Evolution, 2023, **77(7)**, 1720–1729
https://doi.org/10.1093/evolut/qpad079
Advance access publication 27 April 2023
Brief Communication

Ecological and life-history drivers of avian skull evolution

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Abstract

One of the most famous examples of adaptive radiation is that of the Galápagos finches, where skull morphology, particularly the beak, varies with feeding ecology. Yet increasingly studies are questioning the strength of this correlation between feeding ecology and morphology in relation to the entire neornithine radiation, suggesting that other factors also significantly affect skull evolution. Here, we broaden this debate to assess the influence of a range of ecological and life-history factors, specifically habitat density, migration, and developmental mode, in shaping avian skull evolution. Using 3D geometric morphometric data to robustly quantify skull shape for 354 extant species spanning avian diversity, we fitted flexible phylogenetic regressions and estimated evolutionary rates for each of these factors across the full data set. The results support a highly significant relationship between skull shape and both habitat density and migration, but not developmental mode. We further found heterogenous rates of evolution between different character states within habitat density, migration, and developmental mode, with rapid skull evolution in species that occupy dense habitats, are migratory, or are precocial. These patterns demonstrate that diverse factors affect the tempo and mode of avian phenotypic evolution and that skull evolution in birds is not simply a reflection of feeding ecology.

Teaser Text

Almost 200 years ago, Darwin found that Galápagos finches' beaks were different shapes in birds with different diets. Today, it is well established that phylogeny, allometry, and ecology can also be key factors in shaping skulls. Yet, the influence of specific aspects of ecology, as well as life history, on morphological evolution remains poorly constrained. Here, we examined whether three novel factors also influence the shape of bird skulls and rates of evolution: habitat density, migration, or developmental mode. To do so, we combine high-resolution 3D quantification of skull shape with dense taxonomic sampling across living birds. Our analyses revealed that skull shape varies in birds based on vegetation density in their habitats and the extent to which they migrate, but not their developmental mode. Despite these differences, habitat density, migration, and life history all influence the rate at which bird skulls evolve. Birds evolved fastest if they live in densely vegetated habitats, migrate long distances, or are precocial. This adds to the growing body of evidence that avian skull evolution is affected by a diverse range of factors and suggests that habitat density, migration, and life history should be considered in future analyses on drivers of phenotypic evolution.

Keywords: macroevolution, morphological evolution, life-history evolution

Background

The Galápagos finches are a classic "textbook" example of avian adaptive radiations where beak morphology is considered an adaptation to diet (Grant & Grant, 1989). In the last 5 years, there have been significant efforts to robustly quantify this interaction of cranial and beak shape and various ecological and developmental factors, particularly feeding ecology (Bright et al., 2016; Cooney et al., 2017; Felice & Goswami, 2018; Felice et al., 2019; Navalón et al., 2019; Pigot et al., 2020, Natale & Slater, 2022), which have demonstrated that this relationship is highly complex and differs across scales and across lineages. Diet has been found to strongly correlate with beak shape in waterfowl (Anseriformes; Olsen, 2017), and corvids (Corvidae; Kulemeyer et al., 2009), as well as brain shape in kingfishers (Alcedinidae; Eliason et al., 2021) and skull shape in shorebirds and relatives (Charadriiformes; Natale & Slater, 2022). Conversely, beak and braincase morphology is largely controlled by size in raptors (Bright et al., 2016), and diet only predicts 2.4% of skull shape variation in parrots and cockatoos (Psittaciformes; Bright et al., 2019). Large-scale studies across Neornithes have also yielded variable results: Diet can be predicted from linear measurements (Pigot et al., 2020), but there is only a weak correlation between diet and cranial morphology (Felice et al., 2019) or beak morphology (Navalón et al., 2019) when using geometric morphometrics. Recently, Crouch and Tobias (2022) found no association between bursts of morphological evolution and rates of dietary evolution at a global scale.

It is well established that diverse aspects of ecology can be key factors in determining both skull morphology (Bardua et al., 2021; Dumont et al., 2016; da Silva et al., 2018; Vidal-García & Scott Keogh, 2017) and rates of shape evolution (Collar et al., 2010; Millien, 2006). Phenotypic convergence occurs when different lineages adapt to similar habitats

Received February 3, 2023; revisions received April 4, 2023; accepted April 26, 2023

(McGhee, 2011). A range of aspects of ecology has been associated with bursts in morphological evolution, such as transitions to a new ecological niche (Price et al., 2011; Sherratt et al., 2017), ecological opportunity (Losos, 2010), habitat stability (Crouch & Tobias, 2022), and competition (Rosenzweig, 1978). Given that diet, as currently measured, is an incomplete predictor of skull shape variation and evolutionary tempo across birds, alternative aspects of life history or ecology warrant investigation. Chira et al. (2018) found low support for an association between rates of beak evolution and generation length, temperature, UVB levels, range size, proportion living on islands, or competition, but 80% of variation in species-level evolutionary rates remained unexplained. Across Neornithes, there are correlations between ecological traits and morphology, for instance, down feather morphology is adapted to habitats (Pap et al., 2020), and there is widespread convergence linking cranial and postcranial linear measurements to trophic niches (Pigot et al., 2020). Within passerines, there is evidence of correlations between body form and foraging mode (Fitzpatrick, 1985); correlations between the lengths of the tarsus and midtoe and substrate utilization (Miles & Ricklefs, 1984), as well as a correspondence between tangers bill morphology and the filling of ecomorphospace (Vinciguerra & Burns, 2021). So, there is evidently a robust correlation between ecology and avian morphology, but it is not clear which components of ecology are shaping avian skull evolution.

Additionally, phylogeny (Brusaferro & Insom, 2009; Degrange & Picasso, 2010), ontogeny (Navalón et al., 2021), allometry (Bright et al., 2016; Tokita et al., 2017; Yamasaki et al., 2018), phenotypic integration (Felice & Goswami, 2018; Navalón et al., 2020; Shatkovska & Ghazali, 2020), and encephalization (Marugán-Lobón et al., 2021) are all intrinsic factors, which have been found to significantly influence skull morphology within various avian lineages, but most have not been assessed across the breadth of avian diversity. Collectively, this research calls into question the primacy of the relationship between diet and avian skull shape.

Here, we interrogate the relationship between cranial morphology and three key ecological/life-history traits: habitat density, migration behavior, and developmental mode. We chose to investigate habitat density as one of our ecological traits due to evidence that habitat openness influences kingfisher brain shape evolution, with forest dwellers undergoing more rapid rates of brain shape evolution (Eliason et al., 2021). This study did not find any single brain shape associated with forest living and instead suggested that brain shape in the forest dwellers was diverging stochastically, possibly in response to genetic drift in fragmented habitats. Given that the skull roof tracks the brain in birds (Fabbri et al., 2017), factors that drive shifts in brain shape may also result in changes in skull shape. However, the impact of the density of habitats on the tempo and mode of avian phenotypic evolution on a broad macroevolutionary scale has not been investigated until now.

Migration is widespread in seasonal environments, with approximately 40% of all birds migrating (El-Sayed, 2019), and it has well-established adaptive value (Hedenström, 2008; Lack, 1968). It has been proposed that the genes for migratory behavior are ancestral in all birds (Pulido, 2007) and that seasonal migration is heritable and can rapidly change in response to selection (Berthold et al., 1992). Thus, transitions between migratory and non-migratory behavior do not require repeated innovation, but merely selection driving a pre-existing genetic program (Alerstam et al., 2003; Salewski & Bruderer, 2007; Winger et al., 2012; Zink, 2002), which may explain the dynamic fluctuations in migration across extant birds (Piersma et al., 2005; Winger et al., 2012; Zink, 2002). Despite the rate at which avian migration can evolve, the degree to which this affects evolutionary rates has not been assessed. Migratory birds have evolved a suite of adaptations to minimize weight, such as organs reducing size before migration (Battley et al., 2000) and hearts being relatively smaller in migrants (Vágási et al., 2016). Additionally, a negative correlation has been identified between migration distance and brain size (Sol et al., 2010; Vincze, 2016). As there are strong correlations between the shapes and sizes of brains and endocasts in birds (Watanabe et al., 2019), and differences in endocranial anatomy are correlated with craniofacial differences in birds (Iwaniuk & Nelson, 2002; Marugán-Lobón & Buscalioni, 2009; Marugán-Lobón et al., 2021), it is possible that migratory birds have also evolved weight-saving adaptations to cranial anatomy.

Finally, we integrate a fundamental aspect of life history that varies widely across birds: the altricial–precocial spectrum. Precocial developmental mode, where juveniles are relatively mature at birth or hatching, is more common than altricial development among vertebrates. This strategy was proposed to be an adaptation to high rates of predation on juveniles (Arnold & Wassersug, 1978; Wassersug & Sperry, 1977). By contrast, altricial developmental mode is associated with more extensive parental care, which promotes rapid growth rates that can average four times that of similarly sized precocial species (Case, 1978; Ricklefs, 1979), as well as poor locomotor performance, and short developmental periods. This variation in life history creates different selective pressures acting on juveniles that fall into different character states along the altricial–precocial spectrum, so it has been suggested that selection on the juvenile morphology could act more strongly than selection on adult morphology for precocial species (Carrier, 1996; Dial & Carrier, 2012).

Furthermore, there is a correlation between degree of precociality and smaller relative brain sizes across birds (Griesser et al., 2023; Hardie & Cooney, 2022), providing evidence for the altricial–precocial spectrum driving morphological differences. However, the influence of developmental mode on avian cranial shape evolution has yet to be investigated across crown birds.

We used 3D geometric morphometric data from 354 species across Neornithes and a phylogenetic comparative framework to address two key questions about the relationship between avian skull shape and ecological and life-history traits. First, we assessed whether avian skull shape covaries with size, habitat density, migration, and developmental mode. Second, we tested whether evolutionary rates differ between different character states within habitat density, migration, and developmental mode.

Methods

Morphological data

Our analyses use a previously published three-dimensional geometric morphometric data set of 354 adult species, representing 159 families of extant birds (Supplementary Table S1, Felice & Goswami, 2018). One skull was used per species, and species were selected based on the availability of complete or almost complete adult skulls. These were subjected to the previously published procedure of landmarking using IDAV Landmark (Felice & Goswami, 2018; Wiley et al., 2005) to place anatomical landmarks and curve semi-landmarks on digital three-dimensional skull models formed from CT and surface scans. We then used the R package "Morpho" v2.5.1 (Schlager, 2017) to project surface semi-landmarks onto each specimen from a template. A total of 757 landmarks were used to quantify three-dimensional cranial morphology, divided into the rostrum, cranial vault, sphenoid region, palate, pterygoid/quadrate, naris, and occipital, as in Felice and Goswami (2018) (Figure 1). The effects of size, position, and rotation were removed with a generalized Procrustes analysis using the R package "geomorph" v3.0.6 (Adams & Otárola-Castillo, 2013). We extracted log centroid size of the cranium during the Procrustes superimposition and used this as a proxy for size in further analyses. Following the finding by Natale and Slater (2022) that some shorebirds followed different scaling patterns thus body mass was a more appropriate size measure for the skull, we assessed the correlation between log body mass and log centroid size of the cranium and found that they are highly correlated for our sample ($r^2 = 0.885$, Supplementary Figure S1).

Phylogenetic hypothesis

A previously published composite phylogenetic tree was utilized for the phylogenetic comparative analyses (Felice et al., 2019). This composite topology was generated by following the procedure described by Cooney et al. (2017). This tree incorporates the backbone of relationships among major clades from (Prum et al., 2015), with the fine-scale species relationships from a maximum clade credibility tree generated by Jetz et al. (2012). The tree of 9,993 species was then pruned down to the 354 species in our data set.

Ecological and life-history trait data

Habitat density, migration, and developmental mode of birds were all classified using three character states (Figure 1). Habitat density was categorized as "dense" (n = 120), "semi-open" (n = 91), or "open" (n = 143) following Tobias et al. (2016), sourced from Tobias et al. (2022). Dense habitats are those where species primarily occupy dense thickets, shrubland, or forest (except species perching habitually

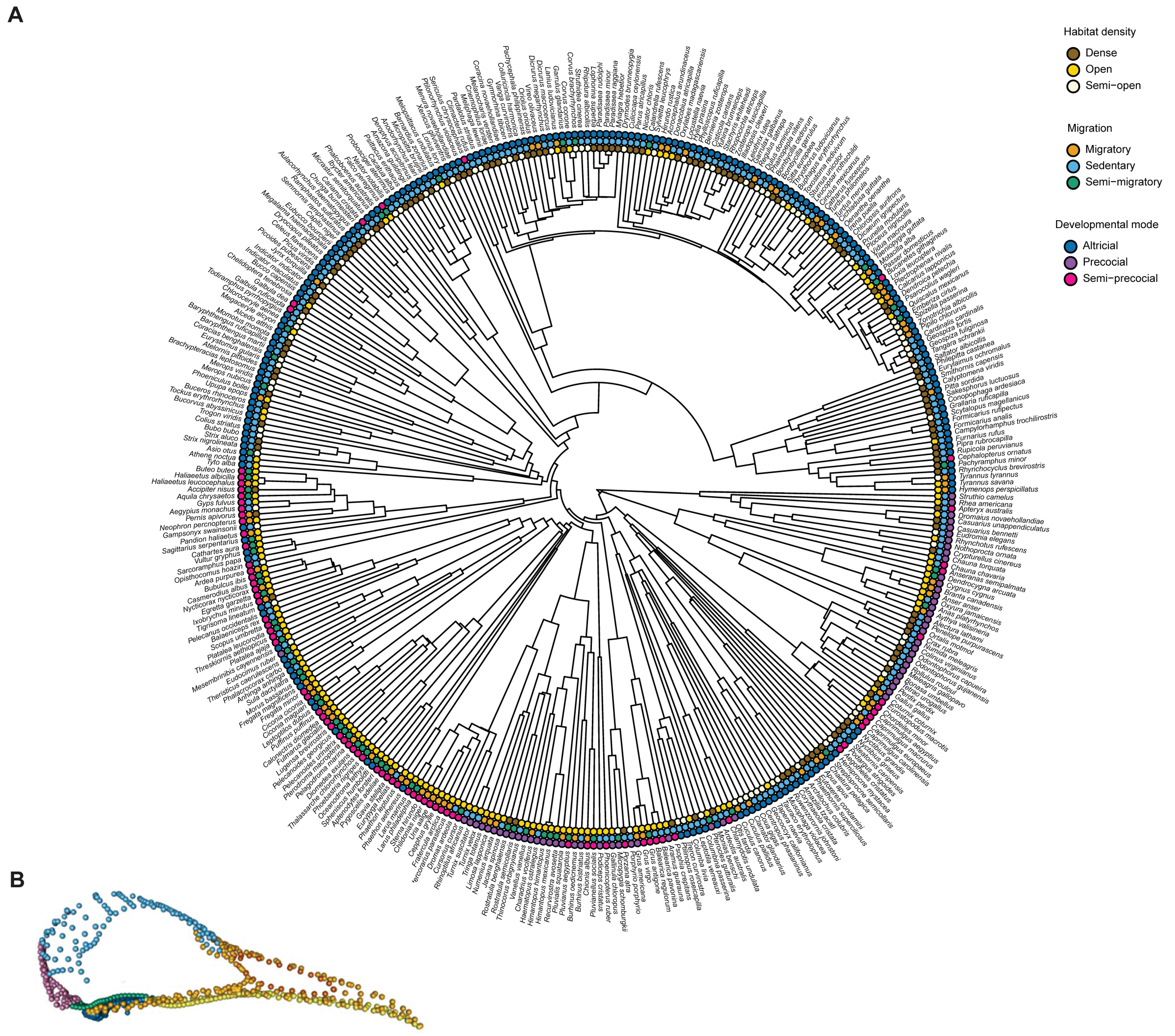

Figure 1. (A) The ecological and life-history trait states of every species in our sample mapped onto the phylogenetic tree used in analyses. (B) The landmarking scheme used in our analyses, presented in lateral view. The landmarks are colored as follows: golden, rostrum; pale blue, cranial vault; green, sphenoid region; yellow, palate; navy, pterygoid/quadrate; orange, naris; and pink, occipital (Felice & Goswami, 2018).

on top of the canopy). Semi-open habitats include primarily living in open shrubland scattered bushes or deciduous forest. Open habitats are where species primarily live in desert, grassland, open water, seashores, cities, or habitually perching on top of forest canopy. Migration behavior was classed as "non-migratory" (n = 218), "partially migratory" (n = 63), or "migratory" (n = 73) following Tobias and Pigot (2019; Tobias et al. 2022). Whereas the migratory class is comprised of species where most of the population embark on long-distance (typically intercontinental) migrations, partially migratory species travel much shorter distances on average. This includes short-distance elevational movements, nomadism, and cases in which a minority of the population migrates relatively short (intracontinental) distances. Finally, non-migratory birds do not migrate and tend to be either sedentary or undergo only local movements. Developmental mode was categorized as "precocial" (n = 60), "semi-precocial" (n = 80), and "altricial" (n = 214; Cooney et al., 2020; Hoyo et al., 1992; Starck, 1993). Where data were not available in an existing database (Cooney et al., 2020), we classified species using Hoyo et al. (1992) and Botelho et al. (2015). Where information was not available at species level, the developmental mode was inferred by information on other species within the genus or family, as previous studies have suggested that there is little intrafamily variation in position on the altricial–precocial spectrum (Ducatez & Field, 2021).

Data analyses

We ran preliminary phylogenetic ANOVAs using the "procD.pgls" function in the geomorph R package (Adams et al., 2022) to assess whether there are any interactions between our three traits (habitat density, migration, and life history) and the previously examined or potentially related traits of diet, habitat, and primary lifestyle, sourced from Tobias et al. (2022) using "trophic niche" as a measure for diet. We found no significant interactions between diet, habitat, or primary lifestyle and our factors at the p < .01 level except a marginally significant interaction between diet and migration (Supplementary Table S2). For this reason, we did not incorporate diet into our further analyses given the heavy focus on this factor in other analyses using npMANOVAs to assess the strength of covariation between diet and shape, as well as estimating rates of evolution for the same morphological data as we use in this study (Felice et al., 2019). We then used type II phylogenetic MANOVAs (phylogenetic regressions) to assess the significance of habitat density, migration, and developmental mode for avian skull shape. We fit these models using the full geometric morphometric data set, with log centroid size, habitat density, migration, and developmental mode as predictors for the "mvgls" and "manova.gls" functions in the R package mvMORPH 1.1.4 (Clavel et al., 2015). We used the "mvgls" function to fit multivariate phylogenetic linear models with Pagel's lambda by penalized likelihood (Clavel et al., 2015). We employed the "manova.gls" function to assess the significance of the four predictors via type II MANOVA tests with Pillai's statistic over 1,000 permutations (Clavel et al., 2019). Principle component analysis was used to visualize the main axes of variation for the whole skull. Morphospaces were plotted in ggplot2 v.3.3.6 (Wickham, 2016), with convex hulls plotted for the different character states of our three traits. The primary axes of shape variation are shown by extreme shapes along the first two principal component (PC) axes.

We further estimated the evolutionary rates for each habitat density, migration, and developmental mode character state following the protocol in Bardua et al. (2021). First, we utilized the "ace" function in ape v5.3 (Paradis & Schliep, 2019) to calculate the ancestral states for habitat density, migration, and developmental mode. We used the "make.simmap" function in the "phytools" package v.1.2-0 (Revell, 2012) to reconstruct the evolutionary history of these factors by stochastic character mapping, which we then used to fit flexible BMM (Brownian motion with multiple rates matrix) models. We conducted model fitting using the "mvgls" function in mvMORPH with the "error = TRUE" setting. We additionally ran our evolutionary rates analyses using this protocol for each the seven anatomical modules of the bird skull (Felice & Goswami, 2018).

Results

PC 1 explains 45.3% of the total variance and mainly describes skull elongation (Figure 2). PC 2 explains 10.2% of variance and represents the dorsoventral beak curvature as well as the mediolateral expansion of the palatine bones (see Supplementary Figure S2 for additional morphospaces). The region of morphospace associated with moderate PC1 and PC2 scores contains the greatest density of taxa and corresponds to passerines and species with passerine-like cranial proportions. Both migration and habitat density states have heavily overlapping convex hulls with broad morphospace occupation, indicating that there are a number of viable phenotypes within each ecological trait state. Non-migratory birds occupy a region of morphospace with higher PC 2 values (Figure 2B), associated with high beak curvature in a convex direction compared with migratory birds which occupy a region of morphospace with lower PC 2 scores. Partially migratory birds overlap with migratory and non-migratory species, but also exhibit both the highest and lowest PC 2 scores of our sample. Whereas altricial species explore a region of morphospace defined by low PC 1 scores and higher PC 2 values, precocial taxa are restricted to a smaller region of morphospace relative to semi-precocial or altricial taxa.

Significant relationships were observed between shape and size, habitat density, and migration categories (P < 0.01), but there was not a statistically significant relationship between shape and developmental mode (p = .096; Table 1). Additionally, there are significant interactions between size and habitat density (p = .001), among size, habitat density, and developmental mode (p = .001), and size and developmental mode (p = .002). There are also significant interactions between size, habitat, and migration (p = .037).

We further identified significant differences in evolutionary rates (σ_{mult}) among the character states of the three traits (Figure 3). Birds living in dense or semi-open habitats evolve approximately three times more rapidly (1.97×10^{-7} and 1.50×10^{-7}, respectively) than those in open habitats (5.85×10^{-8}). Migratory birds have a faster rate of skull evolution (1.64×10^{-7}) than non-migratory or partially migratory birds (7.07×10^{-8} and 1.06×10^{-7}, respectively). Precocial birds have a rate of cranial evolution approximately three times faster (3.03×10^{-7}) than semi-precocial birds (9.63×10^{-8}) and approximately four times faster than altricial birds (7.48×10^{-8}).

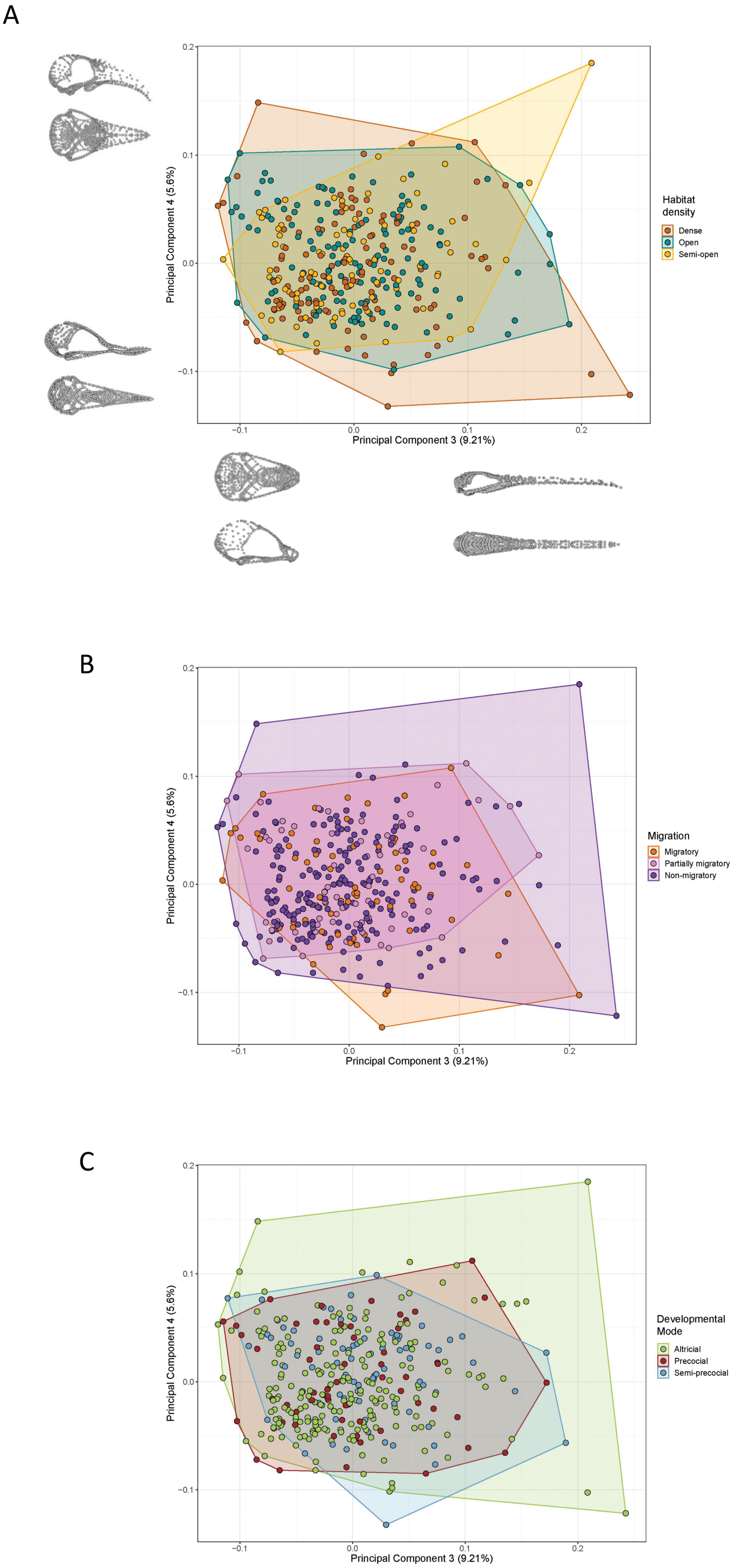

Figure 2. Principal component analyses of whole-skull shape. PC 1 describes 45.3% and PC 2 represents 10.2% of the overall shape variation, as illustrated by the landmark configurations along the PC axes in (A). Convex hulls indicate variation of states for the following ecological and life-history traits: (A) Habitat density; (B) migration; (C) developmental mode.

Discussion and conclusion

Our analyses demonstrate two additional factors, habitat density and migration, are significantly associated with avian skull shape. Furthermore, both ecological and life-history traits affect rates of cranial shape evolution across a globally distributed and speciose sample of birds. These results add

Table 1. Results of Type II phylogenetic non-parametric MANOVA of skull shape against whole-skull centroid size, habitat density, migration, and developmental mode.

	Pillai's test statistics	SES (effect sizes)	*p*-values
Size	0.977	7.48	.001**
Habitat density	1.77	3.35	.001**
Migration	1.79	3.82	.001**
Developmental mode	1.73	1.23	.096
Size:habitat density	1.82	3.67	.001**
Size:migration	1.74	0.749	.248
Habitat density:migration	3.49	1.07	.151
Size:developmental mode	1.79	2.55	.002**
Habitat density:developmental mode	3.50	1.13	.127
Migration:developmental mode	3.44	−0.181	.585
Size:habitat density:migration	3.57	1.69	.037*
Size:habitat density:developmental mode	3.64	2.77	.001**
Size:migration:developmental mode	3.50	0.224	.451
Habitat density:migration:developmental mode	4.36	−0.256	.637
Size:habitat density:migration:developmental mode	2.58	−0.671	.766

Results for MANOVA, including effect sizes, for interactions between our three traits and size are listed with a colon denoting an interaction between the listed traits. Significances of Pillai's test statistics are based on permutations (n = 1,000) with p-values significant at the following alpha levels: *≤.05, **≤.01.

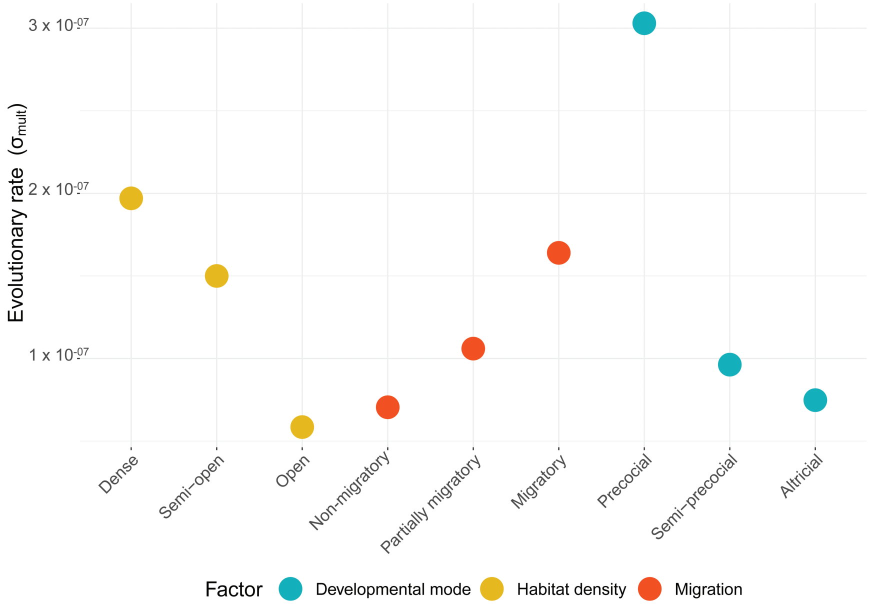

Figure 3. Estimated evolutionary rates (σ_{mult}) for the three different character states of habitat density, migration, and developmental mode.

to the growing body of research suggesting that there is a complex interplay of intrinsic (Bright et al., 2016; Marugán-Lobón et al., 2021; Navalón et al., 2020) and extrinsic factors (Natale & Slater, 2022; Pigot et al., 2020) contributing to avian skull shape evolution.

Our discovery of a significant relationship between skull shape and migration is consistent with previous studies reporting smaller brain sizes in migratory birds (Vincze, 2016), as well as smaller forebrains of migratory "warblers" compared with non-migratory species (Burish et al., 2004). These patterns may be explained by skull size being under strong selection to be lightweight for aerodynamics, driving weight-reducing adaptations in cranial anatomy. Furthermore, brain size may be developmentally or energetically constrained in migrants because of the metabolic costs of migration (Winkler et al., 2004; McGuire & Ratcliffe, 2011) and high-energy use of the brain (Isler & van Schaik, 2009). Alternately, birds with small brains may migrate to compensate for low behavioral flexibility (Winkler et al., 2004). Additionally, the majority of brain size variation is often found superficially in the nidopallium and hyperstriatum regions of the forebrain (Nicolakakis et al., 2003; Rehkämper et al., 1991; Winkler et al., 2004). It is therefore possible that this forebrain region is also responsible for the skull shape covariation with migration which we uncovered.

Analysis of evolutionary rates across character states demonstrated that migrants' skulls evolve faster than those of non-migratory birds. We found that migratory birds evolved faster than partially migratory birds which, in turn, evolved faster than non-migratory birds. Similarly, Winkler et al. (2004) also found the effect of migration on brain size was stronger in long-distance migrants. We propose that these rapid rates of evolution are associated with migratory syndrome, that is., the adaptations of behavior and morphology for migration (e.g. Dingle, 1996; Piersma et al., 2005). In this case, the rapid rates of skull evolution in migrants may be associated with smaller forebrains and dorsoventrally lower skull vaults relative to non-migratory species. Focusing on skull regions, the vault in particular, and to a lesser extent the rostrum, evolves faster in migratory birds compared to non-migratory species (Supplementary Table S3). This result lends further support to the notion that the rapid rates of evolution in migrants is associated with migratory syndrome. Taken as a whole, our results suggest migration exerts a significant selective pressure on brain development, which results in the rapid evolution of different vault morphologies.

Beyond migration, habitat density also affects both avian skull shape and rates of skull evolution across birds. Habitat density covaries with overall skull shape, corroborating work by Kennedy et al. (2020), which found that habitat and strata differentiate corvoid passerine morphology. We discovered heterogenous rates of evolution among birds inhabiting more or less dense habitats, with birds in dense habitats evolving most rapidly. Birds in semi-open habitats evolve more rapidly than those in open habitats which corroborates one of the findings of Eliason et al. (2021) that kingfishers living in forests experience faster brain shape evolution than those in more open habitats. Faster evolutionary rates in dense habitats may be explained by birds in forest habitats adapting to microhabitats, which are not captured by our broad habitat density categories. In addition, birds in open habitats must be highly adapted to extreme environments, which may act as a constraint on cranial morphological evolution; for instance, penguins are adapted to extreme Antarctic conditions and have the slowest evolutionary rates detected in birds (Cole et al., 2022).

In contrast to the results for the ecological traits, developmental mode is not significantly associated with cranial shape variation. The difference in association between ecological and developmental traits may reflect the fact that the two ecological traits are associated with lifelong resource acquisition (Pigot et al., 2016; Ricklefs, 2005; Winkler & Leisler, 1985), while developmental mode may not affect selective pressures experienced by adult birds. Whereas this sample was comprised of adult specimens, an avenue for future research may be investigating whether juvenile bird skull shape or ontogenetic trajectory covary with developmental mode.

Nonetheless, precocial birds have a significantly higher rate of evolution than semi-precocial or altricial species, similar to patterns observed in placental mammals (Goswami et al., 2022). Rates of evolution are fastest in the vault module, particularly for precocial birds (Supplementary Table S3). We hypothesize that these differences are due to precocial hatchlings independently living and interacting with their environment at an earlier age than do altricial hatchlings, including all passerines, which are fed by parents. This earlier independence also drives more rapid neurocranial morphological evolution in precocial birds than in semi-precocial birds such as gulls, which are fed by parents despite being capable of leaving the nest soon after hatching.

This study aimed to comprehensively investigate the role of ecological and life-history traits in the accumulation of phenotypic diversity in a major global radiation. Our results demonstrate that whereas developmental mode only influences evolutionary rates, habitat density and migration shape both the tempo and mode of avian phenotypic evolution. This highlights the importance of investigating a range of factors that may influence evolution, as opposed to presuming a form–function relationship focused on solely one function, particularly for complex, multifunctional structures such as the skull. Skull evolution in birds is not simply a reflection of feeding ecology, but also a product of complex interactions between morphology, life-history, and ecological traits.

Supplementary material

Supplementary material is available online at *Evolution* (https://academic.oup.com/evolut/qpad079).

Data availability

Three-dimensional surface models scans are freely available at www.phenome10k.org. The raw data and code are archived at www.github.com/EloiseSEHunt/Hunt_et_al_2023_Bird_skulls.

Author contributions

R.N.F., J.A.T., and E.S.E.H. collected the data. A.G., R.N.F., and E.S.E.H. conceived the study and designed the analyses. All authors prepared the manuscript.

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

We thank Judith White, Chris Milensky, Christine Lefevre, Steve Rogers, Ben Marks, Janet Hinshaw, Paul Sweet, Lydia Garetano, Kristof Zyskowski, and Greg Watkins-Colwell for facilitating specimen access for morphometric data collection. E.S.E.H. received funding from a Natural Environment Research Council studentship (grant no. NE/S007415/1). Data collection was supported by European Research Council grant STG-2014–637171 (to A.G.), Natural Environment Research Council grant no. NE/I028068/1 (to J.A.T.), and SYNTHESYS grant no. FR-TAF-5635 (to R.N.F.).

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