Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Carrion converging: Skull shape predicts feeding ecology in vultures

K. R. Steinfield[1,2], R. N. Felice[1], M. E. Kirchner[3] & A. Knapp[1,2]

[1]University College, London, UK
[2]The Natural History Museum, London, UK
[3]University of California Berkeley, Berkeley, CA, USA

Keywords
convergent evolution; geometric morphometrics; phenotypic evolution; vultures; feeding ecology; skull shape; ecomorphology.

Correspondence
Andrew Knapp, The Natural History Museum, Cromwell Road, London, UK.
Email: a.knapp@nhm.ac.uk

Editor: Andrew Kitchener
Associate Editor: Lorinda Hart

Received 19 May 2023; revised 15 September 2023; accepted 25 October 2023

doi:10.1111/jzo.13127

Abstract

The link between skull shape and dietary ecology in birds at macroevolutionary scales has recently been called into question by analyses of 3D shape that reveal that cranial anatomy is mainly influenced by other factors such as allometry. It is still unknown whether this form-function disconnect also exists at smaller evolutionary scales, for example within specialized ecological guilds. Vultures are a diverse guild of 23 extant species in two families (Accipitridae and Cathartidae) that exhibit evolutionary convergence as a result of highly specialized feeding ecology. Vultures are the only known obligate scavengers among vertebrates and are usually grouped together under this single dietary category, but within this specialized diet there are three distinct, species-specific feeding strategies termed ripper, gulper, and scrapper. We use three-dimensional geometric morphometrics to quantify the relative contributions of feeding ecology, allometry, and phylogeny on vulture skull shape, along with several non-vulture raptors of similar size, range and ecology. Families show clear separation in shape, but phylogenetic signal is comparatively weak (K_{mult} = 0.33). Taking into account the influence of phylogeny, skull shape is not significantly correlated with either skull size or feeding type, but there are examples of strong, significant convergence and parallel shape evolution across feeding groups. Furthermore, skull shape performs strongly in predicting feeding ecology in a phylogenetic discriminant function analysis. These findings highlight the importance of detailed assessment of feeding behavior in studies of ecomorphology, rather than broader dietary categories alone, and reveal that ecology can be readily inferred from form given appropriate information.

Introduction

The avian skull has long been an exemplar of adaptive evolution due to the incredible phenotypic diversity in extant birds, bringing to mind the most classic examples such as Darwin's finches or Hawaiian Honeycreepers (Cooney et al., 2017; Felice et al., 2019; Gibbs & Grant, 1987; Grant & Grant, 2006; Jønsson et al., 2012; Lack, 1953; Lovette et al., 2002; Olsen, 2017; Pigot et al., 2016; Smith et al., 1995). Attempts to quantify this classic association between form and function through three-dimensional geometric morphometrics have demonstrated that diet insufficiently explains the majority of shape variation, with factors such as allometry or phylogeny contributing significantly more (Bright et al., 2016, 2019; Felice et al., 2019; Navalón et al., 2019). Within more restricted taxonomic groups, geometric morphometric analyses have found that diet has low explanatory power (Bright et al., 2019), whereas allometry often has the strongest effect on shape variation (Bright et al., 2016). Similar results have been found in broad taxonomic studies, with as little as 12% of variation in beak shape associated with diet (Navalón et al., 2019).

In light of these contradictory findings, it has been suggested that traditional dietary categories are too broad to capture the diversity of function in bird skulls (Felice et al., 2019; Navalón et al., 2019; Pigot et al., 2016). In a study mapping avian morphology to associated trophic niche across the breadth of extant bird diversity, a minimum of any four morphological trait measurements were required to parse out phylogenetic noise or convergence of form (Pigot et al., 2020). Likewise, a study successfully linking skull shape with foraging ecology in Charadriiformes (shorebirds, gulls, and auks) found that after collapsing the number of foraging guilds from 36 to 10, the explanatory power of foraging ecology decreased by nearly 50% (Natale & Slater, 2022). Together, these results

suggest the need for more descriptive categorization linking feeding ecology and form.

Vultures are a paraphyletic functional guild formed from members of two avian families; Afro-Eurasian vultures (Accipitridae), and American vultures (Cathartidae; Jarvis et al., 2014). Obligate scavenging in vertebrates is only found in vultures, and it has evolved independently in these two families. Convergent evolution appears to have favored a number of highly specialized traits adapted to foraging for carrion. These birds share exceptionally keen eyesight, specialized digestive tracts, and soaring flight, allowing them to easily locate and rapidly consume detritus material (Houston, 1975; Kane & Kendall, 2017; Ogada et al., 2012; Potier, 2020; Ruxton & Houston, 2004). Given the apparent convergence of such attributes between families in this specialized ecological guild, a strong link between skull morphology and dietary preference might also be expected due to the importance of the skull in feeding. Vultures thus represent an interesting model for investigating the degree to which ecological and evolutionary factors contribute to variation in skull shape.

Across the 23 extant species, vultures exhibit phylogenetic (Jarvis et al., 2014), ecological (Linde-Medina et al., 2021; van Overveld et al., 2020), and morphological diversity (Böhmer et al., 2020; Hertel, 1994; Holmes et al., 2022). Distinctions in sociality (Kendall, 2013; van Overveld et al., 2020), breeding and nesting behavior (Kemp & Kemp, 1975; Kendall, 2013; Krüger et al., 2015; Mundy et al., 1992), migratory and movement patterns (Alarcón & Lambertucci, 2018), habitat preferences (del Hoyo et al., 1992; Kendall, 2014), sensory perception (Jackson et al., 2020; Ogada et al., 2012; Portugal et al., 2017; Spiegel et al., 2013), and feeding and foraging strategies (Houston, 1987; Jackson et al., 2020; Kruuk, 1967; Ogada et al., 2012; van Overveld et al., 2022) have been recorded. For example, *Gypohierax angolensis* and *Gypaetus barbatus* both display unique dietary preferences, with the former primarily a herbivore (Lambertucci et al., 2021) and the latter a bone specialist (Cramp, 1980). Intense competition for spatially and temporally unpredictable food has likely driven many of these differences (Böhmer et al., 2020; Hertel, 1994; Holland et al., 2019). Diversity among vultures is a strong base for testing competing hypotheses for underlying drivers of avian cranial morphology.

Previous behavioral research has provided evidence that vultures fall into three distinct ecotypes based on mode of feeding and dietary preference: ripper, gulper, and scrapper (Hertel, 1994; Houston, 1987; König, 1974, 1983; Kruuk, 1967; Table 1). Additionally, there is evidence that these ecotypes are reflected in the anatomy of the skull (Hertel, 1994), neck (Böhmer et al., 2020) and hindlimbs (Linde-Medina et al., 2021). Morphometric analyses investigating the effects of diet on raptor cranial morphology have consistently placed vultures outside other groups, even in the absence of other dietary trends and to the point of occupying an almost entirely isolated region of morphospace (Bright et al., 2016; Guangdi et al., 2015; Hertel, 1995; Pecsics et al., 2019; Sun et al., 2018). These studies typically classify vultures as 'scavengers', preventing distinctions being made on the basis of different feeding strategies. Few studies have investigated cranial shape variation across vulture feeding types specifically (Hertel, 1994; Linde-Medina et al., 2021), and those that have relied on traditional methods of linear measurements, which describe ratios but omit detailed shape information (Goswami et al., 2019). Geometric morphometric methods allow the accurate quantification of shape, outperforming traditional methods in both accuracy and detail (Adams et al., 2013; Breno et al., 2011; Maderbacher et al., 2008; Mendonca et al., 2013; Parés-Casanova et al., 2020; Zelditch et al., 2004), and allowing for the visualization of shape variation (Breno et al., 2011; Parés-Casanova et al., 2020).

Here, we investigate the relative contributions of allometry, phylogeny, and vulture feeding type on variation in cranial shape using three-dimensional (3D) geometric morphometrics. We predict that vulture cranium shape is correlated with feeding ecology. We expect allometry to have a greater influence on cranial shape than feeding ecology, because there is evidence to suggest that cranium shape in raptors is highly correlated with size and is thought to allow for more effective niche partitioning (Bright et al., 2016). This is likely to be important for scavengers such as vultures because of the strong competition caused by their spatially and temporally scare food source (Hertel, 1994). Finally, because of convergence in feeding ecologies across family groups, we expect that the phylogenetic signal in cranial shape is low, and phenotypic convergence is high (Hertel, 1994; Jarvis et al., 2014; Linde-Medina et al., 2021). Additionally, we use our results to statistically infer the feeding ecology of two extinct taxa, a cathartid vulture (*Breagyps clarki*) and an accipitrid giant eagle (*Hieraaetus moorei*).

Materials and methods

We compiled a dataset of 22 of the 23 extant vulture species, one extinct vulture (*Breagyps clarki*), and eight non-vulture raptors, including the recently extinct *Hieraaetus moorei* (Table S1). Non-vulture raptors were selected on the basis of sharing similarities in body size, ecology (generalists and

Table 1 Vulture feeding classification system

Feeding type	Diet	Mode of feeding
Ripper	Tougher material, skin/hide, muscle, and tendons. Typically feed on the external areas of a carcass.	Strong tearing action away from the carcass.
Gulper	Soft tissue, and viscera. Typically feed on the internal material of a carcass.	Complete insertion of the head into the carcass for swallowing soft food.
Scrapper	Scraps of meat found around the carcass, often the leftover material of another feeding scavenger.	Pecking motion to pick up small scraps on the ground and around the carcass.

frequent scavengers), and geographic overlap in range (Blem, 1997; Cramp, 1980). The two extinct taxa were included because of their completeness and inclusion in previous vulture ecomorphological studies (*B. clarki*: Hertel, 1994; *H. moorei*: van Heteren et al., 2021). Three-dimensional meshes were created from a total of 31 specimens (one representative per species) with data obtained from MorphoSource (www.morphosource.org), Phenome 10K (www.phenome10k.org), Sketchfab (www.sketchfab.com), or scanned from museum collections (see Table S1 for details). Specimens were all adults, but the sex of the majority of specimens was not available. Sexual dimorphism has been documented in a some vultures (Lambertucci et al., 2012; Mabhikwa et al., 2017; Xirouchakis & Poulakakis, 2008), but dimorphic traits are either non-osseus material (i.e. caruncle, plumage), or due to differences in body size (Hirschauer et al., 2018; Mabhikwa et al., 2017; Xirouchakis & Poulakakis, 2008). In general, sexual dimorphism in vultures is low, however (Bildstein, 2022), and unlikely to approach levels of intraspecific variation in shape. Because it is missing from many museum specimens, all specimens were analyzed without the rhamphotheca, a layer of keratin that covers the beak. The rhamphotheca plays an important role in feeding because it comes into direct contact with food and extends beyond the tip of the underlying bone. Nonetheless its shape is strongly influenced by the underlying bone (Hieronymus & Witmer, 2010) and we do not expect its omission to significantly affect our results. We also omitted the mandible from our study, although it plays an important role in feeding. This was for consistency with previous studies using similar methods (Bright et al., 2016; Felice et al., 2019), and because the focus of our study is cranial morphology.

Meshes were processed with Geomagic Wrap 2017 (3D Systems Inc., Rock Hill, SC, USA) to remove non-biological scanning artifacts (i.e. spikes and self-intersections) and fill small holes using interpolation (Bardua et al., 2019). Each mesh was landmarked with 38 anatomical landmarks and 24 sliding semi-landmark curves in Stratovan Checkpoint (Stratovan Corporation, Davis, CA, USA), using a landmark layout adapted from Mitchell et al. (2021; Fig. 1; Tables S2 and S3) designed to capture whole-cranium shape, and taken from a previous study examining whole-cranium shape variation across all birds (Felice et al., 2019). Anatomical landmarks were placed bilaterally and semi-landmark curves were placed on the right side. Specimens damaged on the right side were mirrored in Geomagic Wrap before landmarking. Semi-landmark curves were slid to minimize bending energy, a method that adjusts the spacing of the semilandmarks to minimize the implication that there are shape changes due to differences in that spacing (Bardua et al., 2019; Gunz et al., 2005; Zelditch et al., 2004). This was performed with the 'slider3d' function in the *morpho* package in R (R Core Team, 2021; Schlager, 2017). Right-side landmarks were temporarily mirrored to the left side of the specimen during Procrustes alignment to avoid introducing error and to improve estimates of shape variation and allometry (Cardini, 2016). Mirroring was done with the 'mirrorfill' function from the *paleomorph* R package (Lucas & Goswami, 2017). Landmark data were then superimposed with a generalized Procrustes alignment (GPA) (Rohlf & Slice, 1990) to minimize differences in size, orientation, and location between landmark sets (Kendall, 1989) with the 'gpagen' function in *geomorph* (Adams et al., 2021; Baken et al., 2021). Analyses were repeated on separately aligned subsets of the data to account for the effects that including non-vultures and taxa of unknown ecological categories may have on the results (See Tables S4 and S5). Left side landmarks were removed after alignment, leaving a total of 359 landmarks per specimen. A principal component analysis (PCA) was performed on the Procrustes-aligned shape data to explore shape variation (Collyer & Adams, 2021).

We generated a time-scaled phylogeny from BirdTree.org (Jetz et al., 2012) based on Hackett et al. (2008; Hackett All Species: a set of 10 000 trees with 9993 OTUs each) for all birds of prey (Accipitridae, Pandionidae, Sagittariidae, Falconidae, Cathartidae, and Cariamidae). The resulting tree was pruned in Mesquite (Madison & Madison, 2021) to our dataset. The extinct *Hieraaetus moorei* was substituted in the place of its closest living relative, *Hieraaetus morphnoides* (Bunce et al., 2005). The extinct *Breagyps clarki* was added as a sister taxon to *Gymnogyps californianus* (Emslie, 1988), with the node placed midway along the branch subtending *G. californianus*. The resulting time-scaled tree was read into R using the *ape* package (Paradis & Schliep, 2019). We calculated phylogenetic signal (the degree of similarity explained by shared ancestry) using the K_{mult} statistic, implemented with the 'physignal' function in *geomorph* (Adams, 2014a). Allometric influence on skull shape was tested with raw shape data and phylogenetically corrected shape data respectively with the 'procD.lm' and 'procD.pgls' functions in *geomorph* (Adams, 2014b; Anderson, 2001).

Feeding type was assigned to each species following the classification scheme created by Hertel (1994; Table 1) and based on behavioral observations in the field (Gaengler & Clum, 2015; Hille et al., 2016; Houston, 1987; König, 1974, 1983; Kruuk, 1967; J. Burnett, pers. comms.) with the exception of *Gypohierax angolensis* and *Gypaetus barbatus*, which do not fit these categories (König, 1974; Linde-Medina et al., 2021). These two species along with all extinct and non-vulture raptors were not assigned a type (Fig. 2). A multivariate analysis of variance (MANOVA) was performed on the Procrustes-aligned shape data with feeding type as the independent grouping variable to determine if skull shape correlated with feeding groups. This was repeated for allometry-corrected shape values to identify a potentially significant interaction with size. Interactions between allometry and feeding type as well as phylogeny and feeding type were explored with the 'procD.lm' (for raw shape data) and 'procD.pgls' (for phylogenetically corrected shape data) functions in *geomorph* (Adams, 2014b; Anderson, 2001). Feeding types were plotted over principal component scores in the morphospace. To test the fit of the shape data with feeding categories, we implemented a discriminant function analysis (DFA) with the 'mvgls.dfa' function in the R package *mvMORPH* (Clavel et al., 2015). This method computes a discriminant analysis based on GLS estimates from a phylogenetic regression model and is optimized for high-dimensional data. The output shows both assignment accuracy of specimens of known feeding groups

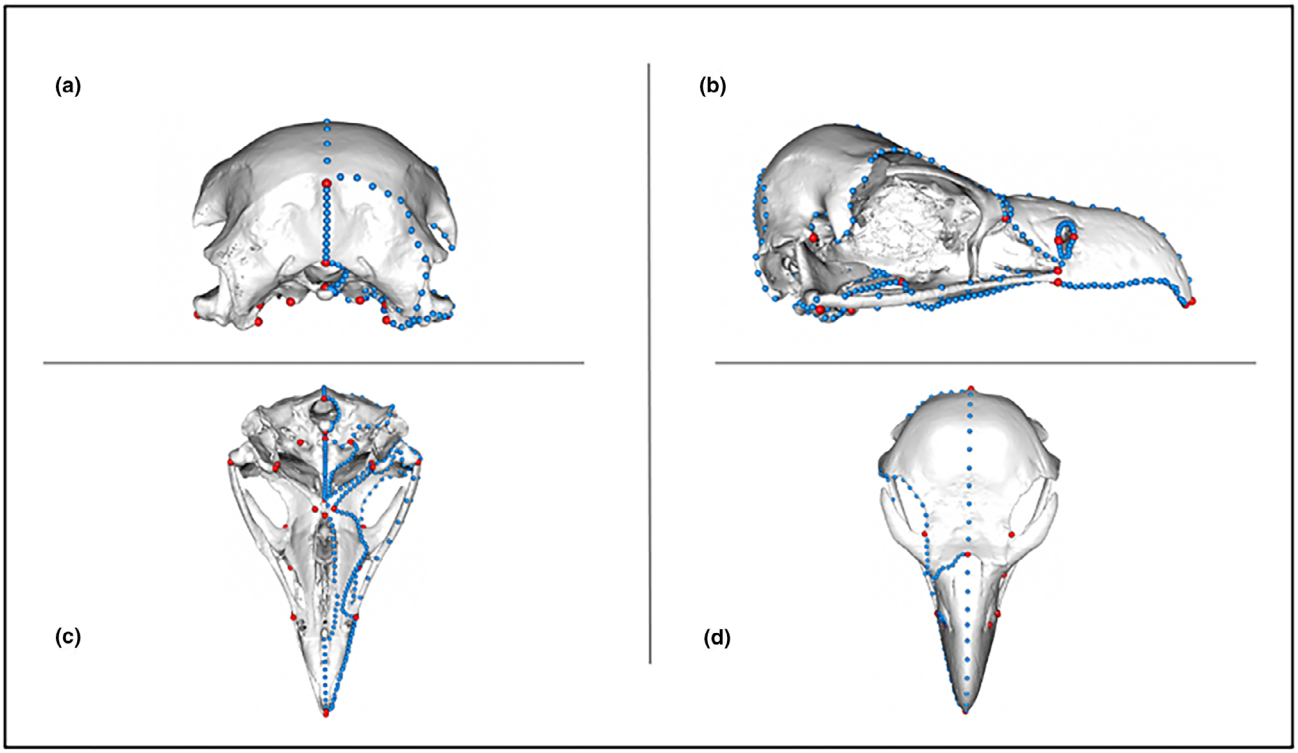

Figure 1 Configuration of the 38 anatomical landmarks (red) and 24 semi-landmark curves (blue) used in this study (shown on *Trigonoceps occipitalis*). Landmarks are shown in (a) posterior, (b) lateral, (c) ventral, and (d) dorsal views.

and predicts group assignment for specimens of unassigned group, including the two extant vulture species that did not fall into any of the three feeding categories (*G. angolensis* and *G. barbatus*), and the extinct vulture, *B. clarki*. Phenotypic convergence within feeding groups was quantified with the distance-based measure, *C*, developed by Stayton (2015), an approach which measures the average phenotypic convergence across a group within phylomorphospace. Results were compared with a set of 100 simulations under a BM null model of evolution to provide a significance value for each cluster, using the first 14 principal components, accounting for a cumulative 95% of total shape disparity to reduce dimensionality, and implemented with the 'convratsig' function in the R package *convevol* (v. 2.0.0, Stayton, 2015). This method has been shown to overestimate convergence in outlying taxa, and so we also applied the method developed by Grossnickle et al. (2023), *Ct*, which measures phenotypic distance at equivalent points on a time-scaled phylogeny. This was implemented in the R package *convevol* (Stayton, 2015), using the same parameters as the *C* measures calculated above.

Results

In the full dataset, the first 14 principal components (PCs) account for ~95% of total shape variation, with the first three PCs cumulatively accounting for ~65% of shape variation (Fig. S1). Shape change along PC1 (proportional variance: 35.8%) is characterized by a transition from a short to elongate beak and naris, tall to low cranium, and an increasingly laterally orientated orbit. Shape change along PC2 (proportional variance: 19.8%) is characterized by a transition from slender to robust beak, an increasingly angular craniofacial hinge, and a large, elongate oval naris to a thin, vertical naris opening. Accipitridae and Cathartidae separate out along PC2. Accipitrids are generally characterized by a comparatively taller and wider cranium, shorter and slimmer nares, a more angular craniofacial hinge, and robust beaks. Cathartids are characterized by a flatter skull, elongate and slender beaks, longer nares, and a distinctly anteriorly sloping cranium. The width of the frontal bone tends to be thinner in accipitrid species anterior to the postorbital process, at which point it expands more laterally than in cathartid taxa. Shape change along PC3 (proportional variance: 9.6%) occurs almost entirely in the beak by shifting towards a more robust and deeply hooked beak (Fig. 3). Phylogenetic signal in shape data was moderately low but statistically significant (K_{mult} = 0.325, P = 0.001, Table S4), suggesting a degree of convergence in shape within the dataset. Allometry accounts for 18.5% of total shape variation (R^2 = 0.185, Z = 3.631, P = 0.001; Table S5), but is not significant after accounting for phylogeny (R^2 = 0.05, Z = 1.463, P = 0.073; Table S5).

Feeding groups mapped over PCs 1 and 2 occupy distinct regions of morphospace, with no overlap along PC1 (Fig. 4 and Fig. S5). Feeding type is significantly correlated with skull

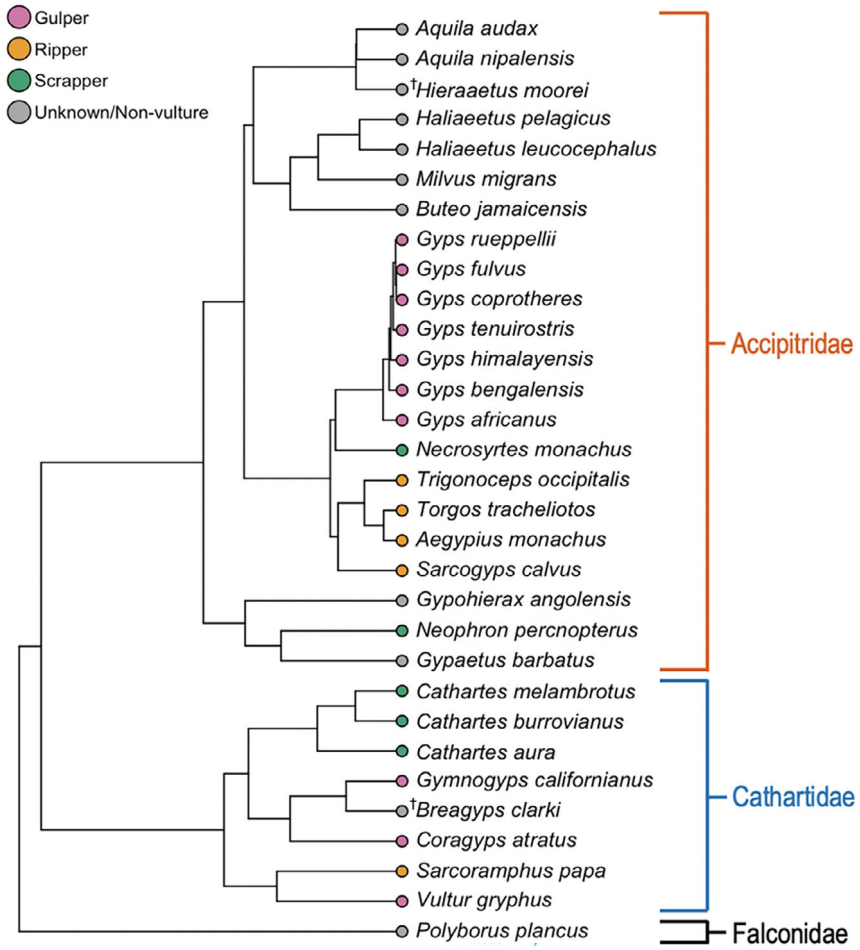

Figure 2 Phylogeny of the 31 species included in this study, adapted from BirdTree.org (www.birdtree.org) (Jetz et al., 2012) and based on Hackett et al. (2008). Taxa are colored according to feeding type. Extinct species are marked (e.g. †*Breagyps clarki*).

shape in non-phylogenetically corrected shape data (R^2 = 0.457, Z = 4.789, P = 0.001; Table S5), but this correlation disappears after correcting for phylogenetic relatedness (R^2 = 0.089, Z = 0.159, P = 0.436; Table S5). Mean phenotypic convergence is statistically significant within all feeding groups with the C measure of phenotypic convergence (Stayton, 2015; gulper C_1 = 0.39, P = <0.001; ripper C_1 = 0.33, P = <0.001; scrapper C_1 = 0.35, P = <0.001). Convergence is not significant across any group when implementing the Ct measure (Grossnickle et al., 2023; ripper, Ct_1 = −0.296, P = 0.47; gulper, Ct_1 = −0.978, P = 0.55; scrapper, Ct_1 = −0.105, P = 0.05). When examining putatively converging taxa rather than all taxa within feeding groups, however, convergence was significant and high for gulper (*Vultur gryphus*, *Gymnogyps californianus*, *Gyps tenuirostris*; Ct_1 = 0.63, P = 0.00, Fig. S2) and scrapper (*Necrosyrtes monachus*, *Neophron percnopterus*, *Cathartes melambratus*; Ct_1 = 0.45, P = 0.00, Fig. S3) taxa, but not for ripper taxa (*Sarcoramphus papa*, *Torgos tracheliotos*; Ct_1 = −0.004, P = 0.38, Fig. S4).

The DFA assigned 100% of specimens of known feeding ecology to the correct group, with a P-value of <<0.001 for each species. The two unassigned extant species (*Gypohierax angolensis* and *Gypaetus barbatus*) were assigned to the scrapper group, each with a P-value of <<0.001 (Table S6). The extinct *Breagyps clarki* was assigned to the gulper group with a P-value of <<0.001. Upon including a non-vulture raptors as a feeding group category, the predicted group assignment for *G. barbatus* changed from scrapper to non-vulture raptor with a P-value of <<0.001 (Table S7).

Discussion

Vulture skull shape is influenced by the interplay of a variety of factors, mainly phylogeny, feeding strategy, and allometry. The distinct shape of vulture skulls compared to non-vulture raptors, coupled with examples of convergence in shape between vultures from both families, suggest that the unique feeding ecologies of vultures are considerable drivers of

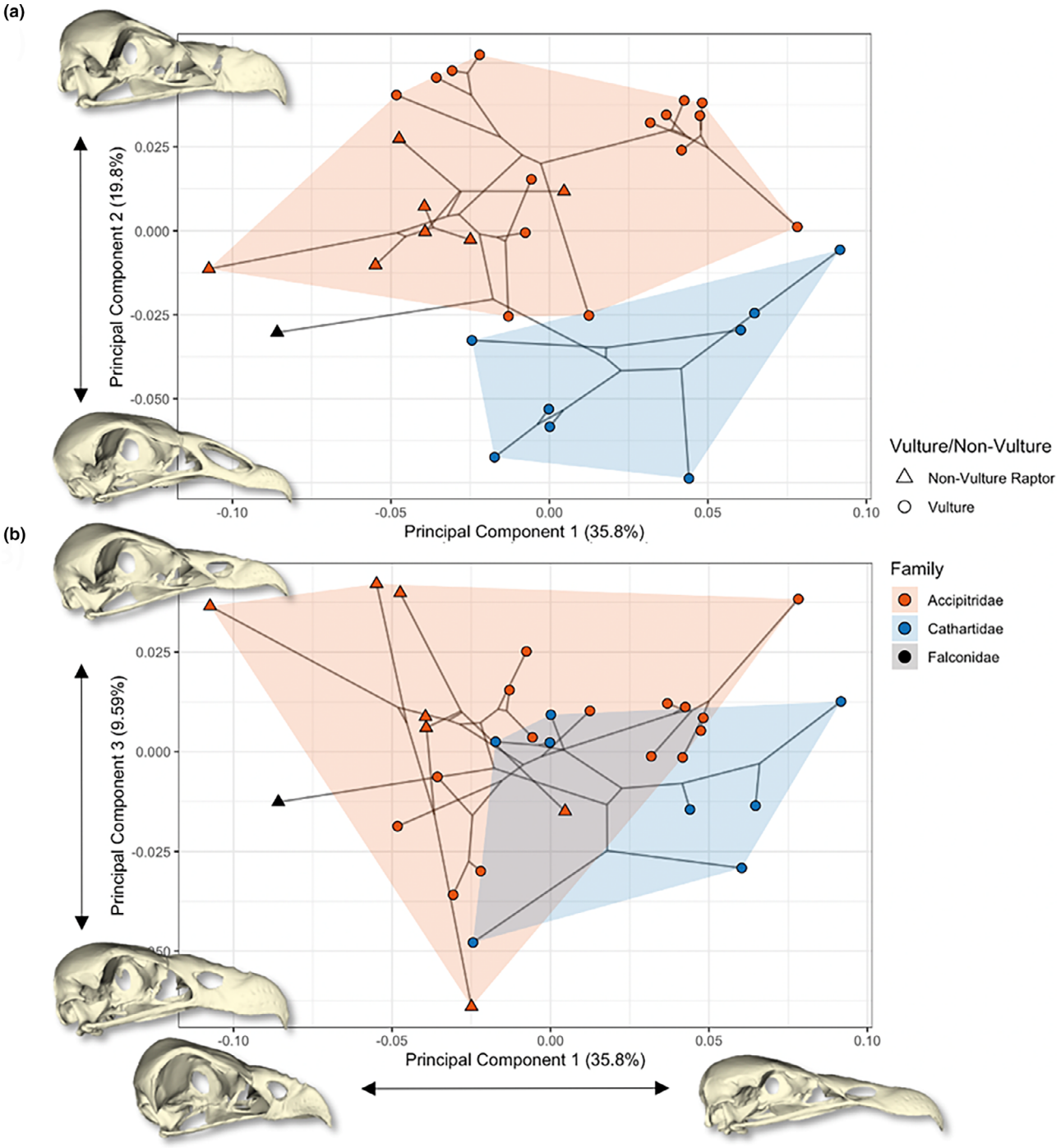

Figure 3 Phylomorphospace showing avian families overlaying the species in this study with transformation along PC1 on the *x* axis and transformations along PC2 (a) and PC3 (b) on the *y* axes. Warped meshes show positive and negative shape values along each axis.

vulture skull evolution, and highlight the evolutionary constraints of ecologically specialized taxa (Bennett & Owens, 1997). Although vulture skull shape is not significantly correlated with feeding ecology after accounting for phylogeny, feeding groups occupy distinct regions of morphospace (Fig. 4), suggesting that adaptation to different feeding ecologies has driven divergence in skull shape within Accipitridae and Cathartidae. This is supported by examples of phenotypic convergence and parallel evolution between these families, and skull shape consequently performs very well in predicting

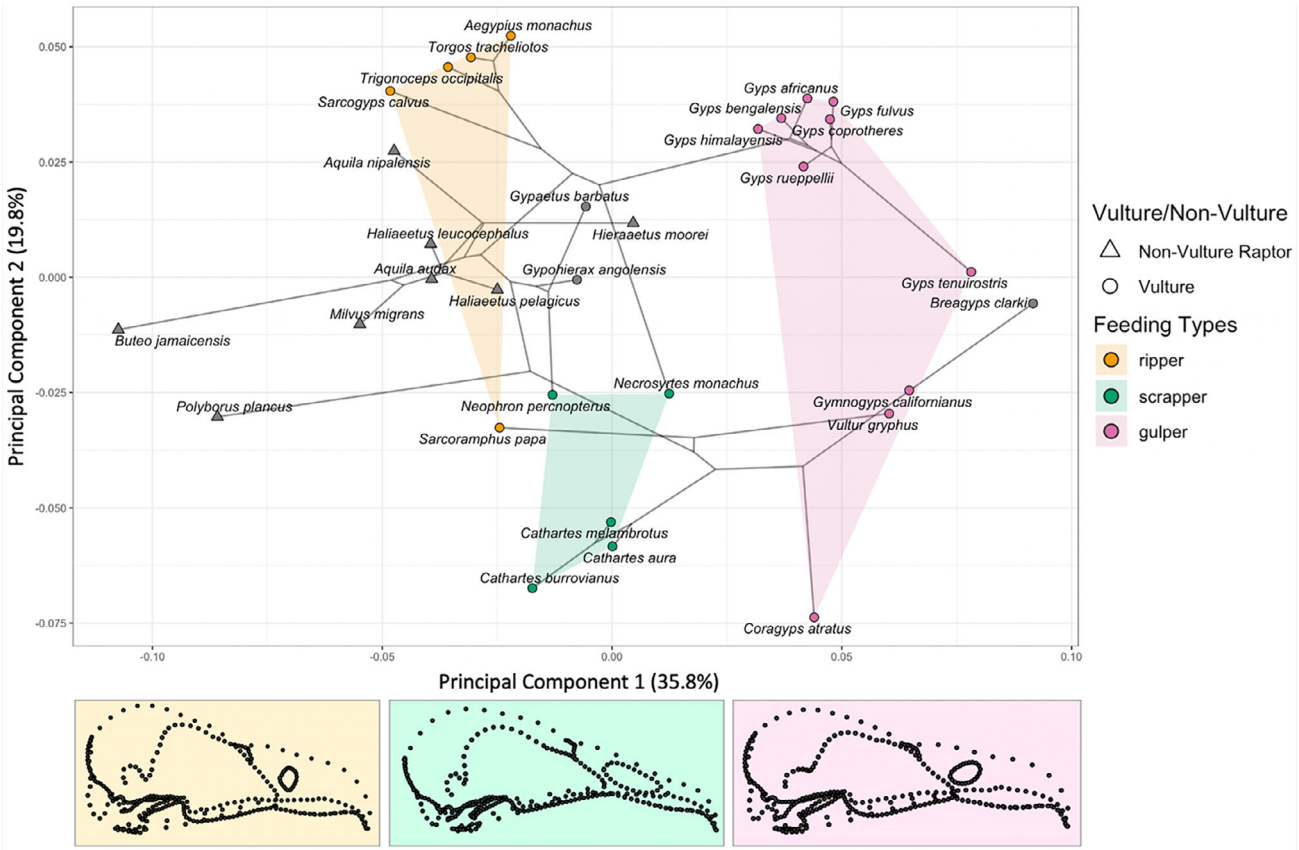

Figure 4 Phylomorphospace of PCs 1 and 2 with vulture feeding types grouped by color and non-vultures and extinct *Breagyps clarki* shown in gray. The color-coded mean shape for each feeding type is shown below the figure, calculated from full-dataset shape data.

feeding ecology. These results reinforce popular hypotheses that the evolution of bird skulls is driven by dietary needs (Gibbs & Grant, 1987; Jønsson et al., 2012; Lack, 1953; Lovette et al., 2002), as well as support recent evidence in the literature that incorporating finer detail within a smaller phylogenetic context could provide more information on the relationship between form and function (Felice et al., 2019; Natale & Slater, 2022; Navalón et al., 2019; Olsen, 2017; Pigot et al., 2016, 2020).

Skull shape variation across the data set yielded a significant, albeit moderately low, phylogenetic signal (K_{mult} = 0.325), revealing that shape is phylogenetically structured, but that phenotypic convergence and parallel evolution play an important role in vulture skull evolution. The separation of Accipitridae and Cathartidae along PC2 reveals the distinct morphologies of each family. Most notably, accipitrid skulls tend to be tall and robust whereas cathartid skulls are low and slender. The description 'low and slender' is commonly used to differentiate all vultures, accipitrids included, from non-scavenging raptors (Guangdi et al., 2015; Hertel, 1994; Pecsics et al., 2019), underscoring the importance of describing feeding ecology in finer detail. Some distinguishing features of the accipitrid skull could offer advantages in the predominantly open, grassland habitats of these vultures (Holmes et al., 2022). Accipitrid vultures tend to soar at higher altitudes and consume larger carcasses than cathartids (Houston, 1984; Mundy et al., 1992), relying primarily on vision to locate both conspecifics and carcasses (Dermody et al., 2011; Potier, 2020). The comparatively larger orbits of accipitrid skulls may indicate greater visual acuity (Hertel, 1995; Ogada et al., 2012; Potier, 2020). Another distinction of the accipitrid skull is a smaller naris, a feature particularly striking in *Gyps* species whose nostrils are partly covered by a bony sheath, leaving a thin vertical opening. No explanation for these sheaths exists in the literature, though protection from dust in semi-arid habitats, viscera when feeding, or wind at high altitudes are all possible explanations. Conversely, visual abilities may be of limited use to American vultures in their often densely forested habitats, thus a reliance on olfaction to locate food in some species may have driven the large, open nares of American vultures (Houston, 1984; Ogada et al., 2012).

In raw shape data, feeding group explained the highest proportion (~45%) of shape disparity, seemingly providing strong evidence that the evolution of skull shape in vultures is driven by feeding behavior. As hypothesized by Hertel (1994), vultures fall into three distinct regions of morphospace based on feeding strategy, with no overlap along PC1 (Fig. 4). When phylogenetic relatedness is accounted for, however, feeding

type is not significantly correlated with shape ($P = 0.436$). This is probably due to clusters of closely related species that share feeding ecologies (e.g. *Gyps*, seven species which are all gulpers) overwhelming the convergence signal of smaller numbers of more distantly related taxa. Nonetheless, there are clear examples of ecological (Fig. 2) and phenotypic convergence (Fig. 4) in the dataset. Notably, *Neophron percnopterus* and *Necrosyrtes monachus*, two accipitrids, converge on Cathartidae taxa along PC2 in the 'scrapper' region of morphospace. For both species, the most closely related taxa do not share the same feeding ecology. Similarly, *Sarcoramphus papa* and *Vultur gryphus* fall into 'ripper' and 'gulper' space respectively, demonstrating strong morphological divergence in these sister taxa along PC1. Using the *C* measure of Stayton (2015), within-group phenotypic convergence was found to be significant, and relatively consistent within all feeding groups, with an average of 39% convergence in gulpers, 33% in rippers and 35% in scrappers. This is contradicted by the results of the *Ct* measure of phenotypic convergence of Grossnickle et al. (2023), with no groups showing significant convergence overall. Examples of significantly converging taxa, however, can be found by focusing on smaller numbers of taxa that appear to show convergence within morphospace, rather than across whole groups. The most conspicuous example of convergence found with this method occurs between *Vultur gryphus*, *Gymnogyps californianus*, and *Gyps tenuirostris* which, despite large phylogenetic distance, have converged on the same region of morphospace ($Ct_1 = 0.63$, $P = 0.00$; Fig. 4). The ripper feeding group did not show any significant convergence with the *Ct* method, despite being clearly separated from other feeding groups along PC1. This is likely to be a combination of the majority of taxa in this group being closely related accipitrids and thus more divergent, with only one more distantly related cathartid species in this group, *S. papa*, 'converging' on this region of morphospace. The *C* method tends to overestimate convergence because it measures phenotypic distance across the entire group, and groups which lie at extremes of the morphospace (e.g. in examples of directional or divergent selection) may accumulate phenotypic distance that contributes to this score (Grossnickle et al., 2023). The *Ct* method only measures phenotypic distance at equivalent timesteps on a time-scaled phylogeny, and so examples of parallel evolution, which can superficially resemble convergent evolution in some circumstances, are not identified as convergent with this method. This contrasts with the *C* measure, which often cannot differentiate between convergent and parallel evolution (Grossnickle et al., 2023). Nonetheless, the apparent parallel evolution along PC1 of *S. papa* with the ripper taxa in Accipitridae is notable in that the evolution of this feeding type coincides with a marked negative shift along PC1. Our results indicate that combining the two methods of convergence analysis, *C* and *Ct*, may be useful in differentiating parallel evolution from convergence, and may highlight directional selection by accumulating phenotypic distance in its calculation.

The mean shapes generated from these groups (Fig. 4) reflect what might be expected by each vulture feeding type. 'Rippers' have a wider cranium (possibly to accommodate larger jaw and neck muscles) and more robust beak for tearing tougher tissue from carcasses. 'Gulpers' have the narrowest skull with the relatively longest beak, supporting ease of maneuverability inside a carcass. 'Scrappers' have the slenderest beak, reflecting the precision necessary for picking up small scraps around the carcass, as also determined by Hertel (1994). In most other respects, and in accordance with Linde-Medina et al. (2021), the 'scrapper' shape is intermediate to the other types, reflecting the less specialized strategies of scrapper species (Ballejo et al., 2018).

Although large bodies allow vultures to maximize food consumption at spatially and temporally unpredictable food sources, the mechanism selecting for and constraining this ability is soaring flight (Poessel et al., 2018; Ruxton & Houston, 2004), rather than feeding behavior. This likely explains the lack of correlation between skull size and shape among vultures. Thus, body size in vultures probably evolved in response to selective pressures acting on searching or foraging efficiency such as flight conditions (Houston, 1987; Ruxton & Houston, 2004), habitat (Xirouchakis & Mylonas, 2004), species interactions (Jackson et al., 2020; van Overveld et al., 2020, 2022), and physiological capacity (Ruxton & Houston, 2004). Future morphometric research investigating the relationship between vulture feeding types and other ecological traits, particularly species interactions, is recommended.

A handful of species included in the study either do not have sufficient behavioral observations to support a vulture feeding type assignment or have been contested in the literature. *Coragyps atratus*, originally identified as a gulper based on behavioral observations (Houston, 1987), has been predicted by morphological research as both a scrapper (Hertel, 1994) and a gulper (Linde-Medina et al., 2021). The overlap with gulpers along PC1 and 'scrappers' along PC2 highlights the limitations of studies based on morphology alone, and the importance of supplementing morphometric data with behavioral observations. Based on morphology alone, *Gypaetus barbatus* has previously been classified as a gulper (Hertel, 1994) and ripper (Linde-Medina et al., 2021), and *Gypohierax angolensis* has been proposed as both a gulper (Hertel, 1994) and scrapper (Linde-Medina et al., 2021). Using a discriminant function analysis to predict unknowns, as both Hertel (1994) and Linde-Medina et al. (2021) did, our study classified both species as scrappers (Table S6). When including non-vulture raptors in the model, however, *G. barbatus* was reassigned as a raptor (i.e. non-specialized; Table S7). These discrepancies further highlight the limitations of morphology-based predictions and the risks of overriding observed behavior. The intermediate positions of these species in morphospace as well as their proximity to non-vulture raptors, suggest that these two species have not undergone such extreme morphological evolution as other, more specialized vultures. In addition, although the gulper assignment of *Gyps tenuirostris* is supported by field observations (Hille et al., 2016), this is the first morphometric study on vulture feeding types to include this taxon and confirm morphological similarities with other gulpers, including the distantly related cathartids *Vultur gryphus* and *Gymnogyps californianus* (Fig. 4). Finally, it is possible to extrapolate feeding assignments to extinct species using discriminant analyses, though results should be interpreted with caution given the inability to obtain observational feeding data. The results of our DFA matched those of Hertel (1994), predicting *Breagyps clarki* a

gulper regardless of the inclusion of a raptor category (Tables S6, S7, S8 and S9). The extinct *Hieraetus moorei* has been the subject of debate regarding its feeding ecology and was recently proposed a gulper on account of its morphological similarity to *V. gryphus* (van Heteren et al., 2021). In contradiction with the obligate scavenger hypothesis, our study finds no morphological evidence to support a vulture feeding type assignment for this species, and based on hindlimb morphology was almost certainly a raptor (van Heteren et al., 2021). Our DFA predicted this species to be a scrapper, but was assigned as a raptor when non-vulture raptors were included (Tables S6, S7, S8 and S9). A better understanding of non-vulture raptor feeding ecology will improve feeding classification and prediction within this group (see Hertel, 1995).

The ability to predict function from form has been a contentious topic in bird skull morphometrics (Natale & Slater, 2022; Navalón et al., 2019), and to do so using a single functional trait has had mixed results (Ballentine et al., 2013; Pigot et al., 2020). The combined dietary and biomechanical information encoded in vulture feeding types is one possible explanation for drawing a successful link between feeding ecology and skull shape. Providing more detail of ecological context has been shown to improve predictive power in morphometric studies (Friedman et al., 2019; Navalón et al., 2019; Pigot et al., 2016) although the task of handling one-to-many or many-to-one ecomorphological relationships remains a challenge (Friedman et al., 2019; Navalón et al., 2019; Pigot et al., 2016). The focus on a single functional guild improved the detail and accuracy of functional traits, supporting the idea that taxonomic categories are possibly too broad to provide meaningful results in such an ecologically and phenotypically diverse class (Felice et al., 2019; Pigot et al., 2020). 'Scavenger' is a broad term applicable to many opportunist and carnivorous species (DeVault et al., 2003), and inclusion under this umbrella term has the potential to group together specialized (ecologically constrained) and generalist (ecologically flexible) taxa.

Conclusion

The use of geometric morphometrics to investigate the evolution and diversification of the avian cranium has yielded new and unexpected discoveries into the various factors contributing to shape variation, while casting doubt on traditional associations between beak shape and ecological niche (Bright et al., 2016, 2019; Felice et al., 2019; Navalón et al., 2019; Tattersall et al., 2017). The avian beak is a multifunctional apparatus, however, and a complex variety of selective pressures influence the tempo, direction, and mode of avian skull morphology, both developmentally and ecologically (Felice et al., 2019). Other factors such as mandible, neck and hindlimb morphology, and jaw and neck musculature, are also likely to be informative (Linde-Medina et al., 2021), but our study has provided robust results using the cranium alone. Broadly applying hypotheses across Aves is likely to provide equally complex results. The ability to link feeding ecology, rather than broader dietary categories to skull shape in the present study is a potentially fruitful avenue of research. Future research testing further competing hypotheses on vulture skull shape variation in relation to cross-species interactions and functional traits is recommended, as this could offer additional insights into the evolution of obligate scavenging. The results of this study also have important implications for the conservation of this rapidly declining guild (Ogada et al., 2012) as vulture conservation initiatives often involve the use of artificially provided food sources such as supplementary feeding sites (Margalida et al., 2010). Furthermore, future research on internal skull morphology could highlight key differences in sensory perception, both at the species level and between feeding types, which would allow for more reliable predictions for human-induced change (Martin et al., 2012).

Acknowledgements

The authors thank Joe Burnett (Ventana Wildlife Society), Daniel Field (University of Cambridge), Ryan Marek (University College London), Paul Scofield (University of Canterbury), and Oliver Kippax-Chui and Judith White (Natural History Museum) for help with data collection. The authors thank the Goswami Lab at the Natural History Museum in London for useful discussions and help with processing and analyzing data.

Conflict of interest

The authors declare no conflict of interest.

Author contributions

KRS and AK conceived the study; All authors contributed to data collection, performed the analyses, and wrote the manuscript.

References

Adams, D. C. (2014a). A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Systematic Biology*, **63**(5), 685–697. https://doi.org/10.1093/sysbio/syu030

Adams, D. C. (2014b). A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution*, **68**(9), 2675–2688. https://doi.org/10.1111/evo.12463

Adams, D. C., Collyer, M. L., Kaliontzopoulou, A., & Balken, E. K. (2021). *Geomorph: Software for geometric morphometric analyses*. R package version 4.0. https://cran.r-project.org/package=geomorph

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2013). A field comes of age: Geometric morphometrics in the 21st Century. *Hystrix*, **24**, 7–14. https://doi.org/10.4404/hystrix-24.1-6283

Alarcón, P. A., & Lambertucci, S. A. (2018). A three-decade review of telemetry studies on vultures and condors. *Movement Ecology*, **6**(1), 13. https://doi.org/10.1186/s40462-018-0133-5

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**(1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Baken, E. K., Collyer, M. L., Kaliontzopoulou, A., & Adams, D. C. (2021). Geomorph v4.0 and gmShiny: Enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology and Evolution*, **12**(12), 2355–2363. https://doi.org/10.1111/2041-210X.13723

Ballejo, F., Lambertucci, S. A., Trejo, A., & De Santis, L. J. (2018). Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis. *Bird Conservation International*, **28**(3), 390–402. https://doi.org/10.1017/S0959270917000211

Ballentine, B., Horton, B., Brown, E. T., & Greenberg, R. (2013). Divergent selection on bill morphology contributes to nonrandom mating between swamp sparrow subspecies. *Animal Behaviour*, **86**(2), 467–473. https://doi.org/10.1016/j.anbehav.2013.06.002

Bardua, C., Felice, R. N., Watanabe, A., Fabre, A. C., & Goswami, A. (2019). A practical guide to sliding and surface semilandmarks in morphometric analyses. *Integrative Organismal Biology*, **1**, obz016. https://doi.org/10.1093/iob/obz016

Bennett, P. M., & Owens, I. P. (1997). Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **264**(1380), 401–408. https://doi.org/10.1098/rspb.1997.0057

Bildstein, K. L. (2022). Vultures of the World: Essential ecology and conservation. *Ornithological Applications*, **125**(3), 20–97.

Blem, C. R. (1997). Handbook of the birds of the World. Volume 2: New World vultures to guineafowl. *The Wilson Journal of Ornithology*, **109**(1), 193.

Böhmer, C., Prevoteau, J., Duriez, O., & Abourachid, A. (2020). Gulper, ripper and scrapper: Anatomy of the neck in three species of vultures. *Journal of Anatomy*, **236**(4), 701–723. https://doi.org/10.1111/joa.13129

Breno, M., Leirs, H., & Van Dongen, S. (2011). Traditional and geometric morphometrics for studying skull morphology during growth in *Mastomys natalensis* (Rodentia: Muridae). *Journal of Mammalogy*, **92**(6), 1395–1406. https://doi.org/10.1644/10-MAMM-A-331.1

Bright, J. A., Marugán-Lobón, J., Cobb, S. N., & Rayfield, E. J. (2016). The shapes of bird beaks are highly controlled by nondietary factors. *Proceedings of the National Academy of Sciences of the United States of America*, **113**(19), 5352–5357. https://doi.org/10.1073/pnas.1602683113

Bright, J. A., Marugán-Lobón, J., Rayfield, E. J., & Cobb, S. N. (2019). The multifactorial nature of beak and skull shape evolution in parrots and cockatoos (Psittaciformes). *BMC Evolutionary Biology*, **19**(1), 1–9. https://doi.org/10.1186/s12862-019-1432-1

Bunce, M., Szulkin, M., Lerner, H. R. L., Barnes, I., Shapiro, B., Cooper, A., & Holdaway, R. N. (2005). Ancient DNA provides new insights into the evolutionary history of New Zealand's extinct giant eagle. *PLoS Biology*, **3**(1), e9. https://doi.org/10.1371/journal.pbio.0030009

Cardini, A. (2016). Lost in the other half: Improving accuracy in geometric morphometric analyses of one side of bilaterally symmetric structures. *Systematic Biology*, **65**(6), 1096–1106. https://doi.org/10.1093/sysbio/syw043

Clavel, J., Escarguel, G., & Merceron, G. (2015). mvMORPH: An R package for fitting multivariate evolutionary models to morphometric data. *Methods in Ecology and Evolution*, **6**(11), 1311–1319. https://doi.org/10.1111/2041-210X.12420

Collyer, M. L., & Adams, D. (2021). Phylogenetically aligned component analysis. *Methods in Ecology and Evolution*, **12**(2), 359–372. https://doi.org/10.1111/2041-210X.13515

Cooney, C. R., Bright, J. A., Capp, E. J., Chira, A. M., Hughes, E. C., Moody, C. J., Nouri, L. O., Varley, Z. K., & Thomas, G. H. (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature*, **542**(7641), 344–347. https://doi.org/10.1038/nature21074

Cramp, S. (1980). *Handbook of the birds of Europe, the Middle East, and North Africa: The birds of the Western Palearctic. Vol. II: Hawks to bustards*. Oxford University Press.

del Hoyo, J., Elliott, A., & Sargatal, J. (1992). *Handbook of the birds of the World*. Lynx Edicions.

Dermody, B. J., Tanner, C. J., & Jackson, A. L. (2011). The evolutionary pathway to obligate scavenging in *Gyps* vultures. *PLoS One*, **6**(9), e24635. https://doi.org/10.1371/journal.pone.0024635

DeVault, T. L., Rhodes, O. E., Jr., & Shivik, J. A. (2003). Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, **102**(2), 225–234. https://doi.org/10.1034/j.1600-0706.2003.12378.x

Emslie, S. D. (1988). The fossil history and phylogenetic relationships of condors (Ciconiiformes: Vulturidae) in the New World. *Journal of Vertebrate Paleontology*, **8**(2), 212–228. https://doi.org/10.1080/02724634.1988.10011699

Felice, R. N., Tobias, J. A., Pigot, A. L., & Goswami, A. (2019). Dietary niche and the evolution of cranial morphology in birds. *Proceedings of the Royal Society B: Biological Sciences*, **286**(1897), 20182677. https://doi.org/10.1098/rspb.2018.2677

Friedman, N. R., Miller, E. T., Ball, J. R., Kasuga, H., Remeš, V., & Economo, E. P. (2019). Evolution of a multifunctional trait: Shared effects of foraging ecology and thermoregulation on beak morphology, with consequences for song evolution. *Proceedings of the Royal Society B: Biological Sciences*, **286**(1917), 20192474. https://doi.org/10.1098/rspb.2019.2474

Gaengler, H., & Clum, N. (2015). Investigating the impact of large carcass feeding on the behavior of captive Andean condors (*Vultur gryphus*) and its perception by zoo visitors. *Zoo Biology*, **34**(2), 118–129. https://doi.org/10.1002/zoo.21202

Gibbs, H. L., & Grant, P. R. (1987). Oscillating selection on Darwin's finches. *Nature*, **327**(6122), 511–513. https://doi.org/10.1038/327511a0

Goswami, A., Watanabe, A., Felice, R. N., Bardua, C., Fabre, A. C., & Polly, P. D. (2019). High-density morphometric analysis

of shape and integration: The good, the bad, and the not-really-a-problem. *Integrative and Comparative Biology*, **59**(3), 669–683. https://doi.org/10.1093/icb/icz120

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, **313**(5784), 224–226. https://doi.org/10.1126/science.1128374

Grossnickle, D. M., Brightly, W. H., Weaver, L. N., Stanchak, K. E., Roston, R. A., Pevsner, S. K., Stayton, C. T., Polly, P. D., & Law, C. J. (2023). A cautionary note on quantitative measures of phenotypic convergence. *bioRxiv*. https://doi.org/10.1101/2022.10.18.512739

Guangdi, S. I., Dong, Y., Ma, Y., & Zhang, Z. (2015). Shape similarities and differences in the skulls of scavenging raptors. *Zoological Science*, **32**(2), 171–177. https://doi.org/10.2108/zs130253

Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in three dimensions. In D. E. Slice (Ed.), *Modern morphometrics in physical anthropology* (pp. 73–98). Springer. https://doi.org/10.1007/0-387-27614-9

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K. L., Harshman, J., Huddleston, C. J., Marks, B. D., Miglia, K. J., Moore, W. S., Sheldon, F. H., Steadman, D. W., Witt, C. C., & Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, **320**(5884), 1763–1768. https://doi.org/10.1126/science.1157704

Hertel, F. (1994). Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology*, **75**(4), 1074–1084. https://doi.org/10.2307/1939431

Hertel, F. (1995). Ecomorphological indicators of feeding behavior in recent and fossil raptors. *The Auk*, **112**(4), 890–903. https://doi.org/10.2307/4089021

Hieronymus, T. L., & Witmer, L. M. (2010). Homology and evolution of avian compound Rhamphothecae. *The Auk*, **127**(3), 590–604. https://doi.org/10.1525/auk.2010.09122

Hille, S. M., Korner-Nievergelt, F., Bleeker, M., & Collar, N. J. (2016). Foraging behaviour at carcasses in an Asian vulture assemblage: Towards a good restaurant guide. *Bird Conservation International*, **26**(3), 263–272. https://doi.org/10.1017/S0959270915000349

Hirschauer, M. T., Zimunya, T., Wolter, K., & Monadjem, A. (2018). Sexing Cape Vulture *Gyps coprotheres* based on head morphometrics. *Ostrich*, **89**(2), 187–190. https://doi.org/10.2989/00306525.2017.1415990

Holland, A. E., Byrne, M. E., Hepinstall-Cymerman, J., Bryan, A. L., DeVault, T. L., Rhodes, O. E., & Beasley, J. C. (2019). Evidence of niche differentiation for two sympatric vulture species in the Southeastern United States. *Movement Ecology*, **7**, 1–12. https://doi.org/10.1186/s40462-019-0179-z

Holmes, J., Sustaita, D., & Hertel, F. (2022). Geometric morphometric analysis of the humerus in New and Old World vultures. *Journal of Morphology*, **283**(4), 379–394. https://doi.org/10.1002/jmor.21449

Houston, D. C. (1975). The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. *Journal of Wildlife Diseases*, **11**(3), 306–313. https://doi.org/10.7589/0090-3558-11.3.306

Houston, D. C. (1984). Does the King Vulture *Sarcorhamphus papa* use a sense of smell to locate food? *Ibis*, **126**(1), 67–69. https://doi.org/10.1111/j.1474-919X.1984.tb03665.x

Houston, D. C. (1987). The effect of reduced mammal numbers on *Cathartes* vultures in neotropical forests. *Biological Conservation*, **41**(2), 91–98. https://doi.org/10.1016/0006-3207(87)90113-3

Jackson, C. R., Maddox, T., Mbise, F. P., Stokke, B. G., Belant, J. L., Bevanger, K., Durant, S. M., Fyumagwa, R., Ranke, P. S., Røskaft, E., May, R., & Fossøy, F. (2020). A dead giveaway: Foraging vultures and other avian scavengers respond to auditory cues. *Ecology and Evolution*, **10**(13), 6769–6774. https://doi.org/10.1002/ece3.6366

Jarvis, E. D., Mirarab, S., Aberer, A. J., Li, B., Houde, P., Li, C., Ho, S. Y., Faircloth, B. C., Nabholz, B., Howard, J. T., Suh, A., Weber, C. C., da Fonseca, R. R., Li, J., Zhang, F., Li, H., Zhou, L., Narula, N., Liu, L., … Zhang, G. (2014). Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*, **346**(6215), 1320–1331. https://doi.org/10.1126/science.1253451

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, **491**(7424), 444–448. https://doi.org/10.1038/nature11631

Jønsson, K. A., Fabre, P. H., Fritz, S. A., Etienne, R. S., Ricklefs, R. E., Jørgensen, T. B., Fjeldså, J., Rahbek, C., Ericson, P. G., Woog, F., & Irestedt, M. (2012). Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences of the United States of America*, **109**(17), 6620–6625. https://doi.org/10.1073/pnas.1115835109

Kane, A., & Kendall, C. J. (2017). Understanding how mammalian scavengers use information from avian scavengers: Cue from above. *Journal of Animal Ecology*, **86**(4), 837–846.

Kemp, A. C., & Kemp, M. I. (1975). Observations on the White-backed Vulture Gyps africanus in the Kruger National Park, with notes on other avian scavengers. *Koedoe*, **18**(1), 51–68. https://doi.org/10.4102/koedoe.v18i1.914

Kendall, C. J. (2013). Alternative strategies in avian scavengers: How subordinate species foil the despotic distribution. *Behavioral Ecology and Sociobiology*, **67**, 383–393. https://doi.org/10.1007/s00265-012-1458-5

Kendall, C. J. (2014). The early bird gets the carcass: Temporal segregation and its effects on foraging success in avian scavengers. *The Auk: Ornithological Advances*, **131**(1), 12–19. https://doi.org/10.1642/AUK-13-201.1

Kendall, D. G. (1989). A survey of the statistical theory of shape. *Statistical Science*, **4**(2), 87–99. https://doi.org/10.1214/ss/1177012582

König, C. (1974). On the behaviour of vultures on carcasses in Spain. *Journal für Ornithologie*, **115**, 289–320. https://doi.org/10.1007/BF01644326

König, C. (1983). Interspecific and intraspecific competition for food among Old World vultures. In S. R. Wilbur & J. A.

Jackson (Eds.), *Vulture biology and management* (pp. 153–171). University of California Press.

Krüger, S. C., Simmons, R. E., & Amar, A. (2015). Anthropogenic activities influence the abandonment of Bearded Vulture (*Gypaetus barbatus*) territories in southern Africa. *The Condor*, **117**(1), 94–107. https://doi.org/10.1650/CONDOR-14-121.1

Kruuk, H. (1967). Competition for food between vultures in East Africa. *Ardea*, **55**(3–4), 171.

Lack, D. (1953). Darwin's finches. *Scientific American*, **188**(4), 66–73.

Lambertucci, S. A., Carrete, M., Donázar, J. A., & Hiraldo, F. (2012). Large-scale age-dependent skewed sex ratio in a sexually dimorphic avian scavenger. *PLoS One*, **7**(9), e46347. https://doi.org/10.1371/journal.pone.0046347

Lambertucci, S. A., Margalida, A., Speziale, K. L., Amar, A., Ballejo, F., Bildstein, K. L., Blanco, G., Botha, A. J., Bowden, C. G. R., Cortés-Avizanda, A., Duriez, O., Green, R. E., Hiraldo, F., Ogada, D., Plaza, P., Sánchez-Zapata, J. A., Santangeli, A., Selva, N., Spiegel, O., & Donázar, J. A. (2021). Presumed killers? Vultures, stakeholders, misperceptions, and fake news. *Conservation Science and Practice*, **3**(6), e415. https://doi.org/10.1111/csp2.415

Linde-Medina, M., Guerra, C., & Alcover, J. A. (2021). A revision of vulture feeding classification. *Zoology*, **148**, 125946. https://doi.org/10.1016/j.zool.2021.125946

Lovette, I. J., Bermingham, E., & Ricklefs, R. E. (2002). Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**(1486), 37–42. https://doi.org/10.1098/rspb.2001.1789

Lucas, T., & Goswami, A. (2017). *Paleomorph: Geometric morphometric tools for paleobiology*. R package version 0.1, 4.

Mabhikwa, N. T., Hirschauer, M. T., & Wolter, K. (2017). Sexual dimorphism and plumage characteristics of juvenile Cape Vultures *Gyps coprotheres*. *Ostrich*, **88**(2), 167–171. https://doi.org/10.2989/00306525.2017.1344742

Maderbacher, M., Bauer, C., Herler, J., Postl, L., Makasa, L., & Sturmbauer, C. (2008). Assessment of traditional versus geometric morphometrics for discriminating populations of the *Tropheus moorii* species complex (Teleostei: Cichlidae), a Lake Tanganyika model for allopatric speciation. *Journal of Zoological Systematics and Evolutionary Research*, **46**(2), 153–161. https://doi.org/10.1111/j.1439-0469.2007.00447.x

Madison, W. P., & Madison, D. R. (2021). *Mesquite: A modular system for evolutionary analysis*. Version 3.70. http://mesquiteproject.org

Margalida, A., Donazar, J. A., Carrete, M., & Sánchez-Zapata, J. A. (2010). Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology*, **47**(4), 931–935. https://doi.org/10.1111/j.1365-2664.2010.01835.x

Martin, G. R., Portugal, S. J., & Murn, C. P. (2012). Visual fields, foraging and collision vulnerability in *Gyps* vultures. *Ibis*, **154**(3), 626–631. https://doi.org/10.1111/j.1474-919X.2012.01227.x

Mendonca, D. A., Naidoo, S. D., Skolnick, G., Skladman, R., & Woo, A. S. (2013). Comparative study of cranial anthropometric measurement by traditional calipers to computed tomography and three-dimensional photogrammetry. *The Journal of Craniofacial Surgery*, **24**(4), 1106–1110. https://doi.org/10.1097/SCS.0b013e31828dcdcb

Mitchell, M. J., Goswami, A., & Felice, R. N. (2021). Cranial integration in the ring-necked parakeet, *Psittacula krameri* (Psittaciformes: Psittaculidae). *Biological Journal of the Linnean Society*, **133**(1), 47–56. https://doi.org/10.1093/biolinnean/blab032

Mundy, P., Butchart, D., Ledger, J., & Piper, S. (1992). *The vultures of Africa* (Vol. **671**). Academic Press.

Natale, R., & Slater, G. J. (2022). The effects of foraging ecology and allometry on avian skull shape vary across levels of phylogeny. *The American Naturalist*, **200**(4), E174–E188. https://doi.org/10.1086/720745

Navalón, G., Bright, J. A., Marugán-Lobón, J., & Rayfield, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution*, **73**(3), 422–435. https://doi.org/10.1111/evo.13655

Ogada, D. L., Keesing, F., & Virani, M. Z. (2012). Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences*, **1249**(1), 57–71. https://doi.org/10.1111/j.1749-6632.2011.06293.x

Olsen, A. M. (2017). Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Functional Ecology*, **31**(10), 1985–1995. https://doi.org/10.1111/1365-2435.12890

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, **35**(3), 526–528. https://doi.org/10.1093/bioinformatics/bty633

Parés-Casanova, P. M., Salamanca-Carreño, A., Crosby-Granados, R. A., & Bentez-Molano, J. (2020). A comparison of traditional and geometric morphometric techniques for the study of basicranial morphology in horses: A case study of the Araucanian horse from Colombia. *Animals*, **10**(1), 118. https://doi.org/10.3390/ani10010118

Pecsics, T., Laczi, M., Nagy, G., Kondor, T., & Csörgő, T. (2019). Analysis of skull morphometric characters in diurnal raptors (Accipitriformes and Falconiformes). *Ornis Hungarica*, **27**(1), 117–131. https://doi.org/10.2478/orhu-2019-0008

Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., Seddon, N., Trisos, C. H., Weeks, B. C., & Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology & Evolution*, **4**(2), 230–239. https://doi.org/10.1038/s41559-019-1070-4

Pigot, A. L., Trisos, C. H., & Tobias, J. A. (2016). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **283**(1822), 20152013. https://doi.org/10.1098/rspb.2015.2013

Poessel, S. A., Brandt, J., Miller, T. A., & Katzner, T. E. (2018). Meteorological and environmental variables affect flight behaviour and decision-making of an obligate soaring bird, the California Condor *Gymnogyps californianus*. *Ibis*, **160**(1), 36–53. https://doi.org/10.1111/ibi.12531

Portugal, S. J., Murn, C. P., & Martin, G. R. (2017). White-headed Vulture *Trigonoceps occipitalis* shows visual field characteristics of hunting raptors. *Ibis*, **159**(2), 463–466. https://doi.org/10.1111/ibi.12448

Potier, S. (2020). Visual adaptations in predatory and scavenging diurnal raptors. *Diversity*, **12**(10), 400. https://doi.org/10.3390/d12100400

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rohlf, F. J., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology*, **39**(1), 40–59. https://doi.org/10.2307/2992207

Ruxton, G. D., & Houston, D. C. (2004). Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology*, **228**(3), 431–436. https://doi.org/10.1016/j.jtbi.2004.02.005

Schlager, S. (2017). Morpho and Rvcg–shape analysis in R: R-packages for geometric morphometrics, shape analysis and surface manipulations. In G. Zheng, S. Li, & G. Székely (Eds.), *Statistical shape and deformation analysis* (pp. 217–256). Academic Press. https://doi.org/10.1016/B978-0-12-810493-4.00011-0

Smith, T. B., Freed, L. A., Lepson, J. K., & Carothers, J. H. (1995). Evolutionary consequences of extinctions in populations of a Hawaiian honeycreeper. *Conservation Biology*, **9**(1), 107–113. https://doi.org/10.1046/j.1523-1739.1995.09010107.x

Spiegel, O., Getz, W. M., & Nathan, R. (2013). Factors influencing foraging search efficiency: Why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? *The American Naturalist*, **181**(5), E102–E115. https://doi.org/10.1086/670009

Stayton, C. T. (2015). The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution*, **69**(8), 2140–2153. https://doi.org/10.1111/evo.12729

Sun, Y., Si, G., Wang, X., Wang, K., & Zhang, Z. (2018). Geometric morphometric analysis of skull shape in the Accipitridae. *Zoomorphology*, **137**, 445–456. https://doi.org/10.1007/s00435-018-0406-y

Tattersall, G. J., Arnaout, B., & Symonds, M. R. (2017). The evolution of the avian bill as a thermoregulatory organ. *Biological Reviews*, **92**(3), 1630–1656. https://doi.org/10.1111/brv.12299

van Heteren, A. H., Wroe, S., Tsang, L. R., Mitchell, D. R., Ross, P., Ledogar, J. A., Attard, M. R. G., Sustaita, D., Clausen, P., Scofield, R. P., & Sansalone, G. (2021). New Zealand's extinct giant raptor (*Hieraaetus moorei*) killed like an eagle, ate like a condor. *Proceedings of the Royal Society B: Biological Sciences*, **288**(1964), 20211913. https://doi.org/10.1098/rspb.2021.1913

van Overveld, T., Blanco, G., Moleón, M., Margalida, A., Sánchez-Zapata, J. A., de la Riva, M., & Donázar, J. A. (2020). Integrating vulture social behavior into conservation practice. *The Condor*, **122**(4), duaa035. https://doi.org/10.1093/condor/duaa035

van Overveld, T., Sol, D., Blanco, G., Margalida, A., de la Riva, M., & Donázar, J. A. (2022). Vultures as an overlooked model in cognitive ecology. *Animal Cognition*, **25**, 495–507. https://doi.org/10.1007/s10071-021-01585-2

Xirouchakis, S. M., & Mylonas, M. (2004). Griffon Vulture (*Gyps fulvus*) distribution and density in Crete. *Israel Journal of Ecology & Evolution*, **50**(4), 341–354. https://doi.org/10.1560/VCL8-FLAK-J2M1-D9KR

Xirouchakis, S. M., & Poulakakis, N. (2008). Biometrics, sexual dimorphism and gender determination of Griffon Vultures *Gyps fulvus* from Crete. *Ardea*, **96**(1), 91–98. https://doi.org/10.5253/078.096.0110

Zelditch, M. L., Swiderski, D. L., Sheets, H. D., & Fink, W. L. (2004). *Geometric morphometrics for biologists: A primer*. Elsevier Inc.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Proportional variance of principal components of the full dataset.

Figure S2. Convergence plot for three gulper species, showing convergence among these taxa (*Vultur gryphus*, *Gymnogyps californianus*, *Gyps tenuirostris*; $Ct_1 = 0.63$, $P = 0.00$).

Figure S3. Convergence plot for three scrapper species, showing phenotypic convergence among these taxa (*Necrosyrtes monachus*, *Neophron percnopterus*, *Cathartes melambratus*; $Ct_1 = 0.45$, $P = 0.00$).

Figure S4. Convergence plot for two ripper species, showing no clear phenotypic convergence (*Sarcoramphus papa*, *Torgos tracheliotos*; $Ct_1 = -0.004$, $P = 0.38$).

Figure S5. Phylomorphospace showing species grouped by vulture feeding types along PC1 on the x axis, and PC2 (top) and PC3 (bottom) on the y axes.

Table S1. List of study species.

Table S2. Anatomical landmark guide.

Table S3. Semi-landmark curve guide (see anatomical landmark guide for initial and terminal landmarks).

Table S4. Summary of phylogenetic signal (K_{mult}) across all datasets.

Table S5. Summary of analyses on all Procrustes-aligned subsets of the data.

Table S6. Flexible discriminant analysis – vulture feeding type.

Table S7. Flexible discriminant analysis – feeding group.

Table S8. Flexible discriminant analysis – vulture/non-vulture.

Table S9. Flexible discriminant analysis – vulture/non-vulture.