Eigensurface analysis, ecology, and modelling of morphological adaptation in the falconiform humerus (Falconiformes: Aves)

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Studies of morphological adaptation aim to quantify the relationship between an organism’s form and its ecology. In the past such studies have been hampered by an over-reliance on either qualitative observations or the collection of a few, marginally representative two-dimensional linear measurements as morphological descriptors. Recent advances in morphometric data acquisition and analysis techniques now provide a means of accurately and comprehensively quantifying the morphological variation inherent in complex three-dimensional (3D) surfaces across a specimen set. Using birds of prey as a model group, we examine how one of these new morphometric methods – eigensurface analysis – can be used to investigate adaptation. Virtual models of the humerus of 50 falconiform species from 29 genera were examined to identify the morphological correlates associated with different flight styles, habitats, and behaviours of these ecologically sensitive predators. Results indicate that strong, consistent, unique, and subtle modes of shape variation are associated with differences in flight speed (fast–slow), flight style (perch hunting, chasing, low flight, soaring flight, hovering), habitat (forested–open landscape) and migratory behaviour (long-distance migrants–sedentary species). In each case, visual modelling of between-groups transitions in morphology can be used to facilitate identification of features of the humerus, such as the size and extent of surface-shape variation within specific regions of muscle attachment, that are important predictors of function and lifestyle. Eigensurface analysis-based representations of 3D morphology, in combination with standard linear discrimination techniques and new shape modelling procedures, represent a way to statistically evaluate hypotheses of morphological adaptation. This approach can be used not only for bird taxa, but more broadly in studies of ecology and adaptation in many vertebrate, invertebrate, and plant species, in ways that cannot be duplicated either by visual observation or by the representation of form using linear measurements, 2D–3D landmark coordinate sets or sets of 2D–3D boundary outline semilandmarks.

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ADDITIONAL KEYWORDS: comparative analysis – flight – morphology – morphometrics.

INTRODUCTION

Ecomorphology is the study of the relationship between an organism’s morphology and its ecology (Ricklefs & Miller, 1999). Ecomorphological analyses can focus either on the way in which the environment affects a group’s functional design or the constraints a given morphology imposes on the way its members interact with the environment (Wainwright, 1991). In this context, ecomorphological analyses can be used to test hypotheses of adaptation (see Endler, 1986).

Quantitative ecomorphology is the variant of this approach to understanding the nature of relationships between ecology and morphology that applies
numerical analysis and statistical testing to the evaluation of ecomorphological hypotheses. Despite the availability of mathematical procedures designed to facilitate this approach (e.g. Bookstein, 1991; Dryden & Mardia, 1998; MacLeod, 1999, 2008; Zelditch et al., 2004), many ecomorphological studies have employed a qualitative-narrative approach to the characterization of morphological variation and the statistical assessment of patterns of covariance between sets of morphological and ecological variables. However, quantitative approaches (1) facilitate formulation of specific and detailed hypotheses, (2) employ more objective forms of data analysis, and (3) support simultaneous consideration of alternative explanations for patterns of morphological variation (e.g. phylogenetic covariation, see Harvey & Pagel, 1991; Martins & Hansen, 1997; Rohlf, 2001, 2006). As a result, a quantitative approach to investigating patterns of morphological variation promotes a more detailed, comprehensive, and nuanced understanding of both the evolutionary sources and the ecological–morphological products of evolutionary processes.

Birds are an excellent example of a taxonomic group in which aspects of both ecological and environmental adaptations are reflected in morphology. The morphology of birds is largely dictated by adaptive requirements associated with flight (Calmaestra & Moreno, 2000). A vulture (Gyps sp.), for example, has large, long wings that are used to soar on rising warm air currents to search for diseased, injured or dead prey. By contrast, a sparrowhawk (Accipiter sp.) has short wings that are used to manoeuvre between branches and make short flights through wooded areas to catch live prey.

Diurnal raptors of the Order Falconiformes are ecologically sensitive predators that occur over a wide variety of habitats, including primary rainforest, desert, coastal cliffs, high mountains and arctic tundra (Ferguson-Lees & Christie, 2001). These birds often have specialized diets and foraging behaviours. Consequently, their geographical ranges can be restricted to those areas – and those habitats – in which their prey occur. This link between morphology and habitat is also one of the primary reasons why many raptor species are currently at risk of extinction as they, and their prey, lose their preferred habitats to deforestation, development, and/or agricultural repurposing (Gamauf, Preleuthner & Winkler, 1998).

Some empirical evidence for covariation in wing morphology with flight styles and habitat has been established through direct studies of raptor behaviour (Janes, 1985; Gamauf et al., 1998). As with aircraft, the main morphological design factors affecting flight performance are wing loading (body weight/wing area) and aspect ratio (wing span/wing area, see Pennycuick, 2008). Having a wing morphology appropriate to its lifestyle enables each bird species to move about efficiently and effectively in its preferred habitat (Norberg & Rayner, 1987) by optimizing the amount of energy required to fly at certain speeds against time spent in various flight modes.

Most muscles responsible for powering flight in birds run from the skeletal thorax (the scapula, coracoid, and sternum) to the humerus. The more energy required for flight, the faster the bird needs to flap its wings at take-off and the larger these muscles need to be. Consequently, muscle size and attachment position have a direct bearing on the flight style of many bird species, as this controls the amount of time a bird spends on the wing and the amount of energy it expends during powered flight. Natural selection will attempt to optimize each species’ wing morphology to maximize performance and minimize the risk of damage, within the constraints imposed by the wing’s composition, its phylogenetically antecedent structure and the needs related to the species’ preferred habitat and lifestyle. These principles apply equally to the wing’s structural support elements, the muscles that move with the wing, the arrangement of wing feathers, the wing size, the wing shape, etc. As the humerus is the largest bone in the wing, it should be possible to use this structure to investigate the manner in which skeletal wing shape varies to solve the functional challenges posed by differing ecologies and behaviours in birds of prey. The basic anatomy of the avian humerus, showing the attachment points of the major flight muscles, is illustrated in Figure 1.

Geometric morphometric techniques provide the tools necessary for detailed study of humerus shape variation, allowing assessment of patterns of co-variation between the detailed morphology of birds and external factors such as habitat and behaviour. Previous attempts to study ecomorphological patterns quantitatively have been hampered by the requirement of selecting morphological characters that accurately represent the form of the organism and that have some functional meaning (Leisler & Winkler, 1991). For example, Janes (1985) used basic body mass, wing area, and wing span measurements to relate avian morphology to aeronautical theory. However, more subtle differences in wing and wingbone form, which cannot be captured by these basic observations, not only have a great effect on flight performance, but constitute the ‘raw material’ for selection. A better way of representing, analysing, and modelling differences in form and shape is to directly pinpoint and compare corresponding features on the surfaces of objects. The complex and sometimes intricate differences in size and shape of these surfaces can be analysed using new, three-dimensional (3D)
geometric morphometric data collection and data analysis techniques (see below). This approach not only provides a more accurate assessment of variation, but allows clearer, more robust tests of the relationship between patterns of morphological and ecological variation.

In this investigation, 3D surface-based morphometric data collection/analysis techniques were used to determine whether variation in humerus morphology among birds is structured in such a way as to reflect species-specific function, lifestyle, habitat, and behaviour. First, covariance between flight style and humerus shape was assessed by examining differences in humeral morphology between slow-flying species, which search for prey using soaring or low quartering flight, and fast-flying species which tend to chase their prey or hunt from an elevated perch. The geometric relationship between morphology and habitat was then investigated by determining distinct humerus shapes which characterize bird species that inhabit forested and more open areas. Next, 3D humerus surface morphology was used to compare birds with sedentary and migratory behavioural tendencies. The cause of any consistent humerus shape differences revealed by these comparisons was also investigated by determining whether the results obtained can be explained by direct adaptation (sensu Gould & Vrba, 1982) or phylogenetic ancestry.

**MATERIAL**

The left humeri of 50 falconiform species were used in this study (Appendix 1), comprising 29 (40%) of the 73 commonly recognized extant falconiform genera (Ferguson-Lees & Christie, 2001). This sample was selected to represent the wide range of body morphologies, flight styles, behavioural ecologies, and habitat preferences present in this group. Members of the Accipitridae, the largest family in the Falconiformes, were drawn from all 14 different subfamilies (as characterized by Lerner & Mindell, 2005). Figure 2 shows a composite falconiform cladogram based on recent molecular and morphological data (Griffiths et al., 2004, 2007; Lerner & Mindell, 2005; Lerner, Klaver & Mindell, 2008).

For many years, phylogenetic relationships within the avian family tree remained poorly resolved (Livezey & Zusi, 2007). Debate continues as to whether the order Falconiformes comprises a monophyletic group or whether the Falconidae are more
closely related to seriemas, parrots, and passerines than to other diurnal birds of prey (see Ericson et al., 2006; Hackett et al., 2008). However, recent evidence (Pacheco et al., 2011), as well as previous work by Livezey & Zusi (2007) and Lerner & Mindell (2005), suggests that the Falconidae should be included with the Accipitridae, Pandionidae, and Sagittariidae within Falconiformes. While the tree presented in Figure 2 does not represent the last word in falconiform systematics, it can be used as a starting point from which to investigate the impact of phylogenetic relatedness upon avian morphological variation. By the same token, although the sample used in this study is by no means comprehensive, specimens were
drawn from a wide range of species, representing clades from across the falconiform evolutionary plexus. This sample is certainly adequate to test the proposition that aspects of function, ecology, and behaviour are reflected in bone morphology.

**METHODS**

**IMAGING**

All 3D scans were taken using a laser scanner and assembled using 3D mesh manipulation software. For each scan, humeri were mounted upright on the distal end with the shaft perpendicular to the scanner’s optic axis on a turntable. Six scans of each humerus were taken, 60° apart. These six scans were then registered and combined in software to create a 3D virtual humerus (see Fig. 3). Once the raw composite scans had been assembled, post-processing of each virtual model involved bringing the resolution of the mesh into approximate conformance and deleting coordinates on the distal and ventral portions of the composite models so that only dorsal surface coordinates of the proximal half of the humerus remained. This was used as the basis for examining morphological differences in the dorsal and bicipital crests, which are the main sites of flight muscle attachment in birds (Fig. 1). Four forms of data from these 3D models were then exported as ASCII point cloud files for eigensurface analysis: (1) the point clouds of the dorsal surface, comprising 2000–3000 3D coordinate points, (2) all points along the outline of this surface (approximately 200 points), (3) two landmark points at the tip of the humeral head and the centre of the shaft at the distal end of the surface, and (4) a mid-line chord joining these two landmarks through the bicipital furrow and along the centre of the shaft (see Fig. 4).

**MORPHOMETRIC ANALYSES**

Morphometric analysis was used to quantitatively compare the shapes of different humeri by constructing a set of variables that model the distribution of morphologies within the set of objects. This study employed eigensurface analysis (MacLeod, 2008; Polly, 2008; Polly & MacLeod, 2008) to determine a number of morphological variables that best model the distribution of 3D surface morphology in the dataset. This comparatively new shape analysis method extends the relatively well-known eigenshape approach to the analysis of 2D curves (see MacLeod, 1999) to 3D surfaces.

Eigensurface analysis relies on the identification of topologically corresponding point locations on all objects in the study group so that the morphologies of objects can be compared on a point-by-point basis. In this investigation eigensurface analysis was performed on the dorsal surface of the proximal end of the humerus.

To implement eigensurface analysis two landmark positions were identified on the periphery of the $x,y,z$ coordinate point cloud at opposite ends of the 3D surface. A fixed number of equally spaced semilandmark points are interpolated along each half-outline and along a chord joining the two landmark points. These inter-landmark curves, segments, and chord form the basis for an adaptive grid of semilandmark point locations that was fit to the surface of the form (for a detailed discussion, see MacLeod, 2008). In this case, after experimentation a sampling net of 30 interpolated points along the mid-line chord and ten points running perpendicular from the mid-line to the outline were found to be sufficient to accurately represent shape variation among the specimens. Steps in the gridding process are described and illustrated in Figure 4.

The advantages of representing the complex topology of the point cloud by an adaptive grid are twofold. First, specification of the grid’s resolution allows the analyst to control the scale of the features that will be included in the analysis. Second, specification of an equal number of grid nodes ensures that each object is represented by the same number of data points, that coverage of the form is complete, and that each node bears a topologically consistent relationship to all other nodes across the sample. It is these features that allow the grids to be compared with one another, and the principal orthogonal dimensions of surface-shape variation to be extracted using the formalisms and algorithms of routine geometric morphometric analysis. This includes the projection of surface configuration points from the shape manifold to a plane, tangent to the manifold at the position of the mean shape, within which ordinations of configurations in a linear space may be obtained (see Bookstein, 1991; Zelditch et al., 2004). Like eigenshape analysis (see MacLeod, 1999), the term ‘eigensurface analysis’ refers to both the method of representing the object of interest – in this case the 3D surface with an adaptively fit, rectilinear grid of semilandmark points – and the linear algebraic operations that align the set of grids with one another and extract the major directions of shape variation within a linear vector space.

In the semi-landmark registration process no attempt was made to ‘slide’ semilandmarks to configurations of minimal bending energy (see Green, 1996; Bookstein, 1997). Given the density of our semilandmark grid and the constraint that semilandmarks cannot slide past one another (otherwise the reconstructed surface becomes artificially folded), even if it was possible to slide semilandmarks along
lines and surfaces in a biologically reasonable manner, the results of this operation would not differ greatly from those of our geometrically more conservative approach. By opting for a dense semi-landmark sampling grid in order to include small-scale features in the analysis, we have automatically reduced the error due to topological non-alignment to a very small value. This can be done without...
Figure 4. Steps in the definition of eigensurface sampling grids as exemplified by the three scans of the proximal–dorsal surfaces of the humeri illustrated in Figure 3. The upper row shows the region selected for analysis. Point clouds of approximately 2000–3000 points representing this region were saved as ASCII text files along with separate files recording the boundary outline coordinates, points along a midline, and the coordinate positions of the two landmarks selected to orient the grid. Lower row: eigensurface form sampling grids. Each eigensurface grid is calculated by selecting a grid resolution (e.g. 10, 15, 20) and then interpolating that number of equally spaced semilandmark points along each half-outline (black) and along the surface trace of the chord joining the orientation landmarks (white). In this analysis a grid resolution of 10 was selected and the landmark chord oriented so that it traced the approximate position of the mid-line running from the humerus head down the centre of the shaft. Lateral or ‘rib’ chords are then drawn along the surface of the form such that each mid-line node is joined to a boundary outline node on either side. Equally spaced rib semilandmarks (grey) were then located along each of these rib chords with the number of semilandmarks used to quantify the shape of the chord being set iteratively as the number required to represent 95% of the length of the most contorted corresponding chord across the entire sample. This iterative procedure is identical to that used by MacLeod (1999) to sample boundary outline form in extended eigenshape analysis. The resulting grids quantify the geometric form of the surface of the humerus using an equal number of semilandmark points for each specimen in the sample and with each point being located in a position that corresponds topologically (relative to the grid point set as a whole) to all other points across the sample.
having to resort to the shape distortions that result from the current convention of sliding 3D semilandmarks along tangents to the surface, rather than along the surfaces themselves, to the position of minimum bending energy, which is itself a biologically artificial limiting protocol.

**Phylogenetic modelling**

To examine the extent to which phylogenetic relationships among higher taxonomic groupings were linked to patterns of shape variation, the phylogenetic generalized least squares (PGLS) technique of Martins & Hansen (1997) was used to subdivide the total covariance matrix \( \text{Cov}_{\text{total}} \) into factors attributable to phylogenetic and non-phylogenetic sources:

\[
\text{Cov}_{\text{total}} = \text{Cov}_{\text{phylogenetic}} + \text{Cov}_{\text{non-phylogenetic}}
\]  

Contrary to much of what has been written about various comparative methods (e.g. Gittleman & Kot, 1990; Harvey & Pagel, 1991; Gittleman & Luh, 1992; Purvis, Gittleman & Luh, 1994; Westoby, Leishman & Lord, 1995; Harvey et al., 1996 [and chapters therein]; Desdevises et al., 2003; Beauchamp & Fernandez-Juricic, 2004), numerical procedures such as PGLS, phylogenetic independent contrasts (PIC) and phylogenetic autocorrelation (PA) are not statistical techniques that remove trait variation patterns correlated with phylogeny from numerical datasets. Rather, these are modelling procedures that, given conformance of the data at hand to the assumptions of various evolutionary process models, are capable of more accurately estimating the standard errors of trait or measurement data. It is this improvement in accuracy that provides a more powerful basis for both the assessment and the statistical testing of associations between traits (for a comprehensive and critical review of approaches to comparative method analysis, see Rohlf, 2001, 2006). These improvements in data analysis results will often be obtained even if the phylogeny is not known to a high degree of accuracy.

In our investigation the cladogram of phylogenetic relationships between major bird groups calibrated against molecular data (see Fig. 2) was used as the basis for the comparative analysis, with branch lengths set to reflect relative assessments of a lineage’s divergence from its sister group. Scores on a number of eigensurface shape vectors sufficient to represent 95% of the observed shape variation were used to calculate lineage mean values and associated standard errors. From these data, Emilia Martins’ COMPARE software was used to model the (phylogenetically) standardized contrasts for the 12 internal nodes of the cladogram using the PIC and PGLS methods.

For both datasets a simple exponential model of constraint was applied with the strength of the constraint on phenotypic evolution estimated via a maximum-likelihood search procedure (see Martins and Hansen, 1997 and online Help documentation for COMPARE: http://www.indiana.edu/~martinsl/compare). Two methods of modelling the phylogenetic component of the shape variation data were used to determine whether the results were robust to changes in the assumptions and methods of the modelling procedure. Based on the results of these analyses a covariance matrix of the standardized contrasts between the terminal branches was determined. This, in turn, was used as the basis for a standardized contrasts principal components analysis (PCA) and standardized contrasts canonical variates analysis (CVA) with the purpose of the latter being to determine whether it was possible to separate ecological groups using only the information included in the non-phylogenetic partition of the total covariance matrix.

**Ecological inferences**

Each species was assigned to ecological categories based on a compilation of data and observations provided by the *Handbook to the Birds of the World* (Del Hoyo, Elloï & Sargatal, 1994), *Raptors of the World* (Ferguson-Lees & Christie, 2001), *Eagles, Hawks and Falcons of the World* (Brown & Amadon, 1968), the *International Union for Conservation of Nature (IUCN) Red List of Threatened Species* (http://www.iucnredlist.org last accessed 1 September 2009), the *Global Raptors Information Network* (http://www.globalraptors.org last accessed 1 August 2011) and *Nature Reserve Explorer* (http://www.naturereserve.org/explorer/ last accessed 1 September 2009). The definitions of all ecological categories used in this study are presented in Table 1.

**Canonical variates analysis**

A CVA of eigensurface analysis results provides a means for creating mathematical functions that best discriminate between groups of objects for which the membership is known a priori. These functions are linear combinations of an initial, more extensive set of variables (e.g. original or Procrustes-registered point coordinate sets, relative warp scores or projection scores from eigenshape or eigensurface analysis, see MacLeod, 2007). The canonical variate functions maximize between-groups variance while simultaneously minimizing within-groups dispersion. Each training-set specimen was then projected onto each discriminant function, the complete set of which defined an empirical falconiform discriminant space.
Low dimensional subspaces derived from the total discriminant space were used to visualize group placements and separations. In addition to providing the set of functions that quantify these various discriminant spaces, coordinate position along the various discriminant vectors can be transformed from the CVA space back into the space of the original variables, and there used to construct geometric models of the modes of shape variation that best express between-group differences (for descriptions of stages of this procedure, see MacLeod, 2007, 2009).

Finally, statistical tests such as the Wilks' $\lambda$ test (Mardia et al., 1979), the $\phi$ likelihood-ratio test (Manly, 1994), and the Hotelling $T^2$ test (Hotelling, 1931) were used to assess the statistical significance of the difference between the positions of group centroids (= projected positions of the set of mean shapes).

CVA was used to assess morphological differences between the humeri of specimens grouped by flight speed, flight style, habitat, and migratory behaviours. In each case, CVA was used to identify a set of functions of eigensurface variables that produced the best segregations of different ecological or behavioural groups of species based on humerus shape. These CVA functions were also used as morphological variables with which to discriminate the groups of specimen shapes. However, given a constant sample size, the statistical power of any discriminant analysis procedure decreases with an increase in the number of variables included in the analysis (Zar, 1999). As a sample size of 50 is a relatively small number of specimens to use in a high-dimensional numerical analysis, it was important to minimize the number of morphological variables used for the CVA to limit this problem of dimensionality by selecting an optimal set of morphological variables for each CVA.

Accordingly, eigensurface axes 22–49 were not used in CVAs, as together the first 21 eigensurface scores represented over 95% of observed humerus shape variation. A sequential series of CVAs were performed to find the optimal number of variables for the best separation of ecological groups – starting with all 21 eigensurface axes, omitting the axis with the lowest eigenvalue, and rerunning the CVA. For each analysis the number of training-set specimens correctly assigned to each group, as well as the probability of observed inter-group centroid differences resulting from random variation, was calculated (see below). In this manner the efficacy of the eigensurface variable sequence was assessed by its ability to separate and distinguish specimens in ecological groups accurately. Variable sets were selected to maximize accuracy, while minimizing the possibility that this result could occur at random.

A Monte Carlo simulation test based on the $\phi$ likelihood ratio test (Manly, 1994) of 10 000 random pseudoreplicate datasets was used to assess how the

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Groups</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Flight speed</td>
<td>Fast</td>
<td>When in flight, uses fast flapping to chase or pounce swiftly on prey (generally includes perch hunting, chase and hovering species)</td>
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<tr>
<td></td>
<td>Slow</td>
<td>Flies using slow wing beats for low quartering or high soaring flight</td>
</tr>
<tr>
<td>Flight style</td>
<td>Chase</td>
<td>Hunts prey by flying in fast pursuit</td>
</tr>
<tr>
<td></td>
<td>Low Flight</td>
<td>Flies slowly at a low height above the ground to search for prey before diving down to seize prey once it is spotted</td>
</tr>
<tr>
<td></td>
<td>Hovering</td>
<td>Remains in a single spot, usually at a low height above the ground, diving to seize prey when it passes</td>
</tr>
<tr>
<td></td>
<td>Perch Hunting</td>
<td>Perches motionless on a low branch or other perch until prey passes. Once prey is spotted it makes a short fast flight to catch the prey item</td>
</tr>
<tr>
<td></td>
<td>Soaring</td>
<td>Searches for prey using slow flight high above the ground, making few wing beats, usually rising through the air on thermals before swooping down to scavenge or capture prey</td>
</tr>
<tr>
<td>Habitat</td>
<td>Forest</td>
<td>$&gt;50%$ canopy cover in foraging habitat</td>
</tr>
<tr>
<td></td>
<td>Open</td>
<td>$\leq30%$ canopy cover in foraging habitat</td>
</tr>
<tr>
<td>Migratory behavior</td>
<td>Long Distance</td>
<td>Most or all individuals migrate long distances each year</td>
</tr>
<tr>
<td></td>
<td>Sedentary</td>
<td>No individuals either migrate or habitually travel long distances</td>
</tr>
</tbody>
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In each analysis, we excluded specimens from species with unknown or highly variable ecologies or behaviours that could not be assigned with confidence to any group. For the habitat analysis, cosmopolitan species, which commonly forage in forested, woodland or open habitats, and species that forage in partially wooded habitats were not used, and for the migration analysis, short-distance migrants and nomadic species were not included.
empirical CVA results compared with the null model of no subgroup-level structure. Use of a Monte Carlo or ‘bootstrap’ comparison approach in this context renders the test free from distributional assumptions and avoids over-interpretation of the statistical significance of results of a high-dimensional discriminant function analysis based on a relatively small sample (e.g. the ‘curse of dimensionality’, see Rao, 1948; MacLeod, 2007). [Note: the $\phi$ test (see Manly, 1994) results reported throughout the article are representative of results obtained using other statistical tests as well, see above.]

A jackknifed cross-validation analysis was also used to test the robustness of the final discriminant classification. This consisted of sequentially sequestering a single specimen from the dataset, recalculating the CVA based on the remaining training set, and using the result of that analysis to assign the sequestered specimen to a group (see Manly, 1994). The jackknifed strategy provides an indication of the overall quality of discrimination result that could be achieved on actual unknown specimens, as well as an indication of the stability of the CVA axes calculated on the basis of the full training set.

**RESULTS**

**EIGENSURFACE ANALYSIS**

The major modes of 3D shape variation in the dorsal surface of the proximal humerus were obtained by singular value decomposition of the raw Procrustes-registered shape covariance matrix. The three most important of these variation modes are expressed as the subspace formed by the first three eigensurfaces (E-Surf) axes (=eigenvectors associated with the largest greatest singular values of the shape covariance matrix). These three axes account for 41.8, 12.8, and 7.8% of observed shape variation, respectively. Into this space we have projected the positions of all specimens in the sample in order to inspect the distribution of shapes in this space (Fig. 5). In addition, qualitative illustrations of the aspects of shape variation subsumed by each axis were obtained and confirmed via inspection of a series of models calculated from a regularly spaced sequence of along-axis point locations (as shown in Fig. 6).

Inspection of the distribution of data points in the PC subspace indicates that there are three loosely clustered regions in the plot of E-Surf 1 and E-Surf 2 (circled in Fig. 5). The first includes two accipiters and three falcons, the second a mix of accipiters, falcons, and eagles, the third includes eagles, vultures, kites, and buzzards as well as an *Accipiter* sp. and a small falcon. The humerus of *Buteo jamaicensis* is a shape outlier to these three groups, but does not fall so far away from the main concentrations of shapes so as to skew the distribution of the other points in the analysis. In the plane formed by E-Surf 2 and E-Surf 3 a large central group of points is evident, with two smaller outlying clusters; one toward the lower end of E-Surf 3 including members of the Aegypinae (vultures). Opposing this, *Elanus caeruleus* and *Geranospiza caerulescens* form a small second cluster. Overall, the low-dimensional ordination of shape variation presented in Figure 5 suggests that, while in some instances species in the same genus exhibit similar morphologies (e.g. *Buteo rufous* and *B. swainsoni* plot adjacent in each scatterplot), there is no obvious broad-scale taxonomic clustering at either generic or subfamily levels.

Comparing the actual specimens with the along-axis shape-variation trends that define the E-Surf 1–3 subspace, it can be seen that a humerus that projects to a position low on E-Surf 1 (e.g. *Falco rusticolus, Accipiter nisus*) possesses a large, pointed deltoid crest and rounded bicipital crest with a distinct bicipital furrow. A higher E-Surf 1 score (e.g. *Gyps bengalensis, Ictiniaetus malayensis*) is indicative of a more slender humerus with a long shaft relative to the much smaller and narrower deltoid crest, and flatter bicipital crest. Note that these eigensurface scores express purely shape-based similarities between the humeri, ignore the effect of size, and carry no necessary implications regarding the biological importance of the shape trends specified on this (or any of the other) shape-variation axes. Nonetheless, there is a highly significant correlation between E-Surf 1 and humerus size as expressed by humerus length as assessed by both the Pearson ($r = 0.524$) and Spearman ($r = 0.580$) coefficients ($\alpha = 0.01$).

The E-Surf 2 axis captures more subtle patterns of shape variation. No significant correlation with humerus length was observed in the scatter of species along E-Surf 2. Furthermore, taxonomically similar hawk taxa (e.g. *Buteo jamaicensis* and *Leucopeters albicollis*, both of which are members of the Buteonines A clade, see Fig. 2) projected to positions at opposing ends of this axis. Based on the calculated models, the main morphological difference expressed along E-Surf 2 is a slight shift in the angle of the apex of the deltoid crest and an increase in the size of the bicipital crest.

Size is again a dominant co-variant of E-Surf 3 (Pearson correlation coefficient $r = -0.618$, Spearman $r = -0.507$, $\alpha = 0.01$). Notably, the humeri of vultures in the Family Aegypinae, which are among the largest Falconiformes, cluster at the low end of this axis. Within the set of E-Surf 3 models (Fig. 6) we note that the deltoid crests are shorter and more pointed in specimens scoring higher on this axis; the
Figure 5. Ordination of the 50 falconiform humerus surfaces in the space formed by the first three eigensurface axes. When taken together this three-dimensional space accounts for 62.4% of observed surface shape variation. Species abbreviations are given in Appendix 1. Note the strong clustering of taxa into non-phylogenetic groups in the subspace, circled in the figure. The locations of these same specimens in the space formed by the first 21 eigensurface (E-Surf) axes (accounting for 95.4% of observed surface shape variation) were used as a summary of biologically important shape variation for all subsequent analyses. See text for discussion.
shafts are also thinner, and the bicipital crests smaller, smoother and positioned further proximally towards the humeral head.

The first 21 eigensurface axes, each representing a subtly different, but mutually independent trend in humerus surface morphology and each accounting for at least 0.5% of shape variation, were used as a set of variables in subsequent discriminant analyses and hypothesis tests. Together these axes accounted for 95.1% of observed 3D surface shape variation.

**Figure 6.** Models of the first three eigensurface (E-Surf) axes that describe the distribution of morphology among the 50 humerus specimens. Eigensurface axis 1 describes 41.8% of observed shape variation and shows clear differences in the shapes of the deltid and bicipital crests between high and low scoring specimens. Eigensurface axis 2 accounts for 12.8% of morphological variation and describes more subtle variation in the shape of the deltid crest. Eigensurface axis 3 includes 7.78% of surface shape variation and exhibits differences in the shape and position of the deltid and bicipital crests between specimens. See text for further discussion of the shape changes and interpretation of the morphological variation described by these model axes.
PHYLOGENETIC COVARIATION ANALYSES

The PGLS method employs a model of stabilizing selection about a constant mean while the PIC method employs a Brownian motion model. These models also differ in the assumptions they make about the data. Both were used in this investigation to provide a check that results obtained would be robust to different assumptions and models of evolutionary change.

As the falconiform cladogram specifies several polytomies, all permutations of the fully resolved cladogram were assessed. [We acknowledge here that one of the reviewers of this article questioned the need to perform analyses of separate forms of the cladogram. We decided to use the more conservative approach of cross-checking all fully resolved cladograms because documentation supplied with the COMPARE program specifies that only fully resolved cladograms can be submitted to COMPARE for analysis.] In both cases the empirical data presented to the procedure were the first 20 humerus eigensurface axes. All standardized contrast CVA spaces and statistical results were very similar. Accordingly, only the computationally simpler PIC analysis results will be reported here. A randomly chosen representative cladogram analysis is shown in Figure 7. Owing to the fact that a PCA of the group mean data captured all of the observed shape variation in 12 vectors, these 12 latent variables were used as the basis for the residual or standardized contrasts CVA.

If phylogenetic covariance (= the relative proportion of covariance values attributable to phylogenetic relationships among the species comprising the dataset) was a dominant factor in controlling the structure of humeral shape relationships within the dataset, the two sets of figures (Fig. 7A–B vs. 7C–D) should exhibit markedly different degrees of group separation in the ordination space. This was obviously not the case. The larger sized groups in particular are, for the most part, well separated from each other in both the total covariance CVA and standardized contrasts CVA ordination.

The impression given by inspection of Figure 7 – of well-developed group separation in the shape spaces irrespective of whether the raw data or the residuals of a PIC phylogenetic model are used as the basis for the CVA – was confirmed statistically using the $\phi$ test (Manly, 1994). In both cases very large values of the $\phi$ statistic were obtained ($\phi_{\text{raw PCA}} = 436.0$, $\phi_{\text{std. contrast PCA}} = 312.8$, d.f. = 144, $\rho = 0.0$), suggesting the probability of the observed ratio of between-group separation to within-group dispersion being obtained via random sampling from a single normal distribution was 0.0 in both cases. The similarity of the $\phi$ statistic values for both datasets is also noteworthy. This suggests that the placement of these phylogenetic groups within the eigensurface shape space does not exhibit a spatial structure that conforms to the predictions of the phylogenetic hierarchy predicted in Figure 2. In fact this can be seen in both Figure 5 and (more clearly in) Figure 7A and B. For example, contrary to the prediction of Figure 2, in both the original eigensurface and canonical variates spaces the centroid of the Accipiter & Harrier group is subequidistant from the centroids of Buteonines A and falcons & caracaras, whereas it is located much further away, but relatively equidistant from, Buteonines B and both elamine and pernine kites. These patterns of shape similarity make no sense from a strictly phylogenetic point-of-view, which is also what the comparison between eigensurface CVA and standardized-contrast CVA results show. The only conclusion that can be drawn from these results is that a factor (or factors) other than simple phylogenetic relationship is responsible for the geometric structure of humeral shape similarities and differences we observed.

NON-PHYLOGENETIC GROUP ANALYSES

The flight speed (1a) test examined the dataset for differences in humerus surface shape between fast and slow flying species. Analysis of flight style (1b) divided the study species into taxa that used chasing, perch-hunting, hovering, continuous low flight, and soaring flight when foraging for prey. A second analysis (2) tested humeral surface shape differences between the humeri of birds that foraged in forests and those that foraged in open areas. Finally, an analysis of population movements was used to investigate differences between sedentary and long-distance migrant species (3). For each CVA, between 10 and 21 of the shape variation axes (= latent shape variables) with the highest associated eigenvalues were used. These represented between 87.2 and 95.1% of the morphological variation within each dataset. In the summaries that follow we present results for the optimal variable set chosen in each case, the eigenvalues of associated CV axes, the shape changes as identified by the CVA models, and the distribution of specimens in the ordination space as a series of along-axis models. The accuracy with which species could be correctly assigned to each group was also evaluated, along with the robustness of the overall shape difference-mediated group classifications.

(1a) Flight speed

Specimens from 26 fast flying and 21 slow flying species were included in this analysis (see Appendix 1). Although flight speed represents a continuous variable, it was clear from published behavioural
Figure 7. Results of a CVA for the original 20 eigensurface variables (A and B), and a projection of the original data into a space formed by the eigenvector decomposition of the covariance matrix of the standardized contrasts between internal nodes of the cladogram in Figure 2 as modelled by the phylogenetically independent contrasts method (C and D, see text for discussion). Note the well-defined lineage-group separation achieved by both analyses and the overall similarities in lineage-group placements relative to one another. The fact that highly structured lineage-specific differences in shape variation remain part of the system even after phylogenetic contrasts have been removed strongly suggests that the dominant shape variation factors being expressed in the eigensurface space cannot be accounted for under a simple model of phylogenetic covariation. See text for discussion.
descriptions that birds of prey fell broadly into two groups: (1) species that generally use chase or perch-hunting which fly fast to capture their prey, and (2) those which use slow, low quartering flight or soaring fight to search for food. In three cases flight speed was either too variable or could not be accurately determined from the behavioural or ecological literature. These species were omitted from this analysis.

Using a dataset comprising the first 21 eigensurface axes, 97.9% of specimens (46 of 47) could be assigned post hoc to the correct flight-speed group. This result indicates that consistent humerus shape differences do reflect the distinction between slow-flying and fast-flying falconiforms. Eigensurface axes 1–4 were the most important components of the model. When fewer or more axes were included the number of specimens correctly assigned did not improve.

The percentage accuracy and the percentage correctly assigned when using a jackknifed cross-validation test was shown to decrease if fewer than 21 axes were used. Using this set of 21 eigensurface axes, the non-parametric \( \phi \) likelihood ratio test (LRT, see Manly, 1994) of 10,000 replicates showed that there was effectively zero (0.003%; d.f. = 21) probability that this result could have been obtained from a dataset of identical composition that did not exhibit subgroup structure. A jackknifed cross-validation (JCV) test was used to assess how effectively the CVA scores would predict group membership of new taxa included in the dataset and to provide a measure of the robustness of these results (see Methods). For this dataset, the JCV method indicated that 84.8% of the specimens could be robustly assigned to the correct flight-style group. This high proportion of correct assignments using a permuted dataset indicates that the orientation of the CVA axes and the shape changes we observe along this axis are consistent and could be used to identify unknown falconiform humeri from species included in the training set.

As this analysis was used to distinguish between specimens in only two groups, a single CVA axis (CV-1) describes the difference between the fast-flying and slow-flying ecological groups. The distribution of falconiform taxa and the variation in morphology modelled along this CVA axis are presented in Figure 8. These models show a clear difference in the morphology of fast-flying and slow-flying taxa, with low and high scores on this axis being determined by the relative size of the deltoid crest and the roundness of the bicipital crest. Taxa with high scores (greater than \(-2.0\)) on the CV-1 axis (e.g. the low flying \( Milvago chimango \) and the soaring \( I. malayensis \)) exhibit more slender humeri with narrower shafts and smaller deltoid crests, i.e. a smaller area available for attachment of the pectoralis muscle. The deltoid crest in these species is also oriented at a slightly more acute angle to the bicipital crest, and the bicipital surface is relatively flat. Low scoring species along CV-1 (e.g. \( A. tachiro \) and \( E. caeruleus \), both of which often use fast bursts of flapping flight to capture prey) exhibit substantially larger deltoid and bicipital crests, with the deltoid crest oriented at a less acute angle relative to the bicipital crest, and the bicipital surface forming a larger, rounded, domed area, medial to the humerus head.

Only one specimen, \( Spilornis cheela \), a fast-flying species (CV score \(-3.12\)), was misclassified as a slow-flying species on the basis of its proximity to the two group centroids. A score of this magnitude is indicative of an intermediate morphology, with a deltoid crest of intermediate size and neither particularly rounded nor flattened bicipital surface. \( Spilornis cheela \), the crested serpent eagle, is known to still-hunt from perches and occasionally soar on thermals over the forest canopy. Other species with intermediate scores included \( H. leucogaster \) and \( B. platypterus \), both of which most frequently use perch hunting, but also use soaring or hovering flight to search for prey. Therefore, these CVA results not only revealed consistent and interpretable humerus shape differences between the fast-flying and slow-flying groups, but also correctly placed species characterized by intermediate flight velocities.

In some cases, all members of recognized phylogenetic clades used in this study fell into the same behavioural group (e.g. \( Aegypini \)ae are all slow-flying scavengers, while \( Accipiter \) sp. are fast fliers). However, no taxonomic clustering was observed within the two flight-speed groups along the CVA axis. Student’s \( t \)-tests highlighted a significant difference in mean humerus length between fast- and slow-flying birds (\( t = -2.075 \), d.f. = 45, \( p < 0.05 \)) and the CV-1 ordination pattern was significantly correlated with humerus length (Pearson correlation coefficient \( r = 0.383, \alpha = 0.01 \); Spearman \( r = 0.434, \alpha = 0.01 \)) as well as with the average body weight for birds in that species (as noted in Dunning, 1993; Pearson correlation coefficient \( r = 0.309, \alpha = 0.05 \); Spearman \( r = 0.323, \alpha = 0.05 \)). These results suggest that taxa which exhibited a more definite ‘fast-flier’ like morphology were generally smaller species, while the more clear-cut slow fliers included larger species such as vultures and eagles. Nevertheless, it should be noted that the highest scoring bird species on the CV-1 axis, \( M. chimango \), is a small, low-flying falconid.

(1b) Flight style
For this test the study set was divided into five flight-style groups consisting of chasing (6), perching (17), hovering (4), low-flying (7) and soaring (8)
species. Eight taxa that had unknown or variable flight styles were not included in this analysis. To assess whether humerus shape is influenced by the way in which muscles are used in flapping flight, it was important to examine whether there are indeed marked differences in humerus morphology between each of these flight style groups.

For this five-group analysis an optimal dataset of the first 13 eigensurface axes was found to give the highest accuracy, with 88.1% (37 of 42 specimens) assigned post hoc to the correct group and effectively 0% (less than 0.000%; d.f. = 52) probability that a group centroid separation this extreme could result from random sampling of a single population. A con-

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**Figure 8.** Ordination of the falconiform species for which accurate flight speed information was available (47 species) within the space of the first two canonical variates axes of 21 eigensurface shape variables. Based on this result 97.9% of the training set species were assigned to their correct flight-speed groups on the basis of proximity of their projected positions to the group means. Shape models below the ordination plot represent along-axis coordinate locations through the canonical variates space for CV-1 calculated using the method of MacLeod (2007). Major differences can be seen in the size of the deltoid crest (DC) and the bicipital crest (BC), and in species with lower scores the bicipital surface (BS) is larger and more rounded, forming a dome. Note the CV-2 axis contains no information with regard to group discrimination and should not be interpreted. Species abbreviations are listed in Appendix 1.
fusion matrix summarizing the number of species assigned to each group is shown in Table 2. Using a JCV test, on average 63.4% of the species included in the study set were correctly assigned using a sequentially permuted dataset. This is a remarkably high accuracy and consistency level considering that there are five groups in this analysis (at best a 20% accuracy level would be expected using a random dataset) and considering the small sample size in the training set for some groups.

Figure 9 illustrates the distribution of humerus surface shapes on the four CVA axes used to distinguish between the five groups. CV-1 and CV-2 together accounted for 73.7% of between-groups shape variation, while CV-3 and CV-4 represented the remaining 26.3% of the variation. In Figure 10, sets of models are presented illustrating the changes in humerus surface shape along the axes that define the flight-style discriminant space.

The first axis, CV-1, representing 42.2% of morphological variation, principally separates the three groups that use continuous flight to search for prey: hovering species (scores \(< -2.0\) ), species that used continuous low flight (\(-2.0\) to 0.0), and soaring species (scores \(\geq -1.0\)). Given the difference in size between soaring and hovering species, CV-1 is strongly correlated with both humerus length (Pearson correlation coefficient \(r = 0.734, \alpha = 0.01\); Spearman \(r = 0.674, \alpha = 0.0\)) and average weight of individuals in each species (Pearson correlation coefficient \(r = 0.738, \alpha = 0.01\); Spearman \(r = 0.632, \alpha = 0.01\)). The sequence of CV-1 models shows a clear difference between high-scoring soaring birds and low-scoring hovering species (Fig. 10). High-scoring species were mostly members of the Aegypiiinae, the vulture subfamily, and were characterized by having slender humeri with narrow deltoid crests, a more domed humeral head, and an external tuberosity in a more proximal position. The low-scoring hovering taxa, including *E. caeruleus* and two species in the genus *Falco*, are characterized by humeri with large, pointed deltoid crests, flatter humeral heads, more rounded bicipital crests, and deeper bicipital furrows (Fig. 10).

The second CV axis represented 31.5% of morphological variation among specimens and captured the difference between the low-flight, perch-hunting and chase-hunting groups. This axis can be interpreted as representing a progressive shift in flight speed and the effort required for each flight style, as well as the amount of time spent on the wing in search of food. As such, species that use continuous flight (hovering, low flight, soaring) all scored below –5 on this axis. The CV-2 axis was not correlated with size parameters (humerus length, average weight). Shape changes were similar to those along CV-1; high-scoring chase-hunting birds (e.g. *F. mexicanus* and *F. rusticolus*) having much broader, robust-looking humeri, with larger, more pointed, and prominent deltoid crests. The bicipital crest is also markedly larger in high-scoring species. Low-scoring taxa (e.g. *Milvus migrans*, *Melierax canorus*, *F. sparverius*) are characterized by slender humeri with a narrow shaft (Fig. 10).

Perch-hunting species clustered in the centre of the CV-1/CV-2 plot; however, on the CV-3/CV-4 plot, low-scoring species along CV-3 are dominated by perch-hunters. On this axis, which represented 14.7% of observed surface-shape variation, perch-hunting species all scored below –2.0. The four lowest scoring species were all accipiters while the three highest scoring species were falcons. This axis was not significantly correlated with size parameters, and differences in shape along this axis were more subtle than was the case for CV-1 and CV-2. Again the most important shape differences between low-scoring and high-scoring species involve the size and shape of the deltoid crest. In low-scoring species (e.g. *Accipiter*

Table 2. Confusion matrix for the five-group flight style analysis

<table>
<thead>
<tr>
<th>Group</th>
<th>Chase</th>
<th>Hover</th>
<th>Low-flight</th>
<th>Perch</th>
<th>Soaring</th>
<th>Total</th>
<th>Percentage correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chase</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>Pbu</td>
<td>0</td>
<td>6</td>
<td>83.3</td>
</tr>
<tr>
<td>Hover</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>100</td>
</tr>
<tr>
<td>Low flight</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>100</td>
</tr>
<tr>
<td>Perch</td>
<td>0</td>
<td>Acf</td>
<td>Stc, Pea</td>
<td>14</td>
<td>0</td>
<td>17</td>
<td>82.4</td>
</tr>
<tr>
<td>Soaring</td>
<td>0</td>
<td>0</td>
<td>Im</td>
<td>0</td>
<td>7</td>
<td>8</td>
<td>87.5</td>
</tr>
<tr>
<td>Total</td>
<td>5</td>
<td>5</td>
<td>10</td>
<td>15</td>
<td>7</td>
<td>42</td>
<td>88.1</td>
</tr>
<tr>
<td>Percentage</td>
<td>100</td>
<td>80</td>
<td>70</td>
<td>93.3</td>
<td>100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Abbreviated names are provided for incorrectly assigned specimens, whose scores indicated a closer proximity to the centroid of a group to which they did not belong; 88.1% of species (37 of the 42 specimens) were assigned to the correct flight style groups. Species abbreviations are listed in Appendix 1.
Figure 9. Ordination of the falconiform species for which foraging flight-style information was available (42 species) within the space of the four canonical variates axes established in a CVA using 13 eigensurface shape variables. The distribution of humerus shapes on the first two CV axes (above) together accounted for 73.7% of between-groups humeral shape variation, while CV-3 and CV-4 (below) together represent the remaining 26.3% of the variation used to distinguish between the five flight-style groups: perch-hunting, chasing, hovering, soaring, and low-flight. Based on this result 88.1% of training set species were assigned to their correct flight-style groups on the basis of proximity to the group means. Shape models representing along-axis coordinate positions through the canonical variates space are shown in Figure 10, highlighting morphological features that were particularly important in distinguishing between high- and low-scoring species on each CV axis. Species abbreviations are listed in Appendix 1.
Figure 10. Shape models representing along-axis trajectories through the canonical variates space for the CVA of flight style [CV-1 (first row), CV-2 (second row), CV-3 (third row) and CV-4 (fourth row)]. Models were calculated using the method of MacLeod (2007). Detailed inspection of the CV-1 models revealed that low scoring hovering taxa had humeri with larger, more pointed deltoid crests (DC), more rounded bicipital crests (BC) and more distinct bicipital furrows (BF); in higher scoring soaring taxa the humerus is more slender with a flatter appearance, the humeral head (H) is more domed and the external tuberosity (ET) is in a more proximal position. The CV-2 axis represented a shift between chase-hunting, perch-hunting, and low-flying species. From the CV-2 models it is clear that higher scoring taxa have more robust humeri with a thicker shaft (S), larger DC and BC. In specimens that have a lower score on CV-3 (which tended to be perch-hunters), the distal portion of the deltoid crest (DC distal) is larger than in higher scoring specimens, which have smaller DCs and less defined BFs. A high score on CV-4 is indicative of a flatter bicipital surface and a smaller DC (particularly the proximal portion) that extends further down the shaft.
that were assigned to different flight style groups, analysis is that species in the same genus or family higher scores along this axis. The lowest scoring species on CV-4 were in the low-flight group, while soaring species tended to have higher scores along this axis.

One striking result obtained in the flight-style analysis is that species in the same genus or family that were assigned to different flight style groups, such as Milvus migrans and M. milvus and members of the genus Falco, were generally assigned to the correct regions of the flight style shape space. This suggests that differences in humerus surface shape in relation to flight style are evident at the species and genus levels. That said, there was clear taxonomic clustering in that most soaring birds were vultures in the subfamily Aegypiinae, all accipiters were perch hunters, and falcons were either chase hunters or hovering species.

In summary, all five flight-style groups could be distinguished by their humerus surface morphologies alone with a high degree of accuracy, with 88.1% of taxa correctly assigned (Table 2). The CVA model was robust to permutations in the dataset and there was effectively no chance that this result could have been generated by random sampling error. The distribution of specimens in the CV shape space indicates that the most marked difference in humerus shape was between soaring and hovering species (expressed along CV-1) followed by a gradation between species that utilize low-flight, perch-hunting and chase-hunting to forage for prey (CV-2). These shifts in the speed and amount of energy required for flight, as well as the amount of time spent on the wing, were reflected in changes in the size and shape of the deltoid and bicipital crests that can be identified clearly on the 3D visual models of the discriminant space axes (Fig. 10).

(2) Habitat
In this analysis the humerus surface shapes of forest-dwelling falconiform species (15) were compared with those living and foraging in open habitats (22). Thirteen taxa that foraged either in a variety of habitats or in sparsely wooded habitats were excluded from this analysis. Using 18 eigensurface axes a single CV discriminant axis was calculated which correctly assigned post hoc 91.9% (34 of the 37 specimens) to the correct habitat group. However, results of a ϕ test (Manly, 1994) indicated that there was a statistically significant probability (ϕ = 15.7%; d.f. = 18) that this degree of separation could be explained as a result of random differences between samples drawn from a single underlying distribution. Using a JCV test, on average 55.6% of taxa could be accurately assigned to forest or open habitat groupings using a permuted dataset. This is a relatively poor level of accuracy compared with the other CVA results in this study, given that there were only two groups in the analysis.

The differences between humerus shapes of open habitat and forest habitat birds are therefore extremely subtle (Fig. 11). The size and shape of the deltoid crest, for example, shows little change between habitat model 1, representing an extreme open habitat-type morphology, and habitat model 5, an extreme forest-type humerus shape. No significant difference in humerus length or the average body weight of species in different habitat groups was evident and there was no significant correlation of CV-1 score with these size parameters. Given access to more data it may be possible to identify statistically significant shape distinctions between forest and open habitat dwellers. However, both ϕ and JCV test results show that although clear differences between the observed humerus surface shapes characteristic of these groups exist, it is not possible to rule out the interpretation that this difference might be an artefact of chance sampling error using the current dataset.

(3) Migratory movements
As a final example, CVA was used to examine the covariation between migratory behaviour and humerus morphology, to test whether there are specific skeletal and muscular requirements necessary for long-distance sustained flight. Only bird species that exhibited long-distance migration (11 species) or were always sedentary (21 species) were used in this analysis. Those which migrate only in certain years, or have dispersive or nomadic behaviours were omitted.

For this test an optimal set of ten eigensurface axes achieved the most robust and accurate results in a CVA: 90.6% (29 of the 32 specimens) were assigned post hoc to the correct behavioural categories. A ϕ test (Manly, 1994) of these data found that the probability of achieving a centroid separation of this magnitude using a dataset that lacked subgroup structure was 2.5% (d.f. = 10), slightly above the traditional level of statistical significance. Owing to the marginal level of statistical significance achieved by this result, and to the large effect only a single misclassification can have on the performance summary in such a small sample, a brief further interpretation of these shape
Figure 11. Ordination of the falconiform species for which foraging habitat information was available (34 species) within the space of the first two canonical variates axes of 18 eigensurface shape variables. Based on this result 91.9% of training set species were assigned to foraging habitat groups correctly on the basis of proximity to the group means; however, a likelihood ratio test showed that there was a 15.6% chance that this result could have been achieved using a dataset that lacked subgroup structure, and a cross-validation test could only accurately assign 55.6% of species to the correct habitat group. Rows of shape models below the ordination plot represent along-axis coordinates through the canonical variates space for CV-1 calculated using the method of MacLeod (2007). Although differences between the models were extremely subtle, in higher scoring specimens the bicipital crest (BC) extends slightly further distally towards the shaft and the bicipital surface is slightly flatter. Note the CV-2 axis contains no information with regard to group discrimination and should not be interpreted. Species abbreviations are listed in Appendix 1.
trends is offered below for heuristic reasons and under the assumption that increasing the size of the dataset would improve the significance of the result.

Differences in morphology between these subgroups are quite subtle (see Fig. 12). Low-scoring species (long-distance migrants such as *F. subbuteo*, *F. vespertinus* and *Hieraetus wahlbergi*) have slightly broader humeri with larger deltoid crests, the region around the humeral head is smoother, and they exhibit a more prominent bicipital furrow. High-scoring species

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**Figure 12.** Ordination of the falconiform species for which migratory behaviour information was available (32 species) within the space of the first two canonical variates axes of ten eigensurface shape variables. Based on this result 90.6% of training set species were assigned to migratory behaviour groups correctly on the basis of proximity to the group means. Rows of shape models below the ordination plot represent along-axis coordinates through the canonical variates space for CV-1, calculated using the method of MacLeod (2007). In high-scoring taxa the external tuberosity (ET) is more prominent and other protrusions may be noted around the humeral head (H), while in lower scoring taxa the humeral head has a smoother, more rounded appearance. See text for further discussion. Note the CV-2 axis contains no information with regard to group discrimination and should not be interpreted. Species abbreviations are listed in Appendix 1.
(representing sedentary taxa) are characterized by relatively slender humeri with a more prominent external tuberosity and other protrusions around the humeral head.

Two sedentary species, B. rufouscus and Gypaetus barbatus, were incorrectly assigned to the migratory group based on proximity to the group centroids. One specimen from a migratory species, Circus cyaneus, also projected to a position much closer to the mean CV score for sedentary taxa. No obvious phylogenetic grouping was evident in the distribution of scores along the CV-1 axis. Although no significant difference in humerus length or body weight was found between species that were either migratory or sedentary, a significant correlation was found between the distribution of species along this CV axis and average body weight (Pearson’s $r = -0.304$, $\alpha = 0.05$), such that specimens with a more characteristic sedentary-type humerus shape are more likely to come from heavier bird species.

Using a JCV analysis, 80.7% of specimens were correctly classified as being in the migratory or sedentary behavioural groups. These results suggest that, despite its marginal statistical significance, the discriminant model is stable to changes in the composition of the training dataset. Overall, this CVA model, which correctly assigned 29 of the 32 specimens in the training dataset to migratory or sedentary groups, suggested that migratory species do tend to have a distinctive and consistent humerus morphology whose variation falls outside the broad range of morphologies observed in sedentary taxa.

**GROUP ANALYSES RESULTS SUMMARY**

A summary of the key shape changes in models for each CVA is presented in Table 3. Considering all analyses, more than 85% of specimens were correctly assigned to the designated ecological/behavioural groups. In both the flight speed and the flight style analyses there was tantamount to 0% probability that their results could have been achieved from datasets that lacked a consistent subgroup structure, and for the analysis used to distinguish migratory from sedentary species there was less than 5% chance of this interpretation being correct. For the analysis of

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Groups</th>
<th>Percentage correct (JCV)</th>
<th>LRT</th>
<th>CV axis length (%)</th>
<th>Morphological changes with increase in CV score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flight speed</td>
<td>Fast / slow</td>
<td>97.9 (84.8)</td>
<td>0.00</td>
<td>CV-1 (100)</td>
<td>More slender humerus with significantly smaller DC and BC. BS is flatter and DC at a more acute angle to BC.</td>
</tr>
<tr>
<td>Flight style</td>
<td>Chase/hover/perch/soaring/low flight</td>
<td>88.1 (63.4)</td>
<td>0.00</td>
<td>CV-1 (42.2)</td>
<td>Narrower DC with less pointed tip; flatter BC; less prominent BF; H more domed; ET in more proximal position.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>CV-2 (31.5)</td>
<td>More robust shape; thicker shaft; larger DC with more pointed tip; larger BC; ET more distal.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>CV-3 (13.7)</td>
<td>Smaller DC (esp. distal portion). Less defined BF</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>CV-4 (11.6)</td>
<td>Smaller BC; flatter BS; smaller DC (esp. proximal portion). DC extends further down shaft.</td>
</tr>
<tr>
<td>Vegetation cover</td>
<td>Forest/open</td>
<td>91.9 (55.6)</td>
<td>15.7</td>
<td>CV-1 (100)</td>
<td>Differences very subtle. BC slightly larger and in a more distal position.</td>
</tr>
<tr>
<td>Migration</td>
<td>Migratory/sedentary</td>
<td>90.6 (80.7)</td>
<td>2.54</td>
<td>CV-1 (100)</td>
<td>More slender humerus shape. More prominent ET.</td>
</tr>
</tbody>
</table>

The percentage correctly assigned in jackknifed cross validation (JCV) analysis gives a measure of the robustness of the results to permutations in the training set. A low likelihood ratio test (LRT) probability (less than 5%) denotes that there is less than a 5% chance that similar results could have been achieved using a random dataset that lacked subgroup structure. The amount of variation explained by each canonical variates axis (CV axis length, %) is also presented, along with key morphological features of the models that are used to distinguish ecological groups. DC, deltoid crest; BC, bicipital crest; BF, bicipital furrow; BS, bicipital surface; ET, external tuberosity; H, humeral head.

foraging habitat, however, it was likely (over 15% chance) that this degree of group separation could have been the expected result of error due to random sampling from a single underlying distribution. Additionally, for the two-group flight speed and migration analyses, a JCV test showed over 80% accuracy using a sequentially permuted dataset, indicating that these results are highly robust to changes in the training dataset. In the five-group CVA of flight style, at 63.4% this measure of robustness was also well above the 20% accuracy level that would be expected under random group assignment.

In all cases in which group separations were clearly and/or marginally significant, the CVA made it possible to identify key morphological features of the humerus that could be used to distinguish falconiforms belonging to different ecological groups via qualitative inspection, despite the fact that qualitative inspections of these structures prior to our investigation had failed to identify these shape differences as reliable indicators of functional or behavioural state. In particular, the size and shape of the deltoid crest was found to be an important feature of all models and was particularly important in distinguishing fast-flying from slow-flying taxa, as well as for distinguishing between taxa that used soaring or hovering flight (flight style CV-1), and between chase/perch hunters and species which use continuous flight to search for prey (flight style CV-2). By looking at the distribution of specimens in the eigensurface-mediated CVA ordinations, it was possible to assess the relationship between taxonomy and morphology in terms of ecological group membership. Although in some cases all members of the same genus or subfamily included in the sample dataset fell in the same ecological group, overall there was little evidence of within-group taxonomic clustering in humerus surface shape variation in any of our analyses.

DISCUSSION

The results obtained by our quantitative ecomorphological analyses indicate that species-level variation in the falconiform humerus contains a number of excellent examples of the way in which aspects of species ecology, habitat, and behaviour are reflected in skeletal morphology. The shape and size of humerus regions vary because different wing shapes and associated muscle anatomies are required for different flight styles. Raptors exhibit significant between-species differences in muscle size and muscle enzyme activity (Corvidae, Bierregaard & Peters, 2006). Previous studies have also identified torsional stress as being the main constraint on the design of bird wing long bones (De Margerie et al., 2005) and that, within an individual’s lifetime, wing bone morphology changes to adapt to shifts in force applied through muscle tension (Mosley et al., 1997).

In this investigation we observed that shape variation in the 50 falconiform humeri showed several distinctive modes of 3D surface-shape variation. This dataset was selected to encompass as much of the morphological, taxonomic, behavioural, and ecological variation within the clade as possible, given a modestly sized dataset. Although in some instances ecology is reflected in phylogenetic groupings (e.g. all Gyps species are large soaring birds, all Accipiter species use perch hunting methods), our results indicate that variation in humerus morphology, as illustrated by the plots of the subspace formed by the three most important eigensurface axes, for the most part did not reflect currently recognized phylogenetic groups. It is also notable that despite many phylogenetic studies questioning the relatedness of the Falconidae and Accipitridae within the avian phylogeny (e.g. Ericson et al., 2006; Hackett et al., 2008) we did not find that the members of the Falconidae represented in this study had humerus shapes that were particularly distinct from those of the rest of the study set.

These findings were confirmed by an explicit comparative method analysis insofar as PIC-estimated and PGLS-estimated models of expected patterns of standardized contrasts covariance between the avian lineages included in our dataset failed to account for shape-related differences in humeral morphology. Provided this result holds true in light of more detailed and robust avian phylogenies and a more taxonomically comprehensive dataset, it represents compelling evidence for our core thesis: that ecological, environmental, and behavioural influences can explain much of the variation in morphologies we see in nature. The extensive reshuffling that has been seen both in raptor systematics and the avian tree as a whole as a result of DNA-based phylogenetic analyses over the last decade (e.g. Lerner & Mindell, 2005; Hackett et al., 2008; Pacheco et al., 2011) is no doubt at least partly related to the high degree of morphological convergence seen among avian clades (see Kemp & Crowe, 1994; Lerner & Mindell, 2005; Haring et al., 2007). Caution should therefore be used when conducting phylogenetic analyses relying on osteological data (such as Holdaway, 1994; Livezey & Zusi, 2007), as many anatomical features are likely to be adaptations to a particular way of life.

FLIGHT SPEED/STYLE AND HUMERUS MORPHOLOGY

The first eigensurface axis (40% of observed shape variation) was the most heavily weighted of all axes when used to separate fast- and slow-flying taxa, and the first four eigensurface axes (68.4%) held the top
four weightings in this CVA. From this we concluded that the principal differences in humerus shape among falconiforms are related to flight speed. This axis was also strongly correlated with size and average body weight, a result that indicates that allometry has a significant influence on aspects of falconiform humerus shape. In itself this is unsurprising as larger and heavier birds will require disproportionately larger and/or more efficient wings to lift them off the ground. Similarly, wing loading (body weight/wing area) affects the amount of power required for flapping flight (Pennycuick, 2008) and so will affect the size and attachment position of wing muscles.

More unexpected was the extent to which localized regions of humerus morphology were found to covary with ecological factors including aspects of flight behaviour and ecology. We may infer that these differences were determined by musculoskeletal requirements for different modes of flight that have been ‘tuned’ by evolutionary processes over time to optimize performance in different environmental or habitat settings.

For example, variation in the size and shape of the deltoid crest was identified as a key feature in distinguishing fast and slow fliers, as well as those which use soaring and hovering (flight style CV-1) and those which use chase-hunting, perch-hunting and low-flight to search for prey (flight style CV-2). Fast-flying birds, including those that use chase-hunting or perch-hunting, have deltoid crests with a much larger attachment area for the pectoralis, the muscle which provides power for the down-stroke in bird flight, than those characteristic of slower fliers. Dial et al. (1997) noted that patterns of forces of torsional stress on the deltoid crest during flight in the magpie (Pica pica) match remarkably well with predictions of aerodynamic power. As flapping fliers have much larger pectoralis muscles than soaring fliers (Corvidae et al., 2006), they require this increased area of muscle attachment to prevent muscle and bone breakage. Slow soaring flight, on the other hand, requires a steady tensional force in the pectoralis, pulling down on the humerus nearer the shoulder joint (Swartz, Bennett & Carrier, 1992). Accordingly, a smaller area for muscle attachment is required.

Previously, pectoralis power indicators have been used to distinguish soaring birds from low-flying and fast-flying species, showing that different styles of flight have different power requirements (Tobalske et al., 2003; Pennycuick, 2008). There are, however, numerous other subtle differences in humerus shape that our investigation found to be associated with different flight-style groups, reflecting functional differences in the size and attachment position of other wing muscles. Our results indicate, for example, that hovering species have distinctive humerus shapes that differed substantially from those of the other species in the sample, and are very distinct from those of high soaring species. This similarity may reflect the specialized rotating wing movements that have been observed in these species during hovering flight (Swartz, Bennett & Carrier, 1992), when power comes not only from the down-stroke, but also the upstroke (supracoracoideus muscle). As the birds sweep their wings forward and backward from a more vertical position they use a distinct set of muscles, including the brachialis and coracobrachialis cranialis (Corvidae et al., 2006). While ours is the first investigation to document shape similarities in humeri of hovering species such as Falco vespertinus, F. sparverius, and Elanus caeruleus, additional comparative anatomical and morphometric research will be needed to determine whether other hovering species (e.g. the osprey, terns, kingfishers) also exhibit this characteristic humerus shape such that a tendency to use hovering flight could be recognized from humerus shape alone.

HABITAT

It had been hypothesized previously that, as forest birds need to use flapping flight to navigate around trees and in forested areas, the use of soaring or quartering flight to search for prey is precluded by vegetation cover that conceals prey items, and forest-dwellers should be more likely to have a humerus shape similar to that of chasing or perch-hunting birds. In this way, foraging mode has been linked to habitat use in some studies (e.g. Gamauf et al., 1998); however, other studies have shown these behavioural and ecological factors to be unrelated (e.g. Janes, 1985).

Here, CVA and humerus shape modelling was used to model the humerus shape distinctions that could be used to distinguish forest and open habitat species. Although $\phi$ and JCV tests showed that there was a significant possibility that similar results could have been achieved by random sampling from a single underlying shape distribution, forest species tended to have slightly larger bicipital crests that extended further distally towards the shaft, providing some support to the argument that forest birds have larger wing flexor and propatagial tensor muscles (Corvidae et al., 2006). Using a larger dataset or by application of this data analysis strategy to a different avian group it may be possible to recover differences that do meet the traditional threshold of statistical justification. Indeed, increasing the mesh resolution of our 3D data may improve the statistical confidence of the falconiform
discrimination. Regardless, our data indicate that although flight style may be related to habitat in some cases (e.g. for species that exhibit a particular preference for open areas), a wide range of flight modes may be used successfully in this type of habitat. Consequently, habitat in itself is not a strong or reliable predictor of humerus shape, at least not in our sample. In attempting to understand the effect of habitat on bird form it might be more informative to link anatomical and physiological adaptations in skeletal morphology directly to the structural, muscular, and energetic requirements associated with a species’ most frequently used flight style and hunting strategy.

MIGRATION

Several previous studies have examined the question of whether wing tip shape varies between migratory and sedentary species, although most have failed to detect significant differences once phylogenetic and morphological adaptations are controlled (Lockwood, Swaddle & Rayner, 1998). Our investigation detected significant differences between the humerus shapes of long-distance migrants and sedentary species. These results indicated that long-distance migrants tended to have smoother, more robust humeri with a larger deltoid crest and less prominent protrusions such as the external tuberosity.

There is considerable selection pressure exerted on long-distance migrants to use energy-efficient flight modes (Lockwood et al., 1998). Consequently, when engaged in long-distance, non-time-restricted migration, raptors typically use soaring flight and fly either at or slightly below the minimum speed required to stay aloft, thus optimizing energy conservation (Lockwood et al., 1998). Based on this theoretical relationship, it would be predicted that migratory raptors exhibit humerus morphologies similar to those of soaring birds (e.g. long, slender humeri with relatively small deltoid crests). The results obtained in this part of our analysis are, therefore, unexpected and interesting in that our sample contains migratory species characterized by robust humeral morphologies with relatively large deltoid crests. This pattern may indicate the presence of unique and novel muscular adaptations in migrating raptors designed to be optimal for prolonged periods of flight covering long distances. In migrants, for example, the ability to use powerful flapping flight when necessary may be important in increasing survival and distance covered when flying along a particular chosen route in the face of changing wind conditions.

Although there did not appear to be any overt phylogenetic clustering of species along the migration CV model axis, the effect of our small sample size for this group cannot be excluded as the ‘cause’ of this result. In addition, it may be that a more complete geometric analysis of humerus morphology would produce results that conformed to the expected pattern. Regardless, additional investigation will be needed to resolve this issue. What can be said at present is that (1) there may be more to the interpretation of this association than has been suspected to date and (2) the tools necessary for a more complete evaluation of the relationship between humeral morphology and migratory behaviour are now available.

NEW METHODS IN ECOMORPHOLOGICAL ANALYSIS

In the study of ecomorphology it is important to use sufficiently large morphological character sets to enable accurate description of shape variation (Leisler & Winkler, 1991). Our eigensurface-based analysis proved to be highly accurate and sensitive to the assessment and summarization of subtle and complex patterns of morphological variation. This, in turn, allowed those aspects of humerus shape variation that exhibited the greatest between-groups variation to be found and used in the characterization, testing, and quantitative modelling of between-group differences. Our results extend the utility of eigensurface analysis as a generalized approach to quantitatively testing a wide variety of morphological hypotheses (for a comparison between eigensurface results with those obtained using 2D eigenshape and landmark-based relative warps methods, see MacLeod, 2008). The CVA modelling method used herein also illustrates how the analyst can qualitatively as well as quantitatively examine and communicate stepwise changes in form between one morphotype and another, thereby highlighting the most important functional differences between groups for different audiences in a seamless and rigorous manner.

In the majority of previous ecomorphological investigations, linear measurements were used to quantify and model variation in form. In avian studies these are usually related to wing length, wing aspect ratio, and feather lengths (e.g. Janes, 1985; Gamauf et al., 1998), despite the widely acknowledged fact that such measurements are often imprecise, difficult to interpret, and influenced strongly by body size (e.g. Lockwood et al., 1998). More to the point, these strategies force a severe abstraction on the assessment of morphological variation in these admittedly complex structures; so much so that the precise nature and locations of covariance between morphology, ecology, and behaviour have been often obscured. As a result, few studies have looked at the functional anatomy of the humerus despite the fact that its complex, 3D
structure shows much more variation in form than bird wings. By looking at points of muscle attachment in the skeletal wing apparatus and on shapes modelled at discrete locations within eigensurface and CVA ordination spaces, important functional differences in muscle placement, orientation and use can be inferred directly.

Eigensurface analysis and related 3D techniques make it possible to determine how the precise form of this bone differs between species, and which parts of the humerus shape covary with aspects of the taxon’s function, ecology, and behaviour. However, morphology, ecology, and behaviour are all aspects of evolutionary relationships (Meloro et al., 2008) and the constraints of phylogeny that have an influence on the morphology of extant species must be kept in mind when making interpretations in any of these areas. Between-group differences in form are the result of a complex concatenation of influences and cannot be interpreted as due purely to the functional requirements of ecological mode. In our study, small sample size and limited sampling of humerus morphology prevented us from providing a truly comprehensive analysis of this fascinating character complex. Nevertheless, our results are valid both for the region of the humerus we studied and the selection of species in our sample, which is representative of the falconiform clade as a whole. Although we do not presume to have said the last word on this subject even in terms of falconiform evolution, we do contend that our results are sufficiently robust and sufficiently complete to answer the questions posed in our Introduction: whether variation in humerus morphology among birds is structured in such a way as to reflect species-specific function, lifestyle, habitat, and behaviour. Our results indicate the answer to each of these questions is ‘affirmative’ in each instance.

CONCLUSIONS

Our findings support a strong relationship between falconiform ecology and humerus morphology, providing a comprehensive demonstration of the way in which 3D morphometric analysis can be used to quantify and accurately model subtle variations in skeletal morphology between species and species groups. Using these types of morphometric data analyses and modelling procedures it is possible to distinguish between alternative ecophenotypic hypotheses and address long-standing issues involving questions of organismal form and function. While previous studies have employed morphometric data to investigate morphological adaptations to flight in different bird species, most have relied on simple linear-distance measurement data of wing and body shape as the subjects of analysis. By looking directly at shape variation in bone surfaces, variation in much more subtle aspects of morphological differences between specimens can be accessed, evaluated, and identified.

Further development of this technique will involve testing whether the models of shape variation like those we have devised can be used to assign specimens to the correct ecological group, without specifying their group assignment a priori. Once tested in this way, and if used with larger datasets and in conjunction with data analysis techniques that take phylogenetic relationships into account, results such as ours have the potential to facilitate a comprehensive 3D understanding of the ecomorphology of both modern and fossil forms. From the standpoint of ultimately using analytical ecomorphological results in the context of ecological and environmental inference, it is important to note here that the humerus is also the wing bone with the highest likelihood of post-mortem preservation. By expanding our approach to the analysis of whether similar trends in functional morphology occur in a wider range of both extant and extinct avian species, fossil humeri could perhaps be used as environmental indicators of palaeohabitat, and inferences could be made about the ecology of poorly known species.

Similar skeleton-based methods could also be applied to the study of the locomotor systems of other animals and in the study of other aspects of functional ecology. Previous work using bovid remains, for example, used morphometric methods to predict palaeohabitat by making inferences about species’ ecologies from the morphology of their locomotor apparatus (MacLeod & Rose, 1993; DeGusta & Vrba, 2005). Taxon-free methods hold a number of advantages over taxon-based methods of inferring palaeoenvironments: they do not, for example, require a robust phylogeny of indicator species and do not assume stasis in the ecology of a lineage through time. With continued ecomorphological research using the morphometric methods presented here, it may even be possible to obtain reliable estimates of functional ranges, ecologies, behaviours, etc., from morphological evidence alone. This would, of course, be of great use in palaeontological contexts, but would also enable a wide range of analyses of modern vertebrate faunas to be undertaken with greater reliability and confidence than is possible at present.

ACKNOWLEDGEMENTS

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Jonathan Krieger and John Stewart (Palaeontology Dept, The Natural History Museum, London) for help and advice throughout this study. This manuscript benefited greatly from thoughtful and constructive reviews provided by P. David Polly and three anonymous reviewers as well as from comments provided by the ZJLRS editor, Peter Hayward. All eigensurface analyses were carried out using Mathematica™ programs written by N.M. or Jonathan Krieger with Mathematica-based data analysis programmes supplied by N.M. These programs may be obtained from N.M. on written request.

REFERENCES


APPENDIX 1

List of 50 Falconiform specimens used in this study and assigned ecological groups. All specimens were sourced from the Natural History Museum, Tring, UK. Species names are consistent with current taxonomic concepts as listed on Avibase (last checked on 17 August 2011). For members of the Accipitrinae, subfamilies correspond to those indicated by Lerner & Mindell (2005); for members of the Falconidae, subfamily divisions are not used.

<table>
<thead>
<tr>
<th>Abbrev.</th>
<th>Subfamily/family</th>
<th>Species</th>
<th>Flight speed</th>
<th>Foraging mode</th>
<th>Habitat</th>
<th>Migratory behaviour</th>
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