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Inter-relationships among body mass, jaw musculature and bite force in birds

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Abstract

Bite force can provide an insight into the feeding biomechanics and ecology of vertebrates. There has been an increasing interest in bite force in birds with data being collected using force transducers although bite forces have also been calculated from the mass of the jaw musculature. Studies have sought to find ecological correlates between bite force and diet or feeding style as well as with morphology. This study collated data reported in the literature for bite force and mass of the jaw musculature in birds and explored the relationships between these variables and their relationships with body mass to test two hypotheses. First, bite force and mass of the jaw musculature would scale with body mass irrespective of the phylogeny. Second, bite force and mass of the jaw musculature would be directly related to each other and be unrelated to phylogeny. Phylogenetically controlled analyses showed that in relation to body mass there were different relationships with bite force, and with the mass of the jaw musculature, for non-passerine (isometry and negative allometry, respectively) and passerine species (both positive allometry). By contrast, a single significantly positively allometric relationship described the relationship between jaw muscle mass and bite force. These relationships were driven in part by the diet of the species concerned but also may reflect morphological differences in jaw musculature. The few studies that compare measured and calculated bite force for the same species show that values derived from muscles were higher. Detaching muscles from their points of origin and insertion to calculate physiological cross-sectional area may be biasing bite force calculations.

Introduction

Bite force has been recognised as a functional trait in vertebrates and so can be used in integrative studies at various levels of organismal biology, including helping in developing an understanding of the functions and capacities of the jaw-cranial musculoskeletal system (Anderson et al., 2008; Smith-Paredes & Bhullar, 2019; Ziermann et al., 2019). The jaw apparatus of the birds has been the subject of anatomical study for many years with many descriptions of the muscle configuration in a range of species (e.g. Bhattacharyya, 2013; Goodman & Fisher, 1962; Sims, 1955; Burton, 1974). More recently studies have started to focus on the functional aspects of the jaw musculature, particularly the bite force generated by a range of birds and other species (Sakamoto et al., 2019) and so provide insight into feeding biomechanics and ecology (Corbin et al., 2015). There has been an increasing number of reports detailing bite forces for birds determined empirically using force transducers (e.g. Corbin et al., 2015; Herrel et al., 2005a, 2005b; Sustaita & Hertel, 2013; van der Meij & Bout, 2004). There are also reports for bite forces have also been determined from the characteristics of the jaw musculature (e.g. Carril et al., 2015; Pestoni et al., 2018). Other studies have modelled bite force using finite element analysis (FEA; Soons et al., 2012, 2015; To et al., 2021).

Sakamoto et al. (2019) showed that bite force in amniotes seems to have evolved in multiple bursts where key groups, for example, Darwin's finches (Thraupidae), experienced significant evolutionary rate changes. However, it was concluded that coevolution with body size was primarily responsible for observed patterns. Across birds, beak shape does not necessarily reflect dietary preferences or inferred bite force, as determined from a mechanical advantage (Navalón et al., 2018). Few bird lineages seemed to have strong bites but this did not reflect beak shape; birds of prey and parrots had similarly shaped maxillae but the latter had much higher mechanical advantage values (Navalón et al., 2018).

Other studies have sought to find ecological correlates between measured bite force and diet or feeding style (e.g. Corbin et al., 2015; van der Meij & Bout, 2004). For instance, the method of removal of seed husks can vary between species ranging from simple crushing in an estrildid (Estrildidae) to more complex mediolateral movements of the jaw in a finch (Fringillidae; Nuijens & Zweers, 1997). Bite forces have also been investigated in relation to head and beak dimensions (Corbin et al., 2015; Herrel et al., 2005a, 2010) and shape (van der Meij & Bout, 2008). A few studies have examined cross-species variation by determining allometric relationships between bite force and body mass (Sustaita & Hertel, 2013; van der Meij & Bout, 2004). The relationship between bite force and body mass for estrildids showed isometry but there was positive allometry exhibited by finches (van der Meij & Bout, 2004). Bite force scaled isometrically with jaw muscle mass for both types of these seed-eating birds (van der Meij & Bout, 2004) and in two raptorial families (Sustaita & Hertel, 2013). To date, however, there has not been a systematic review of the inter-relationships between body mass, jaw musculature and bite force for birds.

The study described here collated data for body mass, the mass of the jaw musculature and bite force from literature sources for as many bird species as possible. The analyses examined allometric relationships between these three variables to test the hypotheses that: (1) bite force and mass of the jaw musculature would both scale with body mass when controlled for phylogeny and (2) bite force and mass of the jaw musculature would also be directly related to each other when controlled for phylogeny.

Materials and methods

Data for avian species were derived from the literature in three categories (see Data S1 for sources). Body mass (in grams) was derived from the actual study, or if this was not reported mean values for the species concerned were derived from Dunning (2008). The total mass (in mg) of the jaw musculature that act to close the jaw (and so will generate bite force) was recorded. Most reports did not state whether values were for one or both sides so it was assumed that the values represented one side of the head (and was confirmed by some authors). The final parameter was maximum bite force measured, or calculated, at the tip of the beak (in Newtons). It was also noted whether the values had been measured using a transducer (e.g. van der Meij & Bout, 2004) or had been calculated from the mass of the jaw musculature (e.g. Carril et al., 2015).

In total, data were collected for 122 species from 14 different orders but data were not always available for all three parameters for each species. For the comparison of bite force to body mass, there were values for 100 species for bite data measured using a transducer and 29 values for bite force calculated from jaw musculature (some species had replicate data). Measured bite force was reported most for various families of passerines with data being available for non-passerines from only two species of woodpecker (Piciformes; Corbin et al., 2015) and 11 species of raptorial birds (Degrange et al., 2010; Hull, 1993; Sustaita & Hertel, 2013). Multiple values for measured bite force and body mass were averaged leading to a subset of data for 77 species. For the comparison between measured bite force and mass of the jaw musculature there was a subset of 51 species. Note that reports of the mass of the jaw musculature were used for species where measured bite force was reported. For the comparison between the mass of the jaw musculature and body mass there were data from a subset of 86 species.

All data were $\log_{10}$-transformed prior to analysis. Graphical representation of the data suggested that two subsets of data were present based largely on passerine and non-passerine species. To test whether this was a significant criterion, 'type' of bird was included as a factor in the analyses and the interaction term was included to assess whether patterns between the dependent variable and the covariate were significantly different. Given the distribution of species between different orders and families, the analyses were made using a phylogenetically controlled general linear model analysis. A phylogenetic tree of the 122 species in the dataset was produced based on a Hackett backbone using birdtree.org (Jetz et al., 2012). Using this tree, phylogenetically controlled general linear modelling (pglm) was performed in R (ver. 3.6.3; R Development Core Team, 2021) using the packages *ape* (Paradis et al., 2004), *mvtnorm* (Genz & Bretz, 2009) and *MASS* (Venables & Ripley, 2002) as used by Deeming (2018) using code provided by Carl Soulsbury (pers. comm.).

Exponents (i.e. 'b' which is the slope of the regression line based on $\log_{10}$-transformed data, or $Y = aX^b$) were tested for isometry using one-sample t-tests (Bailey, 1981). The isometric exponent would be 1.0 for the relationships between body mass and jaw muscle mass because they are the same units. However, for the relationships between mass (a unit proportional to volume, which is 3-dimensional) and bite force (a unit proportional to area, which is 2-dimensional) the isometric exponent would be 0.667 (i.e., 2/3 – unit dimensions for dependent variable/independent variable).

Results

Bite force in birds typically ranged from 1 to 70 N and showed a positive relationship with body mass, when controlled for phylogeny:

$$\text{All Birds : Biteforce} = 0.043 * \text{Body mass}^{1.019}$$

($F_{1,74} = 92.58$, $P < 0.001$, $R^2 = 0.556$, $\lambda = 0.9999$). This was a significant positive departure from isometry (SE for the exponent was 0.106; t-test – $t = 3.29$, $P < 0.01$). However, when plotted against body mass, small passerines (<100 g body mass) had bite forces values that were comparable, or higher, than much heavier non-passerine species (Fig. 1). Phylogenetically controlled analysis showed that there was a significant interaction between body mass and type of bird with the rate of increase in bite force associated with body mass being greater for passerines (Table 1; Fig. 1). Type of bird on its own was not a significant factor in the model but body mass was a significant covariate for bite force (Table 1). The λ value was very high and significantly different from 0 ($P < 0.001$) but not from 1 ($P = 0.414$). In light of this result, the dataset was split into non-passerines and passerines to generate the phylogenetically controlled general linear regressions.

$$\text{For non} - \text{passerines : Bite force} = 0.118 * \text{Body mass}^{0.692}$$

($R^2 = 0.652$, $\lambda < 0.001$; illustrated in Fig. 1). The exponent was not significantly different from an isometric slope of 0.667

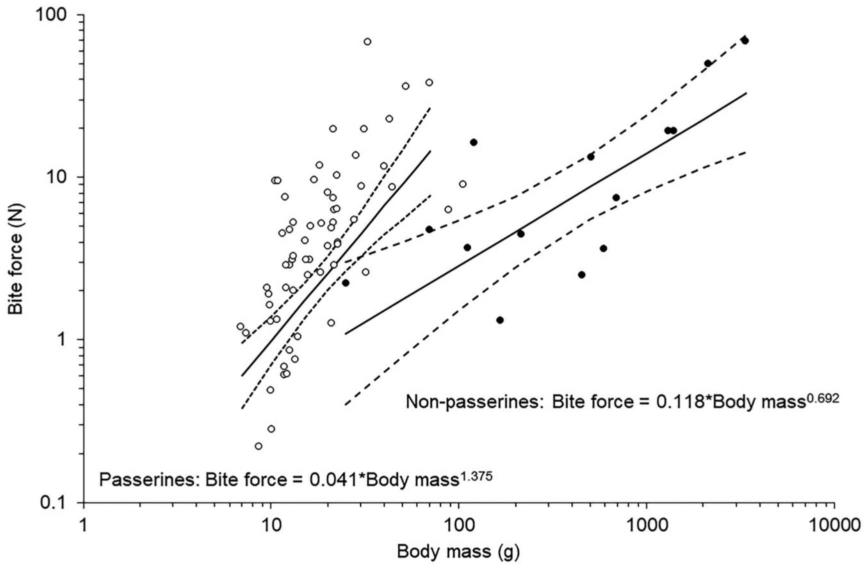

Figure 1 Relationships between body mass and measured bite force for passerine (○) and non-passerine (●) birds. Solid lines are the phylogenetically controlled general linear regression estimates generated by *R* (regression equations are shown) with dashed lines showing the 95% confidence intervals (see text for details). Note the $\log_{10}$ scale on both axes.

Table 1 Results from a phylogenetically controlled general linear model to test the effects of body mass and the type of bird (passerine [$N = 63$] or non-passerine [$N = 14$]), and the interaction of these terms, on the bite force generated by the jaw musculature ($R^2 = 0.589$, $\lambda = 0.999$)

	Exponent (SE)	*t* (*P*-value)
LogBM	1.781 (0.340)	5.25 (<0.001)
Type	0.071 (0.987)	0.07 (0.943)
Type*LogBM	−0.484 (0.211)	−2.30 (0.024)

so the relationship exhibited isometry (standard error [SE] for the exponent was 0.153; *t*-test – $t = 0.20$, $P > 0.05$).

$$\text{For passerine species: Bite force} = 0.041 * \text{Body mass}^{1.375}$$

($R^2 = 0.575$, $\lambda = 0.993$; Fig. 1). This exponent was significantly larger than 0.667 so the relationship was exhibiting positive allometry (SE for the exponent was 0.151; *t*-test – $t = 4.72$, $P < 0.001$).

A plot of the relationship between measured bite force and mass of the jaw musculature also appeared to exhibit a passerine-non-passerine split with the latter group having lower values for bite force for any given muscle mass (Fig. 2). However, whilst phylogenetically controlled general linear regression showed that there was a significant effect of jaw muscle mass there was no significant difference between the two groups, nor was there a significant interaction (Table 2). The λ value was moderately high and significantly different from both 1 and 0 ($P < 0.01$ in both cases). Further analysis to reduce model complexity showed that there was a single relationship for all birds so the phylogenetically controlled general linear regression, which was:

$$\text{Bite force} = 0.044 * \text{Jaw muscle mass}^{0.868}$$

($R^2 = 0.685$, $\lambda = 0.780$; Fig. 2). An isometric slope for this relationship should be 0.667 and in this instance the slope was exhibiting significant positive allometry (SE for the exponent was 0.088; *t*-test – $t = 2.42$, $P < 0.05$).

Jaw muscle mass for passerines and non-passerines seemed to be different when plotted against body mass with non-passerines having relatively lower values for any given body mass (Fig. 3). There was a highly significant interaction term for these data in the phylogenetically controlled general linear model (Table 3). The λ value was moderately high and significantly different from both 1 and 0 ($P < 0.001$ in both cases). In light of the difference in the pattern of the relationships between the dependent variable and the covariate, the non-passerine and passerine data were separated for individual phylogenetically controlled general linear regression analyses.

$$\text{For non} - \text{passerines: Jaw muscle mass} = 6.17 * \text{Body mass}^{0.771}$$

($R^2 = 0.626$, $\lambda = 0.736$) which was a significantly negative allometric relationship (SE for the exponent was 0.097; $t = -2.38$, $P < 0.05$).

$$\text{For} - \text{passerines: Jaw muscle mass} = 3.47 * \text{Body mass}^{1.380}$$

($R^2 = 0.693$, $\lambda = 0.378$) which was showing significantly positive allometry (SE for the exponent was 0.139; $t = 2.75$, $P < 0.05$).

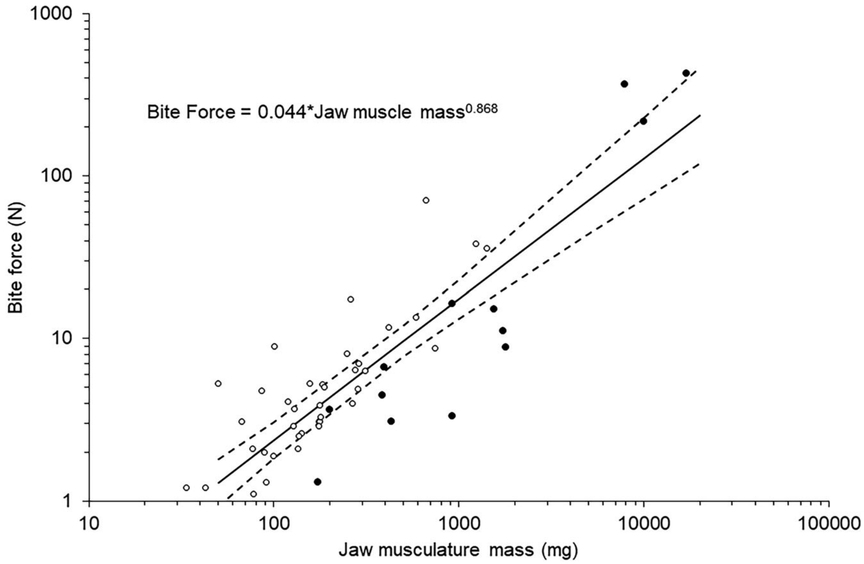

Figure 2 Relationship between the mass of the jaw musculature and measured bite force for passerine (○) and non-passerine (●) birds. The solid line is the phylogenetically controlled general linear regression estimate generated by *R* (regression equation is shown) together with 95% confidence intervals indicated by dashed lines (see text for details). Note the $\log_{10}$ scale on both axes.

Table 2 Results from a phylogenetically controlled general linear model to test the effects of mass of the jaw musculature (MM), the type of bird (passerine [$N = 38$] or non-passerine [$N = 13$]), and the interaction of these terms, on bite force generated by the jaw musculature ($R^2 = 0.704$, $\lambda = 0.762$)

	Exponent (SE)	*t* (*P*-value)
LogMM	0.698 (0.312)	2.34 (0.003)
Type	−0.027 (0.554)	−0.05 (0.962)
Type*LogMM	0.118 (0.181)	0.65 (0.517)

Discussion

The data showed that even when controlling for phylogeny, contrary to prediction, when scaled against body mass both bite force and mass of the jaw musculature showed different patterns in passerines and non-passerines. This difference between types of birds was not observed for the relationship between jaw muscle mass and bite force, and the positive allometry suggests that bite force is disproportionately increasing as the mass of the jaw muscles increases. This relationship means that, in line with our hypothesis, it is possible to predict bite force based on the mass of the jaw musculature with a degree of confidence, irrespective of species.

Biomechanical significance

Despite the small sample size, for non-passerines, bite force scaled with body mass$^{0.70}$, which was not significantly different from isometry (scaling with mass$^{0.67}$). This showed that, with respect to resultant bite force, smaller and larger non-passerines in this dataset appeared to have jaw musculatures that are sufficiently geometrically similar that large non-passerines could be considered ‘scaled up’ versions of smaller birds. Jaw muscle mass, however, of the non-passerines scaled with mass raised to the power 0.77 (i.e. mass$^{0.77}$), which was significantly lower from an isometric prediction, that is, mass raised to the power 1.0 (mass$^{1.0}$); therefore, large non-passerines had proportionally less bite muscle mass than isometry would predict. While we did not have the data for the mechanical advantage for the bite muscles for these birds, the combination of an isometric relationship between body mass and bite force and the negative allometric relationship between body mass and bite muscle mass suggests that the moment arm ratio of the bite muscles (ratio of inlever to outlever lengths) is positively allometric to compensate for the negative allometry of jaw muscle mass. Specifically, the moment arm ratios in non-passerines would need to scale with mass$^{0.18}$ to perfectly reflect our observed relationships between body mass, jaw muscle mass, and bite force (see Appendix S1).

For passerines, however, the bite forces scaled with the body mass$^{1.38}$, significantly higher than what isometry would predict (scaling with mass$^{0.67}$). This relationship appeared to result from larger passerines having proportionately more body mass devoted to biting muscles than did the smaller passerines. Similarly, jaw muscle mass was proportional to mass$^{1.38}$, which was significantly larger than the isometric prediction of jaw muscle mass being directly proportional to body mass (i.e. raised to the power of 1.0). A constant moment arm ratio combined with this allometrically positive muscle mass relationship would predict that bite force would scale with mass$^{0.91}$ (see Appendix S1). Our observed relationship for passerines, that bite force scaled with body mass$^{1.38}$, was significantly higher than just increased muscle mass would predict, suggesting that, as passerines get larger, not only do they get increased muscle mass, but the mechanical advantage of these muscles also

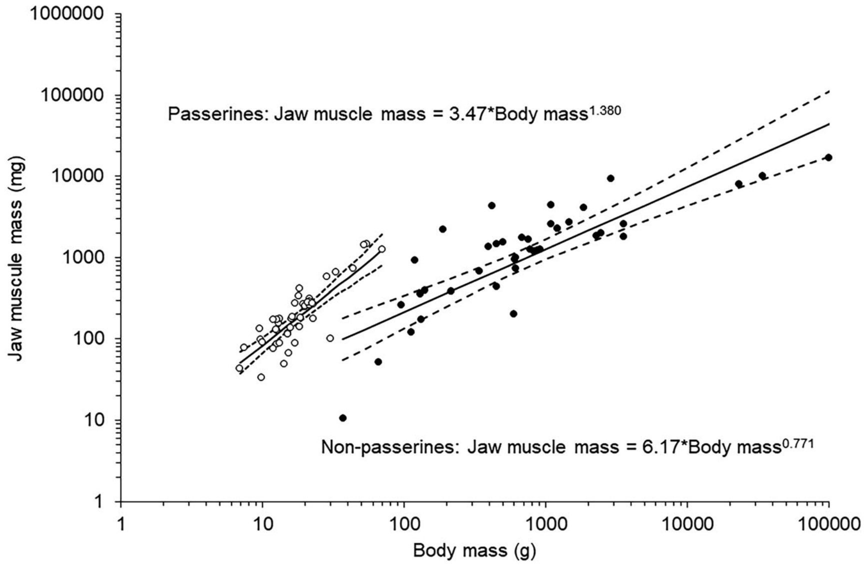

Figure 3 Relationships between body mass and the mass of the jaw musculature for passerine (○) and non-passerine (●) birds. Solid lines are the phylogenetically controlled general linear regression estimates generated by *R* (regression equations are shown) with dashed lines showing the 95% confidence intervals (see text for details). Note the $\log_{10}$ scale on both axes.

Table 3 Results from a phylogenetically controlled general linear model to test the effects of body mass and the type of bird (passerine [$N = 46$] or non-passerine [$N = 40$]), and the interaction of these terms, on the mass of the jaw musculature ($R^2 = 0.723$, $\lambda = 0.822$)

	Exponent (SE)	*t* (*P*-value)
LogBM	0.284 (0.266)	1.07 (0.290)
Type	−0.229 (0.415)	−0.55 (0.583)
Type*LogBM	0.533 (0.208)	2.56 (0.013)

increases, allowing the total bite force to increase at a greater rate than isometry would predict.

One element of these relationships is that taxonomic distribution is not random. For passerines, studies of bite force have focussed on species that are considered to need a strong bite to feed with. For the 90 values for bite force reported for the Passeriformes, 76 values are from either the Fringillidae, Thraupidae or Estrildidae. Similarly, for non-passerines 23 of the 39 reported values for bite force are from the Accipitridae or Falconidae. As a result, our interpretation of these results needs to be tentative because additional data from a wider range of species with a broader range of diets may change the relationships. There is a need to have a wider taxonomic spread for values for bite force to better understand the interrelationships between body mass, jaw musculature and bite force in birds.

Bite force and diet

For a given body mass, the smaller passerines in this study have more jaw muscle mass and so generate more bite force than non-passerines. This pattern may reflect the feeding strategies of the species studied because insectivores and zoophagous birds have lower bite forces (Pestoni et al., 2018). However, the dataset had many values for finches and other granivorous species that feed on seeds, which require force to de-husk them and so gain access to the nutritious kernels (van der Meij & Bout, 2004, 2006). Clabaut et al. (2009) reported that large-billed morphs of the African seedcracker (*Pyrenestes ostrinus*) are able to deal with sedge (*Scleria verrucosa*) seeds that require 153 N to split the testa; by contrast, small-billed morphs feed on sedge (*Scleria goossensii*; mean hardness of 13 Newtons). More generally, lower bite forces in finches were associated with longer husking times (van der Meij & Bout, 2006) and diets that require less processing are associated with lower bite forces (Corbin et al., 2015; Lederer, 1975). In finches (Fringillidae), bill shape and size correlate with the size and durability of seeds that can be processed (Willson, 1971, 1972).

Another aspect of bite force is that it is often determined at the tip of the beak and in this study these values were used for analysis. However, bite force can be applied at the base of the bill and, depending on the species of Darwin's finch, the increase in bite force can be between 20% and 65% of the bite force at the tip (Herrel et al., 2010). Nuijens and Zweers (1997) reported that manipulation of seeds by the beak varied between estrildid and fringillid finches. FEA of skulls of various Darwin's finches suggested that the bite force at the base was also greater at the most distal position of the bill (Soons et al., 2015). This reflected the feeding strategy of some species that crushed seeds using the base of the bill rather than the tip (Soons et al., 2015). It would be interesting to collect more data on a wider range of bird species with a more diverse range of diets to determine whether the relationship between bite force and body mass is directly a consequence of diet (Corbin et al., 2015; Pestoni et al., 2018).

Association between bite force and jaw musculature

It is not surprising that bite force is a direct function of muscle mass given that force generated by the muscle is a function of its size (Fitts et al., 1991). Small, seed-eating passerines can generate a greater bite force because they simply have more jaw muscle. As the number of empirical studies increases in the future the current biases in relation to the diet of the birds involved will diminish. Presumably, differences in feeding strategy and/or diet will be reflected in the mass of the jaw muscle required to deliver an ‘appropriate’ bite force for the species concerned but it is anticipated that this will not affect the pattern described here.

In birds of prey, beak and skull size seem to be a key feature in determining feeding ecology rather than bill shape (Bright et al., 2016). Sustaita and Hertel (2013) showed that accipiters and falcons exhibit different bite forces despite similarities in body size and this is associated with increased muscle mass in falcons. In Japanese sparrowhawks (*Accipiter gularis*) the larger females have relatively larger *m. pterygoideus* that reflects their reversed sexual dimorphism in anatomy and diet (Wang et al., 2017).

The present analysis suggests that bite force is a simple function of the mass of the musculature associated with closing the jaw. Bhattacharyya (2013) suggests that there are 7 muscles that act to close the jaw but nightjars only seem to have 6 muscles (Demmel Ferreira et al., 2019) whereas birds of prey and the guira cuckoo (*Guira guira*) have 8 muscles (Sustaita, 2008). By contrast, cormorants (Suliformes) have 11 muscles (Burger, 1978) whereas finches and Darwin’s finches seem to have around 12–14 muscles that serve to close the jaw (Genbrugge et al., 2011; Soons et al., 2012, 2015; To et al., 2021). The increase in number appears to be associated with subdivisions of muscle complexes and so this may reflect a switch from one large, wide muscle to several narrower muscles that will each have shorter fascicle lengths and so will have larger PCSA values. It is unclear whether there is a link between jaw muscle structure and feeding methodology or diet, or whether this reflects body size; this would be an interesting area for further research.

Comparison between measured and calculated bite forces

Data for calculated bite force are increasingly common for birds (e.g. Carril et al., 2015; Cost et al., 2020; Sakamoto et al., 2019) but there are many more values for measured bite force with the emphasis on passerine species (Corbin et al., 2014; Herrel et al., 2005a; van der Meij & Bout, 2004). There are very few studies that enable comparison between bite force values determined for the same species derived from empirical studies or having been calculated using PCSA values. For Darwin’s finches (Thraupidae) measured bite forces (Herrel et al., 2009) are very similar to those predicted by FEA of skulls (Soons et al., 2015). For the Java finch (*Padda oryzivora*) measured bite force averaged 9.0 N but the value derived from FEA was 6.8 N (Soons et al., 2012). Summing the forces generated by determining the PCSA of the muscles active during closing the jaw gave a bite force of at least 14.0 N for the Java finch but this value may double if the values are given by Soons et al. (2012) only represent one side of the jaw. For falcons (Falconidae) and hawks (Accipitridae), the values for bite force calculated from muscle characteristics were approximately double that derived from *in vivo* measurements of bite force after controlling for body mass (Sustaita & Hertel, 2013).

Although the magnitude of a bite force may reflect the willingness of an individual bird to bite (van der Meij & Bout, 2004), the apparent disparity between measured and calculated values may be a reflection of the methods involved to calculate bite force from muscle dissection. Anatomical studies determine the PCSA of the individual muscles to allow for the calculation of stress forces, which are used in conjunction with moment arms to calculate bite force for the jaw musculature (Carril et al., 2015; Martin et al., 2020; Sustaita, 2008). PCSA is the volume of the muscle multiplied by the cosine of pinnation angle of the muscle fascicles (≤1) and then divided by the fascicle length. Whilst PCSA is often reported (Carril et al., 2015; Sustaita, 2008; Wang et al., 2017) pinnation angles and fascicle lengths are rarely found in the literature (but see Pestoni et al., 2018; Soons et al., 2012). In some instances, pinnation angles are not considered in the calculation of PCSA (Genbrugge et al., 2011) despite their importance in modelling muscle forces (Martin et al., 2020). However, the use of the appropriate PCSA value is essential for accurate modelling of bite force (Gröning et al., 2013).

Fascicle length is typically measured on muscles that have been dissected from the skull (e.g. Demmel Ferreira et al., 2019; Pestoni et al., 2018; Sustaita, 2008) and are subsequently fixed in nitric acid (e.g. Genbrugge et al., 2011; Pestoni et al., 2018; Soons et al., 2012), alcohol (van der Meij & Bout, 2004) or formaldehyde (e.g. Carril et al., 2015). Each of these procedures, however, cause the muscles to shrink reducing the measured fascicle length (as recognised by Genbrugge et al., 2011). A smaller value for the denominator will increase the value of the calculated PCSA and over-estimate the force generated by the muscle in subsequent calculations. This may offer an explanation for the higher calculated values for raptors (Sustaita & Hertel, 2013) but there is an urgent need to provide more comparative studies that allow a test of the validity of the determining fascicle length from dissected muscles (see Martin et al., 2020).

The jaw musculature of birds is characterised by muscles that have multiple points of attachment to the skull and mandible. Often the muscles form broadsheets where the epimysium is attached to wide areas of the bone rather than having point insertions. For example, the *m. adductor mandibulae externus profundus* (*amep*) of the monk parakeet (*Myiopsitta monachus*) has a broad point of origin on the lateral cranium and an elongated point of insertion on the dorsal mandible (Carril et al., 2015). A similar pattern is seen for the same muscle in the guira cuckoo (Pestoni et al., 2018). This means that the *amep* is a broad flat muscle sheet in these species, which would not retain a natural shape once it is dissected from the skull. The determination of pinnation angles and fascicle lengths from photographs of muscles *in situ* would provide a more anatomically realistic determination of the PCSA because the fascicle length would not be distorted. In addition, the area and width of muscle could be determined and so an actual cross-sectional area could be determined based on the calculated volume.

In birds, Herrel et al. (2010) used computed tomography (CT) scanning in conjunction with FEA to study bite force in Darwin's finches. CT scanning has also been used to visualise the points of origin and insertion of the jaw musculature of finches (Genbrugge et al., 2011), the guira cuckoo (Pestoni et al., 2018), a nightjar (*Systellura longirostris*; Demmel Ferreira et al., 2019), and a parrot (*Psittacus erithacus*; Cost et al., 2020). As the costs of CT scanning equipment become more reasonable it is likely that this method will be increasingly used to study the jaw apparatus of birds and will prove useful in providing accurate and direct measures of cross-sectional areas of muscles that generate bite forces. For instance, Santana (2018) reported a method using CT scanning to determine cross-sectional areas of muscles *in situ* in bats (Chiroptera). Such digital dissection techniques have the advantage of determining muscle characteristics without the need to dissect the muscles from points of origin and insertion and so offer a more anatomically accurate view of the musculature (Cost et al., 2020).

Predicting bite force in extinct species

An understanding of the relationship between body mass, jaw musculature and bite force would prove useful in predicting the diet of extinct avian species. Biomechanics of jaws have been considered to gain insight into the feeding preferences of *Diatryma*, a gigantic bird from the Eocene of North America, although bite forces were not estimated (Witmer & Rose, 1991). Degrange et al. (2010) estimated the bite force of the extinct 40 kg 'terror bird' *Andalgalornis steulleti* using data from passerine species to be 133 N at the tip of the bill. Other extinct birds from South America have had their bite forces estimated by the same method and these ranged from 34 N for *Thegornis musculosus* weighing between 1.9–2.3 kg to 343 N for *Brontornis burmeisteri* estimated to have a mass of 319–350 kg (Degrange et al., 2012). However, the analysis presented here suggests that these estimates may perhaps be better estimated using the relationship between body mass and bite force for non-passerine birds described above. Estimates for bite force for *A. steulleti* and *B. burmeisteri* would increase to 180 and 809 N, respectively, whereas *T. musculosus* would have a bite force of only 25 N. It is unclear, which estimate is the more accurate but a better understanding of the relationship between the jaw apparatus and bite force in a wider range of non-passerine birds may be useful in predicting bite force in extinct bird species.

Conclusion

Bite force, and jaw muscle mass, both scale with body mass and appear to exhibit different patterns between non-passerines and passerines. This difference is not observed for the relationship between bite force and jaw muscle mass. Whether these relationships hold true when data more species are available is yet to be seen. Improving our understanding of the role that bite force plays in determining the diet of birds will highlight how morphology can affect the ecology of species (Corbin et al., 2015). Presently, studies have been understandably biased towards species that have specialised diets, or offer interesting comparisons, but it is clear that, given the diversity of birds, our understanding of the inter-relationships between body size, jaw musculature and bite force is limited. The collection of data from a wider range of species will inevitably help in our understanding of the morphological and ecological aspects of the feeding apparatus of birds.

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References

Anderson, R. A., McBrayer, L. D., & Herrel, A. (2008). Bite force in vertebrates: Opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society*, **93**, 709–720.

Bailey, N. T. J. (1981). *Statistical methods in biology*, 2nd ed. Hodder & Stoughton.

Bhattacharyya, B. N. (2013). Avian jaw function: Adaption of the seven-muscle system and a review. *Proceedings of the Zoological Society*, **66**, 75–85.

Bright, J. A., Marugán-Lobónc, J., Cobbe, S. N., & Rayfield, E. J. (2016). The shapes of bird beaks are highly controlled by nondietary factors. *Proceedings of the National Academy of Sciences, USA*, **113**, 5352–5357.

Burger, A. E. (1978). Functional anatomy of the feeding apparatus of four South African cormorants. *Zoologica Africana*, **13**, 81–102.

Burton, P. J. K. (1974). *Feeding and the feeding apparatus in waders*. British Museum.

Carril, J., Degrange, F. J., & Tambussi, C. P. (2015). Jaw myology and bite force of the monk parakeet (Aves, Psittaciformes). *Journal of Anatomy*, **227**, 34–44.

Clabaut, C., Herrel, A., Sanger, T. J., Smith, T. B., & Abzhanov, A. (2009). Development of beak polytmorphism in the African seedcracker, *Pyrenestes ostrinus*. *Evolution & Development*, **11**, 636–646.

Corbin, C. E., Lowenberger, L. K., & Gray, B. L. (2015). Linkage and trade-off in trophic morphology and behavioural performance of birds. *Functional Ecology*, **29**, 808–815.

Cost, I. N., Middleton, K. M., Sellers, K. C., Echols, M. S., Witmer, L. M., Davis, J. L., & Holliday, C. M. (2020). Palatal biomechanics and its significance for cranial kinesis in Tyrannosaurus rex. *The Anatomical Record*, **303**, 999–1017.

Deeming, D. C. (2018). Effect of composition on shape of bird eggs. *Journal of Avian Biology*, **49**, jav-01528.

Degrange, F. J., Noriega, J. I., & Areta, J. I. (2012). Diversity and paleobiology of the Santacrucian birds. In S. F. Vizcaíno, R. F. Kay, & M. S. Bargo (Eds.), *Early Miocene paleobiology in Patagonia: high latitude paleocummunities of the Santa Cruz formation* (pp. 138–155). Cambridge University Press.

Degrange, F. J., Tambussi, C. P., Moreno, K., Witmer, L. M., & Wroe, S. (2010). Mechanical analysis of feeding behavior in the extinct "terror bird" Andalgalornis steulleti (Gruiformes: Phorusrhacidae). *PLoS One*, **5**(8), e11856.

Demmel Ferreira, M. M., Tambussia, C. P., Degrange, F. J., Pestoni, S., & Tirao, G. A. (2019). The cranio-mandibular complex of the nightjar *Systellura longirostris* (Aves, Caprimulgiformes): Functional relationship between osteology, myology and feeding. *Zoology*, **132**, 6–16.

Dunning, J. B. Jr (2008). *CRC handbook of avian body masses*, 2nd ed. CRC.

Fitts, R. H., McDonald, K. S., & Schluter, J. M. (1991). The determinants of skeletal muscle force and power: Their adaptability with changes in activity pattern. *Journal of Biomechanics*, **24**, 111–122.

Genbrugge, A., Herrel, A., Boone, M., Hoorebeke, V., Podos, J., Dirckx, J., Aerts, P., & Adriaens, D. (2011). The head of the finch: The anatomy of the feeding system in two species of finches (*Geospiza fortis* and *Padda oryzivora*). *Journal of Anatomy*, **219**, 676–695.

Genz, A., & Bretz, F. (2009). *Computation of Multivariate Normal and t Probabilities, series Lecture Notes in Statistics*. Springer-Verlag.

Goodman, D. C., & Fisher, H. I. (1962). *Functional anatomy of the feeding apparatus in waterfowl*. Southern Illinois Press.

Gröning, F., Jones, M. E. H., Curtis, N., Herrel, A., O'Higgins, P., Evans, S. E., & Fagan, M. J. (2013). The importance of accurate muscle modelling for biomechanical analyses: A case study with a lizard skull. *Journal of the Royal Society, Interface*, **10**, 20130216.

Herrel, A., Podos, J., Vanhooydonck, B., & Hendry, A. P. (2009). Force-velocity trade-off in Darwin's finch jaw function: A biomechanical basis for ecological speciation? *Functional Ecology*, **23**, 119–125.

Herrel, A., Soons, J., Aerts, P., Dirckx, J., Boone, M., Jacobs, P., Adriens, D., & Podos, J. (2010). Adaption and function of the bills of Darwin's finches: Divergence by feeding style and sex. *Emu*, **110**, 39–47.

Herrel, A., Soons, J., Huber, S. K., & Hendry, A. P. (2005a). Evolution of bite force in Darwin's finches: A key role for head width. *Journal of Evolutionary Biology*, **18**, 669–675.

Herrel, A., Soons, J., Huber, S. K., & Hendry, A. P. (2005b). Bite performance and morphology in a population of Darwin's finches: Implications for the evolution of beak shape. *Functional Ecology*, **19**, 43–48.

Hull, C. (1993). Prey dismantling techniques of the peregrine falcon *Falco peregrinus* and the brown falcon *F. berigora*: their relevance to optimal foraging theory. In P. Olsen (Ed.), *Australian raptor studies* (pp. 330–336). Australian Raptor Association.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Lederer, R. J. (1975). Bill size, food size and jaw forces of insectivorous birds. *The Auk*, **92**, 385–387.

Martin, M. L., Travouillon, K. J., Fleming, P. A., & Warburton, N. M. (2020). Review of the methods used for calculating physiological cross-sectional area (PCSA) for ecological questions. *Journal of Morphology*, **281**, 778–789.

Navalón, G., Bright, J. A., Marugán-Lobon, J., & Rayfield, E. J. (2018). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution*, **73**, 422–435.

Nuijens, F. W., & Zweers, G. A. (1997). Characters discriminating two seed husking mechanisms in finches (Fringillidae: Carduelinae) and estrildids (Passeridae: Estrildinae). *Journal of Morphology*, **232**, 1–33.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.

Pestoni, S., Degrange, F. J., Tambussi, C. P., Demmel Ferreira, M. M., & Tirao, G. A. (2018). Functional morphology of the cranio-mandibular complex of the Guira cuckoo (Aves). *Journal of Morphology*, **279**, 780–791.

R Development Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Sakamoto, M., Ruta, M., & Venditti, C. (2019). Extreme and rapid bursts of functional adaptations shape bite force in amniotes. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20181932.

Santana, S. E. (2018). Comparative anatomy of bat jaw musculature via diffusible iodine-based contrast-enhanced computed tomography. *Anatomical Record*, **301**, 267–278.

Sims, R. W. (1955). The morphology of the head of the hawfinch (*Coccothraustes coccothraustes*). *Bulletin of the Natural History Museum. Zoology*, **2**, 371–393.

Smith-Paredes, D., & Bhullar, B. A. (2019). The skull and head muscles of Archosauria. In J. M. Ziermann, R. E. Diaz Jr, & R. Diogo (Eds.), *Heads, jaws, and muscles* (pp. 229–251). Springer Nature.

Soons, J., Genbrugge, A., Podos, J., Adriaens, D., Aerts, P., Dirckx, J., & Herrel, A. (2015). Is beak morphology in Darwin's finches tune to loading demands? *PLoS One*, **10**(6), e0129479.

Soons, J., Herrel, A., Genbrugge, A., Adriaens, D., Aerts, P., & Dirckx, J. (2012). Multi-layered bird beaks: A finite-element approach towards the role of keratin in stress dissipation. *Journal of the Royal Society Interface*, **9**, 1787–1796.

Sustaita, D. (2008). Muscularskeletal underpinnings to differences in killing behavior between North American accipiters (Falconiformes: Accipitridae) and falcons (Falconidae). *Journal of Morphology*, **269**, 283–301.

Sustaita, D., & Hertel, F. (2013). In vivo bite and grip forces, morphology and prey-killing behaviour of North American accipiters (Accipitridae) and falcons (Falconidae). *Journal of Experimental Biology*, **213**, 2617–2628.

To, K. H. T., O'Brien, H. D., Stocker, M. R., & Gignac, P. M. (2021). Cranial musculoskeletal description of black-throated finch (Aves: Passeriformes: Estrildidae) with DiceCT. *Integrative Organismal Biology*, **3**, 1–11.

van der Meij, M. A. A., & Bout, R. G. (2004). Scaling of jaw muscle size and maximal bite force in finches. *Journal of Experimental Biology*, **207**, 2745–2753.

van der Meij, M. A. A., & Bout, R. G. (2006). Seed husking time and maximal bite force in finches. *Journal of Experimental Biology*, **209**, 3329–3335.

van der Meij, M. A. A., & Bout, R. G. (2008). The relationship between shape of the skull and bite force in finches. *Journal of Experimental Biology*, **211**, 1668–1680.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*, 4th ed. Springer.

Wang, H., Yan, J., & Zhang, Z. (2017). Sexual dimorphism in jaw muscles of the Japanese sparrowhawk (*Accipiter gularis*). *Anatomia Histologia and Embryologia*, **46**, 558–562.

Willson, M. F. (1971). Seed selection in some North American finches. *Condor*, **73**, 415–429.

Willson, M. F. (1972). Seed size preference in finches. *The Wilson Bulletin*, **84**, 449–455.

Witmer, L. M., & Rose, K. D. (1991). Biomechanics of the jaw apparatus of the gigantic Eocene bird *Diatryma*: implications for diet and mode of life. *Paleobiology*, **17**, 95–120.

Ziermann, J. M., Diaz, P. E. Jr, & Diogoi, R. (2019). *Heads, jaws, and muscles*. Springer Nature.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Prediction of exponent of scaling of moment arm ratios with body mass.

Data S1. Data on body mass, jaw muscle mass and bite force in birds used in the analysis.