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Feeding ecology is the primary driver of beak shape diversification in waterfowl

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Summary

1. The diversity of beak shapes among birds is often assumed to be largely the result of adaptations to different feeding behaviors and diets. However, this assumption has only been tested for a small subset of avian diversity, primarily within the order Passeriformes. Moreover, given the role of the beak in behaviors other than feeding and given that most previously identified beak-feeding associations concern beak size rather than shape, it remains unclear how much of beak shape diversity is explained by feeding ecology and what functional explanations account for these differences in shape.

2. I quantified the association between beak shape and feeding ecology for 42 species in the bird order Anseriformes (waterfowl) using 3D curvature of the upper beak collected from museum specimens and continuous dietary data compiled from the literature. I also tested whether leverage or stress resistance of the beak explains the association between beak shape and feeding ecology. Diet is strongly and significantly correlated with beak shape in waterfowl. An ancestral beak shape reconstruction and the reconstructed diet of the anseriform fossil *Presbyornis* both support filter-feeding as ancestral for most waterfowl, followed by multiple, significantly convergent transitions from a duck-like beak toward a more goose-like beak. The evolution of a more goose-like beak is associated with increased consumption of leaves, decreased consumption of invertebrates, and an increase in mechanical advantage of the beak. Moreover, no association was identified between size (measured as either beak size or body mass) and feeding ecology nor between size and beak shape.

3. These results demonstrate that feeding ecology has acted as the primary selective force in the diversification of waterfowl beak shapes, including the convergent originations of geese. Thus, rapid and convergent adaptation of the beak to feeding is not limited to passerines nor is it limited to size-correlated shape changes. The positive evolutionary correlation between mechanical advantage and herbivory shows that lever mechanics can explain the functional evolution of the kinetic upper beak in birds. These results also suggest that functions of the beak other than feeding may play a minor role in explaining overall beak shape diversity.

Key-words: anseriformes, bird, convergence, diet, geometric morphometrics, herbivory, mechanical advantage, *Presbyornis*

Introduction

Bird beaks are frequently invoked as a classic example of the result of adaptive evolution, wherein selection for feeding performance on particular foods influences the diversification of beak size and shape. The distinction of bird beaks among examples of adaptation is largely owed to the decades of work on Darwin's finches, whose diverse beaks have evolved primarily as an adaptation to differing diets and feeding behaviors (Schluter & Grant 1984; Grant & Grant 2006). Significant relationships between beak morphology and feeding ecology have been demonstrated in several avian taxa other than Darwin's finches, including the Great Tit (Gosler 1987), crossbills (Benkman 1988), warblers (Price 1991), scrub-jays (Peterson 1993; Bardwell, Benkman & Gould 2001), shorebirds (Barbosa

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& Moreno 1999), flower-piercers (Schondube & del Rio 2003), and raptors (Bright *et al.* 2016).

Yet, it remains unclear how much of beak shape diversity can be explained by adaptation to feeding. The relationship between feeding ecology and beak morphology is rarely tested outside of passerines (perching birds) and beak shape is generally quantified using caliper measurements rather than more detailed three-dimensional shape data (but see Bright *et al.* 2016). Also unknown is how frequently selection acts on beak shape, beak size, or both. In raptors, beak shape variation and feeding ecology are strongly correlated with skull size (Bright *et al.* 2016). However, it is unclear if this is also true for other clades such as crossbills and seed-eating Darwin's finches, for which divergence in feeding ecology has been described mostly in relation to beak size (Grant 1981; Benkman 1988; Marquiss & Rae 2002). Additionally, the beak has a clearly demonstrated role in functions other than feeding, including modulating the vocal tract during vocalization (Westneat *et al.* 1993; Derryberry *et al.* 2012), preening (Clayton *et al.* 2005), and thermoregulation (Greenberg *et al.* 2012). These non-feeding functions of the beak often show trade-offs with feeding performance (Schondube & del Rio 2003; Herrel *et al.* 2009), thereby limiting the influence of feeding on beak shape. Lastly, it has also recently been suggested that strong covariation between the beak and neurocranium may limit the evolution of beak shape in response to selection on feeding performance, especially in non-passerines (Bright *et al.* 2016).

The reason why particular beak shapes are favored by selection also remains largely unexplored. In seed-eating Darwin's finches, it is known that beak size evolves due to selection on seed handling performance (Grant 1981). Additionally, beak shape in Darwin's finches may evolve due to selection on fracture avoidance since beak shape changes associated with higher bite forces, particularly increases in beak depth (Herrel *et al.* 2005), improve the dissipation of stresses over the beak (Soons *et al.* 2010). Yet outside of Darwin's finches, potential functional explanations for adaptation of the beak to feeding are rarely tested (but see Schondube & del Rio 2003). Mechanical advantage or leverage is a common explanation for morphological and ecological evolution of the feeding system in mammals (Santana, Dumont & Davis 2010; Dumont *et al.* 2014; Varela & Fariña 2015) and fishes (Westneat 1995; Hulsey & García de León 2005). However, whether beak shape evolution in birds can be explained by selection on mechanical advantage has not been tested.

The non-passerine bird order Anseriformes (waterfowl) is an ideal clade in which to test hypotheses relating beak morphology, beak function, and feeding ecology. Comprising approximately 168 species, waterfowl have evolved a diversity of feeding ecologies (Li & Clarke 2015) and show elevated rates of beak shape evolution relative to other bird clades (Cooney *et al.* 2017). Waterfowl feeding behaviors include pursuit diving, aquatic browsing, filter-feeding or dabbling, and grazing (Kear 2005). Pursuit diving is used almost exclusively to capture fish, aquatic browsing is used to glean benthic invertebrates from underwater substrates, filter-feeding is used to obtain small seeds and invertebrates from water (Kooloos *et al.* 1989), and grazing is used to crop the leaves of aquatic or terrestrial plants (Van der Leeuw *et al.* 2003). Owing to their economic and agricultural importance, more is known about the diets of waterfowl than perhaps any other bird order. Additionally, it has recently been shown that a primarily herbivorous diet, and consequently grazing behavior, has likely evolved convergently within waterfowl (Olsen 2015), providing an ideal context in which to test comparative hypotheses.

If feeding ecology is a significant and primary driver of beak shape diversification in waterfowl then feeding ecology should explain most of the variation in waterfowl beak shapes. I test this by quantifying the significance and strength of the correlation between 3D beak shape data obtained from museum specimens and continuous, diet composition data compiled from the literature. Additionally, if feeding ecology has influenced beak shape evolution through selection on mechanical advantage, stress dissipation, or both, then the corresponding functional measures should be significantly associated with feeding ecology. I test this by quantifying the correlation between beak functional metrics (mechanical advantage and aspects of shape predicted to affect stress dissipation) and dietary composition. If filter-feeding is ancestral for waterfowl then (i) the reconstructed diet of the early Eocene anseriform fossil *Presbyornis* (Olson & Feduccia 1980) should consist primarily of seeds and small invertebrates and (ii) beak shapes associated with other feeding behaviors should have evolved secondarily. I test this by (i) reconstructing the diet of *Presbyornis* using the beak-diet relationship among extant waterfowl and by (ii) performing ancestral state reconstructions of beak shape.

Materials and methods

CONTINUOUS DIETARY CHARACTERS

To represent feeding ecology I quantified dietary composition for 42 waterfowl species (37 genera) by compiling data from the published literature using data sources and methodologies similar to a previous study of waterfowl dietary evolution (Olsen 2015). The data compiled for this study include 146 quantitative studies and nine qualitative studies. These studies use different data collection methodologies (e.g. gut dissection, fecal examination, feeding behavior observations) and weigh the relative contributions of food items differently (e.g. mass, volume, frequency of occurrence), which could introduce biases when comparing the results of different studies (Swanson & Bartonek 1970). However, given that the choice of methodology in these studies was not related to beak shape it seems unlikely that such biases would directly influence tests for the relationship between beak shape and diet. Dietary composition for the recently extinct moa-nalo (*Thambetochen chauliodous*) was included from analyses of ancient fecal remains (James & Burney 1997). The sample size, quantification method, portion of the gut examined, season, and locality for each study are available at the Dryad Digital Repository.

The proportion of each food item for each study was expressed as a value from 0 to 1. For quantitative studies reporting the percentage of gut contents or percentage of feeding time, the reported percentages were used. For studies reporting the frequency of occurrence of gut or fecal contents, the relative frequencies were normalized such that the frequencies summed to 1. For the nine qualitative studies, qualitative descriptions (e.g. 'primarily', 'rarely') were used to score items on a scale from 1 to 4. If no such description was given, each item was scored equally. The proportions were then normalized such that the sum of all food item proportions summed to 1 for each study. Diet composition described in this paper as percentages (between 0 and 100%) corresponds to the range of 0 to 1 used for analyses.

Custom code was used to automatically place each recorded food item from each study into one of six categories: leaves, seeds and fruits, roots, algae, invertebrates, and vertebrates. I chose these categories because they correspond to different feeding behaviors among waterfowl and because they represent a compromise between descriptive power and the number of studies that could be included. 'Leaves' includes the leaves, stem, and stalks of plants as well as items belonging to Embryophyta but for which the particular part was not reported; 'Seeds and fruits' includes nuts. For each species, the proportions within each category were averaged across all studies (arithmetic mean) giving equal weight to each entry, to arrive at six continuous dietary characters per species. The use of proportions directly in linear models violates model assumptions since proportions can only take values between 0 and 1. For this reason, dietary proportions were logit transformed prior to analyses, bringing their distributions closer to normality and reducing heteroscedasticity (Warton & Hui 2011).

BEAK SHAPE CHARACTERS

To represent beak shape I measured 3D curvature of the culmen (the dorsal curvature of the beak at the midline) and tomium (the biting margin of the beak) from 136 museum skeletal specimens representing 51 anseriform species and 46 anseriform genera (diet data were not available for all species with shape data). This includes two extinct taxa: the early Eocene *Presbyornis* sp. (Olson & Feduccia 1980) and the recently extinct moa-nalo *T. chauliodous* (Olson & James 1991); both taxa have specimens with excellent three-dimensional preservation of the upper beak. I collected 3D curvature using stereo camera reconstruction, implemented with the R package STEREOMORPH (version 1.5.1; Olsen & Westneat 2015). I photographed each specimen using two cameras and manually digitized the left and right tomia in each camera view using the StereoMorph digitizing application. The digitized tomia were then reconstructed into 3D and unified with culmen curve (digitized from a lateral view) using both culmen curve endpoints and one or two landmarks on the basicranium to ensure proper orientation of the culmen within the midsagittal plane.

Once reconstructed, each curve (culmen, right tomium and left tomium) was described by 50 evenly spaced points (semilandmarks). Each specimen was aligned to the midline plane, reflected, and averaged to produce a bilaterally symmetric set of 150 semilandmarks used in subsequent shape analyses (Klingenberg, Barluenga & Meyer 2002). In some cases damage on one side of a specimen did not allow the tomium to be measured on both sides. In this case, tomium curve points on the undamaged side were simply reflected and not averaged. For each species, semilandmarks from different individuals were aligned by Procrustes superimposition, which scales each shape to the same centroid size and minimizes differences due to translation and rotation, to produce a single mean semilandmark set for each species. All species mean sets were aligned by a second Procrustes superimposition to obtain Procrustes coordinates. Procrustes superimposition was done using the 'gpagen' function in the R package GEOMORPH (version 3.0.1; Adams, Collyer & Sherratt 2016). Two size measures were used to test the relationship between feeding ecology and size: beak size and body mass. Beak size was measured as the mean beak centroid size for each species. Body masses were taken from Dunning (2008). Body masses and beak shape data (by specimen and species) are available at the Dryad Digital Repository.

All phylogenetic analyses were carried out using a published phylogeny of 6714 avian species (Burleigh, Kimball & Braun 2014, 2015), pruned to the species with shape data in this study (available at the Dryad Digital Repository). Constructed from a sparse supermatrix of 22 nuclear loci and seven mitochondrial regions, this tree represents the most current molecular phylogeny of Anseriformes. To this tree, I added *Presbyornis* as sister to the family Anatidae based on phylogenetic analyses using morphological characters (Livezey 1997; Clarke *et al.* 2005; but see Worthy *et al.* 2016). Phylogenetic signal was quantified using the geomorph function 'physignal' (Blomberg, Garland & Ives 2003). When testing for phylogenetic signal the tree was made ultrametric using the 'chronos' function in the R package APE (version 3.4; Paradis, Claude & Strimmer 2004) to account for a few very short branch lengths.

To visualize shape variation I used custom code to generate principal component (PC) backtransformations (MacLeod 2009). In PC analysis, the original input matrix can be recovered by multiplying the PC score matrix by the inverse of the eigenvector matrix. This procedure can be adapted to visualize the shape change along a particular PC axis or axes by constructing a score matrix of evenly distributed scores along the PC axis or axes of interest, within the range of the empirical PC scores, and mean scores for all other PC axes. These backtransform shapes represent the theoretical shape corresponding to a particular PC score or pair of PC scores in multivariate space. Beak shape showed significant phylogenetic signal (K: 0·56, $P < 0{\cdot}001$) and thus I performed phylogenetic PC analysis (pPCA) on the Procrustes coordinates using the 'phyl.pca' function in the R package PHYTOOLS (version 0.5–10; Revell 2009, 2012). The use of backtransformation on the results of phylogenetic PCA requires the additional step of adding the product of a vector of ones and the vector of phylogenetic means (Revell 2009). To visualize the distribution of shapes along two PC axes I plotted lateral silhouettes at evenly distributed points along each axis, creating a 'backtransform morphospace'. I used lateral silhouettes for simplicity of visualization; all shape analyses were performed using 3D data.

BEAK FUNCTION

To test the relationship between feeding ecology and beak function I calculated three beak functional metrics using the 3D beak shape data: mechanical advantage (MA), tomium angle (TA), and culmen angle (CA). Mechanical advantage, a measure of leverage, represents the extent to which a system amplifies relative force. In most birds, nine mobile bones in the skull form a mechanism that enables rotation of the upper beak, referred to as cranial kinesis (Bout & Zweers 2001; Olsen & Westneat 2016). Jaw muscle forces are transmitted through this mechanism to the jugal and palatine bones, which attach to the base of the upper beak. For waterfowl, in particular, the upper beak rotates about a hinge-like joint with the neurocranium, acting like a lever in concert with the lower beak (Dawson *et al.* 2011). I calculated mechanical advantage of the upper beak by taking the ratio of the in-lever (the distance from the beak axis of rotation to the upper beak-jugal joint) to the out-lever (the distance from the beak axis of rotation to the upper beak tip). In waterfowl, the jugal and palatine articulate with the upper beak at nearly the same position so the MA represents force input from either bone.

I chose tomium and culmen angle to represent broad shape changes that have been linked to increased stress resistance during

bending and torsion. Previous studies of stress resistance in archosaur snouts (Rayfield & Milner 2008) and the beaks of Darwin's finches (Soons *et al.* 2010) have found that a more 'cone-like' shape better resists stresses than a broad and flat shape. Increased tomium and culmen angle correspond to increased tapering of the beak (i.e. more 'cone-like') and therefore correspond to potentially greater stress resistance. Tomium angle was calculated as the angle between the midline plane and a line fitted to the tomium landmarks on one side. Culmen angle was calculated as the angle between the average plane of the tomium (i.e. the 'palate' of the upper beak) and a line fitted to the culmen landmarks. Tomium angle could also be interpreted as a 'torsional mechanical advantage', independent of stress resistance. A unilateral bite along the beak margin applies a torque that twists the beak. A wider base, which is likely to increase TA, lengthens the in-lever and increases the torque advantage of the beak in opposing unilateral bite forces.

CORRELATION TESTS

To quantify the correlation between diet and beak shape and between diet and beak function, I used two-block partial least-squares (PLS) regression and pairwise linear regressions. Two-block PLS regression identifies linear combinations of variables (i.e. axes) within two multivariate datasets that are maximally correlated with one another (Rohlf & Corti 2000). PLS regression was performed using the geomorph function 'two.b.pls', with significance of the correlation coefficient (R) determined by a randomization test (1000 iterations) for each PLS axes. To visualize which particular shape features are correlated with particular dietary compositions, custom code was used to generate PLS back-transformations (analogous to PC backtransformations). The PLS backtransformations were obtained by projecting four evenly spaced PLS scores along the PLS regression line, multiplying these scores by the corresponding PLS vectors, and adding the resulting matrix to the corresponding mean shape or diet. Pairwise linear regressions were used to identify the primary associations that contributed to significant PLS correlations. Both non-phylogenetic regressions and phylogenetic regressions were performed. For non-phylogenetic regressions I used the 'lm' function in the R package 'STATS' (R Core Team 2016). For phylogenetic regressions I performed phylogenetic generalized least-squares regression (PGLS) using the 'pgls' function in the R package CAPER, with simultaneous maximum likelihood estimation of lambda (version 0.5.2; Orme *et al.* 2013).

EVOLUTIONARY TRAJECTORY ESTIMATIONS

To estimate the ancestral feeding ecology of waterfowl I reconstructed the diet of the fossil *Presbyornis* using extant diet-beak relationships and created a phylomorphospace of waterfowl beak shapes using ancestral state reconstruction. To reconstruct the diet of *Presbyornis* I used the diet and beak shape datasets from extant waterfowl and the R stats function 'LM' to construct a multivariate model that predicts the six dietary characters from the first two pPCs of beak shape, as only the first two pPCs of beak shape were found to correlate with diet (at $P < 0{\cdot}01$). Model error was quantified by comparing the model's diet predictions against the diet data used to construct the model. Non-transformed diet characters reproduced extant diet data with less error than logit-transformed characters so non-transformed diet characters were used. The diet of *Presbyornis* was then predicted based on the first two 3D beak shape pPC scores. The resulting values were normalized such that they summed to 1.

To create a phylomorphospace of waterfowl beak shapes I simulated trait evolution within the pPC beak morphospace (Sidlauskas 2008; Uyeda, Caetano & Pennell 2015). Five models of continuous trait evolution were compared and a Brownian motion model was found to be the best fit, as determined by corrected Akaike information criterion values. I used the 'fitContinuous' function in the R package GEIGER (version 2.0.6; Harmon *et al.* 2008) to fit each model to each pPC axis used in making the morphospace. The ancestral states of the pPC axes were then reconstructed using the ape function 'ace'. To quantify convergence I used the package CONVEVOL (version 1.0; Stayton 2015). The CONVEVOL package estimates five measures of convergence for a user-defined group of taxa: four distance-based measures ($C_{1\text{-}4}$) that represent different relative measures of phenotypic distances among the selected taxa and a frequency-based measure (C_5) that quantifies the number of transitions into a region of morphospace defined by the selected taxa. Significance was assessed by randomization tests in the CONVEVOL package.

Results

BEAK SHAPE VARIATION

Principal components analysis of 3D beak shape separates ducks, geese, pursuit divers, and screamers into different regions of beak morphospace (Fig. 1a); the common names 'duck', 'goose' and 'swan' are all polyphyletic (Burleigh, Kimball & Braun 2015), based on similar morphological and behavioral traits. Most of the variation in 3D curvature of the culmen and tomium in waterfowl (78%) is explained by the first two PC axes (46% by pPC1 and 32% by pPC2). Low pPC1 values correspond to more 'duck-like' beaks, having a ventrally arcing culmen and tomium and being relatively longer and shorter in height, while high pPC1 values correspond to more 'goose-like' beaks, having a dorsally arcing culmen and tomium and being relatively shorter in length and taller and wider at the base (Fig. 1b,c). Thus, pPC1 is related not only to dimensional proportions, but also convexity vs. concavity of the culmen and tomium. The second pPC axis (Fig. 1d, e) separates the tall, broad beaks of browsing divers, such as steamer ducks (low pPC2 values), from the slender beaks of piscivorous pursuit divers, such as mergansers (high pPC2 values). The third pPC axis, which explains 8% of the total variation, is related to the varying extent to which the rhamphotheca, a layer of keratin overlaying the beak, is preserved on skeletal specimens. Because pPC3 explains relatively little of the variation in beak shape, relates to an artifact, and was not found to correlate significantly with diet, it was not included in further analyses. All remaining pPCs explained <5% of shape variation.

RELATIONSHIP BETWEEN BEAK SHAPE AND DIET

Beak shape is significantly and strongly correlated with diet as evidenced by an overlay of dietary composition onto beak morphospace (Fig. 2a) and the results of partial least-squares regression (Fig. 2b,c). The first PLS axes of beak shape and logit diet are significantly correlated ($P < 0{\cdot}001$; R: 0·805; Fig. 2b) as are the second PLS axes ($P < 0{\cdot}001$; R: 0·645; Fig. 2c). None of the four remaining PLS axes is significant (at $P < 0{\cdot}05$). The first and second PLS axes of beak shape correspond closely to the first and

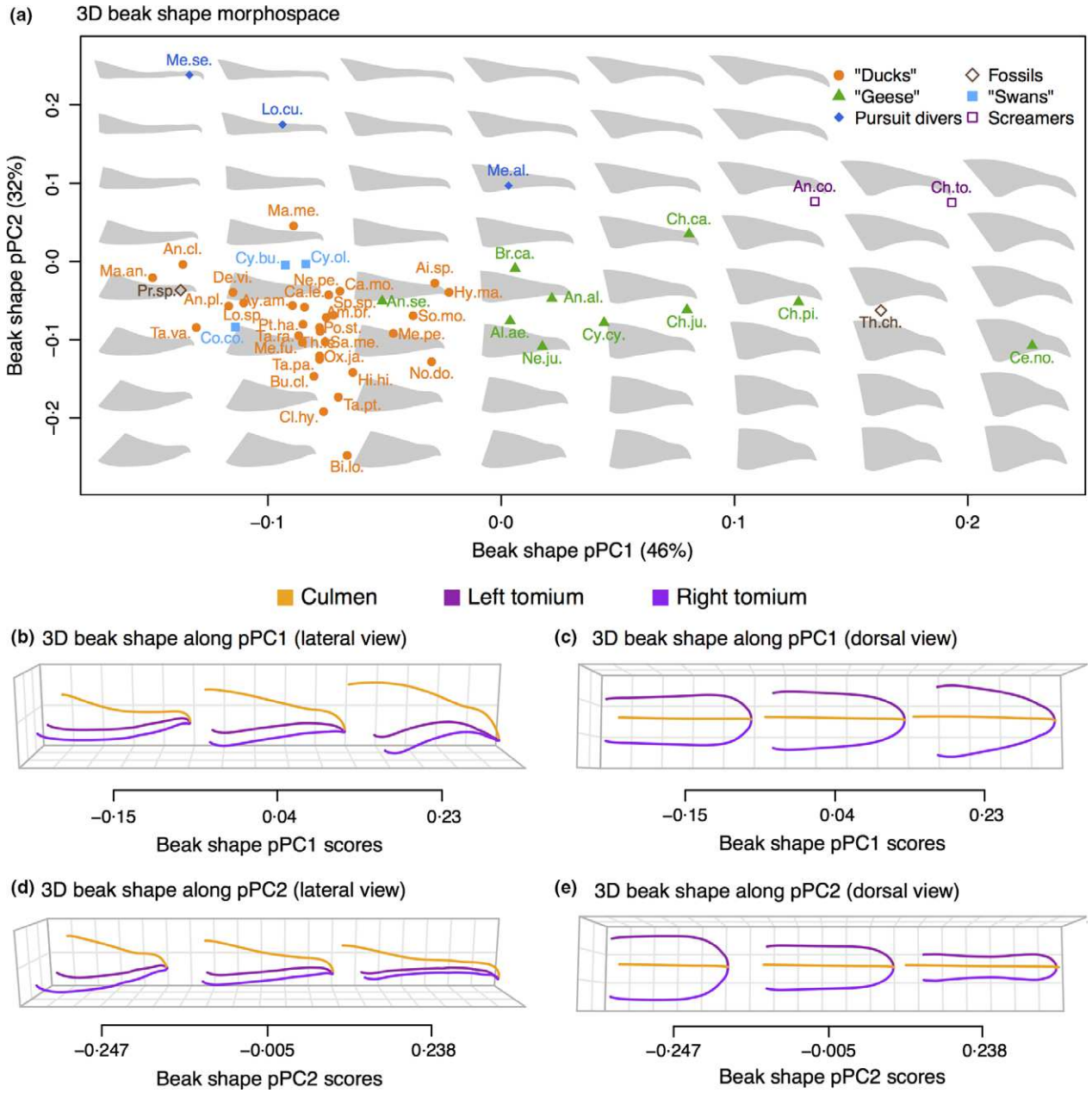

Fig. 1. Waterfowl beak shape diversity. (a) 3D beak morphospace for 51 waterfowl species. Backtransform shapes (gray) in background depict shape variation throughout morphospace. Symbols and colors indicate common name affinities, including the polyphyletic groups 'duck', 'goose', and 'swan'. A subset of backtransform shapes evenly spaced along the first (b–c) and second (d–e) pPC axes show 3D variation in curvature of the culmen (orange) and tomium (purple). The same three shapes are shown in (b) and (c) from a lateral and dorsal view, respectively; likewise for (d) and (e).

second pPC axes of beak shape, respectively, apparent from the resemblance between PLS and pPC backtransform shapes (Fig. 2a–c) and evidenced by strong correlations between beak PLS and pPC scores (R: 0·93 and −0·92, respectively). The first diet PLS axis is negatively associated with invertebrate (R: −0·90) and vertebrate consumption (R: −0·31) and positively associated with leaf (R: 0·81) and root (R: 0·53) consumption (Fig. 2d). The second diet PLS axis is negatively associated with vertebrate (R: −0·55) and root (R: −0·35) consumption and positively associated with invertebrate (R: 0·48) consumption (Fig. 2e). Thus, a more goose-like beak is associated with increased consumption of leaves and roots and decreased consumption of invertebrates, while a more pursuit diver-like beak is associated with increased vertebrate consumption and decreased invertebrate consumption.

Despite significant phylogenetic signal in the diet (K: 0·61; $P < 0·001$) and beak shape (K: 0·56, $P < 0·001$), significant phylogenetic signal (at $P < 0·05$) was not detected in the residuals of any of the non-phylogenetic

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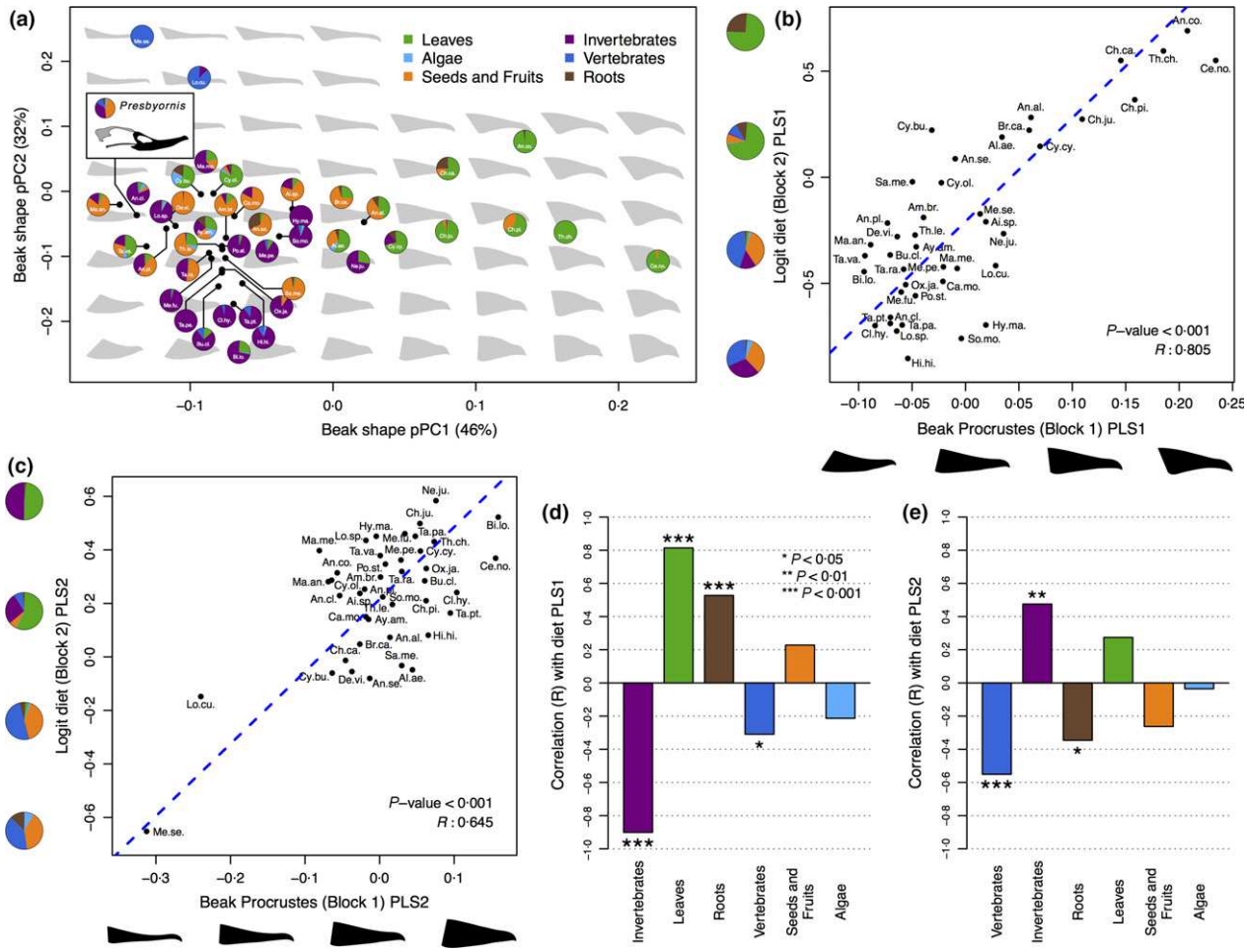

Fig. 2. Diet is associated with beak shape in waterfowl. (a) Pie charts depict dietary composition by species (42 of the 51 species with beak shape data). Inset box shows the diet of *Presbyornis* predicted by extant beak shape and diet data and the 3D beak shape of *Presbyornis*. (b–c) Correlation between diet and beak shape based on partial least-squares (PLS) regression, along the first (b) and second (c) PLS axes. PLS backtransformations of diet (vertical) and beak shape (horizontal) depict maximally correlated character states along each PLS axis. (d–e) Pairwise correlation coefficients (R) between diet PLS axes and each dietary category (logit-transformed).

regressions, indicating that regressions did not require correction for phylogenetic non-independence (Revell 2010). Thus, only the results of non-phylogenetic regressions are shown. Additionally, in terms of significance the PGLS results were completely consistent with the results of non-phylogenetic regressions (i.e. significance was always within the same P-value threshold), indicating these results are insensitive to phylogenetic non-independence.

No evidence was found for an influence of size on feeding ecology, either as a relationship between diet and beak size, between diet and body size, or between beak shape and size (either body mass or beak size). Although all beak shapes are scaled to centroid size as a part of Procrustes superimposition, the resulting axes of shape variation may still correlate with beak size. The residuals of non-phylogenetic regressions of beak shape on log10 beak centroid size, beak shape on log10 body mass, and diet on log10 body mass all show significant phylogenetic signal ($P = 0{\cdot}001$, $0{\cdot}003$, $0{\cdot}002$, respectively) and thus PGLS regressions were used. PGLS regressions of beak shape on centroid size, beak shape on body mass, and diet on body mass are all non-significant ($P = 0{\cdot}065$, $0{\cdot}55$, and $0{\cdot}22$, respectively). If a non-ultrametric tree is used, a PGLS regression of beak shape on beak centroid size is weakly significant ($P = 0{\cdot}014$). However, a PLS regression between diet and beak shape corrected for any potential correlation with beak size (residuals from a regression on centroid size) is just as significant ($P < 0{\cdot}001$; R: $0{\cdot}817$) as when uncorrected beak Procrustes coordinates are used.

RELATIONSHIP BETWEEN BEAK FUNCTION AND DIET

Beak mechanical advantage (MA) and tomium angle (TA) are both significantly correlated with diet ($P = 0{\cdot}003$ and $P < 0{\cdot}001$, respectively) while culmen angle (CA) is weakly correlated with diet ($P = 0{\cdot}039$; Fig. 3). More goose-like beaks have a higher MA, TA, and CA while pursuit diving beaks have a lower MA, TA, and CA (based on correlations with pPC scores, Fig. 3c,f,i). In pairwise regressions, MA is only significantly correlated with increased

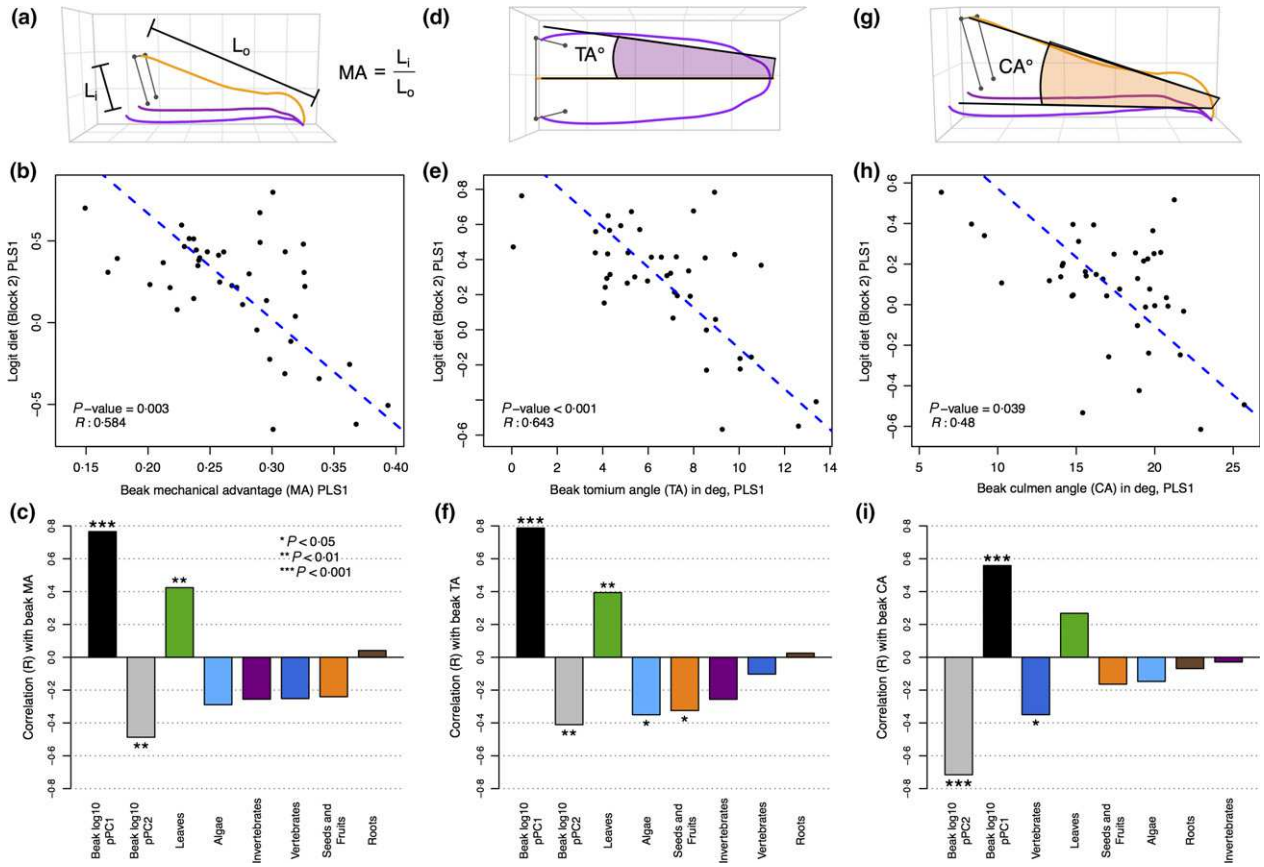

Fig. 3. Multiple beak functional metrics correlate with diet in waterfowl. Top row (a,d,g): Beak function quantified using mechanical advantage (MA), tomium angle (TA), and culmen angle (CA). Middle row (b,e,h): correlation between diet and each functional metric using partial least-squares regression. Bottom row (c,f,i): Pairwise correlation coefficients (R) for each functional metric, beak pPC1-2, and each logit-transformed dietary category.

consumption of leaves (R: 0·42). TA is significantly correlated with increased consumption of leaves (R: 0·39) and weakly with decreased consumption of algae (R: −0·35) and seeds and fruits (R: −0·32). And CA is only weakly correlated with decreased consumption of vertebrates (R: −0·35). Similar to regressions between beak shape and diet, significant phylogenetic signal (at $P < 0·05$) was not detected in the residuals of any of the non-phylogenetic regressions of beak function and diet. Thus, only the results of non-phylogenetic regressions are shown.

EVOLUTIONARY TRAJECTORIES

The reconstructed diet of *Presbyornis* and an ancestral state reconstruction of beak shape are both consistent with a duck-like beak as ancestral for most waterfowl, followed by a single transition toward a pursuit diver beak and multiple transitions toward a goose-like beak. The reconstructed diet of *Presbyornis* based on a multivariate model of diet characters and beak pPC scores is estimated to be 43·8% seeds and fruits, 35·7% invertebrates, 11·4% vertebrates, 4·0% algae, 4·3% roots, and 0·7% leaves (Fig. 2a). The mean error of diet proportions predicted by the model, evaluated against the input dataset, is 12·8%, with mean errors for each taxon ranging from 4·8 to 23·6%.

Simulated trait evolution supports two main patterns of diversification (Fig. 4). The first pattern is a single evolutionary trajectory from low to high pPC2 values in the origin of the piscivorous pursuit divers. The second pattern comprises several independent and parallel transitions along pPC1 from a more duck-like beak to a more goose-like beak. The lineages undergoing these transitions include the screamer lineage (the sister group to all other Anseriformes in the genera *Anhima* and *Chauna*), as well as six to seven independent lineages of 'geese' (genera *Cereopsis*, *Anser*, *Chen*, *Branta*, *Thambetochen*, *Chloephaga*, *Neochen*, *Alopochen*, *Chenonetta*, and *Cyanochen*). These lineages are highlighted by separate colors in Fig. 4.

Taken together, these screamer and goose lineages were found to be significantly convergent using the distance-based measures $C_{1\text{-}4}$ (Table 1). In contrast, these taxa were not found to be significantly convergent using the frequency-based measure C_5, indicating that the number of transitions (here, eight) into the elliptical region defined by these taxa is not significantly greater than would be expected by chance. Significance for $C_{1\text{-}4}$ and lack of significance for C_5 are consistent with parallel, convergent transitions of varying extent. Some of the selected goose lineages have beak shapes intermediate between those of ducks and geese, expanding the selected elliptical and

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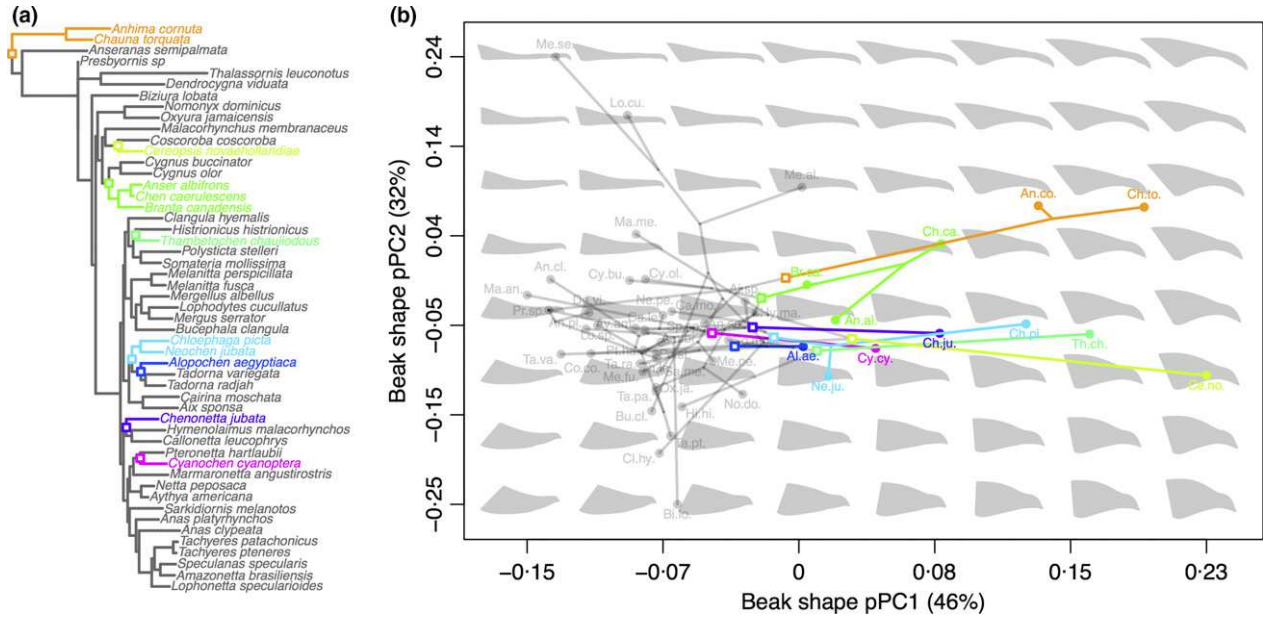

Fig. 4. Waterfowl show several independent transitions toward a more goose-like beak shape. (a) Waterfowl phylogeny (pruned from Burleigh, Kimball & Braun 2015). (b) Waterfowl phylomorphospace, highlighting the screamers (orange) and seven independent goose lineages. Open square symbols (internal nodes) and branch colors correspond between (a) and (b).

decreasing the chance of a significant C_5. However, the $C_{1\text{-}4}$ results indicate that geese are still significantly more similar to one another than would be expected by chance.

Discussion

These results demonstrate that foraging ecology has strongly influenced beak shape diversification in waterfowl. Previous studies have shown significant associations between feeding and beak morphology in birds (e.g. Gosler 1987; Benkman 1988; Price 1991; Peterson 1993; Barbosa & Moreno 1999; Bardwell, Benkman & Gould 2001; Schondube & del Rio 2003; Grant & Grant 2006; Bright *et al.* 2016). However, this is the first study to test how much variation in beak shape, and particularly three-dimensional curvature, is explained by diet and one of only a few studies to test hypotheses on the functional mechanisms underlying beak shape changes. This is also one of only a few studies to demonstrate evolvability of beak shape in adaptation to feeding among non-passerines. This contradicts a recent hypothesis that high integration between the beak and neurocranium in non-passerines may constrain evolvability of beak shapes in adaptation to feeding (Bright *et al.* 2016). These results suggest clade-specific patterns of association between feeding ecology and beak shape throughout birds rather than patterns specific to passerines vs. non-passerines.

Table 1. Convergence test results

Convergence metric	Estimate	*P*-value
C_1	0·41	**<0·005**
C_2	0·10	**<0·005**
C_3	0·02	**<0·005**
C_4	0·02	**<0·005**
C_5	8	0·154

Results of convergence tests for the highlighted screamer and goose lineages in Fig. 4 (N = 200 simulations).

The strength of the correlation between diet and beak shape, explaining 64% of the variation between the first PLS axes (Fig. 2b) and 41% of the variation between the second PLS axes (Fig. 2c), is surprisingly high given that the two datasets were unassociated at the level of the individual (i.e. diet data were compiled from the literature while morphology was measured from museum specimens), and the non-uniform methodologies of the compiled diet studies. A more thorough diet classification, including for example the sizes of ingested seeds and invertebrates, would likely explain even more variation in beak shape (Nudds & Bowlby 1984; Gurd 2008). The high variance explained by diet suggests a relatively minor influence on beak shape by functions of the beak other than feeding, such as preening and thermoregulation. However, it is possible that these additional functional demands in waterfowl are not mutually exclusive with the demands of feeding.

The observed correlations between diet and beak function (Fig. 3) are consistent with selection acting to increase mechanical advantage (MA) for grazing behavior. A lever with a higher MA exerts a higher output force for the same input force. Thus, given the same input muscle force, a more goose-like beak can exert a higher static bite force at the beak tip for cropping plants relative to a more

duck-like beak. Interestingly, ungulates show an analogous pattern: a higher lower jaw MA is associated with increased herbivory (Varela & Fariña 2015). In ungulates, the positive association between MA and herbivory has been attributed to a higher bite force which allows more effective grinding of grasses. Given that geese only use the beak to crop, not grind, grasses, the higher MA in the jaws of grazing ungulates may also be advantageous for cropping. More broadly, lever mechanics also explain patterns of shape diversification in the lower jaws of labrid fishes (Westneat 1995), cichlids (Hulsey & García de León 2005), and bats (Santana, Dumont & Davis 2010; Dumont *et al*. 2014). Thus, this study demonstrates that the kinetic upper beak of birds can function and evolve as a lever in a manner analogous to the lower jaws of other vertebrates.

Additionally, the observed correlation between diet and beak shape is consistent with a previously observed performance trade-off in waterfowl between filter-feeding and grazing. *In vivo* feeding trials comparing the performance of mallard ducks, white-fronted geese, and wigeons showed that mallards have the highest filter-feeding performance while white-fronted geese have the highest grazing performance (Kooloos *et al*. 1989; Van der Leeuw *et al*. 2003). Interestingly, wigeons, which have beak shapes intermediate between ducks and geese, do not appear to suffer much of a deficit in either filter-feeding or grazing performance. This trade-off corresponds well with the first major axis of beak shape variation and associated dietary specializations (Fig. 2): a more duck-like beak (lower pPC1 values) is associated with foods obtained by filter-feeding (invertebrates) while a more goose-like beak (higher pPC1 values) is associated with foods obtained by grazing (leaves and roots).

An increased tomium angle (TA) increases both stress resistance and torsional MA, while increased culmen angle (CA) increases stress resistance with no effect on MA. Thus, it is likely that changes in beak TA are related primarily to torsional MA. The relationship between TA and diet may additionally be due to widening of the beak tip (lower TA) in filter-feeders to increase fluid intake rate (Kooloos *et al*. 1989). Since this study uses shape metrics only approximately related to stress resistance, these results cannot rule out a role for stress resistance as a selective force in waterfowl beak evolution. Finite element modeling (e.g. Soons *et al*. 2010) and *in vivo* strain measurements of beak shapes spanning the duck to goose spectrum are needed to evaluate stress resistance as a selective force.

Although beak shapes corresponding to lower pPC1 and higher pPC2 scores (i.e. more duck-like beaks and beaks of pursuit divers) have lower MA, the consequences of this for filter-feeding and pursuit diving are not entirely clear. Filter-feeding and pursuit diving entail more rapid displacements of the beak relative to grazing, which may favor a relatively lower MA. However, MA can have counterintuitive effects on absolute (as opposed to relative) output force and velocity when energy losses are taken into account. For example, a higher MA can increase the absolute velocity of a lever moving through water since the higher force advantage better counteracts drag (McHenry 2012). Additionally, as a comparative study these data can only support with statistical significance those associations observed in cases of convergence, limited here to the association between a more goose-like beak and higher MA. More detailed study of the musculoskeletal dynamics in waterfowl during filter-feeding and pursuit diving, including a consideration of drag, is needed to resolve the consequences of changes in MA for rapid, opening and closing of the beak in fluid.

The reconstructed diet of the fossil waterfowl lineage *Presbyornis* (Fig. 2a) and the results of an ancestral beak shape reconstruction (Fig. 4) support the evolution of filter-feeding early in the evolution of waterfowl, followed by several independent 'duck-to-goose' transitions. There are several additional lines of evidence that support a goose-like beak and grazing behavior as derived within waterfowl. The first is the widespread, and therefore likely ancestral, presence among waterfowl of lamellae, keratinous comb-like ridges lining the upper and lower beak. The only other extant bird clades in which these have evolved, flamingos and prions, use the lamellae to filter-feed (Klages & Cooper 1992; Zweers *et al*. 1995) indicating that their origin in waterfowl likely coincided with the acquisition of filter-feeding. Most waterfowl, including most geese, have the capacity to filter-feed (Kear 2005). The second is a study of waterfowl dietary evolution (Olsen 2015), which identified several independent transitions toward increased herbivory in waterfowl, both within goose lineages and within some duck lineages.

The third line of evidence is the origin of moa-nalos, a recently extinct clade of flightless waterfowl endemic to the Hawaiian Islands (Olson & James 1991) that had definitively goose-like beaks (Fig. 1) and fed on the leaves of native vegetation (James & Burney 1997). The young age of the Hawaiian Islands and lack of a sister relationship to any extant goose lineage (Sorenson *et al*. 1999) demonstrate the potential for a rapid duck-to-goose transition. Lastly, the grasses upon which geese are largely dependent only became widespread with the emergence of grasslands during the Oligocene and Miocene (Strömberg 2011), well after the origin of the order Anseriformes in the Eocene (Prum *et al*. 2015) or earlier (Clarke *et al*. 2005). The global emergence of grasslands may even have been an ecological impetus for the evolution of geese by opening up new niches, consistent with the presence of independent goose lineages on every continent except Antarctica. The relationship between beak shape and feeding ecology, the pattern of morphological convergence, and the association between a more herbivorous diet and increased efficiency of force transmission during biting provide strong evidence for an adaptive role of beak shape evolution in the repeated expansions of waterfowl into new ecological niches.

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Data accessibility

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.42s0c (Olsen 2017). The phylogeny used in this study (pruned from Burleigh, Kimball & Braun 2014, 2015) is included in the deposited data. The full phylogeny is also accessible via the Dryad Digital Repository, deposited in association with Burleigh, Kimball & Braun 2014 (https://doi.org/10.5061/dryad.r6b87).

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