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Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration

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In this paper we review the existing methods of quantifying avian wingtip shape, and compare their efficiency at detecting morphological adaptations to migration. We use multivariate methods to derive two novel measures of avian wingtip shape, pointedness C_2 and convexity C_3, based on measurements of primary feather lengths. Size-constrained components analysis, a modified form of principal components analysis, is used to ensure that the measures are independent of isometric size, and have a consistent interpretation in terms of the geometric shape of the wingtip. Our measures of pointedness and convexity can be calculated easily for both live birds and museum skins, and can be applied to any ecomorphological or functional analysis of avian wingtip shape. This approach circumvents many of the interpretational problems associated with previous wingtip shape indices that are often based on less accurate wing measurements. To test the suggested interpretations of previously published wingtip shape indices, we use a comparative interspecific analysis to determine the interrelations of our new shape measures with these published indices, and with aerodynamic parameters which have known functional significance. Published indices do not always measure the quantities that they are claimed to do, and are beset with awkward terminological inconsistencies. We assess the efficacy and utility of these wingtip shape measures with regard to predicted and well-known morphological adaptations in the wings for migration. Once phylogenetic bias and extraneous ecological factors are controlled, the majority of published wingtip shape indices are unable to detect morphological differences between migratory and non-migratory species. Our measures of pointedness and convexity confirm that migrants have wingtips that are relatively more pointed and more convex; they also have wings of relatively larger aspect ratio. The biomechanical implications of these adaptations for different flight behaviours are discussed. An appendix discusses some of the statistical problems involved in the analysis of size and shape, and introduces the size-constrained components analysis (SCCA) method, which is applicable to any study of morphological variation.

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Wing shape and the design of the wingtip play a major role in determining the aerodynamic and mechanical performance of the avian wing. Wings are subject to a suite of interacting and conflicting constraints, reflecting among other factors the bird's need to fly economically, to exploit a habitat effectively, and to survive either as predator or as prey. Close ecomorphological relations between wing design (measured by aerodynamic, skeletal and morphometric parameters), ecology and behaviour have been demonstrated both within and between species (see, for example, Norberg 1979, 1981, Leisler and Winkler 1985, 1991, Norberg and Rayner 1987, Rayner 1988, Hedenström and Møller 1992). Until now it has not been possible to take wingtip shape into account since measures of wing outline and wingtip geometry have been imprecise, and have lacked rigorous geometric or biomechanical interpretations.

Wing shape can be quantified in various different ways. Wing outline, or the spanwise distribution of aerodynamic wing chord, can be described by algebraic formulae (Oehme and Kitzler 1975, Dathe 1985, Norberg and Rayner 1987), and can be summarized by various spanwise moments of wing chord (Ellington 1984, Meirte 1987). These methods are limited because they require extensive measurements that cannot readily be made from museum skins or live birds, but can potentially be valuable since the wing chord distribution is related to both wing weight and to aerodynamic lift. However, to provide an accurate measure of wing shape in flight it is desirable to determine the changing wing geometry in three dimensions (incorporating camber as well as variation in chord), and this presents considerable technical difficulties.

To simplify wing geometry, a number of wingtip shape indices have been suggested (Table 1); most of these indices are ratios of the dimensions of one or more of the main flight feathers, and are based either on primary feather lengths or on primary distances. Primary distances are defined as the length of the line between the wingtip and the relevant primary feather tip projected onto a line parallel to the wing chord, on a folded wing spread in which all primaries are approximately parallel (Fig. 1). The indices are on the whole simple to derive, and primary lengths and distances are straightforward to measure. As they are based on the dimensions of the main flight feathers, these indices tend to characterize the shape of the wingtip more than of the whole wing. The indices do not take into account the spacing or separation of the feathers, or the geometry of individual feathers. They have been shown to be sensitive to various behavioural and trophic factors, but rarely lend themselves to straightforward geometrical or functional interpretations. In this paper, we consider a variety of measures of wing shape, including the indices in most common use, and demonstrate the extent to which these measures clarify the relations between wing design and migration in birds.

Wingtip shape indices

Authors proposing formal definitions of wingtip shape have generally asserted that their indices describe wing shape by measuring either the pointedness or the symmetry of the wingtip (Table 1). However, there is little consistency in the use of the term 'pointedness', which has no obvious mathematical definition when the wingtip outline is defined by the envelope of the ends of the feathers. Only Levin et al. (1991) propose indices – based on the rate of change of the feather lengths over the entire handwing (sharpness $I_{\mathrm{L}\alpha}$) or about the wingtip (pointedness $I_{\mathrm{L}\beta}$) – which have an immediate interpretation related to the angle of the wing outline at the tip. Levin's indices are correlated with each other (Levin et al. 1991) and do not measure independent features of wingtip shape; prior to this study they appear not to have been applied to practical analyses of wingtip shape.

Several of the 'pointedness' indices measure wingtip shape according to the position of the wingtip (longest primary) with respect to the leading (distal) edge of the wing: in pointed wings the longest primary is more distal (Sundevall 1834, Dixon 1892, Pettigrew 1905, Averill 1925, Rensch 1938, Kipp 1959, Stegmann 1962, Kokshaysky 1973). There is no obvious aerodynamic reason why wings should change shape only in this way (though this may be a response to developmental constraints): it is possible to envisage an aerodynamically effective pointed wing in which the fourth or fifth primary (from the distal-most) forms the wingtip, but this apparently does not occur in birds.

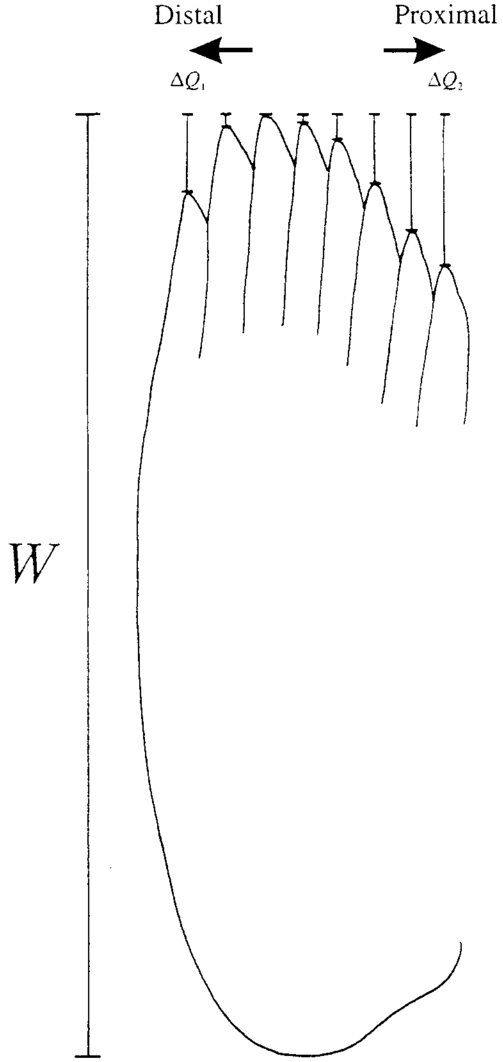

Fig. 1. A typical folded bird wing showing definitions of wing length W and primary distances ΔQ_i.

Table 1. The calculation and interpretation of wingtip shape indices. All measurements are based on folded wing spreads. N, sample size; W, wing length; ΔQ_i, primary length distance of Q_i; Σp, sum of primary distances proximal to wingtip; Σd, sum of primary distances distal to wingtip; ΔS_1, distance for most distal secondary feather, defined equivalently to ΔQ_i. Hedenström's indices are based on the lengths of the 5th and 9th primaries numbered conventionally; in most birds these are primaries Q_5 and Q_1 in our notation. Original author's proposed interpretation of the indices shown in second column: (+) indicates that index increases with pointedness, symmetry etc., (−) that it decreases.

Wingtip shape index		Original authors' interpretation	Source	N	Mean (SE)	Range
Kipp's index	$I_K = 100\frac{\Delta S_1}{W}$	pointedness of wing (+)	Tugarinov (1946), Gladkov (1949), Kipp (1959)†	164	40.38 (0.96)	15.5–74
Holynski's index	$I_H = 100\frac{(\Sigma p - \Sigma d)}{W}$	pointedness of wing (+)	Holyński (1965)	252	88.45 (2.98)	−13.0–215.5
Busse's index	$I_B = 100\frac{(\Sigma p + \Sigma d)}{W}$	symmetry of wing (+) pointedness of wing (+)	Busse (1967) Busse (1967)	252	103.39 (2.34)	21.4–215.5
Tiainen's index	$I_T = \frac{\Sigma p}{\Sigma d}$	symmetry of wing (−)	Tiainen (1982)	186	44.59 (6.40)	0.5–910
Hedenström's P9 index	$I_{H9} = 100\frac{(W - \Delta Q_1)}{W}$	pointedness of wing (+)	Hedenström and Pettersson (1986)	252	94.02 (0.48)	63.7–100
Hedenström's P5 index	$I_{H5} = 100\frac{(W - \Delta Q_5)}{W}$	pointedness of wing (−)	Gladkov (1935), Hedenström and Pettersson (1986)	252	87.70 (0.45)	68.6–100
Mlíkovský's pointedness index	I_{Mp}††	pointedness of wing (+)	Mlíkovský (1978, 1982)	252	1.84 (0.0024)	1.77–2.0
Mlíkovský's symmetry index	I_{Ms}††	symmetry of wingtip (+)	Mlíkovský (1978, 1982)	252	0.15 (0.004)	−0.02–0.34
Levin's α index	$I_{L\alpha}$†††	sharpness of handwing (+)	Levin et al. (1991)	252	14.87° (0.60)	−14.2–37
Levin's β index	$I_{L\beta}$†††	pointedness of wingtip (−)	Levin et al. (1991)	252	68.81° (0.49)	49.6–103.7

† This index was originally proposed by a number of Russian authors, but we follow normal usage in referring to it as Kipp's index.

†† Mlíkovský's indices are computed as weighted third and fourth moments of the distribution of feather lengths; see Mlíkovský (1982) for details of their computation. See Busse (1986) for comments on Mlíkovský's indices. A possible further development of these indices is to use Fisher's statistics of skewness and kurtosis (Sokal and Rohlf 1995), which are effectively normalized equivalents of the indices.

††† Levin's α and β indices are measures of handwing geometry, computed as the regression slope (in degrees) of primary length against primary number for all primary feathers (sharpness α), and as the sum of the slopes for feathers distal to and proximal to the wingtip (pointedness β). See Levin et al. (1991) for details.

It is claimed that some indices measure 'symmetry' through comparison of the variation in primary distances on either side of the wingtip. These indices must be biased by the position of the longest primary forming the wingtip, and therefore cannot be independent of measures of pointedness (Tiainen 1982, Busse 1986, Hedenström 1986, Chandler and Mulvihill 1988).

There have been a few empirical intraspecific tests of the efficacy of wingtip shape indices (Busse 1967, Chandler and Mulvihill 1988, Eck 1992), but only Kipp's index (I_K), which is based on the length of the most distal secondary feather and so is a measure of the pointedness of the entire handwing rather than of the wingtip alone, has been used in comparative surveys of a wide range of species. Indices have been used effectively to quantify variation among populations of the same species (geographical variation, migratory and less-migratory populations, subspecies, age- and sex-classes) (Gladkov 1935, Tugarinov 1946, Yakobi 1964, Nitecki 1969, Gatter 1979, Mlíkovský 1982, Tiainen 1982, Lövei 1983, Tsvyelyikh 1983, 1989, Tiainen and Hanski 1985, Hedenström and Pettersson 1986, Lövei et al. 1986, Norman 1997, Scebba and Lövei 1986, Tsvyelyikh and Dyadichyeva 1986, Heininger 1991, Tsvyelyikh and Goroshko 1991, Eck 1992, Borras et al. 1993), and in ecomorphological and flight-mechanical comparisons among species (Gladkov 1935, Tugarinov 1946, Kipp 1959, 1961, 1976, Yakobi 1966, Eck 1974, Gaston 1974, Gatter 1976, 1979, Bährmann 1978, Leisler 1980, Bairlein 1981, Laske and Immelmann 1981, Pulliainen et al. 1981, Leisler and Thaler 1982, Tiainen 1982, Leisler and Winkler 1985, 1991, Tiainen and Hanski 1985, Winkler and Leisler 1985, 1992, Bairlein et al. 1986, Scebba and Lövei 1986, Landmann and Winding 1993).

An alternative approach to the problem of wingtip shape is to use multivariate statistical methods to summarize a collection of primary length or distance measurements (Chandler and Mulvihill 1988, 1990, Mulvihill and Chandler 1990, 1991, Senar et al. 1994, Mönkkönen 1995, Marchetti et al. 1995). This approach can incorporate the dimensions of all the primary feathers, and therefore has the potential to be applied consistently in a comparative study. Chandler and Mulvihill (1988) applied principal components analysis (PCA) to primary distances for the Dark-Eyed Junco *Junco hyemalis*, and found three significant axes of variation. The first principal component (PC_1) combined increasing wing length with its allometric effects on wingtip shape; PC_2 was interpreted as an increase in distal primary distances, and PC_3 as an inverse relationship between the wingtip and adjacent primary distances. This method describes shape variation within the junco wing effectively, but the shape measures (and their interpretations) which it generates are applicable solely to the junco and cannot be generalized to an arbitrary sample of birds. Marchetti et al. (1995) and Mönkkönen (1995) have applied PCA to primary distances to describe wing shape of *Phylloscopus* warblers and 14 passerine species, respectively, with similar limitations.

Within an individual species, variation of wing proportions and of size is relatively modest. Between species, size variation may be considerable, and it is normal for bird wings to show allometric variation of shape with size: larger birds have relatively large wing areas and long wingspans (Rayner 1988, 1996): accordingly, wingtip shape may also vary with size. PCA is inappropriate for a between-species analysis of wingtip shape because allometric shape variation is distributed across all components (including the first), and therefore the geometric interpretation of the shape components will not be consistent in birds of different sizes (Appendix 1). Senar et al. (1994) and Mönkkönen (1995) have attempted to resolve this problem by size-correcting individual feather lengths by dividing by wing length, but again their analyses are valid only for a limited sample. This method can only separate size and shape if all size variation is included in wing length: the validity of this assumption has not been tested, and is unlikely to be valid. Moreover, the technique is susceptible to various statistical problems associated with the use of ratios (see Appendix 1).

In this study, we apply wingtip shape indices to an interspecific sample comprising a wide range of birds to compare their sensitivity and applicability as measures of wing shape. Where possible we ascribe geometric interpretations to these shape measures. We use the term 'pointedness' to describe a shift in the position of the wingtip feather towards the leading edge of the wing (Fig. 2a, b), and avoid the term symmetry. We introduce the concept of convexity as a measure of the decrease in the acuteness of the handwing (Fig. 2c, d). We also introduce a technique derived from PCA, Size-Constrained Components Analysis (SCCA; see Appendix 1), that describes size by reference to isometric changes between individuals, and therefore successfully differentiates shape from isometric size, and maintains a consistent geometric interpretation of shape across all bird species and all sizes. We assess the usefulness of wingtip shape indices and of our components by applying them to interspecific analyses of wingtip shape in relation to migration behaviour.

Wing shape and migration

Migration represents an important adaptive strategy for many bird species. There has been a broad range of studies of behavioural and physiological strategies appropriate for avian migration (e.g. Pennycuick 1969, Alerstam 1990, 1991, Hedenström and Alerstam 1992, 1995, Lindström and Alerstam 1992, Hedenström 1993,

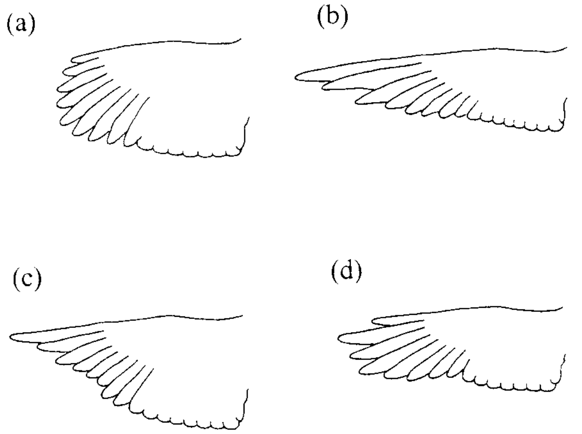

Fig. 2. Theoretical wings constructed to illustrate the extremes of pointedness and convexity according to the definitions used in this paper. (a) Rounded and (b) pointed wings. Pointedness is defined as a shift in the wingtip towards the leading edge. (c) Concave and (d) convex wings. Convexity is defined as a decrease in the acuteness of the wingtip, brought about by a more rapid lengthening of primaries close to the wingtip compared to the most proximal primaries. Wing convexity may be seen in the shape of the outline of the proximal part of the handwing.

Weber et al. 1994), but here we concentrate on morphological adaptations to migration. It has long been accepted that migrants possess longer and more pointed wings (Fredericus II 1240, Seebohm 1880, 1882, Dixon 1892, Pettigrew 1905, Headley 1912), although formal biomechanical explanations of this tendency are surprisingly recent (Greenewalt 1975, Rayner 1988, 1990, Norberg 1990). The trend towards relatively longer, higher aspect ratio wings in migrants has been documented in intraspecific (Gladkov 1935, Niethammer 1937, Tugarinov 1946, Potapov 1967, Nitecki 1969, Gatter 1979, Lövei 1983, Tsvyelyikh 1983, 1989, Hedenström and Pettersson 1986, Scebba and Lövei 1986, Tsvyelyikh and Dyadichyeva 1986, Lo Valvo et al. 1988, Chandler and Mulvihill 1990, Haberman et al. 1991, Mulvihill and Chandler 1991, Tsvyelyikh and Goroshko 1991, Senar et al. 1994, Marchetti et al. 1995) and interspecific (Seebohm 1880, Averill 1920, 1925, Gladkov 1935, Kipp 1936, 1942, 1958, 1959, Tugarinov 1946, Meise 1949, Dilger 1956, Gaston 1974, Gatter 1979, Keast 1980, 1996, Bairlein 1981, Pulliainen et al. 1981, Fitzpatrick 1985, Leisler and Winkler 1985, Winkler and Leisler 1985, 1992, Bairlein et al. 1986, Norberg 1990, Levin et al. 1991, Yong and Moore 1994, Mönkkönen 1995) analyses. However, some studies have failed to ascribe variation in wingtip shape unambiguously to migration alone (Rensch 1938, Tugarinov 1946, Keast 1980, Niemi 1985, Mulvihill and Chandler 1990, Eck 1992), and hitherto a properly controlled, broad, comparative analysis of wingtip shape in migrants has been lacking.

Wing morphology in birds evolves within a complex of mechanical and other constraints, and is sensitive to many aspects of ecology and behaviour which may be independent of migration (Magnan 1922, Lorenz 1933, Saville 1957, Kipp 1959, Kokshaysky 1973, Norberg 1981, 1990, Rayner 1988, 1996, Marchetti et al. 1995). For instance, wingtip shape is known to vary with high altitude habitat (Hamilton 1961, Lo Valvo et al. 1988, Heininger 1991, Landmann and Winding 1993, 1995a, b), latitude (Scebba and Lövei 1986), flocking (Gatter 1976, Kipp 1976) and the ability to respond to wind (Laske and Immelmann 1981); and wing shape may also change in individuals between juvenile and adult states (Alatalo et al. 1984). The constraints and demands experienced by birds vary between species and populations, and despite its importance there is no reason to think that adaptation for migration dominates the evolution of wing morphology in all flying birds. However, migration represents a critical selective pressure on adaptation and on the behaviour of species which undertake it, since failure to migrate successfully can often mean death or failure to reproduce.

Aerodynamic arguments predicting wing design for migration have been based on the hypothesis that selection for low cost of transport (or high range per unit fuel) outweighs other pressures on wing design. For the reasons outlined above, this may not always be the dominant pressure. Cost of transport is minimized by evolving wings with high aspect ratio (wingspan squared divided by wing area, or a measure of wing shape) (Rayner 1988), and is influenced only weakly by wing loading (weight divided by wing area, or a measure of wing size). Thus, migrants should have longer and more pointed wings (Rayner 1988, 1990, Norberg 1990). It has also been suggested that long, pointed wings may be adaptive because they increase load-carrying capacity (Ward 1964), but no mechanism was proposed, and in fact a wing designed for load carrying should have a lower wing loading; many migrants such as ducks and auks have relatively high wing loading because fast flight speeds are adaptive for them (Rayner 1988). In addition to high aspect ratio, migrants and other sustained fliers are predicted to have a tapering, pointed wingtip, which minimizes induced drag by optimizing the configuration of the wingtip vortices. These predictions have not been formally tested across a broad range of species. One previous study has shown a trend for aspect ratio to increase between migratory and non-migratory birds (Norberg 1990), but this trend is non-significant at the 5% level. Winkler and Leisler (1992) found that aspect ratio is higher in migrants within some taxonomic groups; exceptions included Charadriiformes, Columbiformes and Trochilidae. Mönkkönen (1995) has indicated that wingtip pointedness is related to migratory distance in 14 passerine species.

Across a broad range of avian taxa, relationships between migration, phylogeny and ecology are evident. To test hypotheses concerning the response of design to migration *per se* it is essential to minimize the possibility that variation within an interspecific sample is attributable to ecology and flight behaviour, or to common adaptations in related species (Harvey and Pagel 1991). In this study we isolate migration from other factors as a possible influence on wing morphology by using pairwise comparisons (Felsenstein 1985) of measures of flight morphology and wingtip shape between congeneric pairs of species that occupy the same ecological niche, but exhibit different migratory behaviours. Previous studies of flight morphometrics in relation to migration have not controlled for both phylogenetic and ecological bias.

Materials and methods

Flight morphology measurements

Lengths Q_1-Q_8 of the eight distal-most primary feathers were measured from museum skins for adults of 148 avian species spanning 12 orders (Sibley and Ahlquist 1990), primarily from the Western Palaearctic. Primary feather lengths were defined as the distance from the tip of the feather to the point where it enters the skin. The eight distal-most primaries were numbered ascendingly as 1–8 (with feather 1 the most distal, i.e. forming the leading edge of the wing). Vestigial feathers (Averill 1925, Stegmann 1962), defined as distal-most primary feathers shorter than the most proximal primary, were ignored. This unconventional primary feather notation (Jenni and Winkler 1994) was adopted to account for interspecific differences in absolute numbers of primaries between species (Stresemann 1963). This numbering sequence also helped to minimize interspecific differences between insertion points of primary feathers onto the wing bones. In both passerine and non-passerine species, the four distal-most primaries are attached to the digits and the rest are attached to the metacarpus (Jenni and Winkler 1994). Therefore, by numbering primaries ascendingly from distal to proximal, we have generally accounted for any variation in points of feather attachment. Lengths were measured with Vernier callipers to 0.1 mm accuracy for primaries up to 150 mm in length, and with a metal rule to 1 mm accuracy for longer feathers. Primary distances $\Delta Q_1-\Delta Q_8$ (Fig. 1) and ornithological wing length (sometimes termed wing chord) were also measured from folded wing spreads of the museum skins with a metal rule. Measurements of individual primary feather lengths for adults of 212 species were obtained from the literature (Brown et al. 1987), and primary distances were calculated for these species by subtracting the length of each primary feather from the length of the longest primary. We defined wing length for these species as the length of the longest primary. The validity of the literature measurements was determined by correlating the primary lengths, primary distances, and wing lengths for the literature sample with the mean values of those measured from museum skins on a species by species basis for 116 species in both datasets. The literature data were highly correlated with the museum data (range of Spearman rank correlation coefficients $r_S = 0.972 \leq r_S \leq 0.985$, $p < 0.0001$, for primary lengths; $0.626 \leq r_S \leq 0.919$, $p < 0.0001$, for primary distances; $r_S = 0.982$, $p < 0.0001$, for wing length; $N = 116$ in all cases), and so the measurements for the additional 96 species from the literature were combined with our measurements to total 244 species for analysis. Eight species were included twice in the database reflecting geographical races with different migratory behaviours.

Estimates of body mass (kg), wingspan (m), wing area (m^2), aspect ratio and wing loading ($N\ m^2$) were collected from the literature for as many of the 244 species in the original data set as possible. These data were analysed previously by Rayner (1988); additional mass estimates were obtained from Dunning (1993).

Repeatability and normality of feather measurements

Previous wingtip shape indices have mostly been based on primary distances. We identified a number of practical and statistical problems associated with the use of distances, and therefore based our analysis on primary lengths.

Measurement error

Primary distances are much shorter than primary lengths, and therefore are more susceptible to measurement errors.

Repeatability of measurements

By testing the repeatability of primary distance and length measurements in sample species we found that primary distances could not always be measured consistently. This was not exclusively ascribed to measurement error, but also to the potential variability in folded wings, even of the same individual. Primary distances measured with a metal rule (accuracy 1 mm) from three repeated folded wing spreads of each of 18 mixed sex, live adult European Starlings *Sturnus vulgaris* selected at random from a large wild-caught, free-flying captive population were not always significantly repeatable (range of intraclass correlation coefficients r_I (Zar 1984) for individual primaries: $-0.207 \leq r_I \leq 0.969$; $0.654 \leq F_{5,2} \leq 64.06$; $0.015 \leq p \leq 0.69$; $N = 18$). Primary feather lengths measured with Vernier callipers from the same individuals were far more repeatable than primary distances (range: $0.963 \leq r_I \leq 0.998$; $34.5 \leq F_{5,2} \leq 1288$; $0.00093 \leq p \leq 0.018$; $N = 18$; for all primaries). Primary lengths from three repeated measurements with a metal rule of skins of six adult Mallard *Anas platyrhynchos* were also highly repeatable (range: $0.963 \leq r_I \leq 0.999$; $53.1 \leq F_{5,2} \leq 8244$; $0.00012 \leq p \leq 0.019$; $N = 6$; for all primaries). The high repeatability of primary length measurements has previously been noted by Berthold and Friedrich (1979), Jenni and Winkler (1989) and Swaddle and Witter (1994).

Normality of primary lengths

The frequency distribution of recorded primary feather lengths differed significantly from the normal (range of Kolmogorov-Smirnov goodness of fit D with intrinsic normal distribution (Rohlf and Sokal 1995, Sokal and Rohlf 1995): $0.136 \leq D \leq 0.165$, $p < 0.0001$). When log-transformed, primary lengths again differed from normal, but to a much smaller extent (range: $0.060 \leq D \leq 0.082$, $0.001 \leq p \leq 0.05$), largely because most feather length distributions were platykurtic. The Kolmogorov-Smirnov intrinsic test detects very slight differences from normality, which in this analysis are insufficient to disrupt the multivariate techniques that we employ (Mardia 1975). Therefore log-transformed feather lengths were used for subsequent analysis.

Normality of primary distances

The frequency distribution of primary distances ΔQ_i differed significantly from the normal both when untransformed and log-transformed (untransformed range: $0.112 \leq D \leq 0.330$, $p < 0.0001$; log-transformed [$\ln(\Delta Q_i + 1)$] range: $0.070 \leq D \leq 0.206$, $p \leq 0.01$). We did not use $\ln(\Delta Q_i)$ because of the zero values in the distance measurements for all longest primaries. Because of the way they are defined, we do not expect the untransformed primary distances to be normally distributed; distances incorporate interspecific size variation, they are confined to be non-negative, and must include zero values (i.e. they obey a Dirichlet distribution including lower bound 0). They are also sensitive to the identification of the longest primary, which may vary in an individual with factors such as condition and moult, as well as with the extent to which the wing is folded. Logarithmic transformation is appropriate for both lengths and distances because of the size variation in the sample, and its ability to test isometric hypotheses expressed in power-law form (Rayner 1985); it is, however, unable to transform all primary distances to a normal distribution.

From these preliminary analyses we concluded that primary lengths are more reliable and accurate measures of wing morphometrics than are primary distances derived from the folded wings of live birds or skins. Therefore, we used log-transformed primary feather lengths in our multivariate analyses. We caution against the use of primary distances in any interspecific or intraspecific (e.g. Chandler and Mulvihill 1988) analysis of wingtip shape, or in the comparative analysis of wingtip shape indices, unless attention is paid to their unfavourable statistical distributions.

Wingtip shape indices

Wingtip shape indices were calculated from our measures of $Q_1 - Q_8$ and $\Delta Q_1 - \Delta Q_8$ (see Table 1 for definitions), with the exception of I_K, for which we used median values from the ranges given in the literature (Kipp 1959, 1961, 1976). Mlíkovský's and Levin's indices can be calculated for variable numbers of primaries; we consistently used the distances and lengths, respectively, of the eight primaries measured.

Size-constrained multivariate analysis

We applied size-constrained components analysis (SCCA, Appendix 1; derived from Burnaby 1966) to length measurements of the eight distal-most primaries for each species. Measurements were log-transformed, which increased normality (above), and were standardized to equal unit variances for each Q_i. SCCA, which is closely related to PCA, constrains the first component to measure isometric size, and unambiguously identifies allometry in the shape components (Appendix 1).

Classification of ecology and migration behaviour

All 244 species were classified according to ecological niche and migratory behaviour. Nine ecological categories were established on the basis of foraging modes (Cramp and Simmons 1977, 1980, 1983, Cramp 1985, 1988, 1992, Alerstam 1990, Cramp and Perrins 1993): (i) birds in wetlands; (ii) birds which forage on lakes and the sea bottom; (iii) birds which feed on terrestrial plants; (iv) birds which feed on fish; (v) birds which obtain food at the water surface; (vi) birds of prey; (vii) insectivores; (viii) seed-eaters; (ix) and omnivorous birds. Migration was ranked into four categories (Cramp and Simmons 1977, 1980, 1983, Harrison 1982, Cramp 1985, 1988, 1992, Cramp and Perrins 1993): (i) migratory (*Mig*, all or most individuals make regular seasonal movements between breeding and wintering ranges); (ii) partially migratory (*Part*, populations contain substantial migratory and non-migratory elements); (iii) dispersive (*Disp*, population can undergo infrequent, random movements over a long distance); (iv) and non-migratory (*Non*, either resident or sedentary species).

Statistical procedures

Univariate statistical analyses were performed with Minitab v 10.1 (Minitab Inc. 1994). Where appropriate, significance levels were adjusted by the Bonferroni correction procedure for multiple comparisons (Zar 1984). Two-tailed tests of probability are used throughout. Software for multivariate analyses was written by JMVR.

Results

Wingtip shape indices

Means and ranges for the computed indices are shown in Table 1. Tiainen's index I_T is infinite for many birds in which the most distal primary is the longest; these values were omitted from correlation computations below; for this group of birds I_H and I_B were identical.

Multivariate analysis

SCCA on length measurements of the eight most distal primary feathers produced three significant axes of variation (Fig. 3, Table 2, Appendix 2); subsequent axes correlated with no other wing shape parameters and explained less than 0.40% of the size variance or 9% of the variation in shape, and were ignored. The first component C_1 was, by definition, a measure of isometric size. A decrease in C_2 represented an increase in wingtip pointedness (decrease in wingtip roundedness) and a shift of the wingtip towards the leading edge of the wing (Fig. 2a, b). Increasing C_3 corresponded to an increase in the convexity of the outline of the proximal portion of the handwing, and a decrease in the acuteness of the wingtip (Fig. 2c, d). C_2 was not significantly allometric ($\rho_2 = 0.056$, (A9)), but C_3 included significant positive size allometry ($\rho_3 = 0.437$): small birds tend to have more rounded wings. The pooled coefficient of allometry was 0.496 (243 d.f.).

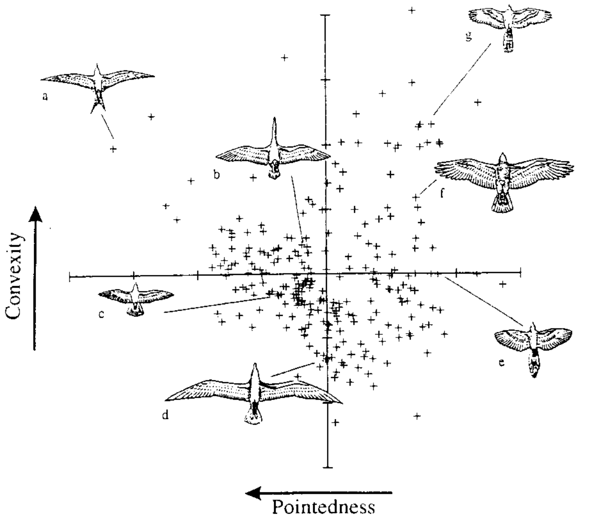

Fig. 3. Distribution of species in terms of the two size-constrained components of wing shape. C_2 is a measure of wingtip pointedness, decreasing as pointedness increases; C_3 increases with increasing wingtip convexity. Each point on the graph represents a single species: a, tern; b, duck; c, pigeon; d, gull; e, magpie; f, buzzard; g, sparrowhawk. Bird outlines from Herzog (1968).

Table 2. Results of the SCCA on primary feather lengths. Component loadings (correlations) between the original variables and the derived components. Q_1 - Q_8 refer to primaries 1 to 8, numbered ascendingly from the distal, leading edge of the wing. Shape variance is the partitioning of variance after the isometric size variance explained by C_1 is removed. Loadings with C_3 are all positive because of size allometry in this component.

	C_1	C_2	C_3
Q_1	0.977	−0.149	0.376
Q_2	0.993	−0.054	0.452
Q_3	0.997	0.001	0.475
Q_4	0.998	0.054	0.480
Q_5	0.998	0.105	0.469
Q_6	0.995	0.137	0.440
Q_7	0.994	0.155	0.403
Q_8	0.988	0.195	0.376
% total variance explained	98.46	1.19	0.22
% shape variance explained		77.3	14.0

The interpretations of the components can be visualized by plotting idealized bar diagrams of the primary lengths (Q_1–Q_8, left to right) for a range of values of C_2 and C_3 (extending beyond the range occupied by our broad sample) with constant size C_1 and with C_4 to C_8 equal to zero (Fig. 4). Each bar diagram indicates the relative primary lengths of species distributed in that region of the plot; the diagrams should not be interpreted as outlines of real wings.

The scatter plot of C_2 and C_3 summarizes variation in wingtip shape, and these components clearly differentiate birds with visibly different wingtip outlines (Fig. 3). C_2 and C_3 are statistically uncorrelated, but the distribution of C_2 and C_3 is not even. Birds with very low values of C_3, corresponding to extreme trailing edge concavity, tend to have average to low pointedness. Very low values of C_2 (high pointedness) are associated with high C_3 in the upper left quadrant: these are the pointed wings of birds such as terns (Laridae) for which the wingtip formed by Q_1 or Q_2 is very pointed but has little concavity in the more proximal primaries. No bird possesses a very pointed and concave wing (i.e. more concave than Fig. 2c), possibly because an isolated extended feather could not tolerate extreme mechanical loads.

We considered correlations between the wingtip shape components and flight morphology. Apart from the expected strong correlations between size-dependent

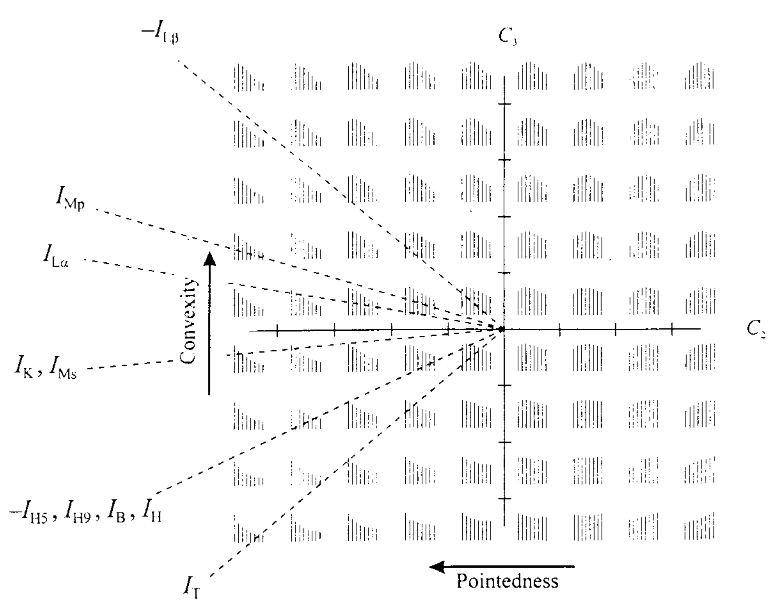

Fig. 4. Bar diagrams of primary feather lengths for a range of values of the two wingtip shape components C_2 and C_3 derived from SCCA. Each bar diagram represents eight primary feathers, from distalmost to proximal ordered ascendingly from left to right. The diagrams should not be interpreted as outlines of real wings. Dashed lines show the approximate trends of variation of components with increases in the various wingtip shape indices computed for these idealized wings. These trends are only indicative, because the indices were not, in general, linear with C_2 and C_3; several of the indices were particularly nonlinear when C_2 was large, and I_T was undefined for a large portion of the left side of the figure. I_K was approximated for this figure by the length of the eight primary Q_8, rather than that of the first secondary. Levin's β index and Hedenström's fifth primary index both reduce with increasing pointedness, and hence are shown here as their negatives.

morphological parameters (mass, wingspan, wing area, wing length, wing loading) and C_1, the only appreciable correlations were log aspect ratio with C_2 (Pearson product-moment correlation $r_{233} = -0.584$, $p <$ 00001), and log wing loading with C_3 ($r_{233} = -0.322$, $p < 0.00001$). Therefore, the wingtip shape components explain additional dimensions of wing design beyond those described by the flight morphology parameters.

We propose that C_2 and C_3 can be used as interspecific measures of wingtip shape. Unlike wingtip shape indices they give geometrically consistent measures of shape independent of wing size, and are easy to interpret in interspecific comparative analyses of birds with widely differing size and wing design. C_2 (pointedness) and C_3 (convexity) may be calculated quickly and easily for any species by the formulae presented in Appendix 2. The coefficients in the equations (Appendix 2) depend on our sample, and would vary if a different interspecific sample was analysed. However, we believe that our sample is sufficiently broad to be representative of birds in general, that the structure of the components is robust, and therefore the components are applicable across most data sets.

Relations among indices

Spearman rank correlations were used to relate the wingtip shape indices, aspect ratio and our size-constrained components, because not all the variate pairs displayed a bivariate normal distribution; results with Pearson product-moment correlations showed the same levels of significance. Many of the wingtip shape indices measure similar, but not identical, quantities (Table 3, Fig. 4). I_H, I_{Ms}, I_{H5}, I_B, $I_{L\alpha}$ and I_K all varied very closely with one another, with C_2 and with aspect ratio A, and were not significantly correlated with C_3. With the exception of the pair I_T and I_{H9}, which were not correlated with I_{Mp} and $I_{L\beta}$, all indices were significantly correlated with each other, and therefore to some extent measure a common factor. Notably, I_K, I_{H9}, I_{Mp} and $I_{L\beta}$ were significantly correlated with isometric size C_1 and therefore confound elements of size and shape. All indices were significantly correlated with wingtip pointedness C_2 (Fig. 4) and with aspect ratio A; I_K was particularly closely correlated with A (see below), and the correlation between $I_{L\beta}$ and C_2 was almost unity, although the relationship between these two quantities was not linear. Wingtip convexity C_3 was closely correlated with few indices: I_{Mp} and $I_{L\beta}$ were more closely correlated with C_3, but all other indices correlated more closely with C_2. There is little to distinguish the indices which purport to measure symmetry (I_H, I_T, I_{Ms}) from those designed to measure pointedness, indicating that these features are not independent.

Wingtip shape and migration

Wingtip shape varied with migratory behaviour (Table 4; Fig. 5). Within our pooled sample, all wingtip shape indices that are reputed to measure wingtip pointedness, including C_2 but with the exception of I_{Mp}, demonstrated that migrants have significantly more pointed wings than non-migrants (for statistical details see Table 4). There was also a significant difference in wingtip convexity C_3 between migratory and non-migratory species (Fig. 5l) as a result of the low C_3 in dispersive species; Kipp (1959) has demonstrated that

Table 3. Spearman rank correlation coefficients (Siegel and Castellan 1988) between all wingtip shape indices, wingtip shape components C_i and aspect ratio A. All correlations are significant at $p = 0.05$ unless coefficient is given in parentheses. Correlation coefficients Bonferroni corrected. Sample size ranges from 108 (I_K vs I_T) to 252 (most other comparisons).

	I_K	I_H	I_B	I_T	I_{H9}	I_{H5}	I_{Mp}	I_{Ms}	$I_{L\alpha}$	$I_{L\beta}$	A
I_H	0.748										
I_B	0.768	0.899									
I_T	0.506	0.832	0.472								
I_{H9}	0.527	0.788	0.523	0.944							
I_{H5}	−0.664	−0.954	−0.869	−0.773	−0.745						
I_{mp}	0.568	0.479	0.723	(−0.011)	(0.027)	−0.392					
I_{ms}	0.720	0.973	0.911	0.746	0.698	−0.932	0.600				
$I_{L\alpha}$	0.696	0.865	0.746	0.776	0.739	−0.854	0.381	0.855			
$I_{L\beta}$	−0.612	−0.462	−0.660	(−0.072)	(−0.095)	0.410	−0.796	−0.550	−0.562		
A	0.864	0.625	0.606	0.421	0.519	−0.578	0.369	0.590	0.603	−0.332	
C_1	0.533	(−0.019)	(0.156)	(−0.153)	−0.214	(0.070)	0.387	(0.019)	(−0.010)	−0.332	0.429
C_2	−0.688	−0.869	−0.734	−0.790	−0.759	0.863	−0.343	−0.851	−0.997	0.526	−0.599
C_3	0.314	(0.097)	0.370	(−0.193)	−0.310	(−0.037)	0.745	0.214	(0.156)	−0.784	(0.127)

eruptive passeriform species have unusually rounded wings.

This trend in wingtip shape in migrants might have arisen because migrants in our sample share common phylogeny, or because wing design is a response to extraneous ecological or behavioural factors, such as a need for manoeuvrability in a particular environment (Norberg and Rayner 1987, Rayner 1988), and are not adaptations that occur specifically to facilitate migration. To test whether wings become more pointed in response to migration behaviour we controlled for phylogenetic and ecological bias by comparing the wingtip shapes of closely related pairs of species that exhibit different degrees of migratory behaviour, but occupy similar ecological niches. Paired t-tests for 27 pairs of species, representing 22 genera (Table 5), produced different results from the uncontrolled analyses (Table 4). Only I_K, $I_{L\alpha}$, $I_{L\beta}$ and our shape components (C_2 and C_3) detected differences in wingtip shape between migratory and less-migratory species. Only these latter indices and our new measures are effective at discerning the morphological adaptations to migration.

Flight morphology and migration

It is also expected that migrants should have longer wings. The only flight morphology parameter to show a significant difference between migratory and non-migratory species was aspect ratio (Fig. 5m). Body mass, wingspan, wing area and wing loading did not differ significantly between migratory and less-migratory species (mass, $F_{3,247} = 1.41$, $p = 0.24$; wingspan, $F_{3,245} = 1.86$, $p = 0.136$; wing area, $F_{3,231} = 1.27$, $p = 0.284$; wing loading, $F_{3,231} = 2.11$, $p = 0.100$). These relationships did not alter when phylogenetic and ecological factors were controlled: migratory species had a higher aspect ratio than less-migratory species (Table 4), but there was no significant difference in other flight morphology parameters (mass, $t_{26} = -1.85$, $p = 0.076$; wingspan, $t_{26} = -1.74$, $p = 0.093$; wing area, $t_{24} = -2.04$, $p = 0.053$; wing loading, $t_{24} = 0.07$, $p = 0.94$). These results strongly support the conclusion from the wingtip shape indices: migrants have more pointed wings. Since aspect ratio may be viewed as a measure of relative wing spread, migrants also have relatively longer wings, even though there is no absolute difference in either wingspan or wing area between migratory and less-migratory species.

Discussion

Wing shape and aerodynamics

Selection in response to aerodynamic factors may influence wing shape in several interacting and possibly conflicting ways.

Table 4. Summary of analyses of variance (ANOVA) between migratory categories and wingtip shape indices. Values given in table are F-ratios for the analysis of variance, p values (statistics as follows: ** <0.01; *** <0.001; **** <0.0001; NS, $p>0.05$) and Student's t statistics. Uncontrolled analyses are broad interspecific analyses of variance: Sample size ranges from 108 (I_K) to 250 (most other indices). Significant ($p<0.05$) pairwise comparisons shown were identified with Tukey tests (Minitab Inc. 1994). Migration categories: *Mig.* = 1; *Part.* = 2; *Disp.* = 3; *Non.* = 4 (see Methods). Phylogenetically and ecologically controlled analyses were paired t-tests of closely related pairs of species that occupy the same ecological niche, but exhibit differing migratory behaviours.

	No control			With phylogenetic and ecological control	
	ANOVA		Tukey comparisons		
I_K	$F_{3,104} = 12.5$	****	1 vs 4; 3 vs 4	$t_{15} = 4.40$	***
I_H	$F_{3,248} = 17.2$	****	1 vs 3; 1 vs 4	$t_{26} = 0.97$	NS
I_B	$F_{3,248} = 12.55$	****	1 vs 3; 1 vs 4	$t_{26} = 1.16$	NS
I_T†	$F_{3,183} = 5.59$	***	1 vs 4	$t_{17} = 1.22$	NS
I_{H9}	$F_{3,248} = 8.60$	***	1 vs 4	$t_{26} = -0.34$	NS
I_{H5}	$F_{3,248} = 16.63$	****	1 vs 3; 1 vs 4; 2 vs 4	$t_{26} = -1.49$	NS
I_{Mp}†	$F_{3,248} = 2.08$	NS		$t_{26} = 0.15$	NS
I_{Ms}	$F_{3,248} = 14.12$	****	1 vs 3; 1 vs 4	$t_{26} = 1.18$	NS
$I_{L\lambda}$	$F_{3,248} = 22.02$	****	1 vs 3; 1 vs 4; 2 vs 4	$t_{26} = 3.14$	**
$I_{L\mu}$	$F_{3,248} = 4.90$	*	1 vs 4	$t_{26} = -3.39$	**
C_2	$F_{3,248} = 22.10$	****	1 vs 3; 1 vs 4; 2 vs 4	$t_{26} = -2.93$	**
C_3	$F_{3,248} = 1.33$	NS		$t_{26} = 3.87$	***
A†	$F_{3,231} = 14.87$	****	1 vs 4; 3 vs 4	$t_{24} = 2.81$	**

† These variates were transformed to natural logarithms to approach a normal distribution of the residuals.

Overall wing proportions

The quantity usually used to model the gross shape of the wing is the *aspect ratio*, which is defined as the ratio of wingspan squared to wing area, and which is equivalent to wingspan divided by mean wing chord. Aspect ratio affects the relative magnitudes of induced and profile drags: if mass, wing area and other wing shape parameters remain constant, a long, thin high-aspect-ratio wing gives a low cost of transport or high range (Norberg and Rayner 1987, Rayner 1988). Large values of this quantity have always been considered by aerodynamicists to provide the prime evidence for selection for flight economy in sustained flights, though large aspect ratio is not necessarily associated with high speed (which is favoured by small wings), or low power (which is favoured by relatively long, broad wings) (Rayner 1988). In accordance with this prediction, high aspect ratios occur in birds for which flight economy is critical, as, for instance, the larger long-distance migrants, marine soaring birds, and many aerial predators. This correlation between long, thin wings and migration is formally confirmed, for the first time, by our analyses with ecological and phylogenetic controls (Table 4): migrant birds have wings of higher aspect ratio. This study represents the first stringent test of this hypothesis across a broad range of avian species.

Kipp's index I_K is determined by the length of the handwing and the length of the first secondary feather. The first secondary usually lies approximately perpendicular to the leading edge of the wing, and its length is a reasonable estimate of wing chord; the handwing represents a considerable proportion of the wingspan. Of all of the indices we consider (Table 1), this is the only one which measures the overall proportions of the handwing rather than some aspect of the geometry of the wingtip. It identifies a different dimension of wing shape from the other indices, and it is not surprising that this index is closely correlated with aspect ratio, and shows similar patterns of variation with migration classes (Fig. 5a, m).

Wing outline

The spanwise distribution of wing chord affects the distribution of aerodynamic lift or bound wing circulation across the wing, and therefore is related to the aerodynamic force moments acting at the wing root, to the geometry of the vortex wake, and to the induced drag. We do not yet know fully the criteria and constraints which determine wing outline in birds of different behaviours, particularly in flapping flight. The accepted wisdom is that an elliptic wing outline is optimal for low-speed wings because this profile minimizes induced drag for given lift and given wing area. However, this criterion is probably simplistic for many birds: a more rounded wing can maximize thrust from flapping, while a more pointed wing with a sharp wingtip minimizes wing weight and wing inertia (Rayner 1986, 1993). A short wing must be flapped at high frequency to provide sufficient thrust, and is therefore more likely to be subject to selection to minimize inertia, and hence to have a pointed, low-inertia outline. This explains the wing form of birds such as waders, auks and ducks, which fall in the upper left quadrant of Fig. 3, and have very pointed but convex wings; C_3 as a measure of primary feather convexity is very effective in identifying this group of birds. On the

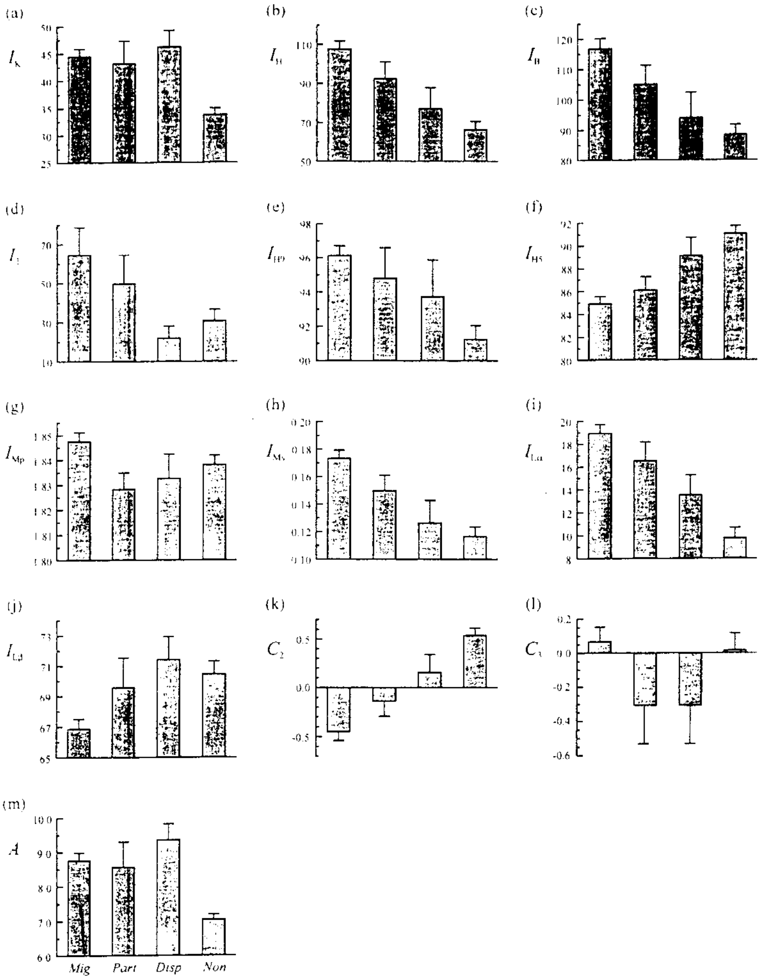

Fig. 5. Mean (+SE) wingtip shape in relation to migratory categories. See Table 4 for statistics.

other hand, relatively larger wings are more diverse in shape (cf. gull and buzzard in Fig. 3), and are probably not influenced by constraints on wing weight or inertia. Our convexity coefficient C_3 distinguishes between species with a relatively convex wing providing high thrust and those with a relatively concave wing with reduced wing weight and inertia.

The elliptic wing is optimal in the theoretical case of a straight wing, lying perpendicular to the line of flight. Bird wings are rarely straight and perpendicularly aligned, but are often designed with a forward or backward sweep. This can reduce induced drag compared with the elliptic value: a backward swept wing is more efficient if it is pointed, while a forward swept wing should be rounded (Aschenberg and Weihs 1984, D. Weihs, pers. comm.). It appears that bird wings have evolved in this way – pointed wings are backward swept, while square and rounded wings tend to sweep forwards (Fig. 3 in Rayner 1988) – though these patterns have not been formally tested. Backward swept, pointed wings, for example in gulls and swans, often show appreciable concavity of the tips of the proximal primaries.

More rounded wings (larger C_2) generate a greater proportion of their lift towards the wingtip, where the wing is moving faster. They are particularly effective for birds which fly at slow speeds (including taking off from the ground), or which need high levels of acceleration or of lateral manoeuvrability. All of these conditions benefit from the larger moments when lift is generated more distally on the wing. Many small passerines often fly slowly or among clutter, or need rapid acceleration to escape predators or during the flapping phases of bounding flight. Many of the same factors also apply to woodland predators such as sparrowhawks, buzzards and corvids. The latter pressures correlate with the relatively rounded and convex wings of these species, and the prevalence of extremely rounded wings in passerines explains the appreciable allometry of C_3 with size. Similar trends occur within species: take-off in European Starlings shows a significant increase in angle of ascent with wingtip roundedness (increasing C_2) (J. P. Swaddle, unpubl. data). This probably reflects the greater thrust available from a more rounded wing at low flight speeds. Marine gliding and soaring birds do not experience pressures of this kind, and tend to have convex but pointed wings.

Wingtip geometry

The geometry of the wingtip affects the way the wingtip vortices are shed into the wake, but the aerodynamic processes at the feathered wingtips are relatively poorly understood. Tip shape can theoretically have a significant effect on induced drag, especially when the primary feathers are highly separated and each feather acts as a separate aerofoil (e.g. see Tucker 1993, 1995). A pointed tip should allow the tip vortex to be shed smoothly and to roll up quickly, while on a more rounded wing the tip vortex will occupy a larger volume and presumably, therefore, rolls up more slowly, and gives rise to a higher induced drag. However, recent flow visualization studies of gliding wakes reveal that the rounded but highly cambered wings of owls are remarkably efficient; not only do they not have the high induced drag expected with this wing shape, but they appear to function more effectively than a planar elliptic wing (Rayner 1995); this may be due to the vertical as well as horizontal spacing of the primary feather tips. Moreover, while a very pointed wingtip formed of one narrow feather should shed wake vortices with minimum tip losses, it would also be susceptible to deformation under aerodynamic loads, as well as to physical damage and abrasion.

Table 5. Pairs of species used in phylogenetically and ecologically controlled analyses. More-migratory and less-migratory species in con-generic pairs that occupy the same ecological niche, but exhibit differing migratory behaviours. Species that are more migratory have more pointed and convex wingtip shapes and have a higher aspect ratio (Table 4) than less-migratory species.

Family	More-migratory species	Less-migratory species
Ardeidae	*Ardea purpurea*	*Ardea cinerea*
Anatidae	*Cygnus columbianus*	*Cygnus olor*
Anatidae	*Anser albifrons*	*Anser anser*
Anatidae	*Branta bernicla*	*Branta canadensis*
Anatidae	*Anas clypeata*	*Anas crecca*
Anatidae	*Anas querquedula*	*Anas platyrhynchos*
Anatidae	*Aythya ferina*	*Aythya fuligula*
Accipitridae	*Circus aeruginosus*	*Circus cyaneus*
Accipitridae	*Buteo lagopus*	*Buteo buteo*
Rallidae	*Gallinago media*	*Gallinago gallinago*
Laridae	*Larus fuscus*	*Larus argentatus*
Laridae	*Larus eburnea*	*Larus marinus*
Laridae	*Larus melanocephalus*	*Larus ridibundus*
Columbidae	*Streptopelia turtur*	*Streptopelia decaocto*
Strigidae	*Asio flammeus*	*Asio otus*
Hirundinidae	*Hirundo rustica*	*Hirundo daurica*
Passeridae	*Motacilla flava*	*Motacilla alba*
Muscicapidae	*Saxicola rubetra*	*Saxicola torquata*
Muscicapidae	*Turdus iliacus*	*Turdus merula*
Muscicapidae	*Turdus philomelos*	*Turdus viscivorus*
Regulidae	*Regulus ignicapillus*	*Regulus regulus*
Paridae	*Parus ater*	*Parus palustris*
Fringillidae	*Emberiza hortulana*	*Emberiza calandra* (*Miliaria*)
Fringillidae	*Emberiza aureola*	*Emberiza citrinella*
Fringillidae	*Fringilla montifringilla*	*Fringilla coelebs*
Fringillidae	*Carduelis spinus*	*Carduelis chloris*
Fringillidae	*Acanthis cannabina*	*Acanthis flavirostris*

Our pointedness coefficient C_2 distinguishes the shape of the wingtip largely by the location of the longest primary feather (Fig. 4). Its aerodynamic interpretation is presently not entirely clear. Work is currently in progress predicting and measuring tip vortices of wings of different design with the aim of differentiating between conflicting aerodynamic and mechanical pressures on wingtip adaptation. Our pointedness and convexity indices will prove invaluable in quantifying tip geometry. We believe they will also prove particularly valuable in moult studies, by permitting quantification of the variation in wing geometries of moulting birds by a measure which may be understood in terms of flight aerodynamics.

Wingtip shape indices

Although they all correlate with C_2 (wingtip pointedness), the wingtip shape indices are not identical to one another; our analysis raises several questions regarding the compatibility and interpretation of these measures. Some authors have concluded that particular between-index comparisons are valid for closely related species (Tiainen and Hanski 1985, Hedenström and Pettersson 1986), but it is evident that different indices measure different aspects of wing shape variation (see also Busse 1967, Chandler and Mulvihill 1988). A criticism made of the indices has been that wingtip pointedness and symmetry are not independent quantities (Tiainen 1982, Tiainen and Hanski 1985, Chandler and Mulvihill 1988). Our study supports this finding, since all published indices, including those supposed to measure symmetry, tend to increase with decreasing C_2 (Fig. 4), and symmetry indices (I_H, I_T and I_{Ms}) are significantly correlated with most pointedness indices. However, despite the significant correlations between indices and the measures of wingtip shape as derived by SCCA, the majority of indices tested in our analyses were unable to detect ecologically-relevant shape variation across a wide range of species when phylogenetic and ecological biases were controlled. Our analyses of migratory wingtip shape adaptations suggest that $I_{\mathrm{L}\alpha}$ and $I_{\mathrm{L}\beta}$ are the most powerful wingtip shape indices in identifying species adapted for migration (although their calculation may be prohibitively time-consuming); our measures are more straightforward and simpler to calculate than Levin's indices, and are therefore recommended as sensitive measures of wingtip pointedness and concavity that are independent of size bias.

We have tested the congruence and significance of indices in interspecific analyses. As Chandler and Mulvihill (1988) predicted, all indices detect gross morphological changes associated with the transformation from a rounded to a pointed wing. With the exception of I_{T}, I_{H9}, I_{Mp} and $I_{\mathrm{L}\beta}$, all indices were highly correlated with each other, and therefore may be supposed either to measure the same features of wingtip shape, or to combine aspects of the wingtip design which, for mechanical or structural reasons, are constrained to vary together. For these reasons, the indices measure primarily wingtip pointedness, despite the various claims that they measure 'symmetry' or 'sharpness'.

High correlations among indices were not apparent in Chandler and Mulvihill's (1988) intraspecific analysis of the Dark-eyed Junco, in which I_{H9} was not significantly correlated with I_{H5}, and I_{H9} was only occasionally correlated with I_{B}. Chandler and Mulvihill also found that the indices were insensitive to a high percentage of the wingtip shape variation in Dark-eyed Juncos, as quantified by principal components analysis. Our failure to find many indices varying closely with C_3 (Fig. 4) shows that the same is true in interspecific analyses. The indices (in the main, at least) are straightforward to compute and in interspecific studies are convenient as measures of pointedness, if their geometrical and statistical limitations are set aside. They are not effective in measuring hand wing convexity, and can have little validity in comparative analyses across a broad range of species. SCCA has identified two significant axes of interspecific wingtip shape variability; it is possible that within certain individual species these axes do not form the most significant trends of variation, and indices may continue to prove useful in intraspecific problems, provided that the problem of size bias is addressed for I_{K}, I_{H9}, I_{Mp} and $I_{\mathrm{L}\beta}$.

There is a further source of close relations among the indices. There are strict geometric constraints on feather length at and around the wingtip, since in most wings feather lengths must decrease monotonically away from the longest primary. For instance, only in rare cases is Q_8 longer than Q_7, or Q_6 than Q_5; such extreme concave wings would fall in the lower right quadrant of Fig. 4, where there are few real wings (Fig. 3). These constraints are reflected in the form of our indices (Appendix 2). C_1 has an approximately equal weight with all Q_i (it can be expressed symbolically as $\Sigma \ln(Q_i)$): this is in part a consequence of its definition as an isometric size component. C_2 is structured as a weighted and centred first moment of feather lengths, of the form $\Sigma\, i \ln(Q_i)$, and C_3 is essentially a centred second moment $\Sigma\, i^2 \ln(Q_i)$, weighted slightly to the most distal and most proximal feathers. Ramsay and Silverman (1997) provide a mathematical explanation for why our indices take the form of moments. The algebraic similarity of our indices to Mlíkovský's indices (Table 1) based on the statistics of skewness and kurtosis (Mlíkovský's indices are uncentred third and fourth moments) is evident. The appearance of these simple algebraic forms in primary feather SCCA reflects structural and biological constraints on primary feather lengths.

Wing shape, morphometrics and migration

The results of our phylogenetically and ecologically controlled analyses highlight the importance of controlling for both of these biases in any interspecific study of adaptations for migration. The significant difference in wingtip pointedness between migratory and less-migratory species supports both practical and theoretical analyses of morphological migratory adaptations. Theoretical analyses (Rayner 1988, Norberg 1990) predict that migratory species should have wings with higher aspect ratio, and these predictions are broadly confirmed by previous morphometric studies (Fitzpatrick 1985, Winkler and Leisler 1985, 1992, Yong and Moore 1994). In both our broad interspecific and controlled analyses we found a significant difference in aspect ratio, which is independent of size, with migration, but no difference in mass, wingspan, wing area or wing loading, all of which depend on size. Some previous studies of migration may have failed to detect morphological adaptations in the wings because of the confounding effect of phylogenetic and ecological bias, and because of a failure to compensate adequately for isometric variation in size.

The size-constrained measures of wingtip shape introduced in this study are straightforward to calculate and are applicable to ecomorphological analyses of the function and consequences of wingtip design in birds. Unlike the previously published indices, our measures statistically isolate shape from size in an interspecific sample and are free of the interpretational problems from which the other indices suffer. C_2 and C_3 can be utilized in any subsequent interspecific study of wingtip shape and interpreted in terms of the aerodynamic and biomechanical predictions of pointedness (C_2) and convexity (C_3). This cannot be achieved with any other previously published index of wingtip shape. Our analyses also provide a phylogenetically and ecologically controlled indication that migrants have a more pointed and more convex wingtip shape and a higher aspect ratio. This is the first study to provide unambiguous support for these morphological adaptations to migration at the interspecific level.

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Appendix 1. Size-corrected components analysis (SCCA)

This appendix describes a modification to principal components analysis (PCA) which incorporates a rigorous geometric model of size, defined, in most cases, as that axis which maintains constant isometric shape. It is intended for morphometric problems that have defined shape isometry, and is applicable to other cases in which it is necessary to constrain variation relative to an externally-imposed vector or geometry. The method is presented here for p variates X which are logarithmically transformed and standardized (for rationale see main text, also Bookstein et al. 1985, Rayner 1985); logarithmic transformation is not essential, but is convenient when the size vector, and associated hypotheses, are formulated in power-law form. The method is derived from a discriminant function method of Burnaby (1966), which is also extended by derivation of the appropriate form of the isometric size vector with a standardized multivariate sample.

Principal components analysis (PCA) is frequently used in morphometric studies because it often reduces dimensionality, and produces a set of p orthogonal principal components which may be easier to interpret than direct measurements with a complex correlation structure. When most of the variates are dimensions of organisms spanning a reasonable size range, the first principal component (PC_1) is likely to be positively weighted to all input variates, and is usually interpreted as a measure of size (e.g. Shea 1985, Bookstein 1989; for examples see Chandler and Mulvihill 1988, Rayner 1988, Rising and Somers 1989, Leisler and Winkler 1991). The remainder of the variance is encompassed in the remaining principal components (PC_2–PC_p) which are deemed to be independent of size and are usually identified as measures of shape. Those components with small eigenvalues, representing insignificant partitions of the sample variance, can be ignored.

A limitation of PCA is that the terms 'size' and 'shape' are poorly defined. Since the formulae for the component loadings depend on the sample, they have no predictable geometric interpretation. In many morphometric problems both terms 'size' and 'shape' are ambiguous, and there is considerable confusion in the literature surrounding their use. Bookstein (1989) has reviewed PCA and other measures of size and shape in multivariate morphometrics, and has made a strong case for the need for greater precision in the definition of these quantities: "we may see fewer arguments over what size and shape are supposed to mean, and fewer arguments that size-your-style does not have property-X-my-style." Similar confusion surrounds the terms 'isometry' and 'allometry', which are used to describe the extent to which shape depends on size: these can only be consistently meaningful in the context of a rigorous geometric definition of size (and shape). With a strict geometric definition, a sample can be said to obey isometric scaling if shape is independent of size, and to show positive or negative allometry according to whether a shape variable increases or decreases as size increases (e.g. Rayner 1985, 1996). If shape and size are ill defined, and if they partition variance to different extents when estimated by different methods, allometry cannot be uniquely quantified. Allometry is an important biological phenomenon (e.g. Gould 1966), and arises frequently in the course of growth, or as a consequence of adaptation within size-dependent constraints (e.g. Rayner 1988, 1996). The investigator must often expect *a priori* that shape will depend upon size; a goal of a morphometric study may be to quantify allometry or to test its significance, or to control for the effects of size and/or allometry before testing hypotheses about shape. The principal component method, although it appears to separate 'size' and 'shape' into independent components, cannot give a robust model of the geometrical relationships of the variates in the presence of allometry.

Various other methods have been proposed to separate size and shape (for reviews see Humphries et al. 1981, Reist 1985, Bookstein 1989), but all reflect different, and often inconsistent, definitions of size. The two most familiar methods correct each variate for size independently. Variates can be converted to ratios, so that if X_i is expected to vary with a certain size variate X_1 as $X_1^{a_1}$, then X_i is replaced by $X_i' = X_i/X_i^{a_1}$, and subsequent analyses are performed with the $p-1$ variates X_2' to X_p'. In general the first principal component is no longer positively weighted with all the X_i', because scaling has eliminated variation with size. This approach is unsatisfactory because X_1 is unlikely to encompass all size variation, because it may not be possible to choose a single most approrpiate X_1, and because ratios are subject to severe statistical and conceptual difficulties and rarely satisfy the normality and linearity criteria required for methods such as PCA (Atchley and Anderson 1978, Humphries et al. 1981). (It should be noted that the use of wingtip shape indices as variates in a PCA is an example of this method, and would be subject to the problems inherent in the use of ratios.)

A more sensitive approach is to compute X_i' as the regression residual $X_i' = X_i/X_i^{b_1}$, where b_i is determined from the sample as the log-linear regression coefficient of X_i on X_1 (Humphries et al. 1981); for examples of this method see Senar et al. (1994) and Mönkkönen (1995). As with the method above, this approach remains subject to statistical limitations of ratios, and can only eliminate that component of size which is measured by X_1. Both methods are highly sensitive to measurement errors in X_1, but their more serious limitation is that they do not provide an unique measure of size. This information is retained in the principal component approach as PC_1, albeit confounded by the apparent, though illusory, removal of allometry.

Two approaches are available to circumvent these problems. Humphries et al. (1981), Bookstein et al. (1985) and Rohlf and Bookstein (1987) have developed a 'shearing' path analysis model by which size is extracted by regression of the individual

PCA component loadings on a within-group size component (for a similar method see also Sampson and Siegel (1985)). This method is intended primarily for landmark or Cartesian co-ordinate data, and is not intended for size correction or control. The primary limitation of shearing for our purposes is that it determines the measure of size from the sample, and therefore the numerical measure and the structural formulation of size are dependent on the sample measured and the variates chosen, and as with PCA could have no consistent geometric interpretation between different analyses of the same phenomenon.

For problems in which strict control of geometry and of the definition of size are important, it is preferable to use the growth-invariant discriminant function of Burnaby (1966) (see also Rohlf and Bookstein 1987, Reyment 1991). The method starts with an *a priori* geometric definition of the size vector. If $p-1$ shape variables (some of which may not be significant) are defined to be constant in isometrically similar animals (as isometric measurement functions, *sensu* Mosimann (1970)), then the remaining variable is a measure of *isometric run*. Burnaby's method was originally applied to discriminant analysis, but translates readily to the components problem with a single population. We term the method size-constrained components analysis (SCCA), following the terminology of Sundberg (1989); SCCA is similar to PCA in that it rotates the co-ordinate system to partition variance; the rotation is equivalent to mapping component 1 to the pre-defined size vector, and then performing a PCA on the subsequent components.

Suppose that size is measured by the known vector $\boldsymbol{g}$. Then if $\boldsymbol{R}$ is the sample estimate of the dispersion matrix of the standardized and log-transformed input variates $\boldsymbol{x}$ (i.e. $\boldsymbol{R}$ is the correlation matrix of the unstandardized input variates $\log(\boldsymbol{X})$), the eigensolution $\boldsymbol{l}$ must minimize $\boldsymbol{l'Rl}$ subject to the constraints $|\boldsymbol{l}| = 1$, $\boldsymbol{l} \cdot \boldsymbol{g} = 0$ and $|\boldsymbol{l}| = 1$, and can be written as

$$(\boldsymbol{L} - \lambda \cdot \boldsymbol{I})\boldsymbol{l} = 0, \tag{A1}$$

where

$$\boldsymbol{L} = (\boldsymbol{I} - \boldsymbol{gg'})\boldsymbol{R} \tag{A2}$$

(after Burnaby (1966), eqn (5); see also Rohlf and Bookstein (1987) and Reyment (1991)). $\boldsymbol{L}$ is a $p \times p$ idempotent matrix with, at most, $p-1$ non-trivial eigenvectors; projections of $\boldsymbol{x}$ onto these eigenvectors give the shape components $C_2 - C_n$. The size factor C_1 is estimated from the projection of $\boldsymbol{x}$ onto $\boldsymbol{g}$. The first (size) component derived by this method is not an eigensolution, and the components should therefore not be referred to as *principal*.

Somers (1986) proposed an alternative approach to this problem based on an iterative matrix reduction, which has some similarities to the present method. His approach is subject to a number of statistical limitations, in particular to a tendency to predict negative eigenvalues (Rohlf and Bookstein 1987, Somers 1986, 1989). Sundberg (1989) raised a number of specific criticisms of Somers' method; problems due to inappropriate data scaling are significant (and were corrected by Somers (1989)), but the problem of non-zero correlations between the size and shape components is neither an error (Somers 1989) nor a disadvantage, and is a valuable feature of both Somers' and Burnaby's methods, as we demonstrate below.

It remains to estimate the size vector $\boldsymbol{g}$. Burnaby (1966) firmly recommended that this should not be estimated from the data themselves, but should be determined independently; this rules out using the first principal component of the within-groups variation (Burnaby 1966, Reyment 1991). Somers (1986) and Rohlf and Bookstein (1987) suggest using the vector

$$\boldsymbol{g}_1 = (p^{-\frac{1}{2}}, p^{-\frac{1}{2}}, \ldots, p^{-\frac{1}{2}}), \tag{A3}$$

which they termed an isometric size vector, following Jolicoeur (1963) and Mosimann (1970). $\boldsymbol{g}_1$ is the first eigenvector of a dispersion matrix with all variances equal and all co-variances equal; at first sight it appears the natural choice for the size vector. However, it is misleading to term this vector 'isometric', since it does not measure sample isometry in the geometric sense defined above. This can readily be demonstrated by considering the bivariate case. The dispersion and correlation matrices of a standardized bivariate sample are identical and of the form

$$\begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix} \tag{A4}$$

for some ρ; therefore all bivariate samples have 'isometric size' eigenvector $\boldsymbol{g}_1 = (2^{-(1/2)}, 2^{-(1/2)})$ and corresponding eigenvalue $1 + \rho$, regardless of the population variance structure. This eigensolution $y = x$ is the bivariate reduced major axis (Rayner 1985), and is not independent of sample variances v_{xx} and v_{yy} since, in the equation for the relation $Y = X^{\beta}$ between centred unstandardized variates, $\beta = (v_{yy}/v_{xx})^{1/2}$ and is not in general unity. The isometric equation must be of the form $Y = X^1$. The vector $\boldsymbol{g}_1$ is geometrically isometric only in the special case in which all sample variates have equal variance.

To represent sample isometry, $\boldsymbol{g}$ in the standardized space must reflect the centring and standardizing transformations employed to reach that space. Suppose isometric variation in the untransformed sample variates can be written as the line

$$a_1 X_1^{b_1} = a_2 X_2^{b_2} = \ldots = a_p X_p^{b_p}, \tag{A5}$$

with unit vector of scaling indices

$$\boldsymbol{G} \propto (b_1, b_2, \ldots, b_p), \tag{A6}$$

for some a_i; the b_i are determined by the geometrical relationships and physical dimensions of the X_i (and in many cases will be identically 1). After log-transformation and standardization the isometric line becomes

$$b_1 V_1^{\frac{1}{2}} x_1 = b_2 V_2^{\frac{1}{2}} x_2 = \ldots = b_p V_p^{\frac{1}{2}} x_p, \tag{A7}$$

where V_i is the sample variance of $\log_e(X_i)$. Therefore $\boldsymbol{g}$ (which for convenience has unit modulus) should be proportional to the vector

$$(b_1^{-1} V_1^{-\frac{1}{2}}, b_2^{-1} V_2^{-\frac{1}{2}}, \ldots, b_p^{-1} V_p^{-\frac{1}{2}}). \tag{A8}$$

The geometry of this transformation of the isometric vector and the SCCA method is illustrated in Fig. 6. The key feature of this method is that the geometry of the isometric vector is prescribed *a priori* in the sample dataspace (in the transformed and standardized dataspace $\boldsymbol{g}$ will depend on the sample variances). If all the X_i have the same physical dimension (for instance they are all measurements of length) and the size hypothesis is that they vary isometrically with one another, then all the b_i are unity. This is not always the case: if for example the sample comprised three variates mass, wingspan, wing area (as in Norberg and Rayner (1987) and Rayner (1988)), then the isometric similarity hypothesis would be represented by $b_1 = \frac{1}{3}$, $b_2 = 1$ and $b_3 = \frac{2}{3}$.

The result of SCCA is a vector C_i of component loadings for each sample. As in PCA, it is convenient to standardize the loadings, though in some applications it may be appropriate not to standardize the C_1 so that the size measure is not dependent on the sample. Small eigenvalues of $\boldsymbol{L}$ are associated with insignificant components of variance, and may be identified by the same tests as used for PCA, but applied only to the $p-1$ shape components. Correlations ρ_i between C_1 and the $C_2 - C_p$ scores are not in general zero, and can be used

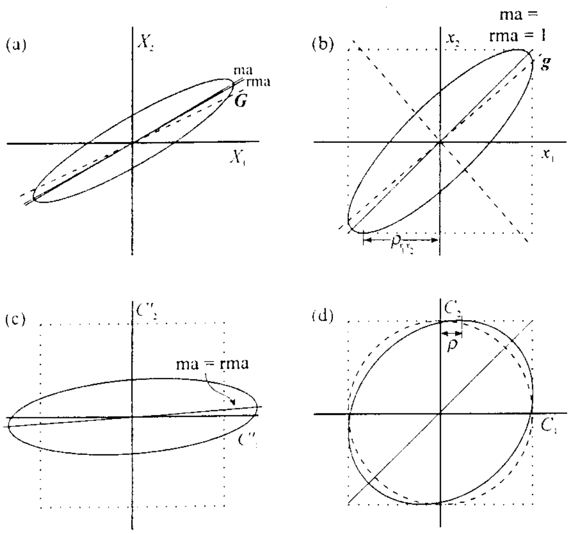

Fig. 6. Geometry of size-constrained components analysis (SCCA), illustrated by the bivariate case. (a) log-transformed variates X_1, X_2 for a bivariate sample with moderate correlation, showing reduced major axis (rma) and major axis (ma) structural relations (see Rayner 1985) and an externally specified size or hypothesis vector $\boldsymbol{G}$. The sample variates are assumed to obey a bivariate normal distribution, indicated by the ellipse, and show modest positive allometry because rma and ma are steeper than $\boldsymbol{G}$. (b) The sample after standardization: standardized variates x_1, x_2 have unit variances, and the sample ellipse is bounded by a square of side 2, whose diagonal with unit slope is the now-coincident rma and ma; the transformed hypothesis vector $\boldsymbol{g}$ has a lower slope. (c) The sample after rotating so that C'_1 corresponds to $\boldsymbol{g}$, but before normalization. C'_1 and C'_2 axes are orthogonal, but sample loadings on C'_1 and C'_2 are correlated because of allometry. SCCA has partitioned variance so that isometric size variation lies along C'_1, shape variation lies along C'_2, but this shape variation includes some allometry. (d) The final step (which is convenient but not essential) is to normalize the component loadings to C_i so that the sample ellipse is again bounded by a square. In the absence of allometry the distribution would be circular; the skew of the distribution (measured by the correlation coefficient ρ, which with two variates has the geometric interpretation shown) is a measure of allometry.

to test the significance of allometry either of each component, or, using the multiple correlation coefficient

$$\rho = \left(\sum_{i=2}^{p} \rho_i^2 \right)^{\frac{1}{2}}, \tag{A9}$$

with $N-p-1$ d.f., of pooled allometry (Fig. 6d); in the two-dimensional case ρ_2 is equivalent to the expected slope regression test for allometry (Rayner 1985).

In real applications for which PC_1 would be an acceptable measure of size, the components derived by SCCA will normally differ only slightly from those of conventional PCA, even when allometry is significant. SCCA can be obtained from PCA by an orthogonal rotation. The distinction between them is in the partitioning of variance. In PCA, PC_1 is that linear combination of the variates which explains maximum variance, and although conveniently described as 'size' will differ from isometric size unless allometry is absent because it must include some shape variation. PC_2–PC_p are measurements of shape independent of allometry. In applications such as our measurement of avian wingtip geometry where an exact quantification of shape is needed, the inclusion of allometry in PC_1 is disruptive. Two animals with identical wingtip geometry but differing isometrically in size would have different PCA size components, but would also have different shape components. PCA cannot identify consistency of geometric shape. By defining a size vector *a priori*, SCCA circumvents this problem: these two animals will have identical shape components, and their size components C_1 will differ by the exact ratio of the linear dimensions. In SCCA, C_1 is defined to measure size only, and subsequent shape components are geometrically orthogonal to it (though the sample correlations between size and shape components need not be zero; Fig. 6d). The method is valid for any definition of the size vector $\boldsymbol{g}$, but when all input variates are linear measurements, there is a natural *a priori* formulation of size as isometry. Like PCA, SCCA is intended for use with a multivariate normal sample, but usually responds well with samples which are not normally distributed. The advantages of SCCA lie in its explicit formulation of size in terms of a shape measurement function, in its retention of the most useful properties of PCA (sequentially partitioned variances, uncorrelated shape components), and in its explicit quantification of the magnitude of allometry.

Appendix 2. Formulae for SCCA components

The wingtip shape indices derived in this study can be calculated directly from the formulae below. C_1 is a measure of isometric size. C_2 and C_3 are measures of wingtip pointedness ($-$) and convexity, respectively. Q_1–Q_8 are the lengths of primaries 1 to 8, numbered ascendingly from the distal, leading edge of the wing, but omitting any vestigial distal-most primaries (see text).

$$\begin{aligned} e^{C1} &= 4.705 \times 10 - 4 Q_1^{0.209} Q_2^{0.200} Q_3^{0.198} Q_4^{0.195} Q_5^{0.192} \\ &\quad \times Q_6^{0.192} Q_7^{0.204} Q_8^{0.210} \end{aligned} \tag{A10}$$

$$\begin{aligned} e^{C_2} &= 3.332 Q_1^{-3.490} Q_2^{-1.816} Q_3^{-0.893} Q_4^{-0.003} \\ &\quad \times Q_5^{0.829} Q_6^{1.351} Q_7^{1.661} Q_8^{2.363} \end{aligned} \tag{A11}$$

$$\begin{aligned} e^{C_3} &= 0.0879 Q_1^{-6.231} Q_2^{1.683} Q_3^{4.033} Q_4^{4.721} Q_5^{3.955} \\ &\quad \times Q_6^{1.349} Q_7^{-3.185} Q_8^{-6.326} \end{aligned} \tag{A12}$$