E-Article

The Effects of Foraging Ecology and Allometry on Avian Skull Shape Vary across Levels of Phylogeny

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abstract: Avian skull shape diversity is classically thought to result from selection for structures that are well adapted for distinct ecological functions, but recent work has suggested that allometry is the dominant contributor to avian morphological diversity. If true, this hypothesis would overturn much conventional wisdom regarding the importance of form-function relationships in adaptive radiations, but it is possible that these results are biased by the low taxonomic levels of the clades that have been studied. Using 3D morphometric data from the skulls of a relatively old and ecologically diverse order of birds, the Charadriiformes (shorebirds and relatives), we found that foraging ecology explains more than two-thirds of the variation in skull shape across the clade. However, we also found support for the hypothesis that skull allometry evolves, contributing more to shape variation at the level of the family than the order. Allometry may provide an important source of shape variation on which selection can act over short timescales, but its potential to evolve complicates generalizations between clades. Foraging ecology remains a better predictor of avian skull shape over macroevolutionary timescales.

Keywords: adaptation, ecomorphology, geometric morphometrics, Charadriiformes, macroevolution.

Introduction

Arguably, no morphological feature is more intimately associated with the central biological concept that natural selection drives adaptive diversification than the avian skull (beak and braincase). Some of the most iconic examples of island adaptive radiation, such as the *Geospiza* finches of the Galápagos Islands (Darwin 1845; Lack 1947; Grant 1981; Schluter and Grant 1984), Hawaiian honeycreepers (Fringillidae; Freed et al. 1987; Lovette et al. 2002), and Malagasy vangas (Vangidae; Jønsson et al. 2012; Reddy et al. 2012), occurred along morphological axes associated with distinct foraging ecologies. Evolution along diet or foraging-mode-related axes of skull shape variation is also thought to have facilitated adaptive diversification in clades such as waterfowl (Anseriformes; Guillemain et al. 2002; Olsen 2017), kingfishers (Alcedinidae; Eliason et al. 2020), corvids (Corvidae; Kulemeyer et al. 2009), and warblers (*Phylloscopus*; Price 1991), as well as in guilds of unrelated but ecologically similar taxa, such as carnivorous raptors (Hertel 1995). Analysis of rates of beak shape evolution across the entire extant avian radiation by Cooney et al. (2017) has revealed pulses of rapid shape change that may suggest expansion in ecomorphospace associated with dietary shifts, and Pigot et al. (2020) have shown that it is possible to predict the foraging guild of extant birds from a few beak measurements. Intraspecific variation in beak morphology has also been associated with spatial variation in diet and foraging ecology (Peterson 1993) and even with distinct patterns of resource use within populations of the same species (Smith 1987).

Recently, a number of studies have presented results that cast substantial doubt on the limits of the form-function relationship between the avian skull and the foraging ecology. Miller et al. (2017) noted that morphology and foraging guild exhibit an "imperfect" relationship in Australian honeyeaters (Meliphagidae), with many morphologically similar species foraging in divergent ways. In an analysis of 2D morphometric data from a broad taxonomic sample of extant birds, diet explained only 12% of beak shape variation, and birds with different feeding ecologies shared similar morphologies, leading the authors to suggest that selection for broad performance outcomes (e.g., mechanical advantage), combined with limited axes of potential shape variation, might impose constraints on beak diversification

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(Navalón et al. 2019). Other authors have more specifically implicated allometry as the critical source of avian morphological diversity. Using 3D geometric morphometrics of the entire skull, Bright et al. (2016) found that body size and covariance between the beak and braincase explained nearly 80% of skull shape variation for a polyphyletic assemblage of birds of prey, while birds with distinct diets could not be discriminated from one another on the basis of skull shape. Similar findings have been recovered for Psittaciformes (parrots and relatives; Bright et al. 2019), and evolutionary allometry has even been found to explain a significant proportion of skull shape variation in the two iconic examples of adaptive, diet-driven evolution: Hawaiian honeycreepers and the finches of the Galápagos (Tokita et al. 2017; Navalón et al. 2020). Furthermore, an analysis of 3D landmark data from bird skulls spanning the entire class Aves found that although relative rates of evolution in some skull components vary between dietary groups, a weak relationship between overall shape and diet is seen in avian skulls (Felice et al. 2019). Allometry-related changes in skull shape have been associated with specific patterns of resource use that have facilitated macroevolutionary radiations in some mammalian clades (Marroig and Cheverud 2005; Machado 2020) and may represent a relatively common mode of evolution if size represents the direction of maximum intraspecific genetic and phenotypic variance along which evolution can occur (Schluter 1996). Collectively, this work has called into question the strength of the relationship that both foraging ecology and body size have to avian skull shape.

These highly variable results may be driven by the use of analytical frameworks that assume common allometric trends across clades in which allometry itself may have evolved. Body size and associated allometric shape variation can act as a line of least evolutionary resistance (Marroig and Cheverud 2005) in young radiations and might facilitate resource partitioning and optimization of foraging efficiency in ecologically similar assemblages of taxa (Hutchinson 1959; Sherry and McDade 1982; Kiltie 1984, 1988; Wheelwright 1985; Dayan and Simberloff 1994; Werdelin 1996). However, given that genetic covariances decay rapidly over macroevolutionary timescales (Schluter 1996), extrapolating results between clades at different taxonomic levels may be flawed. Furthermore, allometric parameters themselves can evolve, generating distinct scaling relationships between shape and size within and between clades (Pélabon et al. 2014; Voje et al. 2014; Uyeda et al. 2017). As a result, the processes responsible for generating morphological variation at both the same and different hierarchical levels across a phylogeny are not necessarily the same (Erwin 2000; Jablonski 2007; Slater and Friscia 2019), and the assumption of a common allometric scaling of shape with size in avian clades should be tested against models allowing for variable allometric scaling among clades.

Charadriiformes (shorebirds, gulls, and auks) is an ideal clade within which to evaluate the relative contributions of foraging ecology and evolutionary allometry to skull shape variation. Charadriiformes comprises about 380 species and encompasses a great diversity in body size, ranging from the ~20-g least sandpiper (*Calidris minutilla*) to the ~1,850-g great black-backed gull (*Larus marinus*; del Hoyo et al. 1996). The order is also ecologically disparate, occupying a broad range of habitat types (e.g., shorelines, tundra, forest, grasslands), possessing diverse dietary specializations (e.g., small mammals, succulent plants), and utilizing foraging behaviors ranging from visually guided pecking to tactile probing (del Hoyo et al. 1996). Several studies have demonstrated links between charadriiform skull morphology and foraging ecology. Research on 17 species of Charadriiformes (excluding gulls, terns, and relatives; suborder Lari) found that longer beaks were associated with tactile foraging modes and shorter beaks were associated with visual foraging modes (Barbosa and Moreno 1999). A detailed biomechanical study of seed snipes (Thinocoridae) showed evidence of musculoskeletal adaptations for efficient tearing of vegetation (Korzun et al. 2009), while the skull morphology of skimmers (*Rynchops* spp.) has been proposed to be well adapted to reduce drag as these birds fly over the water with their lower jaw submerged (Zusi 1962; Withers and Timko 1977; Martin and Bhushan 2016). Other lines of evidence suggest that size might also play an important role in charadriiform foraging ecology and skull shape evolution, although this has yet to be tested explicitly across the order. For example, studies in both terns (Sterninae; Hulsman 1981) and auks (Alcidae; Swennen and Duiven 1977) have demonstrated that gape width is correlated with maximum and preferred prey size.

We used a phylogenetic comparative framework and 3D geometric morphometric data from 262 species (approximately 70% of recognized species) of Charadriiformes to address three critical questions regarding the relationship between foraging ecology, allometry, and avian skull shape evolution. First, we assessed the relative explanatory power of foraging ecology, body size, and their interaction for charadriiform skull shape. Second, we explicitly evaluated whether a model of common or evolving allometry is supported across the charadriiform order. Finally, we asked whether allometric relationships and the relative importance of foraging ecology varied in strength and direction between charadriiform families. Our results highlight how the assumption of common allometry in previous work may have generated variable conclusions about the main factors explaining avian skull shape variation.

Methods

Morphological and Body Size Data

Three-dimensional surface scans were obtained from nonjuvenile museum specimen skulls of 262 species of Charadriiformes (see table S5 for specimen information as well as specific scanner settings for each specimen). For 206 species, two individuals were scanned, while the remaining 66 were represented by a single specimen. Scans were obtained with either a Comet L3D blue-light scanner (Carl Zeiss, Jena, Germany) or a Capture Mini desktop structured-light scanner (3D Systems, Cary, NC). Each surface scan was processed using the software Geomagic Design X (3D Systems) to remove small holes and scanning artifacts. Models were subsequently decimated to 300,000 triangles and exported as standard tessellation language (STL) files, which are available on the MorphoSource data repository. A total of 255 landmarks (42 type I, normal landmarks placed at discrete points, and 213 type II, semilandmarks placed along curves; fig. 1; see table S4 for written descriptions) were digitized on each skull using Checkpoint (Stratovan 2018). We based our landmark configuration on a synthesis of the configurations in Olsen and Westneat (2016) and Olsen (2017), as well as the documentation for the R package linkr (Olsen 2016). Dense sampling along the beak was used to prevent the Pinocchio effect (Walker 2000; Zelditch et al. 2004), where one distant landmark (e.g., tip of the beak) dominates any signal when analyzing the entire landmark configuration. The landmark set used here aimed to capture differences in overall skull shape as well as features of biomechanical or ecological interest (e.g., points on the quadrate and orbits, respectively).

Figure 1: Landmark scheme on a surface scan of a least tern (*Sterna antillarum*; FMNH 376281) skull. Blue dots indicate type I landmarks, and red lines indicate placement of type II (sliding) semilandmarks. Description of landmarks are available in table S4.

We ran all subsequent analyses (unless otherwise noted) in R (RStudio Team 2019). We found that 157 specimens had missing landmarks where the skull was either damaged or the scanner did not capture the bone as a result of shadow, reflectance, variation in coloration, or the delicate nature of some components (e.g., the jugals) of the avian skull. These missing landmarks were estimated in one of two ways (details on which landmark sets were completed in which manner are given in table S4). For 118 specimens, landmarks from one side of the skull were mirrored across the plane created by the top of the beak, using the paleomorph (Lucas and Goswami 2017) package's mirrorfill function. For 68 other instances where mirroring was not possible, the fixLMtps function in the Morpho package (Schlager et al. 2020) was used. This function works by comparing complete landmark sets with those with missing points and uses thin-plate spline interpolation to impute the missing landmarks. To help minimize estimation errors, the function up weights specimens that are closer to the deficient specimen in morphospace. For this study, deficient landmark sets were completed by comparing specimens from the same genus to minimize both potential deviations from actual shape and the computational intensity of this estimation process.

Once complete landmark sets were obtained for all specimens, type II semilandmarks were slid along the curves using the slider3d function in the package Morpho (Schlager et al. 2020). Species-average configurations were obtained for species represented by two specimens by first performing a Procrustes superimposition using the procSym function in the Morpho package (Schlager et al. 2020) to remove the effects of orientation, size, and translation and then taking the average of each landmark coordinate using the mshape function in the package geomorph (Adams et al. 2020). Once averaged landmark configurations were obtained, the sliding procedure described above was repeated using the same slider3d function on these species-level landmark configurations. The final product of these steps was a set of 255 three-dimensional, aligned coordinate points for 262 charadriiform species. This data set was used for all further analyses and is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.pc866t1p0; Natale and Slater 2022). We also created two additional data subsets (see table S4 for details): one for the braincase and one for the beak and its biomechanically associated structures (i.e., quadrates, pterygoids, palatines).

To assess how shape relates to body size, an average body mass in grams was obtained for each species from the *Handbook of the Birds of the World* (del Hoyo et al. 1996; Cornell Lab of Ornithology 2020). When a range was given,

the midpoint was taken. As body mass is a volumetric measurement, we transformed these values by taking the log of the cube root. We chose to use body mass as opposed to centroid size in subsequent analyses, as comparisons of body mass with centroid size calculated from both the whole skull and a subset of landmarks that excluded points along the beak (a method that has been used to limit potential bias in centroid size estimation from elongated shapes; Kulemeyer et al. 2009) revealed subsets of taxa that follow different scaling patterns (see the figs. S1–S3).

Phylogeny

The phylogenetic tree used in all analyses here is taken from Černý and Natale (2021). This tree was inferred under a maximum likelihood framework using the program RaXML (Stamatakis 2014) from a supermatrix of 9 nuclear genes, 13 mitochondrial protein-coding genes, 2 mitochondrial ribosomal genes (all downloaded from GenBank; Benson et al. 2013), and 69 morphological characters taken from Chu (1995), representing a total of 336 species. The resulting topology was time scaled under a relaxed, uncorrelated molecular clock using 18 fossil calibrations in the program mcmctree (Yang 2007). Taxa not present in the morphological data set used here were pruned from the tree using the drop.tip function in the R package ape (Paradis et al. 2020).

Coding of Foraging Guild

We compiled descriptive ecological data for each sampled species from *Handbook of the Birds of the World* (del Hoyo et al. 1996; Billerman et al. 2020). Additional information was recorded from a variety of sources, including online videos, scholarly literature, and other online databases (details on additional sources are available in table S5). As most Charadriiformes are migratory, we recorded information related to foraging for the breeding and nonbreeding seasons separately. We then used the accumulated descriptive data to place each species into a foraging substrate and a foraging technique category adapted from the scheme in DeGraaf et al. (1985). We established 14 substrate categories (marsh, shoreline, semiaquatic generalist, water surface, shallow water, lower canopy, pelagic, rocky shore, wet and dry grassland, meadow, arid ground, generalist, ground and air, air, water) and 14 technique categories (facultative prober, facultative ground forager, ground forager, grazer, pursuit diver, dipper, plunge diver, facultative scyther, facultative terrestrial forager, aquatic scavenger, facultative diver, skimmer, hawker, predator). Definitions of each category are available in the supplemental PDF. A foraging guild was then assigned to each species for both breeding and nonbreeding seasons by combining substrate and technique for that season (e.g., pelagic and pursuit diver). Of the 91 possible unique combinations, many were implausible (e.g., arid ground and plunge diver), leaving only 36 occupied foraging guild categories. The breeding guild and nonbreeding guild classifications for each species are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.pc866t1p0; Natale and Slater 2022).

How Well Do Body Mass and Foraging Ecology Predict Charadriiform Skull Shape?

We used Procrustes ANOVAs to assess the proportion of skull shape variation attributable to foraging guild while still considering variation due to allometry (table 1, row 1). Significance was assessed via residual randomization in a permutation procedure (RRPP) as implemented in the procD.lm function of the geomorph package (Adams et al. 2020). The sum of squares argument was set to type II for each Procrustes ANOVA to ensure that we evaluated the effect of each variable despite the impacts of the others (Adams and Collyer 2018). The pgls implementation of Procrustes ANOVA assumes that residual error in the model is perfectly explained by the phylogenetic covariances among species (Adams and Collyer 2018). Revell (2010) has shown that this assumption can lead to increased variance in parameter estimates, reduced power, and, in some cases, elevated type I error rates. Instead, we performed a series of analyses as part of each ANOVA to estimate the amount of phylogenetic signal in the residual error of our model and thus appropriately account for it (Navalón et al. 2019; M. Zelditch, personal communication). We first fitted a nonphylogenetic Procrustes ANOVA using the procD.lm function and extracted the matrix of residuals from this model. We then estimated phylogenetic signal in the residual error term by fitting a multivariate Pagel's λ model to the residuals using the transformPhylo.ML function from the motmot package (Puttick et al. 2019). The maximum likelihood estimate of λ was then used to transform the phylogenetic covariance matrix derived from our charadriiform phylogeny, which was in turn used to define the correlation structure in a second Procrustes ANOVA using the original data and model notation in the procD.lm function.

In each ANOVA, we assessed how much of the variation in skull shape could be attributed to foraging ecology, body mass, and the interaction between the two. We repeated the ANOVAs using foraging guild classifications for both the breeding season and the nonbreeding season; results were similar for both (see table S4 for breeding season results), so for the rest of this article, we focus on guild classifications for the nonbreeding range and make note of one instance when results differed substantially.

To understand whether any relationships between shape, size, and ecology are driven by different parts of the avian skull, we repeated Procrustes ANOVA on subsets of the aligned landmarks corresponding to the beak and braincase separately.

Has Allometry Evolved in Charadriiformes?

It is possible that the strong support for allometry-driven skull shape variation, relative to ecology-driven shape variation, in some avian clades is an artifact of the phylogenetic level studied. Evaluating whether allometric parameters have evolved in geometric morphometric data is challenging, but significantly different slopes between clades in regressions of shape on size may be taken as evidence for shifts in size-shape scaling over macroevolutionary timescales. To assess this possibility, we fitted a set of Procrustes ANOVAs (table 1, row 2) with body mass and family as predictors. We fitted two forms of this model: one in which the two predictors were treated as additive effects and one in which an interaction between the two (indicative of evolution of allometry) was included. Model selection was performed using the anova function in R to assess whether including the interaction term significantly reduced the residual error in the model. We tested for significant differences in the orientation of allometric slopes between families based on vector correlations using the pairwise function in the RRPP package (Collyer and Adams 2018, 2019). The arccosine of the vector correlation between unit-normed vectors gives the angle between them, which can be evaluated against the null model based on the RRPP fit.

Is Allometry of Variable Importance in Charadriiform Families?

To further evaluate how allometric trends vary across different taxonomic levels, Procrustes ANOVAs assessing how much of the variation in skull shape could be attributed to foraging guild, body mass, and the interaction between the two (table 1, row 3) were also run on families that contain more than 20 species, as defined by Boyd (2019). This included four families: the Alcidae (auks and relatives), Charadriidae (plovers, lapwings, and relatives), Scolopacidae (sandpipers and relatives), and Laridae (gulls, terns, and relatives). To visualize how shape changes with size, both in Charadriiformes as a whole and in each of these families, the plotRefToTarget and shape.predictor functions from the geomorph package (Adams et al. 2020) were used to warp the mean landmark configuration of the clade to the predicted shape at high and low body masses for that clade.

Results

How Well Do Body Mass and Foraging Ecology Predict Charadriiform Skull Shape?

We found that body mass, foraging guild, and the interaction between body mass and foraging guild were all significant predictors ($P < .05$) of whole-skull, beak, and braincase shape (table 2). Foraging guild explained ~71% of whole-skull shape variation, body mass explained ~2%, and the interaction between them explained ~7%. The strong relationship between whole-skull shape and foraging ecology appears to be driven predominantly by the beak, given that foraging guild explained ~73% of beak shape variation but only ~44% of the variation in braincase shape. A larger amount of shape variation could be explained by both body mass (~7%) and the interaction term (~11%) for the braincase relative to the beak (where body mass explained ~0.5% and the interaction explained ~7%). Effect sizes (Z) for foraging guild were uniformly high ($Z > 10$) in the whole-skull, beak, and braincase analysis.

Table 1: Summary of the Procrustes ANOVA models run at various phylogenetic levels and on various sets of the morphological data to address three different research questions

Phylogenetic level	Morphometric data	ANOVA syntax	Question addressed
Order	Whole skull, beak, braincase	Shape ~ foraging guild × mass	How well do body mass, foraging guild, and their interaction predict charadriiform skull shape?
Order	Whole skull	Shape ~ mass + family Shape ~ mass × family	Has allometry evolved in Charadriiformes?
Families	Whole skull	Shape ~ foraging guild × mass	Is allometry of variable importance in charadriiform families?

Note: See "Methods" for full details of the pipeline used to conduct these models. "Mass" refers to the transformed body mass variable, and "whole skull, beak, braincase" indicates that the analyses were repeated on these three different sets of morphological data. Each analysis listed that required foraging guild data was repeated twice, once using the foraging guild for the breeding season and once using the foraging guild for the nonbreeding season.

Table 2: Results of Procrustes ANOVAs

Morphological structure	Percent variation explained by foraging guild	Percent variation explained by body mass	Percent variation explained by interaction
Whole skull	$R^2 = .70583$, $F_{31,187} = 23.4181$, $Z = 16.2542$, $P = .001$	$R^2 = .01584$, $F_{1,187} = 17.3472$, $Z = 3.4643$, $P = .001$	$R^2 = .06986$, $F_{31,187} = 2.3177$, $Z = 5.5991$, $P = .001$
Beak/associated structures	$R^2 = .73219$, $F_{31,187} = 24.3698$, $Z = 16.8077$, $P = .001$	$R^2 = .00574$, $F_{1,187} = 6.3021$, $Z = 2.7261$, $P = .002$	$R^2 = .06816$, $F_{31,187} = 2.2686$, $Z = 5.4276$, $P = .001$
Braincase	$R^2 = .43543$, $F_{31,187} = 7.9998$, $Z = 11.8971$, $P = .001$	$R^2 = .06694$, $F_{1,187} = 40.5862$, $Z = 4.6251$, $P = .001$	$R^2 = .10773$, $F_{31,187} = 1.9793$, $Z = 4.3505$, $P = .001$

Note: These series of ANOVAs assess the impact of body mass, foraging ecology, and the interaction between the two on whole-skull, beak, and braincase shape across the charadriiform order.

Has Allometry Evolved in Charadriiformes?

A model including an interaction term between family and body mass is strongly preferred over an additive model ($F_{12,257} = 4.0105$, $Z = 5.96$, $P < .001$), indicating that there are variable allometric relationships among families and that a common allometric model is not appropriate for charadriiform skull evolution. Family explained ~66% of skull shape variation in this interaction model ($R^2 = 0.6591$, $F_{12,232} = 53.8425$, $Z = 12.5951$, $P = .001$). Body mass explained ~2% ($R^2 = 0.02457$, $F_{1,232} = 24.0877$, $Z = 3.9253$, $P = .001$), while the interaction term explained ~5% of skull shape variation ($R^2 = 0.04909$, $F_{12,232} = 3.9901$, $Z = 5.9498$, $P = .001$).

Pairwise vector correlations revealed significant differences in allometric slopes between several families (fig. 2; table 3). These tend to be restricted to comparisons in which one family or both families are relatively species rich ($n > 20$; e.g., Laridae, Scolopacidae, Alcidae, Charadriidae), although significant differences were recovered for comparisons involving some smaller families (e.g., Glareolidae, Thinocoridae, Haematopodidae).

Is Allometry of Variable Importance in Charadriiform Families?

We performed family-level Procrustes ANOVAs on four charadriiform families with more than 20 species to assess how much skull shape variation could be explained by body mass, foraging guild, and the interaction between the two. The explanatory power of foraging ecology was substantially lower relative to the ordinal-level analysis in three of the families: ~23% in the Laridae,

Figure 2: Variable allometric relationships among different charadriiform families. Each of the 13 nonmonotypic families from the charadriiform order is encoded by a different color. The regression scores summarize how skull shape changes with body mass. Slopes are shown with a solid line for families, denoted with an asterisk where significant differences in allometric slopes were recovered between that family and at least one other (see table 3).

Table 3: Pairwise comparisons of allometric slopes between clades

Comparison	*r*	Angle	95% UCL	*Z*	*P*
Alcidae/Laridae	−.0390	1.610	1.170	2.383	.006
Charadriidae/Laridae	.008	1.562	.879	2.833	.002
Charadriidae/Scolopacidae	.674	.831	.964	1.333	.089
Glareolidae/Laridae	−.426	2.011	1.951	1.700	.037
Haematopodidae/Scolopacidae	−.620	2.240	2.225	1.613	.044
Jacanidae/Laridae	−.066	1.637	1.823	1.408	.095
Laridae/Scolopacidae	−.246	1.820	.672	3.845	.001
Laridae/Thinocoridae	−.071	1.642	1.704	1.579	.067

Note: These pairwise comparisons are in the form of vector correlations (*r*) for allometric slopes between clades that are significantly different at $P < .1$. "Angle" refers to the angle between allometric slopes expressed in radians, 95% UCL is the upper confidence limit for the difference between slopes based on randomized residuals in a permutation procedure, *Z* is the effect size, and *P* is the probability that the observed angle came from the same distribution as the full randomized sample.

∼19% in the Charadriidae, and ∼32% in the Scolopacidae. We excluded foraging ecology as a predictor in the Alcidae after it was found that all species shared one foraging guild.

Across these four families, the amount of skull shape variation attributable to body mass was variable but was consistently higher than the <2% of skull shape variation that could be attributed to body mass at the ordinal level (fig. 3). The proportion of shape variation attributable to body mass ranged from ∼8% in the Laridae to ∼24% in the Alcidae. We found no consistent trends in how shape changes with size (fig. 3). For Scolopacidae and Charadriidae, larger species have longer, narrower skulls and smaller species tend to have shorter, wider skulls, although elongation is less extreme in the Charadriidae. In the Laridae and Alcidae, larger species tended to have beaks that curved downward but varied in how the length of the skull changed with body size. Results using the breeding-season-specific foraging data (available in the supplemental PDF; table S3; fig. S4) were broadly consistent with those presented here, but in our analysis of the Charadridae, breeding-season-specific foraging guild did not significantly relate to skull shape.

Discussion

Recently, support has emerged among comparative biologists for the idea that foraging ecology explains a relatively small proportion of avian skull shape variation (Felice et al. 2019) and that a significant amount of skull shape variation is instead attributable to variation in body size (Bright et al. 2016, 2019; Tokita et al. 2017; Young et al. 2017; Navalón et al. 2019). If true, this hypothesis would overturn much conventional wisdom regarding the importance of form-function relationships in adaptive radiations (Lack 1947; Schluter and Grant 1984). Using 3D landmark data from the skulls of 262 species from the ecologically diverse order Charadriiformes, we evaluated this hypothesis and recovered evidence that allometric trajectories have evolved over charadriiform evolution. While the relative importance of allometry increases in younger clades, the specific relationship between skull shape, foraging ecology, and body mass is highly clade specific. These results both point to fruitful directions for future research and help to explain why past research on the predictors of avian skull shape variation has appeared so contradictory.

The Influence of Foraging Ecology on Skull Shape

The substantial relationship between foraging ecology and skull shape found here for Charadriiformes contrasts strongly with results for other clades. Charadriiformes is an ecologically disparate clade, with diets ranging from herbivory (Korzun et al. 2009) to predation on other birds (de Almeida Reis et al. 2021). It is possible that this ecomorphological diversity, which is greater than many other avian clades that have been comprehensively examined to date, is necessary to recover significant relationships between skull shape and foraging ecology. It is also worth noting that in clades such as parrots (Psittaciformes; Bright et al. 2019) and guilds such as birds of prey (Guangdi et al. 2015; Bright et al. 2016; Sun et al. 2018), where weak or nonexistent relationships between foraging or dietary ecology and skull morphology have been found, both the beak and the feet are used to acquire and manipulate food items (Brown and Magat 2011; Felice et al. 2019; Tsang et al. 2019), while Charadriiforms tend to rely solely on the beak to obtain food items. These results hint that ecomorphological diversity in the skull may be reduced when feeding involves multiple independent musculoskeletal systems.

Some studies conducted at higher levels of phylogeny and encompassing a broader range of ecological variation than that found in parrots or birds of prey have also recovered weak relationships between foraging ecology and skull shape (Felice et al. 2019; Navalón et al. 2019). These findings suggest that clade choice is not the only explanation

Figure 3: Variable relationships between skull shape, foraging ecology, and body mass in several charadriiform clades. All results are based on phylogenetically corrected Procrustes ANOVAs. The *n* given denotes the number used in our final analysis after species occupying their own unique foraging guild were removed. These results are shown for the charadriiform order as a whole as well as four families with sufficient sample sizes: the Scolopacidae (sandpipers and relatives), Charadriidae (plovers and relatives), Laridae (gulls, terns, and relatives), and Alcidae (auks). The thin-plate splines illustrate the morphology 1.5 SDs above and below the mean body size, warped relative to the mean. The bar chart on the right shows the amount of skull shape variation attributable to foraging guild, body mass, and the interaction between these two factors in each clade. The images are representative examples of small and large species from that clade. From left to right, row by row: little tern (*Sternula albifrons* by Agustín Povedano), brown skua (*Catharacta antarctica* by Zakhar V. Akulov), least sandpiper (*Calidris minutilla* by Fernando Flores), Far Eastern curlew (*Numenius madagascariensis* by John Harrison), three-banded plover (*Charadrius tricollaris* by Charles J. Sharp), southern lapwing (*Vanellus chilensis* by Mdf), whiskered tern (*Chlidonias hybrida* by Derek Keats), Pacific gull (*Larus pacificus* by J. J. Harrison), parakeet auklet (*Aethia psittacula* by Dave Govoni), common murre (*Uria aalge* by thelastweasel). Full image licensing available in figure S5 and table S6.

for the differences between our results and those of previous work. We suspect that the intensity of sampling within and between clades may also exert a substantial influence on results. Felice et al. (2019) found a significant but weak relationship between diet and skull shape variation based on a sample of 352 extant species, a 35% increase in size on our data set. However, their sample spanned the entirety of the class Aves, with the result that individual orders and families were only sparsely represented. In finding that diet explained only 12% of variation in beak shape across a sample of 175 species spanning 94 families of birds, Navalón et al. (2019) suggested that one-to-many mapping of morphology to ecology may cloud form-function relationships at higher phylogenetic levels (see also Friedman et al. 2019). Alternatively, these results may suggest that broad but sparse sampling fails to capture sufficient instances of convergence on similar morphological solutions in response to similar foraging ecologies. Indeed, Pigot et al. (2020) found that foraging ecology could be reliably predicted from nine trait measurements, many taken from the beak, in a sample that comprised ∼99% of extant bird species. Notably, Pigot et al. (2020) also found that beak morphology is predictive of both diet (the food types consumed) and foraging mode (the way in which it is obtained). It is therefore possible that the low proportion of skull shape variation recovered in some higher-level studies (e.g., Felice et al. 2019; Navalón et al. 2019) is also due to the use of relatively coarse dietary categorizations. Indeed, repeating our analyses after collapsing the 36 foraging guilds used into 10 more coarse guilds that cluster species that forage in generally similar ways (e.g., birds that dive) irrespective of specific foraging technique reduced the amount of skull shape variation that could be attributed to foraging ecology by ∼46% (see the supplemental PDF; table S2).

Approaching Allometry as an Evolving Factor Shaping Avian Skull Evolution

Although allometry is known to evolve (Voje et al. 2014), most morphometric studies assume common scaling of shape with size across a clade. On the one hand, failure to account for these evolving relationships might contribute to the low amount of skull shape variation attributable to body size in analyses that have looked across broad taxonomic scales. On the other hand, this assumption has the potential to obscure the detection of unique allometric trajectories in subclades and therefore de-emphasizes the importance of allometry as a source of ecomorphological variation on which selection can act over relatively short timescales. Support for a Procrustes ANOVA that included an interaction between family and size, significant differences between allometric trajectories for families in pairwise tests, and the distinct allometric trends seen in individual family-level analyses all support the idea that size-shape relationships for the avian skull have evolved over time. The variability seen in the size-shape relationships for charadriiform families, combined with the relatively low proportion of shape variation explained by size at the level of the order, helps explain the discrepancy between studies that have found strong contributions of allometry to skull shape at lower taxonomic levels (Bright et al. 2016, 2019; Tokita et al. 2017) and those that have found relatively modest or insignificant contributions at higher levels (Felice et al. 2019). Our findings indicate that extrapolating results between different taxonomic levels is not advisable. More research is needed to understand at what scale these evolving size-shape relationships differ enough to impact the recovered patterns in taxonomically broad studies.

At the family level, we found substantial variation in the amount of skull shape variation attributable to body mass, foraging ecology, and the interaction between these two factors. Body-size-related change may function as an evolutionary line of least resistance, particularly in young clades (Schluter 1996), and can facilitate rapid ecological divergence, such as the rapid changes we often see in young island radiations (Cooney et al. 2017), in spite of otherwise strong phenotypic covariance (Felice et al. 2018). Here, we found that allometry explained more of the variation in skull shape in individual charadriiform families than in the order as a whole, supporting the role of allometry as an important source of variation in younger, relatively ecologically conservative clades. It is notable that previous work on a relatively similar scale (Tokita et al. 2017) found that evolutionary allometry accounted for ∼11% and ∼28% of total shape variation in the skulls of Hawaiian honeycreepers and Galápagos finches, respectively, suggesting that the age of the clade studied may indeed affect the strength of the allometric relationship recovered.

Our results additionally highlight how, even if allometry is of relatively greater importance at lower taxonomic levels, the importance of size-related shape variation may differ among clades of a similar age. Body size is known to serve a particularly important role in species sorting when prey type is relatively uniform, but prey size serves as the primary axis of niche divergence or resource partitioning (Hutchinson 1959; Kiltie 1984, 1988; Dayan and Simberloff 1994; Werdelin 1996). We did not quantify relative prey size for charadriiform species here, but it is notable that one of the clades to exhibit a strong and substantial allometric component of variation, the Alcidae, consumes a wide range of prey sizes (del Hoyo et al. 1996), often feeds sympatrically (Linnebjerg et al. 2015), and exhibits a correlation between preferred prey size and gape width (Swennen and Duiven 1977), leaving open the possibility that size-based resource partitioning may be an important driver of morphological

evolution at lower taxonomic levels when foraging modes are relatively more conserved. Similarly, both body size and foraging ecology explained relatively large portions of skull shape variation in the Scolopacidae. Allometric variation in this family appears to relate to changes in specific foraging niches: most large scolopacid species possess elongated skulls that tend to be associated with probing behaviors, while most smaller species possess less elongated skulls that tend to be associated with pecking behaviors (Barbosa and Moreno 1999). The distinct patterns recovered for Scolopacidae and Alcidae further emphasize that while allometry may generally be an important source of shape variation in younger clades, extrapolating results across clades at the same taxonomic level may also generate conflicting results. Given the substantial differences between families in the same order recovered here, future work aiming to understand the magnitude of size-shape relationship differences across all birds is warranted.

Conclusions

Through the use of comprehensive taxonomic sampling and 3D landmark data from the entire skull and the application of phylogenetically informed statistical analyses, we recovered two important conclusions regarding the roles of allometry and foraging ecology in explaining morphological diversity in the avian skull. First, our support for evolving allometric relationships in Charadriiformes highlights the need to use an analytical framework that accounts for these evolving relationships when studying allometry at a relatively broad taxonomic scale. Second, the relatively higher importance of allometry at the familial level, relative to the ordinal level, coupled with the highly variable relationship between skull shape, foraging ecology, and body mass seen in these families, provides strong reasoning not to extrapolate results across different taxonomic scales and suggests that the importance of allometry and foraging ecology may be clade specific. Collectively, our results suggest that foraging ecology is likely a critical predictor of avian skull shape at macroevolutionary scales, as has been classically thought, and that the recent shift toward an allometry-dominated perspective is likely the result of methodological choices and the taxonomic scale of study. Future work is needed to better understand both the relationship between allometry and foraging ecology at lower levels of avian phylogeny and how allometry itself evolves at higher levels.

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Statement of Authorship

Both authors contributed to the conceptualization of the study, funding acquisition, experimental design, and writing, editing, and reviewing the manuscript. R.N. performed data collection, analysis, and visualization, with G.J.S. providing feedback on these portions.

Data and Code Availability

All data files and R scripts are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.pc866t1p0; Natale and Slater 2022). The 3D surface scans used are available on MorphoSource (project ID: 00000C909).

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Associate Editor: Tony D. Williams
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"I will first mention the St. Lucas Thrush (*H. cinereus*); it agrees with the thrasher, and differs from all the rest, in being thickly speckled with brownish-black over most of the under parts. It is dull brownish-gray above; the shape of the bill is shown [as figured]." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 7:321–331).