Multiple Origins of a High Force Feeding System in Waterfowl

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Abstract

Convergent biomechanical systems offer unique insight into musculoskeletal systems because the repeated association of structure and function by independent evolutionary events constitutes strong evidence for adaptation. Owing to their great diversity, bird feeding systems are ideal for identifying convergent systems. We collected beak shape data from 32 genera within the order Anseriformes, which includes ducks, geese, swans and mergansers. We find that the goose beak shape and the associated foraging behavior, grazing, have evolved multiple times from a duck-like ancestor. Differences in beak shape and other predictors of relative bite force indicate that the evolution of a goose-shaped beak is associated with the evolution of a higher bite force. By identifying aspects of the musculoskeletal system that are shared among goose feeding systems we can better understand how bones, muscles and joints adapt to producing and sustaining higher forces.

Introduction

Anseriforms can be divided into three foraging groups, based on diet and beak shape (Fig. 1).

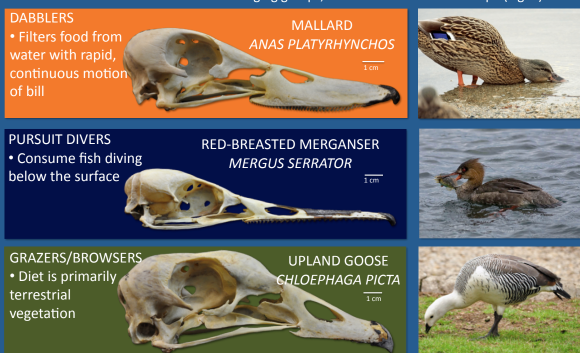

Figure 1. Examples of major foraging behaviors among anseriforms

Anseriforms in different foraging categories differ not only in beak shape but in overall cranial shape as well. Particularly structures in the skull associated with beak movements. Anseriforms can move both their lower and upper bill. However, no muscles insert directly onto the upper bill. Instead, muscles pull on the quadrate, pterygoid, jugal and palatine (Fig. 2), which trasmit force to the upper bill, causing it to rotate. In engineering, this closed loop of kinetic bones is known as a linkage. Upper bill shape is a good predictor of foraging category and both beak shape and linkage geometry predict how force production varies across anseriforms.

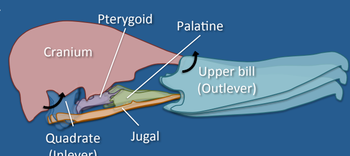

Figure 2. The cranial linkage bones cause upper bill rotation

Methods

Our study includes a total of 79 specimens representing 32 genera within Anseriformes. Morphological landmarks were obtained using a custom stereo camera setup (Fig. 3) and direct linear transformation for reconstructing 3D points from multiple camera views (Fig. 4; Miller *et al.* 1980). Upper bill morphology was characterized by fitting 3D curves to the tomium and culmen. An anseriform supertree was prepared by combining several phylogenies (sources listed in Fig. 5).

Figure 3. Two camera stereo setup

An upper beak morphospace plot (Fig. 6) was prepared by performing PC analysis on Procrustes superimposed landmarks and curves. Tiled background images of beaks in Figure 6 show the changes in upper beak shape associated with the first two principal components (PC).

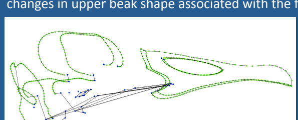

Figure 4. 3D Landmark and curve reconstruction

The evolutionary trajectories of anseriforms through upper beak morphospace (summarized in Fig. 6) were determined by ancestral state reconstruction (Felsenstein 1985) without branch lengths. PC1 and PC2 scores were used as states in the ancestral state reconstruction.

Results

Geese have origins across the anseriform phylogeny

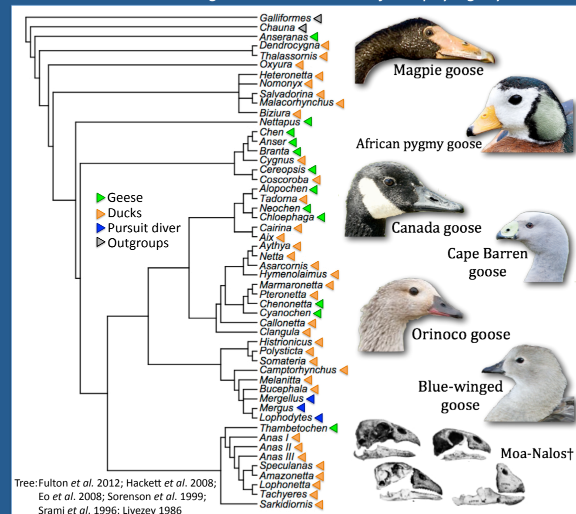

Figure 5. Supertree of 52 Anseriform genera. Representatives of several goose lineages at right.

- Geese do not form a monophyletic group within Anseriforms (Fig. 5)
- The simplest explanations for the distribution of geese across the anseriform phylogeny are:
  (1) multiple origins of geese from a duck-like ancestor, or
  (2) a greater number of multiple origins of ducks from a goose-like ancestor

Geese have evolved independently from a duck-like ancestor

- Ancestral state reconstruction of upper beak shape supports multiple origins of geese and a single origin of pursuit divers from a duck-like ancestor (Fig. 6)

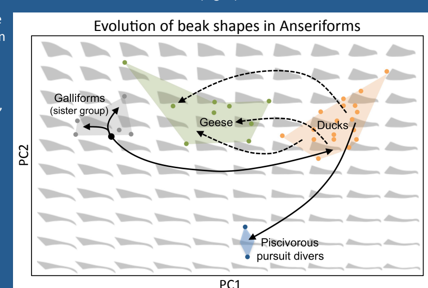

Figure 6. Morphospace of upper beak shapes in Anseriforms. Morpho-space supports common division of anseriforms into geese, ducks and piscivorous pursuit divers. Arrows summarize results of ancestral state reconstruction which supports at least three independent origins of geese (dashed lines) from a duck-like ancestor.

Geese have evolved a higher force feeding system

Grazing requires more force than dabbling

- Ducks feed primarily by dabbling, which involves rapid motion of the bill through water or mud to filter out food particles
- Geese feed primarily by grazing, which involves cutting tough vegetation at the tip of the bill
- Thus, grazing likely requires a more force-advantaged system relative to dabbling

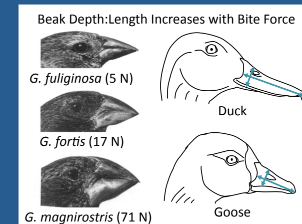

Figure 7. Beak depth:length increases with bite force (shown in newtons) in Darwin's Finches. A similar pattern is seen in ducks and geese.

Higher Beak Depth to Length Ratio

- The ratio of beak depth to beak length has been shown to increase with the evolution of higher bite forces in Darwin's Finches (Figure 7, left; Herrel *et al.* 2005; Grant & Grant 2003)
- A similar pattern is observed in the evolution of geese from a duck-like ancestor (Fig. 7, right)

Higher Beak Effective Mechanical Advantage

- Effective mechanical advantage (EMA) measures the force advantage of a lever (Westneat 2003)
- Geese have beaks with a significantly higher EMA relative to ducks (Fig. 8)

Lower Inlever-Outlever Ratio

- The ratio of inlever to outlever length (Fig. 2) influences the force advantage of a 4-bar linkage
- A shorter inlever relative to outlever (*i.e.* lower ratio) produces a force-advantage system
- The 4-bar linkage of geese has a significantly lower ratio relative to that of ducks (Fig. 9)

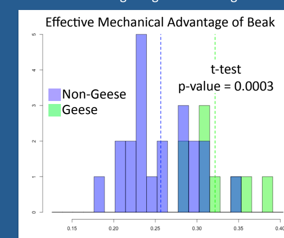

Figure 8. Geese have beaks with a significantly higher EMA relative to non-geese.

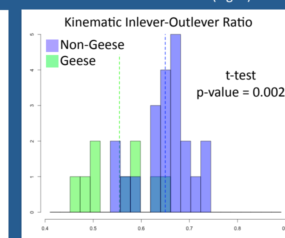

Figure 9. Geese have cranial linkages with a significantly lower inlever-outlever ratio.

Discussion

- Multiple origins of geese are supported by ancestral state reconstruction of upper beak shape
- Since the sister group to anseriforms (Galliformes) and the sister group to all other anseriforms (*Chauna*; Fig. 5) have galliform-like beaks, the ancestor of all anseriforms was likely galliform-like
- Although both galliforms and geese are terrestrial herbivores, they have distinct beak shapes:
  (1) Geese have a broad beak tip like ducks, while the beak tip of galliforms is pointed
  (2) Goose beaks are intermediate in height between galliforms and ducks (Fig. 6)
- That geese have a similar diet to galliforms but yet share aspects of beak shape with ducks suggests that these beak features are remnants retained in geese from a duck-like ancestor
- Differences in diet, beak shape and key aspects of the beak musculoskeletal system are all consistent with the evolution of higher bite forces as geese evolved from duck-like ancestors
  (1) The evolution of grazing from dabbling is expected to increase bite force
  (2) Anseriform beak shape evolution parallels higher bite force evolution in Darwin's finches
  (3) Differences in the lever and linkage geometry of geese indicate that geese are significantly better than non-geese at amplifying force from cranial musculature to the beak tip

Conclusion

Geese have convergently evolved beaks that generate higher forces during feeding. Identifying aspects of the musculoskeletal system that are shared among goose feeding systems will inform our understanding of how bones, muscles and joints adapt to producing and sustaining higher forces. *In vivo* bite force data from geese would be useful in confirming higher bite forces in geese. Also, nothing is known of how beak movements differ among geese or between ducks and geese. Lastly, continued research into beak evolution across the additional 32 orders of birds will likely reveal additional convergent feeding systems that will provide rich insight into how diverse musculoskeletal systems function and evolve.

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Acknowledgments

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