Correlated evolution of sternal keel length and ilium length in birds

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Abstract

The interplay between the pectoral module (the pectoral girdle and limbs) and the pelvic module (the pelvic girdle and limbs) plays a key role in shaping avian evolution, but prior empirical studies on trait covariation between the two modules are limited. Here we empirically test whether (size-corrected) sternal keel length and ilium length are correlated during avian evolution using phylogenetic comparative methods. Our analyses on extant birds and Mesozoic birds both recover a significantly positive correlation. The results also provide new evidence regarding the integration between the pelvic and pectoral modules. The correlated evolution of sternal keel length and ilium length may serve as a mechanism to cope with the effect on performance caused by the tradeoff in muscle mass between pectoral and pelvic modules, via changing moment arms of muscles that function in flight and in terrestrial locomotion.

Introduction

Although the pectoral module (the pectoral girdle and limbs) and the pelvic module (the pelvic girdle and limbs) of birds are specialized for different functions, they are likely to be linked during evolution (Allen et al. 2013; Gatesy & Dial 1996; Heers & Dial 2015). This linkage could be a result of developmental and functional constraints (Allen et al. 2013; Young et al. 2005) as the pectoral and pelvic limbs share a broad range of development pathways, though they acquire distinct identity in adult in tetrapods (Young et al. 2005). Restricted by overall resources availability, pectoral and pelvic modules are negatively correlated in skeletal mass and muscle mass (Heers & Dial 2015). Changes of the forelimb size could change the position of center of mass, further affecting the hindlimb posture and functions (Allen et al. 2013;

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Dececchi & Larsson 2013; Hutchinson & Allen 2009). But functional specialization could also weaken the integration between pectoral and pelvic limbs, as suggested by morphometric analyses of avian and mammalian limbs (Bell et al. 2011; Schmidt & Fischer 2009; Young et al. 2005). This conflict between drivers of limb evolution necessitates empirical studies to understand whether and how traits of pectoral and pelvic modules co-vary ~~during evolution~~.

Along the theropod to avian lineage leading to the origin of crown birds, a series of morphological changes in the pectoral and pelvic girdles have previously been identified. These include In the pectoral girdle, the changes include the enlargement of the sternum and keel (O'Connor et al. 2015; Zheng et al. 2014; Zheng et al. 2012), the elongation of the coracoid (Zheng et al. 2014), the origin of an acrocoracoid process and the triosseal canal (Baier et al. 2007; Longrich 2009), the reorientation of the glenoid fossa from laterally directed to dorsolaterally directed (Jenkins 1993), and the transformation of the furcula from boomerang-shaped to U-shaped (Nesbitt et al. 2009; Zhou & Zhang 2002). While In the pelvic girdle we find the elongation of the ilium and the loss of the pubic symphysis ~~have been identified~~ (Hutchinson 2001). Of these changes two major derived features that characterize derived birds are the larger sternal keel and the longer ilium (Hutchinson 2001; O'Connor et al. 2015). This pattern of similar first appearances of these two key features could result from the correlated evolution between the sternal keel and the ilium, since pectoral and pelvic modules are suggested to be integrated in evolution (Allen et al. 2013; Heers & Dial 2015). Here we compile morphometric data on extant birds and Mesozoic birds to empirically test this hypothesis based on sternal keel length and ilium length...

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Material and Methods

Data collection on extant birds

We sampled 224 skeleton specimens with body mass data of 137 volant bird species from 45 families of 19 orders. All the specimens are housed in the collection of Beijing Museum of Natural History (Supporting Information Table S1). Sternal keel length and ilium length were taken with a digital caliper (± 0.01 mm) (Fig. 1). When multiple specimens were measured for a species, the mean values of those specimens were used. These variables were log10-transformed before subsequent analyses.

Phylogenetic comparative methods

All analyses were carried out in R 3.3.3 (R Core Team).

Phylogeny and size-correction

We used 1000 time-calibrated phylogenetic trees for the 137 species included in our study from birdtree.org (Jetz et al. 2012). Phylogenetic size-correction of log10-transformed ilium length and keel length was conducted using the function phyl.resid in the “phytools” (Revell 2012).

Evolutionary rate matrix

Under the assumption of Brownian motion model, the variance of a trait at a given time interval is equal to the length of the time interval times the Brownian motion rate parameter, σ^2. The multivariate Brownian motion is governed by the evolutionary rate matrix, which contains the evolutionary variances or rates (σ^2) for individual characters on its diagonals and the evolutionary covariances on its off-diagonals (Revell & Collar 2009; Revell & Harmon 2008). The Pearson correlation coefficient (r) can be calculated based on these values. This analysis was implemented using the function evol.vcv in the "phytools" (Revell 2012). The Pearson correlation coefficients from iterations across the 1000 trees were averaged, weighted by their Akaike weights based on AICc (Burnham & Anderson 2002). As the Pearson correlation coefficient does not follow a normal distribution, Fisher transformation was used during the process.

Mesozoic birds

To determine whether keel length and ilium length are correlated during early evolution of birds, we sampled 10 Mesozoic avian species housed in the collection of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Sternal keel length, ilium length and femur length were measured (Supporting Information Table S1). They were log10-transformed before subsequent analyses. Calibration dates for these taxa were adapted from Wang & Lloyd (2016a; 2016b). A phylogenetic tree including these 10 species

was constructed manually based on a recent phylogenetic analysis (Wang & Zhou 2017). The fossil bird tree was time-calibrated using the function timePaleoPhy with the "equal" method in the "paleotree" (Bapst 2012), with tip dates drawn randomly from a uniform distribution between the maximum and minimum dates, producing 1000 trees. The estimate of the evolutionary rate matrix was iterated across these 1000 trees to account for the uncertainty in time-calibration. The estimated correlation coefficients from 1000 iterations were averaged, weighted by Akaike weights.

Results

In extant birds, the correlation between sternal keel length and ilium length is 0.77 (95% Confidence interval: 0.69 to 0.84). Similarly, the correlation is 0.90 in Mesozoic birds (95% Confidence interval: 0.61 to 0.98). Both are positive and statistically significant, as their 95% confidence intervals do not include 0.

In the morphospace defined by sternal keel length and ilium length (Fig. 2), several outliers are identifiable in these extant birds. *Phalacrocorax carbo* deviates from other taxa by entering the upper-left space, indicating that it has relatively long ilia but a relatively short keel. By contrast, *Brachyramphus marmoratus* enters the lower right space, by having a relatively long keel but relatively short ilia. *Gavia stellata* also deviates from others, but it largely follows the pattern of a positive correlation between sternal keel length and ilium length.

In the phylomorphospace defined by sternal keel length and ilium length of Mesozoic birds (Fig. 3), the enantiornithines are located in the lower left part, while the ornithuromorphs in the upper right part, indicating that the ornithuromorphs have a longer keel and longer ilia than enantiornithines. An exception is *Piscivorenantiornis inusitatus*, which has relatively longer ilia than most ornithuromorphs except *Iteravis huchzermeyeri*. *Piscivoravis lii* differs from other ornithuromorphs in having a comparatively shorter keel and shorter ilia.

Discussion

Our results support the hypothesis that ilium length and sternal keel length are correlated during avian evolution and further provide quantitative support of the integration between pelvic and pectoral modules (Allen et al. 2013; Gatesy & Dial 1996; Heers & Dial 2015). Among basal birds, an ossified sternal keel is absent in *Archaeopteryx*, *Jeholornis* and *Sapeornis*, and only a faint keel is present in *Confuciusornis* (Chiappe et al. 1999; O'Connor et al. 2015; Zheng et al. 2014). The keel is small and restricted to the caudal part of the sternum in Early Cretaceous enantiornithines (O'Connor et al. 2011; Wang & Zhou 2017; Zheng et al. 2012), while comparatively larger in ornithuromorphs (e.g., Zhou & Zhang 2001; Zhou & Zhang 2006). Despite these differences the recovered positive correlation between the sternal keel length and ilium length based on data of enantiornithines and ornithuromorphs suggests that this pattern appears very early during avian evolution.

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Heers & Dial (2015) showed that the pectoral and pelvic modules are negatively correlated in muscle mass and skeletal mass and suggested the tradeoff in investment is associated with a tradeoff in performance. In other words, the less-invested module has to cope with a larger burden. The correlated evolution of sternal keel length and ilium length may serve as a mechanism to offset, to some extent, the effect on performance caused by the tradeoff in muscle mass via changing moment arms of pectoral muscles and hindlimb muscles, because the torque produced by a muscle is determined by its mass and moment arm and the effect caused by a decrease in the muscle mass can be offset by an increase in the muscle moment arm. This requires that the mass and moment arm of a muscle can be modified independently to some extent. The sternal keel provides a surface for the attachment of muscles essential for flight, i.e., m. supracoracoideus and m. pectoralis; therefore, their moment arms can be directly affected by changes of sternal keel length. Though sternal keel length is correlated with the mass of these muscles (R^2 = 0.47; Wright et al. 2016), parts of their variances cannot be statistically explained by each other. These facts imply that during evolution of flight, birds have the potential to modify masses and moment arms of pectoral muscles independently. Similarly, evolution of hindlimb functions may be achieved through changing the masses or moment arms of hindlimb muscles, though their relationship has not been empirically estimated. These inferences need to be tested in future studies.

In the sampled extant birds, two birds, i.e., *Brachyramphus marmoratus* and *Phalacrocorax carbo*, exhibit large deviation from other taxa in the morphospace defined by sternal keel length

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and ilium length (Fig. 2). As a wing-propelled diver, the elongated keel *Brachyramphus marmoratus* accommodates the enlarged m. supracoracoideus and the elongated m. pectoralis to flap the wing in the water (Kovacs & Meyers 2000; Spear & Ainley 1997). To adapt to this situation, the pelvic girdle of *B. marmoratus* shifts to an upright posture rather than acquires an elongated ilium as in other birds (Fig. 2) (Storer 1945). The relatively long ilium in *Phalacrocorax carbo* is an adaptation of foot-propelled diving (HiniĆ-Frlog & Motani 2010). Its comparatively shorter sternal keel than that of other foot-propelled divers, for example, *Gavia stellata*, is associated with its weak flight ability; it can only slope soar in strong winds (Norberg 1990). *Phalacrocorax carbo* is an example of the evolution towards flightlessness with the pelvic module enhanced and the pectoral module reduced (Wright et al. 2016), which is seen in some flightless bird species such as the Galápagos cormorant (*Phalacrocorax harrisi*) (Livezey 1992) and ratites (Cracraft 1974).

Among our sampled Mesozoic birds, *Piscivorenantiornis inusitatus*, a fish-eating enantiornithine (Wang & Zhou 2017; Wang et al. 2016), differs from other enantiornithines (*Longipteryx chaoyangensis*, *Bohaiornis guoi* and *Longirostravis hani*) in that it has relatively longer ilia (Fig. 3). The functional significance of this feature in *Piscivorenantiornis* is unclear, but in extant birds it is associated with an aquatic lifestyle (HiniĆ-Frlog & Motani 2010; Stoessel et al. 2013). This provide a side evidence of its ecology besides the pellet found associated with the holotype skeleton (Wang et al. 2016).

In summary, pectoral and pelvic modules are linked in a more complicated way than just

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negatively correlated in overall investment. Besides modifying moment arms of muscles, birds may change behaviors to cope with the effect caused by tradeoff in investment. More integrative studies in the future can provide more insight into the relationship between pectoral and pelvic modules.

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I do want to suggest the authors read the new article by Stoddard et al. (2017) entitled "Avian egg shape: Form, function, and evolution" that just appeared in the June 23rd edition of Science. It mentions how selection for flight may have influence egg shape, which undoubtedly has an effect on pelvic shape, thus showing another potential mechanism to link these two systems together. I don't think this article is critical for the authors argument, but it could be used as supporting evidence.

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