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Relative skull size as one of the factors limiting skull shape variation in passerines

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1 Abstract

2 Despite a considerable interest of researchers to the issue of variation in skull shapes of birds and
3 factors influencing it, some drivers associated with the design features of an entire bird body, which
4 are important for both successful terrestrial locomotion and flight, are overlooked. One of such
5 factors, in our opinion, is relative skull size (skull length in relation to body mass), which can affect
6 the position of the body's center of gravity. We tested effects of relative skull size, allometry (i.e.
7 absolute skull size), and diet on variation in skull shape. The study was conducted on 50 songbird
8 species with a wide range of body mass (8.3g to 570g) and dietary preferences (granivores,
9 insectivores/granivores, insectivores, omnivores). Skull shape was analyzed using 2D geometric
10 morphometrics. We revealed that similar patterns of skull shape occur among passerines with
11 different body sizes and diets. The relative skull size predicted skull shape to a similar extent and
12 with a similar pattern as the absolute size. In our opinion, the effect of the relative skull size on
13 skull shape variation is likely due to biomechanical constraints related to flight.

14 **Keywords:** granivores, insectivores, omnivores, geometric morphometry, allometry, songbirds,
15 passerine birds

1 Introduction

2 Birds have a dramatically wide variety of skull shapes, which is the subject of constant
3 research interest (Hospitaleche and Tambussi 2006; Degrange and Picasso 2010; Klingenberg and
4 Marugán-Lobón 2013; Bright et al. 2016; Tokita et al. 2016; Felice and Goswami 2017). Observing
5 this diversity, one gets an impression that possibilities for variation in bird skull shape are endless.
6 But is this really the case? Birds, as flying vertebrates, should have strong restrictions on change of
7 body parts and skull in particular that are associated with biomechanical requirements imposed by
8 flight.

9 Several aspects can be distinguished in this respect. Firstly, birds have significant
10 restrictions on increases in body size. Evolutionary loss of the teeth, bone reduction, a fusion of
11 most bones in the skull, and formation of cranial kinesis in birds are associated with the need to
12 reduce the skull weight to meet the requirements of active flight (Judin 1970; Dzerzhinsky 1972).
13 Secondly, it is the position of the body's centre of gravity, which is important for both terrestrial
14 locomotion and flight (Gladkov 1949; Stegmann 1949; Judin 1970). The center of gravity of a bird
15 body is close to the intersection of the longitudinal axis of the body with the line connecting wing
16 pressure centers and does not change its position significantly in movements of birds (Gladkov
17 1949; Judin 1970). Consequently, a relationship between body parts must be such that it does not
18 significantly affect the position of the body's center of gravity during flight. The possibility of
19 independent transformation of a skull in this regard seems rather limited.

20 We hypothesize that the relative skull size, specifically its influence on the position of the
21 center of gravity of the body may be the limiting factor in the variation of skull shapes. The results
22 of recent study support this assumption (Shatkovska and Ghazali 2020). It was found that the skull
23 length scaled isometrically on the body mass, the beak length was positively allometric while the
24 cranium length was negatively allometric. The isometric pattern of change of the total skull length
25 on the body mass indicates a limited range of alteration in the relative skull size; and the opposite
26 trends in the beak and cranium length reveal restricted variability in the proportions of these regions
27 within the skull.

On the other hand, trophic specialization can significantly influence skull shape. Passerines have a very diverse food spectrum. The relationship between the shape of a beak and diet in passerines has been repeatedly noted by different researchers (Grant and Grant 1993; Lovette et al. 2002; Jönsson et al. 2012; Tokita et al. 2016). Passerines with different dietary preferences, like insectivores and granivores, are completely different from each other in food items, and load on the jaw apparatus when holding and processing food items (Dzerzhinsky 1972; Nekrasov 1978). Even within granivores, there is a variation in beak width and depth depending on hardness of seeds used (Boag and Grant 1981; Price et al. 1984; Grant and Grant 1995; Herrel et al. 2005). In turn, food specialization can affect not only beak shape but also cranium shape since jaw muscles, which responsible for holding and processing food items, are positioned at the cranium (Bowman 1961; Nekrasov 1978). A high degree of integration between shapes of the upper beak and the cranium (braincase) was confirmed by several researchers based on studies of skull shape variation using geometric morphometrics (Kulemeyer et al. 2009; Klingenberg and Marugán-Lobón 2013; Bright et al. 2016; Tokita et al. 2016). Although Felice and Goswami (2017) using a large number of landmarks found that the avian skull is highly modular, consisting of seven independently evolving anatomical regions.

At the same time, similarity of skull shapes in birds with different food specializations has been repeatedly noted (Bright et al. 2016; Tokita et al. 2016), which may indirectly indicate the presence of factors constraining skull shape variation. We assume that the relative skull size, specifically its influence on the position of the center of gravity of a body, may be the limiting factor in the variation of skull shapes in birds with different food specializations.

The shape of a skull is also largely determined by allometry (Kulemeyer et al. 2009; Klingenberg and Marugán-Lobón 2013; Bright et al. 2016; Tokita et al. 2016). A general pattern of allometric changes in skull shapes is that the skull enlargement is associated with beak elongation, skull roof flattening, and rotation of the occipital from a ventral to a posterior orientation. A mechanism that is at the base of the correlative transformation of these regions may be a developmental constraint (Linde-Medina and Diogo 2014), which is considered an important factor

that channeled evolutionary change (Gould and Lewontin 1979). However, it should be noted that allometry takes into account only the overall dimensions of a body or skull, but does not consider an interrelation of different skeletal regions within the body and their possible mutual influence on each other.

We aim to estimate and compare the effect of relative skull size (skull length in relation to body mass), allometry (absolute skull size) and diet on skull shape variation. We carried out this study on songbird species that were previously subjects of research on the integration of different skeletal regions (skull, sternum and pelvis) (Shatkovska and Ghazali 2020). This, it seems to us, will allow a more reasoned analysis of the influence of the relative size of a skull on its shape, taking into account the relationship between sizes of different skeletal regions within a body. Since the species under study belong to different families (Table S1), we also took into account the influence of phylogeny on the variation of skull shape. It was noted earlier that the shape of a skull is associated with phylogeny, so that related bird species have more similar skull shapes (Brusaferro and Insom 2009; Degrange and Picasso 2010).

Firstly, we examined the variation of skull shapes in passerines with a wide range of body mass (8.3g to 570g) and dietary preferences (granivores, insectivores/granivores, insectivores, omnivores) by a principal components analysis. In choosing the dietary categories, we were guided mainly by a principle that the studied species have the most varied loads on the jaw apparatus. Different functional loads on the jaw apparatus can affect the overall proportions of a skull, which in turn can be under pressure from biomechanical limitations associated with flight. Secondly, we performed phylogenetic regression analyses to predict skull shapes based on diet, absolute and relative sizes and to evaluate the influence of diet on sizes of skull. Thirdly, the degree of beak-braincase shape covariation was tested by phylogenetic two-block partial least squares (PLS) analysis.

Previously, the variation of skull shapes was examined within several songbird clades - i.e., Corvidae family (Kulemeyer et al. 2009), Darwin's finches and Hawaiian honeycreepers (Tokita et al. 2016; Navalón et al. 2020). Among the studied groups, the birds were similarly sized and

phylogenetically closely related. We believe that our study of passerines with a wider range of body mass, dietary preferences, and taxonomic groups will expand our understanding of the factors that determine the skull shape.

Materials and methods

Data acquisition

Our sample consists of skulls of 50 species (1 specimen per species) of passerines representing 21 families. Only adult individuals were considered. Taxonomy is given according to Jetz et al. (2012). For a complete list of the studied species see Table S1. Materials were gathered from the collection of National Natural Science Museum of NAS of Ukraine (Kyiv).

We digitized two-dimensional coordinates of homologous landmarks and equally spaced semilandmarks on curves in lateral (14 landmarks and 55 semilandmarks) and dorsal (6 landmarks and 30 semilandmarks) views of a skull (Fig. 1). We tried to take into account as much as possible both overall proportions of a skull and shapes of beak, braincase and orbit orientation when digitizing the landmarks and semilandmarks. The landmarks and semilandmarks in dorsal projection were located on the midline and left side of the beak and braincase. Anatomical description of landmarks and semilandmarks is presented in Table S2. Digitization of landmarks and semilandmarks was done with tpsDig2 v. 2.31 (Rohlf 2017).

Since the main purpose of our study was to test the effect of relative skull size on skull shape variation, the correct expression of the relative skull size was important to us. The necessity to unify the dimensions of analyzed values was in the foreground. The body size was expressed through a linearized value - cubic root of body mass ($m^{1/3}$). Data on body mass (m) were taken from Dunning (2007). The absolute skull size was expressed via the greatest length of the skull (Lsk), which was measured using a caliper to the nearest 0.1 mm according to a standard methodology (von den Driesch 1976) (Lsk , the distance between the beak tip (apex praemaxillaris) and the most caudal end of the supraoccipital bone (protuberantia occipitalis externa)) (Fig. 1). The greatest skull length is the same for both the dorsal and lateral views (Fig. 1). This fact served as an argument for

choosing *Lsk* as the skull's size proxy since skull shapes variation in lateral and dorsal views can appreciate across the unified parameter - *Lsk*. The relative size of the skull was determined as the ratio of skull length to cubic root of body mass ($Lsk/m^{1/3}$). Although the correlation coefficient between *Lsk* and centroid size was high ($r > 0.97$ for both projections, $p < 0.001$), we did not use centroid size as a value representing the skull size because we needed the same descriptor for relative size for both projections of the skull. Results of basic statistical analysis of skull traits are given in Table 1.

Separating birds according to dietary groups was somewhat difficult as many birds use mixed feed within a year. In classifying the dietary groups, we were guided by dietary preferences, which are leading for birds throughout a year. Birds were divided into following dietary categories: insectivorous, granivorous, omnivorous, walnut specialists and mixed group of insectivorous/granivorous. The last group included birds that use insectivorous diet in summer and switch to mainly granivorous diet in winter. Information about diet was collected from Dement'ev et al. (1954).

Statistical methods

Skull shape morphospace

We performed Procrustes superimposition for skull configurations in dorsal and lateral projections to remove effects of size, position, or orientation of skull. Procrustes shape coordinates were used in further analyses. Analysis and visualizations were made in R v. 3.6.3 (R Core Team 2020) with the packages geomorph v. 3.2.1 (Adams et al. 2019) and phytools v. 0.6-99 (Revell 2012). We conducted an ordinal principal components analysis to assess skull shape variation (geomorph function gm.prcomp).

Phylogenetic hypothesis was reconstructed as the maximum clade credibility tree of 4000 trees imported from the database <http://birdtree.org> (Jetz et al. 2012). Hackett All Species subset was chosen (Hackett et al. 2008). Best tree (Fig. 2) was chosen with the function maxCladeCred in R package phangorn v. 2.4.0 (Schliep 2011). Phylogenetic signal was tested with the function

physignal of the geomorph package with 1000 permutations: multivariate test showed significant deviation from random distribution of traits values along the tree (skull shape both projections $K_{mult} = 0.8, p < 0.001$). Thus, we accounted for phylogeny by implementing phylogenetic comparative methods.

Testing of factors affecting skull shape

Phylogenetic generalized least squares analyses of shape data were applied to test the interaction of effects of diet, absolute and relative skull size on skull shape variation (geomorph function `procD.pgls`, 2000 iterations). The effects of diet, skull size and relative skull size were evaluated with R^2 (portion of the total variance explained by factor after controlling for others). Pairwise comparison of skull shapes between dietary groups was also performed with `procD.pgls` function.

Phylogenetic ANOVA and pairwise post-hoc comparisons (`phytools` function `phylANOVA`, 2000 simulations) were applied to test the differences between dietary categories in the absolute and relative skull size. Skull length and relative skull size were $\log_{10}$ -transformed to normalize data.

We applied false discovery rate (FDR) correction for multiple tests when interpreting pairwise comparisons, but we reported uncorrected p -values with bold highlighted values that remain significant after FDR-correction in the tables. We used function `p.adjust` of the `stats` package of R (R Core Team 2020).

Estimation of covariation between blocks

Phylogenetic two-block partial least squares (PLS) analysis between shapes of upper beak and cranium were carried out to produce first PLS-axes and associated shape changes for ordination plots (geomorph function `phylo.integration`). Following formula of Escoufier (1973) we calculated RV coefficient to evaluate the level of covariation between blocks; covariance matrices of

phylogenetically corrected PLS-scores were used. Null hypothesis of complete independence of two blocks ($RV = 0$) was tested with permutation test with 10000 randomization rounds.

To assess whether skull size or relative skull size influenced skull shape variation or skull integration we estimated minimal angles between coefficient vectors of phylogenetic regressions, the major axis of skull variation (PC1) and the major axis of skull integration (PLS1). Calculations were conducted with the functions `angle.calc` and `angleTest` of package `Morpho` (Schlager 2017). The angles can range from 0° to 90° . If the angle between vectors is close to 0° , this is an indication of the correlated change of vectors. If the angle is close to 90° , it means that the change of traits is orthogonal.

Results

Skull shape variation

The first three principal components explained 80% (lateral view) and 87% (dorsal view) variation of skull shapes (Fig. 3, scores of PC1 and PC2 are in Table S3). PC1 accounted for 53% (lateral view) and 65% (dorsal view) variation and was connected to braincase size, size and orientation of orbits, beak length in both lateral and dorsal views, and depth of a beak and bending between a jugal arch and a ventral border of a premaxillary bone and size of nares in lateral aspect. PC2 described 19% variation (lateral view) and 15% (dorsal view) and was linked with braincase size in both views, and depth and curvature of the beak in lateral projection, and width of the beak and an interorbital space in dorsal one. PC3 explained 8% variation (lateral view) and 7% (dorsal view) and was related to minor changes in skull depth in lateral view, and width of the beak and interorbital space in dorsal view (Fig. S1, S2).

In the morphospace of the first two principal components in both lateral and dorsal aspects (Fig. 3) species, although overlapping, are noticeably divided into two clusters on PC1. One of the clusters included granivores and insectivores/granivores, while the other involved insectivores, omnivores and walnut specialists. Granivores and insectivores/granivores have mainly shorter and deeper beak with pronounced bending between the jugal arch and the ventral border of the

premaxilla, reduced nasal fossa, large orbits with more frontal orientation and large and deeper braincase. Insectivores and omnivores have a more flattened, narrowed skull with a longer beak, less pronounced angle between the premaxillary bone and the jugal arch, enlarged nasal fossa, smaller orbits that are laterally shifted and decreased braincase (Fig. 3, 4).

Highly specialized granivores (members of Fringillidae) and large omnivores and walnut specialist (Corvidae) are distinguished by PC2 (the upper part of the plot in the lateral aspect, Fig. 3a; the lower part of the plot in the dorsal aspect, Fig. 3b). They had a wider, more curved and deeper beak, increased interorbital space, expanded and somewhat shortened cranium. The opposite extreme included mainly insectivores and insectivores/granivores, which have the narrower beak, narrowed and somewhat elongated cranium.

Effect of various factors on skull shape variation

PGLS analysis revealed that diet and size influenced skull shape variation if the analysis took into account diet and one of the sizes, absolute or relative skull length (Table 2). After all of the three factors were included in the PGLS analysis, the effect of the diet remained marginal (lateral view) or became unreliable (dorsal view). The effects of skull sizes (absolute or relative) reduced but remained highly significant. This fact indicated that dietary preferences were mediated mainly by changes in absolute and relative skull size.

Pairwise comparisons of skull shapes between different diets indicated that insectivores differed significantly from granivores and insectivores/granivores ($p < 0.05$, Tables 3, 4). Measurements were better determined by diet (phylANOVA, $p < 0.001$): length of skull ($R^2 = 68\%$), relative skull size ($R^2 = 61\%$). Pairwise post-hoc comparison (Table 5) revealed that omnivores differed significantly in Lsk from the other three groups ($p < 0.001$); omnivorous were the largest (Table 1). Pairwise tests of relative size ($Lsk/m^{1/3}$) were significant only between granivores and insectivores, $p < 0.01$; insectivores had the largest relative skull size (Table 1).

Phylogenetic regression analysis of shape data on skull length revealed that 16% ($p < 0.001$, lateral view, Fig. 5a) and 22% ($p < 0.001$, dorsal view, Fig. 5b) of the variation in shape can be

predicted from size that indicated a moderate allometric relationship between skull shape and its absolute size. For both the lateral and dorsal aspects, increasing skull size led to the lengthening of the beak, shortening of the cranium and more lateral orientation of the orbits. In addition, skulls were flattened within the lateral view and narrowed within the dorsal aspect, the bending angle decreased between the premaxillary bone and the jugal arch in lateral projection towards the regression vector. Phylogenetic regression analysis of skull shape against relative skull length showed that 14% ($p < 0.001$, lateral view, Fig. 6a) and 23% ($p < 0.001$, dorsal view, Fig. 6b) of shape variation is related to the relative skull size that is similar to the results of regression analysis of skull shape on absolute skull size.

Features of skull morphology associated with absolute or relative size are similar to the overall shape variation described with PC1. The influence of size on skull shape variation is confirmed by analyses of angles between regression vectors and the main axis of skull shape variation (PC1) (Table 6). Small values of angles indicated a high degree of consistency in changing skull shape and sizes, both absolute and relative.

Distribution of species in the morphospace of the regression analyses was similar to that along PC1 (Fig. 3, 5). It is noteworthy that small insectivores and large omnivores are similar in lengthened beak, decreased braincase, flattened and more laterally oriented orbits, enlarged nasal fossa, and no pronounced curvature between the jugal arch and premaxillary bone. Granivores and insectivores/granivores are also similar by their short, deeper, and curved beak, smaller nasal fossa, enlarged braincase, and large and more frontal oriented orbits.

Covariation between shapes of beak and cranium

Phylogenetic PLS analysis indicated a high degree of overall strength of association between beak and cranium shapes ($r = 0.9$, $p < 0.001$; $RV = 0.68$, $p < 0.001$, lateral view; $RV = 0.76$, $p < 0.001$, dorsal view). The first PLS axis (PLS1) explained most of the covariation (74 % in lateral view and 97% in dorsal view), scores are in Table S3.

According to PLS1 for lateral view, the elongated and straightened beak correlated with the flattened cranium, flattened and more laterally oriented orbits and reduced braincase, which were typical for omnivores and insectivores (Fig. 7a). Conversely, the shortened curved beak correlated with the deeper skull with enlarged frontally oriented orbits and large braincase, which were observed mainly in granivores and insectivores/granivores. The described correlative changes in beak length, braincase size and orbits' orientation are also seen in the dorsal projection (Fig. 7b).

Analyses of angles between PLS1 and vectors of regressions showed that similarity between shape changes associated with sizes (regression vectors) and covariation of beak and cranium (PLS1) was weak, although highly significant (Table 6).

Discussion

The results of our study showed that most variation of the skull shapes is distributed within a continuum. One extreme of the continuum is represented by species with an elongated beak, a flattened and somewhat reduced braincase with flattened laterally oriented orbits and the second one is expressed by birds with a shortened beak, which correlates with an enlarged braincase and enlarged frontally oriented orbits. A part of the variation in skull morphology is related to allometry. In our sample of species, the influence of allometry is most noticeable in large species. The modifications of their skulls are described above as the first extreme of continuum. Similar transformations in skull shapes with an increase in its absolute size were observed previously for many bird groups (Kulemeyer et al. 2009; Klingenberg and Marugán-Lobón 2013; Bright et al. 2016; Tokita et al. 2016).

Despite the long-recognised allometric pattern of skull shape change in birds, little is known about factors that underlie this pattern. We assume that the decreasing cranium in large passerines is associated with allometric pattern of brain changes in birds and close relationship between brain growth and surrounding cranium bones (Zusi 1993; Fabbri et al. 2017). Birds have negative allometric pattern scale of brain size on body size (Martin 1981; Bennett and Harvey 1985; Font et al. 2019; Ksepka et al. 2020), although large-scale allometric differences occur in the brain-body

relationship across bird clades (Ksepka et al. 2020). This negative allometric pattern corresponds to Haller's rule of brain size alteration in animals (Lüps 2010). Although we have not investigated the regression of skull shape on body mass, it is obvious that birds with the largest body mass have the longest skull (Tables 1, S1). It is noteworthy that there are no large species with enlarged braincase among our sample. This fact could be explained by the small sample size. However, given that members of Corvidae family are the largest representatives of the order (Ilichev et al. 1991), an increase in the sample is unlikely to affect the observed pattern. Passerines with large body mass apparently cannot develop sufficiently large relative sizes of braincase as small birds.

An unexpected point in our study is the presence of similar skull shapes in insectivores and omnivores: pairwise comparison of lateral or dorsal projections of their skulls did not reveal significant differences in skull shapes between these bird groups (Tables 3, 4). Obviously, the similarity of skull shapes, in this case, is not related to allometry, since insectivores and omnivores differ in absolute skull size (Table 5). This fact indicates that skull shape alterations are limited and that skull shape is not always associated with skull size or food specialization. Interestingly, Tokita et al. (2016) found many examples of convergent skull shapes among Darwin's finches and Hawaiian honeycreepers with dissimilar diets. Bright et al. (2016) found that beak-braincase covariation in birds of prey remained even after removal of the allometric or phylogenetic signal, which seems to us to indicate a limited variability in the proportions of these skull parts for birds as a whole.

A question arises: Why is beak lengthening inevitably associated with a decrease of the cranium and vice versa? The occurrence of the described trends, in our opinion, is associated with the relative size of a skull, which limited skull shapes alteration. The analysis of angles between regression vectors and PLS1 revealed the moderate correlation between both absolute or relative skull sizes and covariant changes in shapes of the beak and braincase. The relative size of a skull determines skull shape variability to a similar extent and in a similar pattern as the absolute size.

Despite this fact, we believe that the influence of the relative skull size represents an entirely different phenomenon from allometry. The effect of the relative skull size on skull shape variation

is likely due to biomechanical constraints related to flight. The relative skull size can influence the center of gravity of a body, which supports a balance between cranial and caudal parts of the bird's body. If this balance is disturbed and the center of pressure of wings shifts concerning the center of gravity of a body, this leads to an emergence of a twisting moment (torque) that affects the balance of a bird in flight (Gladkov 1949). Our previous study of bird skeletal integration on the same sample of species showed that passerines with different body mass vary in body proportions (Shatkovska and Ghazali 2020); birds with small body mass have relatively shortened postcranial axial body length. As a result, their entire body mass is brought together on the long axis of the body. An additional instability of the body is created with such distribution of mass: the bird can more easily get out of its equilibrium position (Gladkov 1949). For passerines with small body mass, the restriction on the increase in skull size is especially significant since the increase in the skull size without balancing increase in the postcranial skeleton can lead to overturning birds in flight although to some extent this can be offset by lengthening a tail (Gladkov 1949).

The limiting effect of the relative skull size on the variability of its shape is most clearly seen in an example of insectivores. Birds of this dietary group have a number of specific features: an elongated beak with reduced braincase and the largest relative skull size among studied groups. This combination of characteristics may be caused by several factors. Firstly, the elongated and thinned beak, combined with peculiarities of adductor muscles morphology, probably contribute to an increase in speed of beak closing (Dzerzhinsky 1997). Secondly, insectivores have restrictions on decreasing of brain size given the negative allometric pattern scaling brain size on body mass in birds (Martin 1981; Bennett and Harvey 1985) and small body size of insectivores (Table 1). The decrease of the braincase in insectivores is therefore also limited. However, lengthening of the beak cannot be accompanied by a proportional enlargement of the braincase since this would lead to a significant increase in the skull size relative to the entire body. Thus, the presence of relatively large skull in insectivores seems to be a compromise between the need to lengthen the beak, preserve of the largest possible braincase and limit variability in the relative skull size.

Changes in skull sizes mediate transition to specific diets in birds studied. PGLS analysis revealed that diet was not an independent factor influencing skull shape variation (Table 2). Our findings are partially consistent with those obtained on birds of prey (Bright et al. 2016), namely, the relationship between allometric changes in skull shape and diet alteration. Among the studied passerines, this pattern is observed mainly in large species, which are omnivores.

A new finding in our study is that the relative skull size also mediates dietary transition. Insectivores and granivores, which differ in relative skull sizes (Table 5), also differ in skull shapes (Tables 3, 4). Diet alteration is likely a driving force that affects skull shape and its relative size in this case. Patterns of skull shape variation are connected with a necessity to vary beak shape as an organ directly related to obtaining food. The close relationship between the structure and size of the beak and the specificity of food items in passerines has been repeatedly noted by different researchers (Bowman 1961; Ziswiler 1965; Nekrasov 1978; Grant and Grant 1993). Most granivorous passerines crack and peel seeds by their beaks before eating, which requires complex jaw movements that resemble chewing in mammals (Nekrasov 1978). The load on the jaw apparatus in these birds can be orders of magnitude greater than the weight of the bird itself (Sims 1955; Nekrasov 1978). Given these facts, the skull of granivores requires substantial strengthening in comparison with the skull of insectivores.

Strengthening of the skull of granivores involves both the jaw apparatus and cranium since loads from the upper and lower jaws are transmitted through the fronto-nasal hinge and os quadratum to the occipital segment of the skull (Nekrasov 1978). Shortening and increasing the width and depth of the beak, reducing the nasal fossa, as well as the pronounced ventral bending of the skull between jugal arch and ventral border of upper beak, which are observed in granivores (Fig. 3), lead to strengthening of their beak and enhance the ability to more effectively compress food items (Dzerzhinsky 1972; 1997; Nekrasov 1978). Increasing depth and width of the beak are also significant predictors of bite force among birds adapted to the granivorous diet, as shown in an example of Medium Ground Finch (*Geospiza fortis*) (Herrel et al. 2005). In addition, granivores have reinforced adductor jaw muscles (especially m. adductor mandibulae externus and m. adductor

mandibulae internus), which contribute to the development of muscular processes (proc. postorbitalis, proc. zygomaticus and to a lesser extent proc. suprameaticus), crests of the dorsal part of the posterior wall of the orbit, larger parietal and occipital crests (Nekrasov 1978), and probably the relative increase of the cranium depth as a whole. Thus, diet preferences require not only changes in the shape of the beak, but also correlative transformations of the braincase that is confirmed by the PLS analysis results. A high degree of integration between these regions was previously detected for other birds (Bright et al. 2016; Tokita et al. 2016). Members of insectivorous/granivorous dietary group are similar in analyzed characteristics to granivores; they do not have significant differences in skull shapes and relative skull sizes. The need to consume seeds apparently requires significant strengthening of the jaw apparatus, which in turn is accompanied by cranium changes in both groups.

We did not investigate the size and shape of a mandible. The lower jaw in birds is longer and weaker than the upper one and its shape and size are strongly related to food specialization of birds (Dzerzhinsky 1997). A ventral curvature of the beak in birds, especially those experiencing increased loads on the jaw apparatus, such as granivores, is associated with a decrease in the functional length of the mandible (Dzerzhinsky 1997; Nekrasov 1978). Taking this into account, we can expect a correlation between the shape and size of upper and lower jaws. Although more detailed research is desirable to clarify this issue.

Various factors discussed above that influence variation of skull shape in passerines are not exhaustive, as much of the variation in skull shape remains unexplained. With that, they clearly show that the adaptive landscape of the skull morphology is not determined by the impact of single selective force. As Rayner (1985) suggested a variety of environmental, mechanical, aerodynamic and physiological factors influence bird adaptation. In our case, the more diverse shapes of the skulls in passerines with small body mass are mainly a compromise between the influence of food specialization, brain development and the limiting influence of the relative size of the skull.

Although our study was performed on the small sample of species, increasing the sample is unlikely to affect the conclusions. Our conviction is based on the fact that we investigated species

1 with the range of body mass, which is close to the maximum among passerines (Ilichev et al. 1991).
2 On the other hand, our sample includes species with similar body mass, but completely different
3 food specialization, which allows us to take into account other factors unrelated to allometry that
4 affect skull shapes. However, increasing the number of species in separate dietary categories or
5 including other dietary categories can expand our understanding of patterns of skull shape within
6 highly specialized groups of birds. A more detailed study of skull shapes may also reveal other
7 features of skull morphology that are related to food specialization, which has been repeatedly
8 noted even among relatives with similar diets (Dzerzhinsky 1972; 1997; Nekrasov 1978; Herrel et
9 al. 2005). At the same time, the variability of body parts and the skull in particular in birds will
10 always be subordinated to the main adaptation of members of the class - ability to fly. In this regard,
11 it is necessary to take into account the integration and mutual influences of different parts within a
12 body and their compliance with biomechanical requirements imposed by flight.

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1 **Figure legends:**

2 **Figure 1.** Skull of *Garrulus glandarius* in lateral (a) and dorsal (b) views with labelled landmarks
3 and semilandmarks. Numbers of the landmarks correspond to those given in Table S2.

4

5 **Figure 2.** Maximum clade credibility tree of the studied birds. Symbols refer to different diets.

6

7 **Figure 3.** Ordinal principal components analysis (PCA) of shape of the lateral (a) and dorsal (b)
8 skull projections. Grey wireframe represents mean shape. Dietary categories are marked with
9 different types of points. Phylogenetic relationships of species are presented with connecting lines.

10

11 **Figure 4.** Outlines of the studied species by dietary categories. Mean shape in each category is
12 colored in black. Landmarks and semilandmarks are omitted.

13

14 **Figure 5.** Shape allometry estimated with the multivariate regression of the lateral (a) and dorsal (b)
15 projections of the skulls on $\log_{10}$ -length of skull. Grey wireframe represents mean shape. Each point
16 type corresponds with the dietary category. Correlated with the size shapes are given at
17 corresponding ends of the Regression Score Axis. Phylogenetic relationships of species are
18 presented with connecting lines.

19

20 **Figure 6.** Regression of the skull shape on relative skull length, lateral (a) and dorsal (b)
21 projections. Grey wireframe represents mean shape. Each point type corresponds with the dietary
22 category. Correlated with the size shapes are given at corresponding ends of the Regression Score
23 Axis. Phylogenetic relationships of species are presented with connecting lines.

24

25 **Figure 7.** Integration between shapes of lateral (a) and dorsal (b) projections of the beak and
26 cranium estimated with the phylogenetic PLS analysis. Grey wireframe represents mean shape.

- 1 Each point type corresponds with the dietary category. Phylogenetic relationships of species are
- 2 presented with connecting lines.
- 3

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Supplementary material:

Table S1. A list of skeletal specimens, along with information about catalogue number, dietary groups, and measurements of body mass and skull.

Table S2. Definitions of the landmarks and semilandmarks used on the skull.

Table S3. Scores of the PCA (PC1, PC2) and PLS (PLS1 Axis) analyses.

Figure S1. Scatterplot and shapes of the 2nd and 3rd principal components of the lateral projection. Grey wireframe represents the mean shape. Scatterplot of the species values is colored by dietary categories. Correlated with the axis shapes are given at corresponding ends of the axes.

Figure S2. Scatterplot and shapes of the 2nd and 3rd principal components of the dorsal projection. Grey wireframe represents the mean shape. Scatterplot of the species values is colored by dietary categories. Correlated with the axis shapes are given at corresponding ends of the axes.

Table 1. Basic statistic estimates of body mass (m) and skulls traits (skull length (Lsk) and relative skull length ($Lsk/m^{1/3}$)) in birds of different dietary category

Dietary category	Statistical parameter	m (g)	Lsk (mm)	$Lsk/m^{1/3}$
omnivorous ($n=9$)	Min	67.8	46.2	10.1
	Max	570.0	92.8	12.1
	Mean	207.8	59.9	10.8
	SD	180.3	17.2	0.6
	CV (%)	86.8	28.8	6.0
granivorous ($n=11$)	Min	13.0	22.1	7.9
	Max	42.2	32.2	12.1
	Mean	25.2	27.2	9.4
	SD	7.8	3.0	1.2
	CV (%)	31.2	10.9	12.4
insectivorous ($n=24$)	Min	8.3	26.0	10.5
	Max	79.0	58.0	14.7
	Mean	25.4	34.6	12.4
	SD	17.7	7.1	1.1
	CV (%)	69.8	20.4	9.1
insectivorous/granivorous ($n=5$)	Min	11.5	25.0	9.8
	Max	43.5	35.2	11.6
	Mean	24.6	29.7	10.6
	SD	14.7	4.8	0.7
	CV (%)	60.0	16.1	6.2
Total CV (%)		169.7	39.6	13.8

n , number of species; SD , standard deviation; CV , coefficient of variation.

Table 2. Results of PGLS analyses of shape regression on diet, skull length and relative skull length as covariates.

Model	view	diet		$\log_{10}Lsk$		$\log_{10}(Lsk/m^{1/3})$	
		$R^2, \%$	p	$R^2, \%$	p	$R^2, \%$	p
coords ~ diet	lateral	16.5	0.005	-	-	-	-
	dorsal	18.9	0.008	-	-	-	-
coords ~ $\log_{10}Lsk$	lateral	-	-	16.0	0.001	-	-
	dorsal	-	-	21.9	0.001	-	-
coords ~ $\log_{10}(Lsk/m^{1/3})$	lateral	-	-	-	-	14.4	0.001
	dorsal	-	-	-	-	22.5	0.001
coords ~ diet + $\log_{10}Lsk$	lateral	13.9	0.004	13.5	0.001	-	-
	dorsal	15.4	0.003	18.4	0.001	-	-
coords ~ diet + $\log_{10}(Lsk/m^{1/3})$	lateral	11.5	0.026	-	-	9.4	0.001
	dorsal	11.4	0.029	-	-	15.0	0.001
coords ~ diet + $\log_{10}Lsk$ + $\log_{10}(Lsk/m^{1/3})$	lateral	9.5	0.048	9.0	0.001	5.0	0.003
	dorsal	8.4	0.053	11.0	0.001	7.6	0.001

Table 3. Pairwise comparison of lateral projections of skull by diet (coords ~ diet). Lower triangle - p -values, upper triangle – factorial R^2

Dietary category	granivorous	insectivorous	insectivorous/ granivorous	omnivorous
granivorous	-	13.2	5.4	11
insectivorous	0.003	-	10.3	3
insectivorous/granivorous	0.512	0.006	-	14.6
omnivorous	0.083	0.445	0.047	-

Table 4. Pairwise comparison of dorsal projections of skull by diet (coords ~ diet). Lower triangle - *p*-values, upper triangle – factorial *R*²

Dietary category	granivorous	insectivorous	insectivorous/ granivorous	omnivorous
granivorous	-	17.7	9.2	10.3
insectivorous	0.003	-	13.4	3.8
insectivorous/granivorous	0.222	0.007	-	15.4
omnivorous	0.131	0.284	0.068	-

Table 5. Pairwise phylogenetic analysis of variance of absolute (Lsk) and relative skull size ($Lsk/m^{1/3}$) between dietary categories. Lower triangle – p -values of Lsk , upper triangle – p -values of $Lsk/m^{1/3}$. Values that remain significant after FDR-correction are in bold.

Dietary category	granivorous	insectivorous	insectivorous/ granivorous	omnivorous
granivorous	-	0.001	0.161	0.141
insectivorous	0.112	-	0.050	0.018
insectivorous/granivorous	0.643	0.333	-	0.906
omnivorous	0.001	0.001	0.001	-

Table 6. Minimal angles between coefficient vectors of phylogenetic regressions, principal component and integration analyses. All of the angles are significant, $p < 0.001$.

Lateral view	PC1	PLS1	coords ~ log ₁₀ <i>Lsk</i>
PLS1	29°		
coords ~ log ₁₀ <i>Lsk</i>	34°	61°	
coords ~ log ₁₀ (<i>Lsk</i> / <i>m</i> ^{1/3})	28°	57°	26°
Dorsal view	PC1	PLS1	coords ~ log ₁₀ <i>Lsk</i>
PLS1	9°		
coords ~ log ₁₀ <i>Lsk</i>	13°	64°	
coords ~ log ₁₀ (<i>Lsk</i> / <i>m</i> ^{1/3})	10°	59°	18°

Figure 1. Skull of *Garrulus glandarius* in lateral (a) and dorsal (b) views with labelled landmarks and semilandmarks. Numbers of the landmarks correspond to those given in Table S2.

Figure 2. Maximum clade credibility tree of the studied birds. Symbols refer to different diets.

177x228mm (600 x 600 DPI)

Figure 3. Ordinal principal components analysis (PCA) of shape of the lateral (a) and dorsal (b) skull projections. Grey wireframe represents mean shape. Dietary categories are marked with different types of points. Phylogenetic relationships of species are presented with connecting lines.

182x237mm (300 x 300 DPI)

Figure 4. Outlines of the studied species by dietary categories. Mean shape in each category is colored in black. Landmarks and semilandmarks are omitted.

177x203mm (600 x 600 DPI)

Figure 5. Shape allometry estimated with the multivariate regression of the lateral (a) and dorsal (b) projections of the skulls on log₁₀-length of skull. Grey wireframe represents mean shape. Each point type corresponds with the dietary category. Correlated with the size shapes are given at corresponding ends of the Regression Score Axis. Phylogenetic relationships of species are presented with connecting lines.

182x237mm (300 x 300 DPI)

Figure 6. Regression of the skull shape on relative skull length, lateral (a) and dorsal (b) projections. Grey wireframe represents mean shape. Each point type corresponds with the dietary category. Correlated with the size shapes are given at corresponding ends of the Regression Score Axis. Phylogenetic relationships of species are presented with connecting lines.

182x237mm (300 x 300 DPI)

Figure 7. Integration between shapes of lateral (a) and dorsal (b) projections of the beak and cranium estimated with the phylogenetic PLS analysis. Grey wireframe represents mean shape. Each point type corresponds with the dietary category. Phylogenetic relationships of species are presented with connecting lines.

182x237mm (300 x 300 DPI)