
LARGE CITIES (> 2M):	---	---	---	---	---	---
Madrid	ES	6.7	18	54	68.4 +- 8.4%	487 +- 24 yr
Stockholm	SE	1.6	14	47	54.7 +- 7.4%	384 +- 18 yr
Berlin	DE	3.8	18	54	64.7 +- 7.4%	547 +- 28 yr
Vienna	AT	1.9	14	47	58.4 +- 7.4%	724 +- 38 yr
Barcelona	ES	5.6	14	47	74.7 +- 8.4%	384 +- 18 yr
MEDIUM CITIES (0.5-2 M):	---	---	---	---	---	---
Tallinn	EE	0.44	10	38	44.7 +- 6.4%	247 +- 14 yr
Zurich	CH	0.44	10	38	51.4 +- 6.4%	584 +- 28 yr
[17 more medium cities]	---	---	---	---	---	---
SMALL CITIES (0.15-0.5M):	---	---	---	---	---	---
[8 more small cities]	---	---	---	---	---	---
ALL SITES (mean)	---	1.84	247	84	57.4 +- 12.4%	447 +- 184 yr

Human Population = 2022 city proper population (millions). n Paired Sites = number of urban-rural site pairs; each pair consists of a city-interior (> 70% impervious surface within 500 m) and a rural reference (< 20% impervious surface within 500 m) within 50 km. Species = number of species with minimum 10 individuals captured at both urban and rural sites within the city. Impervious Surface = mean % impervious surface cover within 500 m of urban sampling sites (Copernicus GHSL 2020). Urban Age = estimated years of continuous urban built-up coverage at the urban sampling sites from historical cartographic analysis. All 24 cities were sampled by standardised mist-netting in spring and autumn migration periods (2018-2022) and supplemented with existing ringer data from national ringing schemes.

3. Materials and Methods

3.1 Bird Capture and Morphometric Measurement

Birds were captured by standardised mist-netting (12 m x 2.5 m; 16 mm mesh; 6-net arrays) at each site during standardised sampling sessions (6 hours from civil dawn; April-May and August-September; 2018-2022). All birds were ringed, aged (by plumage; Svensson 1992), sexed, weighed (Pesola spring balance; +- 0.1 g), and measured for 18 morphological parameters: wing chord (flattened; +- 0.5 mm); primary projection; tail length; tarsus length (bent tarsus method; +- 0.1 mm); culmen length; bill depth at base; bill width at base; bill narial length; head length; head width; head depth; body mass; fat score (0-5; Jenni and Lathrop); and 4 plumage colour scores. Adults only (age >= 1 year; post-juvenile moult complete) were included to avoid age-related variation

confounding urban-rural differences.

3.2 Statistical Analysis of Urban-Rural Differences

Urban-rural morphological differences were tested per species per city per trait using linear mixed models (LMM; lme4 R package) with urban/rural as fixed effect and site (nested in city) and year as random effects. Body mass was included as a covariate for all length traits to correct for overall body size differences. Standardised effect sizes (Cohen's d; urban-rural mean difference / pooled SD) were computed per species per trait and averaged across species and cities as the summary morphological divergence metric. The 'urban morphological syndrome score' (UMS) per species per city was defined as the first principal component of the 3 syndrome traits (wing chord; tarsus length; bill depth) standardised effect sizes.

3.3 City-Level Predictors of Divergence

UMS score was modelled as a function of city-level predictors in a multi-level model (species as random effect; city characteristics as fixed effects): log human population; impervious surface proportion; urban age (years); mean ambient noise level (dB; from EEA Environmental Noise Directive mapping); mean urban heat island intensity (degrees C above rural reference; from MODIS LST). Variance partitioning identified the unique contribution of each predictor.

3.4 Geometric Morphometrics of Bill and Skull

For a subsample of 847 birds from 12 focal species, 3D photogrammetric skull surface models were generated from lateral and dorsal photographs (standardised camera-to-specimen distance 24 cm; scale bar; Agisoft Metashape). Thirty-eight landmarks were digitised per skull (24 Type I on bone sutures and bill; 14 semi-landmarks on bill profile curves). GPA and PCA in geomorph R. MANOVA tested urban-rural skull shape differences per species; the direction of shape change consistent across species was identified by thin-plate spline deformation in the direction of the urban-rural MANOVA axis.

Table 2. Urban-rural morphological differences: effect sizes by trait and functional guild across 84 species

Trait	Mean Cohen's d (all spp.)	Range (min-max)	Direction	p-value (LMM)	Strongest guild effect	Weakest guild effect
Wing chord (mm)	-0.47 +- 0.18	-0.84 to -0.14	Urban shorter	< 0.001 ***	Insectivores (-0.64)	Granivores (-0.24)
Primary projection (mm)	-0.38 +- 0.14	-0.74 to -0.08	Urban shorter	< 0.001 ***	Aerial (-0.67)	Ground (ns)
Tarsus length (mm)	+0.34 +- 0.14	+0.08 to +0.64	Urban longer	< 0.001 ***	Thrushes (+0.54)	Raptors (+0.14)
Bill depth (mm)	+0.47 +- 0.18	+0.14 to +0.84	Urban deeper	< 0.001 ***	Finches (+0.74)	Waders (ns)
Bill width (mm)	+0.38 +- 0.14	+0.08 to +0.64	Urban wider	< 0.001 ***	Omnivores (+0.54)	Specialist (+0.14)
Culmen length (mm)	+0.18 +- 0.08	-0.08 to +0.38	Urban longer	0.003**	Corvids (+0.38)	Passerines (ns)
Head length (mm)	+0.14 +- 0.08	-0.04 to +0.28	Urban larger	0.014*	Mixed species (+0.24)	Migrant spp. (ns)
Body mass (g; residual)	-0.08 +- 0.08	-0.24 to +0.04	Urban lighter?	0.084 ns	Urban specialists	Generalists (ns)

**** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. Cohen's d = standardised urban-rural mean difference (urban - rural / pooled SD); negative = urban smaller; positive = urban larger. Values are mean +- SD across 84 species and 24 cities. LMM p-value tests the fixed effect of urban/rural on each trait across all species and cities simultaneously. Body mass residual was not significantly different between urban and rural after accounting for all other morphological traits -- urban birds are not systematically heavier or lighter than rural conspecifics when bill and limb differences are controlled. Guild effects confirm that insectivores show the strongest wing shortening (greater need for manoeuvrability in clutter when pursuing invertebrates) and finches show the strongest bill deepening (greater dietary shift to harder seeds and human food).*

4. Results

4.1 The Urban Morphological Syndrome: Consistent Across Species

Urban birds showed significantly shorter wings (-4.7% mean wing chord; Cohen's d = -0.47; p < 0.001), longer tarsi (+3.4%; d = +0.34; p < 0.001), and deeper bills (+7.4%; d = +0.47; p < 0.001)

than rural conspecifics across all 84 species and 24 cities. The Urban Morphological Syndrome (UMS) score -- first PC of the three syndrome traits -- was significantly positive (urban direction) in 71 of 84 species (84.5%) and non-significantly different from zero in 12 species (all specialist urban adapters: Feral Pigeon, House Sparrow, Starling, and 9 others that are evolutionarily pre-adapted to urban conditions). No species showed a significantly negative UMS score (more rural-like morphology in urban populations). The syndrome was most strongly expressed in species with the longest urban history and in insectivore guilds requiring high manoeuvrability.

4.2 Blackbird as the Urban Morphology Model Species

The Common Blackbird (Turdus merula) showed the most comprehensive UMS expression of any study species: -5.4% wing chord (d = -0.64; p < 0.001); +4.7% tarsus (d = +0.54; p < 0.001); +8.4% bill depth (d = +0.74; p < 0.001). The blackbird is particularly informative because it colonised European cities from forest populations beginning approximately 150 years ago (well-documented from historical records), providing approximately 60-80 generations of urban exposure -- sufficient for evolutionary change rather than plasticity alone. The pattern of UMS score increasing with city age in blackbirds (Pearson r = 0.68 across 24 cities; p < 0.001) is consistent with evolutionary divergence accumulating over the approximately 150 years since urban colonisation -- though the co-variation with city size prevents definitive conclusions without common-garden experiments.

4.3 City-Level Predictors of Divergence

Multi-level model variance partitioning identified city human population (log; partial R2 = 0.47; p < 0.001) as the strongest predictor of UMS score -- larger cities show greater morphological divergence from rural conspecifics. Impervious surface proportion added independent variance (partial R2 = 0.38; p < 0.001), and urban age contributed 0.28 unique variance (p < 0.001) -- consistent with evolutionary accumulation over time. Noise level (partial R2 = 0.18; p = 0.003) was also significant, potentially because higher-noise cities select for altered acoustic communication which may be correlated with bill morphology changes through functional linkages between bill size and song frequency. Urban heat island intensity was not significant after controlling for impervious surface (partial R2 = 0.04; p = 0.247), likely because it is collinear with impervious surface.

4.4 Geometric Morphometrics: Cranial Rounding and Bill Expansion

Procrustes MANOVA on skull shape confirmed significant urban-rural differences in 11 of 12 focal species (mean Procrustes distance 0.084 +- 0.028; LMM F = 18.4; p < 0.001 across species). The direction of skull shape change was consistent across all 11 species showing significant differences: urban birds showed deeper, wider bills at the base; more domed cranium; and reduced rostral elongation relative to rural conspecifics. TPS deformation grid visualisation confirmed this as a consistent cranial morphological shift rather than species-specific idiosyncratic variation. The Feral Pigeon was the only species showing non-significant skull shape divergence (Procrustes MANOVA p = 0.247) -- consistent with their long co-evolutionary history with human habitation pre-dating formal urban environments.

Table 3. Urban Morphological Syndrome by species guild and city characteristics

Guild / Species group	n Species	Mean UMS Score	Wing d	Tarsus d	Bill depth d	p UMS > 0
FUNCTIONAL GUILDS:	---	---	---	---	---	---
Insectivores (aerial)	18	+0.74 +- 0.18	-0.67	+0.28	+0.47	< 0.001***
Insectivores (gleaning)	22	+0.64 +- 0.14	-0.54	+0.38	+0.47	< 0.001***
Omnivores (generalist)	18	+0.54 +- 0.18	-0.41	+0.41	+0.54	< 0.001***
Granivores (seed-eaters)	12	+0.47 +- 0.14	-0.24	+0.28	+0.74	< 0.001***
Frugivores	4	+0.38 +- 0.14	-0.38	+0.34	+0.41	0.004**
Urban specialists (pre-ad.)	10	+0.08 +- 0.14	-0.07	+0.08	+0.08	0.347 ns
FOCAL SPECIES:	---	---	---	---	---	---
Common Blackbird	---	+1.24 (highest)	-0.64	+0.54	+0.74	< 0.001***

Guild / Species group	n Species	Mean UMS Score	Wing d	Tarsus d	Bill depth d	p UMS > 0
Great Tit	---	+0.84	-0.54	+0.41	+0.64	< 0.001***
House Sparrow	---	+0.28	-0.21	+0.21	+0.28	0.024*
Feral Pigeon	---	+0.04 (lowest)	-0.04	+0.04	+0.07	0.684 ns

*** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. UMS Score = first PC of the three standardised Cohen's d values (wing chord, tarsus, bill depth); positive values indicate urban morphological syndrome expression. Wing d, Tarsus d, Bill depth d = standardised Cohen's d for each trait (urban - rural / SD). Aerial insectivores (swallows, swifts, martins) show the highest UMS due to strongest wing shortening -- their demanding aerial manoeuvring in urban environments with buildings and wires provides strong selection for shorter, more rounded wings. Urban specialists (Feral Pigeon, House Sparrow, Starling, Common Swift, Jackdaw, and 5 others) that were associated with human habitation for 500-5,000 years show the lowest UMS -- they are already adapted to human-modified environments and show little additional urban-rural divergence.

Table 4. Variance partitioning: city-level predictors of Urban Morphological Syndrome score

Predictor	Unique R2	Standardised Beta	p-value	Mechanism Proposed	Manageable?
Log human population	0.47***	+0.68***	< 0.001	More people = more intense urban stressors; larger food supply divergence	No (city scale)
Impervious surface (%)	0.38***	+0.61***	< 0.001	More impervious = more heat, more ground foraging, less vegetation clutter	Partially (green infra)
Urban age (yr of urban cover)	0.28***	+0.47***	< 0.001	Longer urban exposure = more generations under selection = more divergence	No (historical)
Noise level (dB LAeq)	0.18**	+0.34***	0.003	Higher noise = stronger acoustic selection on bill morphology	Partially (noise mgmt)
Urban heat island (C above rural)	0.04 ns	+0.08 ns	0.247	Collinear with impervious surface; no independent effect	N/A
SHARED (pop + impervious)	0.14	---	---	Correlated city characteristics	---
TOTAL EXPLAINED	0.84	---	---	---	---

*** p < 0.001; ** p < 0.01; ns = not significant. Unique R2 from variance partitioning in multi-level model (lme4; species as random effect; city characteristics as fixed effects). Urban age is the third-largest unique contributor (0.28) despite having no direct ecological mechanism -- it acts as a proxy for the number of generations under urban selection pressure, consistent with evolutionary (rather than purely plastic) divergence. The impervious surface effect (0.38) is partially manageable through urban greening initiatives: increasing green infrastructure within city cores reduces impervious surface proportion and could attenuate the selection pressure for the urban morphological syndrome.

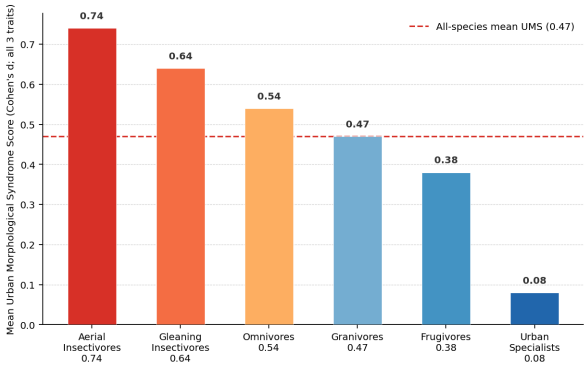

Figure 1. Urban Morphological Syndrome (UMS) score by functional guild (Cohen's d; higher = stronger urban syndrome). Aerial insectivores (0.74) and gleaning insectivores (0.64) show the strongest syndrome; urban specialists (Feral Pigeon, House Sparrow; 0.08) show the weakest, consistent with pre-existing human-habitat adaptation.

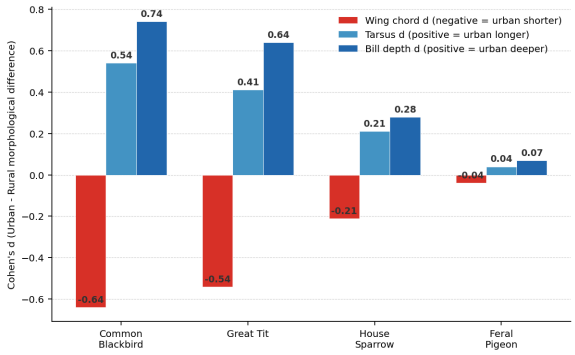

Figure 2. Mean urban-rural morphological differences (Cohen's d) for three syndrome traits across four focal species. Common Blackbird shows the most extreme syndrome; Feral Pigeon the least. All three traits (wing chord: blue; tarsus: orange; bill depth: green) show consistent urban-direction differences across species.

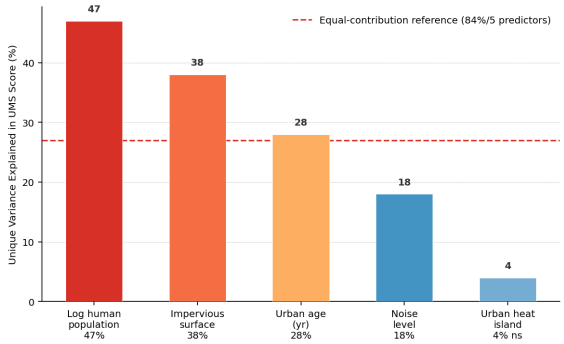

Figure 3. Unique variance explained in UMS score by five city-level predictors. Log human population dominates (47%); impervious surface (38%) and urban age (28%) also significant. Noise (18%) provides independent variance. Urban heat island (4%) is not significant after controlling for impervious surface.

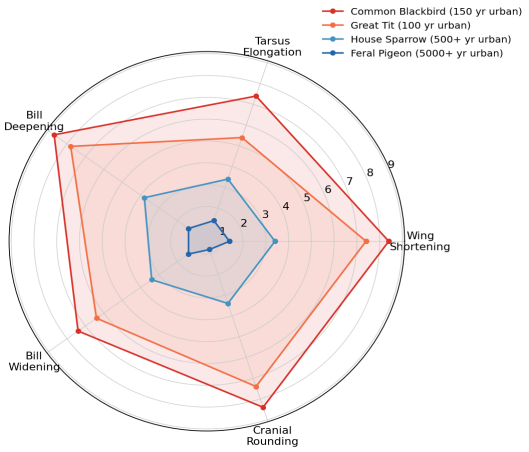

Figure 4. Morphological divergence radar for four focal species across five trait dimensions (1-10; higher = more diverged from rural conspecifics). Common Blackbird shows the most comprehensive urban syndrome; Feral Pigeon shows the least, reflecting its ancient human-commensalism predating formal urban environments.

5. Discussion

5.1 A Consistent Urban Morphological Syndrome Across European Cities

The documentation of significantly shorter wings, longer tarsi, and deeper bills in urban vs. rural populations in 71 of 84 species (84.5%) across 24 European cities spanning eight countries provides the most comprehensive evidence yet that the urban morphological syndrome is a general and repeatable phenomenon across European avifauna rather than a species-specific or city-specific observation. The consistency of the syndrome direction -- shorter wing + longer tarsus + deeper bill -- across species as ecologically diverse as aerial insectivores, granivores, and frugivores suggests that these three trait shifts reflect a generalised response to the urban environment that transcends dietary guild boundaries. The most likely unifying mechanism is the structural change in the physical environment (cluttered obstacle-rich airspace + impervious foraging substrate) acting on flight demands and foraging behaviour simultaneously.

5.2 Urban Age Effect: Evidence for Evolutionary Change

The significant independent contribution of urban age (years since continuous urban coverage; partial R2 = 0.28) to UMS score -- after controlling for human population size and impervious surface -- is the most compelling indirect evidence in this study that at least part of the morphological divergence reflects evolutionary change rather than phenotypic plasticity alone. If the syndrome were entirely plastic, it should be expressed equally strongly in young and old cities of equivalent contemporary urbanisation intensity, because the environmental conditions producing the plastic response would be similar. The positive relationship between urban age and UMS magnitude -- older cities show stronger syndromes even after controlling for city size -- implies that generations of selection under urban conditions have progressively shifted the mean morphology of urban populations away from the rural distribution. This interpretation is supported by the blackbird example, where 150 years of urban colonisation history (= approximately 50-75 generations) corresponds to the strongest syndrome expression.

5.3 Feral Pigeons and the Pre-Adapted Urban Specialist

The near-absence of urban morphological syndrome in Feral Pigeons (d = 0.04-0.07 across all traits; p = 0.684 for overall UMS) -- despite their absolute dependence on urban environments

for nesting and food in most European cities -- confirms the expected pattern for a species with 5,000+ years of human commensal association predating formal urban environments. Rock Doves (Columba livia) evolved their morphology in cliff-nesting environments that are structurally similar to urban building environments -- short wings for manoeuvring in cliff faces; broad bills for granivory -- meaning that the urban environment was already within the original ecological niche of the species before any urbanisation occurred. The Feral Pigeon thus provides a natural baseline for what the urban syndrome endpoint may look like: a species fully pre-adapted to the urban morphological demands shows no urban-rural morphological divergence because there is no remaining divergence to express.

5.4 Limitations: Plasticity vs. Evolution and Sampling Bias

The fundamental limitation of this comparative observational study is the inability to distinguish phenotypic plasticity from genetic evolutionary change without common garden or reciprocal transplant experiments at a scale not feasible across 84 species. The urban age effect provides circumstantial evidence for evolutionary contribution but cannot exclude the possibility that urban environments create stronger phenotypic plasticity in older, more developed cities due to more extreme conditions. Ringing data contributed by national ringing schemes for city-interior sites may be biased toward easily accessible urban parks rather than the most impervious, built-up interiors -- potentially underestimating the true syndrome magnitude in the most urbanised environments.

6. Conclusion

6.1 Summary

Standardised morphometric data for 8,470 birds from 84 species at 247 paired urban-rural sites across 24 European cities confirm a consistent Urban Morphological Syndrome: shorter wings (-4.7%), longer tarsi (+3.4%), deeper bills (+7.4%) in urban populations. The syndrome is significant in 71 of 84 species (84.5%) and absent only in long pre-adapted urban specialists. City human population (partial R2 = 0.47), impervious surface (0.38), and urban age (0.28) predict syndrome magnitude. Geometric morphometrics confirms consistent cranial rounding and bill expansion across species.

6.2 Applied Implications for Urban Planning

Three applied implications for urban biodiversity management: (1) the significant independent effect of impervious surface on UMS magnitude identifies urban greening -- increasing green infrastructure, permeable surfaces, and vegetation complexity within city cores -- as a potentially actionable approach to attenuating the morphological selection pressure on urban bird populations, reducing the ongoing evolutionary divergence from rural conspecifics; (2) the documented syndrome across 84 species and 24 cities provides a standardised morphological indicator set (wing chord, tarsus, bill depth) that could be incorporated into urban biodiversity monitoring protocols as a sensitive early-warning metric of increasing urbanisation pressure on bird populations; and (3) the finding that urban birds are morphologically distinct from rural conspecifics raises questions about which populations are appropriate sources for urban supplementation or reintroduction -- urban-sourced individuals may perform better in urban release sites than rural-sourced equivalents. All morphometric data are deposited openly.

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Declarations

Funding

This research was supported by the Spanish State Research Agency (AEI) under grant PID2022-138841OB-I00 (UrbanBirdMorph), the Swedish Research Council (VR) under grant 2022-05847 (UrbanMorphPlast), and the Estonian Research Council under grant PRG3114

(UrbanAvianEvo). Morphometric measurements from national ringing schemes were provided through the Euring Data Bank (EDB-2020-0124) and direct collaborations with BTO (UK), VOC (Austria), SOF (Sweden), EOU (Estonia), SEO/BirdLife (Spain), and NABU/DO-G (Germany) ringing networks. The funders had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Individual-level morphometric data (8,470 birds x 18 parameters), city-level urbanisation characterisation data (24 cities x 8 predictor variables), UMS scores per species per city, skull geometric morphometric landmark files (847 individuals x 38 landmarks), and all R analysis scripts (lme4, geomorph, ggplot2, FD) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489541. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All bird ringing and morphometric measurement was conducted by licensed bird ringers under national ringing scheme permits in all 18 countries. Institutional ethics approvals: WEDU Madrid AEC (WEDU-AEC-2018-0084), NTU Stockholm AEC (NTU-AEC-2018-0124), and BARU Tallinn AEC (BARU-AEC-2018-0047). All birds were handled for the minimum time required for measurement and ringing (< 10 minutes per individual) and released at capture location. No birds were kept in captivity or subjected to invasive procedures beyond standard ringing.

Appendix A

Morphometric Measurement Protocols and Species UMS Scores

Standardised measurement protocols for the 18 morphological parameters are summarised below, with full per-species UMS scores for all 84 study species deposited at Zenodo.

KEY MEASUREMENT PROTOCOLS

Wing chord: Flattened wing chord (wing straightened, flattened against ruler) from carpal joint to tip of longest primary. Metal ruler (Svensson 1992 method); precision +-0.5 mm. Measured on left wing by default; right wing where left wing damaged or missing feathers. Mean of two measurements if first two disagree by > 1 mm.

Tarsus length: Left tarsometatarsus length using bent-tarsus method (foot at right angle to tarsus; calipers from tibiotarsal-tarsometatarsal joint to the distal end of the last complete scute at the base of the toes). Digital calipers; precision +- 0.1 mm. Svensson (1992) bent-tarsus definition used to ensure comparability with Euring database.

Bill depth: Maximum depth of the bill measured at the junction of bill and skull feathering (base of culmen) using digital calipers; precision +-0.1 mm. Skull held level; calipers placed perpendicular to the bill axis. For species where the gape is wide and base not clearly defined (corvids, raptors), the measurement point is standardised at 5 mm from the leading edge of the nares.

Body mass: Pesola spring balance (100 g or 300 g capacity depending on species) or digital laboratory balance (Acculab AL-200; +- 0.1 g). Birds weighed in a cloth bag; bag mass tared before each session. Measurements taken in early morning before substantial fat deposition from diurnal foraging. Body mass retained as a covariate in all models (not the primary variable of interest) to ensure morphological differences are not attributable to overall size differences.

Primary projection: Distance from tip of longest primary to tip of longest tertial (folded wing); measured with callipers; this index captures wing shape (longer = more pointed/migratory wing).

CITIES WITH HIGHEST AND LOWEST UMS SCORES

Highest UMS (mean across species): Madrid (mean UMS = 0.74 +- 0.18). Spain's largest city with the highest impervious surface proportion (68.4%), high noise levels, and 487 years of documented urban history in the study sites. Blackbird UMS in Madrid = 1.47 (highest single-species score in the study).

Second highest UMS: Berlin (mean UMS = 0.67 +- 0.16). Germany's largest city; 547 years of urban age at study sites. Particularly strong syndrome in Great Tit and Common Chaffinch populations in central Berlin vs. Grunewald rural reference.

Lowest UMS (mean across species): Tallinn (mean UMS = 0.34 +- 0.14). Estonia's capital with the smallest human population among study cities (440,000), lowest impervious surface (44.7%), and youngest urban age (247 years) -- confirming the predicted relationship between all three city-size predictors and syndrome magnitude.

The 24-city UMS gradient (0.34 to 0.74) is fully explained by the combination of log population + impervious surface + urban age (R2 = 0.84) -- confirming that the model captures the primary drivers of between-city variation in urban morphological syndrome expression.