SHORT COMMUNICATION

A morphospace-based test for competitive exclusion among flying vertebrates: did birds, bats and pterosaurs get in each other's space?

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Abstract

Three vertebrate groups – birds, bats and pterosaurs – have evolved flapping flight over the past 200 million years. This innovation allowed each clade access to new ecological opportunities, but did the diversification of one of these groups inhibit the evolutionary radiation of any of the others? A related question is whether having the wing attached to the hindlimbs in bats and pterosaurs constrained their morphological diversity relative to birds. Fore- and hindlimb measurements from 894 specimens were used to construct a morphospace to assess morphological overlap and range, a possible indicator of competition, among the three clades. Neither birds nor bats entered pterosaur morphospace across the Cretaceous–Paleogene (Tertiary) extinction. Bats plot in a separate area from birds, and have a significantly smaller morphological range than either birds or pterosaurs. On the basis of these results, competitive exclusion among the three groups is not supported.

Introduction

Flapping flight is a key evolutionary innovation, opening up a wide range of ecological opportunities for groups that have evolved aerial capabilities (Norberg, 1994). We know that three vertebrate clades – birds, bats and pterosaurs – evolved flapping flight independently over the last 200 million years (Ma); a question that has never been satisfactorily answered is whether any of these clades excluded either of the other two from diversifying within the aerial niche. Because ecology and wing morphology so clearly overlap across the three clades, some degree of competitive exclusion might be expected.

Studies that address morphological diversification between, and within, clades are not new. Previous approaches, however, have focused on comparing taxonomic diversity in time with emphasis on identifying patterns where one clade declines whereas another possible ecological competitor increases in taxonomic diversity. This so-called 'double wedge' pattern has formed the basis for debate in this area (Benton, 1996; Sepkoski, 1996). Benton (1996) developed the concept of 'Candidate Competitive Replacements' (CCRs), defined a range of event types based on the fossil record and stressed that the strongest cases for CCRs must be those for which spatio-temporal overlap and direct resource competition hypotheses can be made (Benton, 1996). Although debates have continued over whether it is really possible to identify CCRs in the fossil record using taxonomic data alone (Gould & Calloway, 1980), especially in the case of vertebrates (Fountaine *et al.*, 2005), mathematical approaches to the morphometrics of flighted taxa have been widely applied with these transitions in mind (Ricklefs & Miles, 1994) – to birds (Rayner, 1988), bats (Norberg & Rayner, 1987; Norberg, 1994) and pterosaurs (Hazlehurst & Rayner, 1992). Some efforts have also been made to directly compare the morphospace occupation patterns of the three groups (Rayner, 1988; Hazlehurst & Rayner, 1992; Middleton & Gatesy, 2000; Dyke *et al.*, 2006).

Does competition among flying vertebrates occur in modern faunas? Birds and bats co-exist today, but their broad temporal subdivision into 'day' and 'night' activity

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means the two groups avoid direct competition to a degree. The oldest fossil bats (*Icaronycteris* from the Eocene Green River Formation; Simmons & Geisler, 1998) could echolocate, indicating that these aerialists were probably primitively nocturnal (Jones & Teeling, 2006). These fossils also come from the same Eocene localities as fossil birds indicating that the two groups have co-existed for at least 55 Ma. Similarly, we know that birds and pterosaurs inhabited the same environments during the Mesozoic (*c.* 150 to 65 Ma) – pterosaurs and *Archaeopteryx* are both found in the famous German Jurassic Solnhofen deposits, and many birds and pterosaurs have been recorded from the Cretaceous Jehol Group of China (Zhou *et al.*, 2003; Zhou, 2004). Birds and bats both had the opportunity to exploit niches vacated by the extinction of pterosaurs at the Cretaceous–Paleogene boundary. Clades that do not overlap temporally, but that would have competed for similar resources, can be viewed as candidate competitors (see Benton, 1996), making it valid for us to consider whether pterosaurs and birds prevented bats from evolving during the Jurassic and Cretaceous by pre-emptive occupation of flying vertebrate niches.

In this paper we compare the occupation patterns of limb morphospace among the three flying vertebrate clades to test for any overlap between them. As the wing membrane is attached to the hindlimbs in bats and in some pterosaurs (Unwin, 2006), the range of possible interactions among locomotor modules (Gatesy & Dial, 1996) might be restricted; this constraint may be reflected by pterosaurs and/or bats having a significantly lower total range in morphospace (corrected for sample size). We employ rarefaction analysis to eliminate effects of different sample sizes (see Wills, 2001), allowing us to test whether bats and/or pterosaurs have a smaller total range in limb morphospace than birds. Previous studies (Dyke *et al.*, 2006) have provided qualitative descriptions of the range and area of morphospace occupied by birds and pterosaurs, and birds, bats and pterosaurs. However, earlier studies did not correct for differences in sample size, a shortcoming that undermines the validity of previous statements on the disparity within, and among, the respective clades.

Materials and methods

Measurements of six variables (hand length, forearm length, humerus length, foot length, tibia length and femur length) were taken from 894 specimens, representing 795 species of nonavian dinosaurs, birds, pterosaurs and bats (G.J. Dyke, R.L. Nudds, J.M.V. Rayner, unpublished data; see Nudds *et al.*, 2004; Nudds & Rayner, 2006; Nudds *et al.*, in press). In this analysis most species are represented by a single individual, some by both male and female specimens. No species are represented by more than two specimens. Included pterosaur taxa take account of recent taxonomic

revisions of the clade (Bennett, 1995, 1996, 2005; Jouve, 2004; Unwin, 2006). Tarsometatarsus length in birds is considered equivalent to foot length in nonavian theropods, bats and pterosaurs. Lengths in millimetres were log_{10}-transformed to render them multivariate normal, and principal components analysis (PCA) was performed on the derived variance–covariance matrix. Group total ranges are the sum of ranges on all six PC axes for each group; all groups were subject to rarefaction analysis to a sample size of 30 and rarefaction results are based on 1000 replications to generate 90% confidence intervals. The Python computer code for this procedure is available on request (to AJM).

Results

Correlations among the six limb variables are shown in Table 1 alongside the PCA results in the form of specimen biplots in the PC I–PC II and PC II–PC III morphospace planes (Figs 1a and 2a). To clarify the regions occupied by nonavian dinosaurs, Mesozoic (non-neornithine) birds and palaeognaths, these groups are highlighted in Figs 1b and 2b. All bones included in analyses load positively on PC I, indicating this component is largely a 'size' axis, although it also contains some 'shape' information as loadings are not all equal (Bookstein *et al.*, 1985). This 'size' factor interpretation of our data is supported by the position of hummingbirds at the negative end of PC I and nonavian dinosaurs and palaeognaths at the positive end (Fig. 1b) (Table 2).

PC II shows that the forelimb measurements load positively, the hand most strongly, whereas hindlimb bones load negatively, with the foot most strongly (Figs 1a and 2a). Pterosaurs and bats, with elongated forelimb digits, have large positive PC II scores whereas flightless kiwis and cassowaries have high negative scores. PC III has the forelimb long bones loading

Table 1 Correlation among the six morphological variables in the fore- and hindlimbs.

	Humerus	Forearm	Hand	Femur	Tibia	Foot
Humerus	1.00	0.94	0.53	0.89	0.88	0.74
Forearm	0.88	1.00	0.71	0.75	0.72	0.53
Hand	0.28	0.51	1.00	0.37	0.25	−0.02
Femur	0.78	0.57	0.14	1.00	0.95	0.82
Tibia	0.77	0.52	0.06	0.91	1.00	0.92
Foot	0.54	0.28	0.00	0.68	0.85	1.00

The upper triangle (values to right of diagonal of 1.00s) shows the correlations, the lower triangle (values to left of diagonal of 1.00s) shows the square of the correlations, which is equivalent to a r^2 value. The r^2 values give some indication of how much variation in a variable can be explained by the morphological variable of interest. These are bivariate relationships, so percentages do not sum to 100%. Values are rounded to two decimal places. The most notable feature of the relationships is the low correlation between the hands and feet and the longer bones of the fore- and hindlimbs.
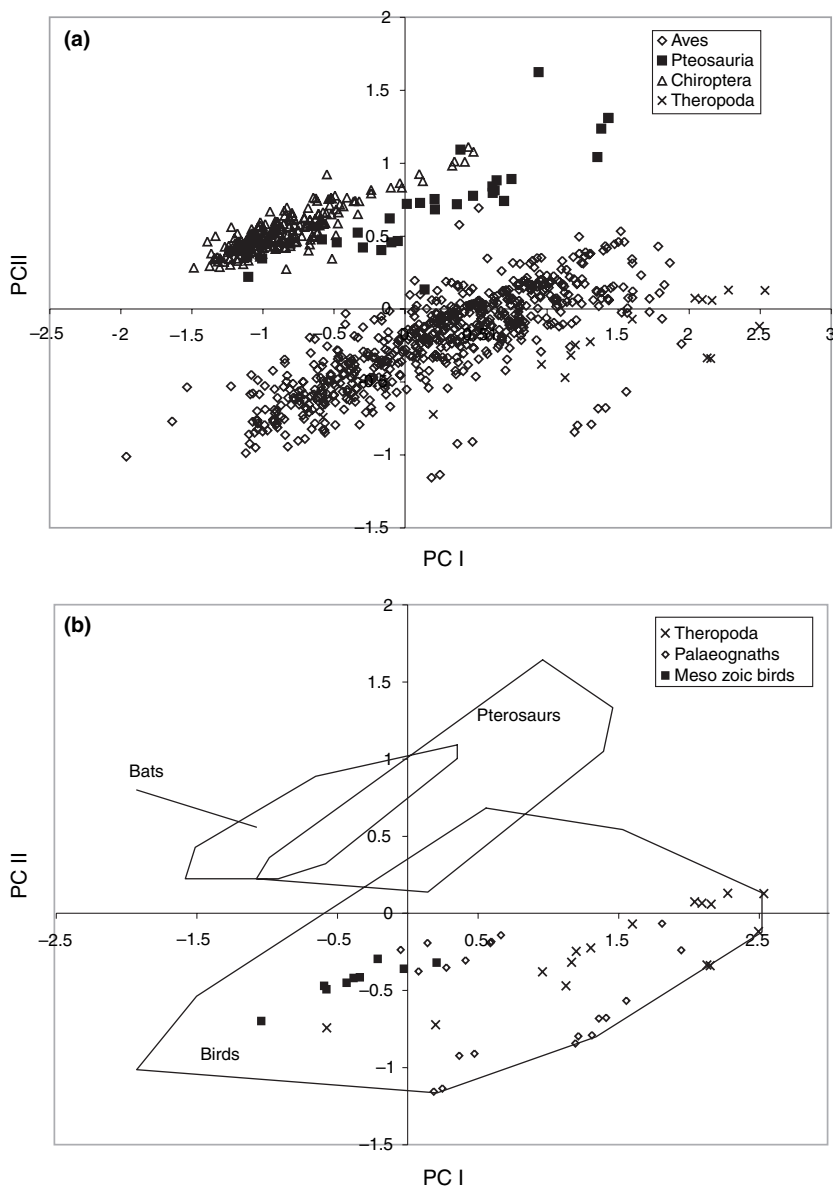
Fig. 1 Biplot of PC I vs. PC II. (a) The full samples of birds, bats and pterosaurs plotted in morphospace. PC I is a 'size' axis. Separation of birds from bats and pterosaurs is almost complete along the PC II axis. The morphological character responsible for this separation is the elongation of the hand in bats and pterosaurs. (b) Areas of morphospace occupied by the three major clades. A single pterosaur is responsible for the overlap between birds and pterosaurs in this plane of morphospace. Palaeognaths, theropods and Mesozoic birds are plotted to help understand the amount of space occupied by these groups. The lack of monophly of two of the groups is not important in this context, as the main reason for plotting these groups up is to understand the overlap, and get some idea of where these group lie relative to the overall avian portion of morphospace. Mesozoic birds plot very close to the centre of avian morphospace, and the overlap between palaeognaths and nonavian theropods is clear.

negatively whereas all other bones load positively (Figs 1a and 2a).

Discussion

What evolutionary insights can be offered by comparing the limb morphospaces occupied by extinct and extant flying vertebrates? Morphospaces can be seductively simple in the explanations and insights they appear to offer; Hulsey & Wainwright (2002) illustrated the dangers of assuming 1 : 1 scaling between morphospace and ecospace. Flight, however, has been extensively studied in terms of functional morphospaces (Norberg, 1994), and the bones considered here are homologous;

we have met the most stringent criteria of Ricklefs & Miles (1994) for an ecomorphological analysis, increasing confidence in our conclusions.

Our analyses show that the three clades do not overlap in limb morphospace. This contrasts with some previous studies – Rayner (1988) and Hazlehurst & Rayner (1992) reported overlap between birds and pterosaurs and birds and bats in wing proportions, but the addition of hindlimb data shows that these taxa are segregated in limb morphospace and are nonoverlapping (Figs 1 and 2). This means that competitive exclusion among the three clades over the course of their evolution is unlikely. Segregation in morphospace among the clades was maintained even after the
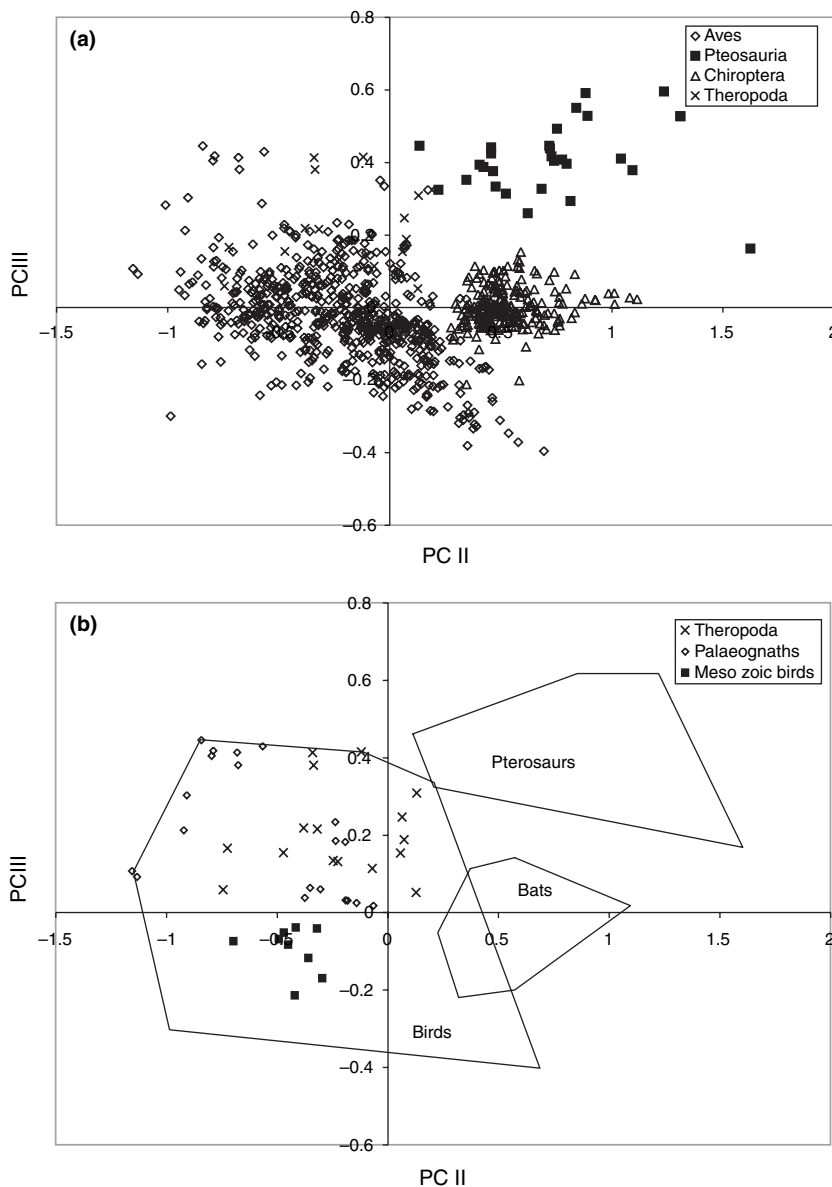
Fig. 2 Biplot of PC II vs. PC III. (a) The full samples of birds, bats and pterosaurs plotted in morphospace. Pterosaurs and birds occupy separate areas in this plot, which means they have no overlap in three dimensions. Bats show some overlap, with *Icaronycteris* being one of the bat taxa in bird space. Separation along PC III is between taxa with short humerus and forearm, but long hands. (b) Areas of PC II vs. PC III space occupied by the different clades, along with theropods, palaeognaths and Mesozoic birds plotted individually. Mesozoic birds once again plot towards the centre of the space.

Table 2 Results of principal components analysis (PCA) of variance–covariance matrix for specimens used in the study.

	PC I	PC II	PC III	PC IV	PC V	PC VI
Humerus	0.40	0.21	−0.51	0.16	0.02	−0.72
Forearm	0.31	0.36	−0.57	−0.09	0.07	0.66
Hand	0.16	0.77	0.49	−0.36	−0.02	−0.12
Femur	0.37	0.04	0.35	0.66	0.54	0.13
Tibia	0.45	−0.08	0.19	0.29	−0.81	0.13
Foot	0.62	−0.48	0.13	−0.57	0.22	−0.01
Eigenvalue	0.68	0.20	0.02	0.02	0.00	0.00
Percentage of variance explained	73.63	22.07	2.13	1.66	0.30	0.21
Cumulative percentage of variance explained	73.63	95.70	97.83	99.49	99.79	100.00

extinction of pterosaurs. Neither birds nor bats occupied pterosaur morphospace after the Cretaceous–Paleogene event. Some overlap does exist between pterosaurs and bats in the PC I–PC II plane, but none in the PC II–PC III plane (Figs 1b and 2b). Birds as a group do not overlap with pterosaurs at all and during the Mesozoic were even less similar (Figs 1b and 2b). This could be interpreted as damping out of Mesozoic bird diversification by pterosaurs (Unwin, 1988), but as neither birds nor bats occupied pterosaur morphospace after pterosaurs became extinct, this interpretation of these data is unlikely. Mesozoic birds at least are more similar in their morphospace occupation to nonavian theropods than they are to pterosaurs.

Our data also show that with one exception birds and extant bats do not overlap in either plane of limb morphospace. The Eocene *Icaronycteris* is the only bat to plot within bird morphospace in either plane; although the addition of more limb data from fossil bats would be required to elucidate the presence of a trend, the combination of a nocturnal mode of life and possible differences in developmental gene expression (e.g. *BMP2*; Sears *et al.*, 2006) may explain why the rapid diversification of bats went unhindered by the parallel diversification of birds. Sears *et al.* (2006) measured the correlation between body size and the length of the fifth metacarpal among fossil and extant bats. All taxa plotted close to a single regression line. This is important evidence for a change in a single change in a developmental pathway opening the aerialist niche to mammals, but then confining them to a particular region of morphospace.

Because birds and nonavian dinosaurs are subsets from within the same larger clade, it is not surprising that our data demonstrate overlap in limb morphospace between the two groups. Our study is however, the first time that this has been shown empirically for both fore and hindlimbs, and supports the proposal of Zweers *et al.* (1997) that the extant flightless palaeognaths may have converged on theropod morphologies. Mesozoic birds occupy an area of morphospace close to their nonavian relatives. The large overlap of Mesozoic birds with passerines (modern perching-songbirds) and nonpasserines (all other neornithines) (Figs 1b and 2b) does support the hypothesis of Nudds *et al.* (2004) that Mesozoic birds may have excluded modern birds from aerial niches. The similarity goes beyond wing form, encompassing body size and shape, and provides us with a stronger basis for drawing inferences about ecological overlap (Jones *et al.*, 2003).

The fact that birds span the Cretaceous–Paleogene boundary means that the trends reported in this paper supports the statement of Jablonski (2005) that much of the evolution that takes place after mass extinctions appears to be 'nonconstructive' or without a clear trend, but can nevertheless be a major determining factor in the subsequent trajectories of surviving clades.

Morphological data, when employed as proxies for ecology, can be an important complement to phylogenetic data in understanding the timing and dynamics of evolutionary radiations, particularly those in which mass extinctions are regarded as driving clade turnovers (Penny & Phillips, 2004). Morphospaces provide additional insights about morphological evolution are not always apparent from phylogenetic data. Phylogenetic data will tend to concentrate on characters that inform us about evolutionary relatedness, while more general morphological data can tell us more about convergence and analogy because they are not collected and analysed with the purpose of reconstructing evolutionary relationships .

Penny & Phillips (2004) encouraged researchers to combine phylogenetic, morphological and ecological data to attempt to choose among a range of possible models of clade radiations around mass extinction boundaries. The morphospace occupation patterns presented in this study demonstrate that birds had already occupied much of their morphospace (and by extension ecospace) during the Mesozoic. The additional areas of morphospace occupied (nonavian dinosaur areas) were not occupied until the Paleogene. Pterosaur morphospace has not been occupied by birds, which suggests that the radiation of birds was not inhibited by the presence of pterosaurs. Bats were likewise probably not constrained by birds or pterosaurs, and the evidence of Sears *et al.* (2006) for internal control of the timing of the evolution of flight in bats provides a viable alternative hypothesis as to why bats did not appear earlier.

Penny & Phillips (2004) presented a continuum of five models, which they split into cases which required a 'macroevolutionary' explanation and those that could be explained by 'microevolutionary' processes. The evolution of birds involves a long phylogentic 'fuse' in the Mesozoic, and there is evidence of both the appearance of crown groups and ecological transformations to modern niches (e.g. granivory) during the Cretaceous. This would fall into the category of microevolutionary explanations. Bats may have radiated slightly earlier than their fossil record suggests (E. Teeling, personal Communication) but they are probably a Tertiary group that radiated into a nocturnal, insectivorous niches at the expense of other mammals. The removal of pterosaurs had no influence on the radiation of bats.

Statements about evolutionary dynamics can be extracted from Fig. 3 which shows the rarefaction results for total range data; these indicate that birds and pterosaurs occupy similar range areas in their overall
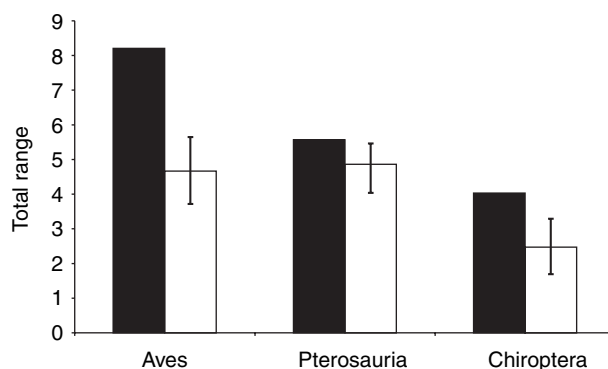

Fig. 3 Results of total range analysis for all six PCs. Filled bars represent the observed total range before rarefaction, unshaded bars represent mean total range after rarefaction to $n = 30$. Bats have the lowest total range, which is significantly lower than that for birds and pterosaurs. When birds and bats are rarefied to $n = 216$ bats still have a significantly lower total range than birds.

limb morphology even after correcting for sample size differences whereas bats occupy a significantly smaller range of morphospace. Taken in conjunction with Figs 1 and 2, this indicates that birds and pterosaurs occupied similar volumes of morphospace, but the areas of morphospace are mutually exclusive. The amount of morphological diversification required to fill the aerialist niche is similar between the birds and pterosaurs, despite the greater time for which pterosaurs occupied the skies (c. 190 Myr), compared with birds (c. 150 Myr).

Even though flapping flight constrains the range of morphologies available to vertebrate aerialists our results show that birds, bats and pterosaurs have evolved in different – yet mutually exclusive – directions. The demise of the pterosaurs at the Cretaceous–Paleogene boundary does not appear to have opened up new niches for birds and bats. Explanations for the higher absolute disparity and diversity are more likely to lie in the ability of birds to exploit granivory, and the evolution of secondary flightlessness. Birds may have gained as much as mammals from the demise of the nonavian dinosaurs.

Acknowledgments

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Scores on PCs I–VI for specimens used in the study.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/full/10.1111/j.1420-9101.2006.01285.x

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