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Digest: Evolution of shape and leverage of bird beaks reflects feeding ecology, but not as strongly as expected*

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Is feeding ecology the main driver of beak diversification in modern birds? Taking a broad-scale interspecific comparative approach, Navalón et al. (2019) found a relationship between feeding ecology (diet and feeding behavior) and beak morphology (shape and leverage), although much of the observed variation remained unexplained. This low explanatory power may suggest that variation in the multitude of nonfeeding functions of the beak also influences its evolution.

The wide variety in shapes and sizes of birds' beaks is a textbook example of the remarkable versatility of this structure to adapt to a bird's preferred food or feeding behavior. This versatility led to the common perception that beaks are specialized for the primary feeding method of the birds bearing them: small beaks peck, heavy beaks crush, long beaks probe, and hooked beaks tear (Collard 2002). This perception is in line with the fact that some of the best examples of evolution by natural selection are known from birds evolving toward different beak shapes in response to changes in the available food (e.g., Smith 1993; Grant and Grant 2006; Ryan et al. 2007). Yet, despite these prime examples of beak evolution in response to diet at a micro-evolutionary scale (i.e., within, or among closely related species), remarkably little is known about whether beaks also reflect trophic ecology at the macro-evolutionary scale (i.e., across the entire avian order).

Navalón et al. (2019) took up this challenge and examined the shape of the upper beak as well as the leverage of the main beak-closing muscles on skulls of 176 bird species (Fig. 1). These leverage characteristics reflect the degree to which the beak is adapted to generate strong bite forces (Fig. 1D). Using literature data on diet and feeding behavior (Fig. 1A, B) and up-to-date information on the phylogenetic relationships among bird species, the researchers studied how these different beak properties evolved in relation to overall feeding ecology.

Using state-of-the-art methods in geometric morphometrics and phylogenetic comparative statistics, Navalón et al. (2019) found a significant link between beak morphology and feeding ecology across modern birds. However, the variation in feeding ecology only accounted for a relatively small portion of the observed variation in beak morphology. For instance, variation in the use of the beak during feeding (Fig. 1B) only explained approximately 9% of the total variation in beak shape, and variation in dietary preferences (Fig. 1A) accounted for 17% of the total variation in leverage. Moreover, the authors showed that species with different dietary preferences were sometimes equipped with similarly shaped beaks.

These findings by Navalón et al. (2019) offer a significant and novel contribution to the field for at least two reasons. First, their results suggest that not only at the micro-, but also at the macro-evolutionary level, feeding ecology plays a significant role in driving beak morphology diversification in birds. Second, the low explanatory power of feeding ecology on beak morphology diversity might suggest a strong effect of functional and ecological trade-offs in beak evolution. This is not unexpected, as aside from feeding, the beak is involved in a variety of functions, such as singing, preening, fighting, drinking, and thermoregulation, among many others. Because these tasks may require different (and sometimes conflicting) morphologies, functional trade-offs

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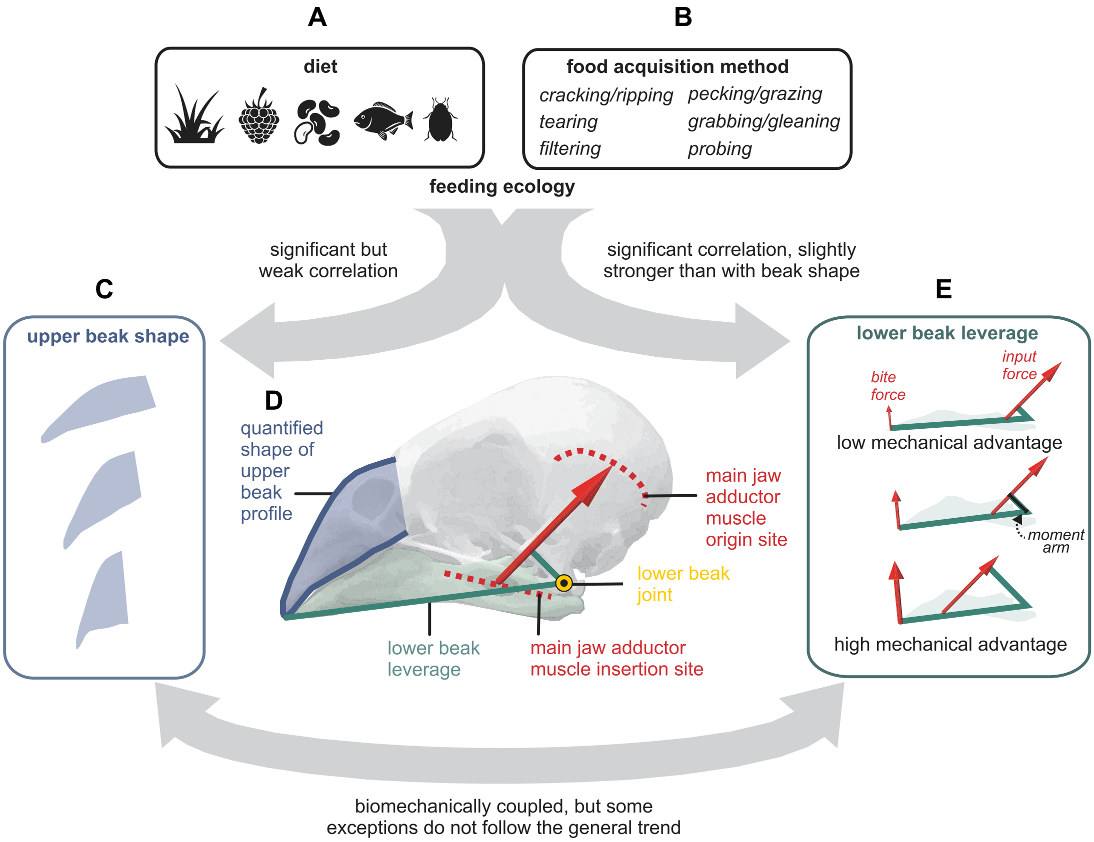

Figure 1. **Overview of the analysis and results from Navalón et al. (2019). Feeding ecology was divided into (A) diet classes and (B) food acquisition methods, and their evolutionary correlation with two important characteristics of cranial morphology was tested: (C) the shape of the upper beak, and (E) the leverage (or gearing) of the main jaw closer muscles by the lower beak, for which high mechanical advantages (to efficiently generate high bite forces) are reached when the moment arm of the muscles' input force is relatively high (E). These properties were inferred from (D) lateral-view photographs of bird skulls.**

may occur that constrain beak morphology evolution. In addition, the relative importance of each function may vary strongly among species (e.g., some birds rarely sing), causing differential selection pressures across species.

While shedding light on the role of trophic ecology on the macroevolution of the bird beak, Navalón et al. (2019) also illustrate that the morphological demands of certain feeding styles, especially those relying on beak movements, remain unclear. Consequently, to better understand the observed eco-morphological relationships, further biomechanical analyses of the cranial musculoskeletal system of birds are required (e.g., Dawson et al. 2011). Such studies can unravel, for example, how upper beak shape affects birds' efficiency of performing certain tasks during feeding.

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