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Effects of body mass and taxonomic order on the masses of functionally classified groups of the jaw musculature in birds

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Abstract There is increasing interest from evolutionary biologists in the evolution of avian bill shape, how the bill is used during feeding and, in particular, the bite forces the bill can deliver. Bite force exhibits isometry with the total mass of the jaw musculature, but there is variation in the functional categories of the jaw muscles in different avian taxa. Qualitative descriptions of the jaw musculature do not allow analysis of the relative contributions that adductor or retractor muscles play in generating a bite force. This study is a meta-analysis of published data for body mass and the mass of the jaw musculature in 66 bird species from 10 orders. The masses of the different muscles contributing to adduction and retraction in closing the jaw, and to depression and protraction in opening the jaw, were summed and allometric relationships explored before investigating the effects of taxonomic order on these relationships. The categories of muscles, and the masses of each category of jaw musculature varied among avian orders. Some species, such as the flightless ratites, had relatively small jaw muscle mass but parrots had an additional adductor muscle. Phylogenetically controlled relationships between body mass and the mass of each muscle category irrespective of taxonomic order were isometric. However, analysis of covariance revealed significant interactions between body mass and taxonomic order. Most orders had low values for body-mass-specific muscle masses in the jaw with the notable exceptions of the Passeriformes (songbirds) and Psittaciformes (parrots). The values of these orders were 3–4 times greater, although the relative amounts of muscles contributing to adduction and retraction were similar in Psittaciformes, but adduction was markedly higher in Passeriformes. The results of these analyses highlight the lack of species-specific data for most birds, which is adversely impacting our understanding of the anatomical features that are determining the functional properties of the bill during feeding.

Keywords: anatomy, jaw, adductor muscles, allometry, depressor muscles, protractor muscles, retractor muscles

Összefoglalás Az evolúcióbiológusok egyre nagyobb érdeklődést mutatnak a madárcsőr alakjának evolúciója, a csőr táplálkozás közbeni használata, és különösen a csőr által kifejtett harapási erő iránt. A harapás erőssége izometriát mutat ("pozitívan korrelál") az állkapocs teljes izomzatának tömegével, azonban eltérések vannak az állkapocs izmok funkcionális kategóriáit illetően az egyes madártaxonok között. Az állkapocs izmainak minőségbeli leírása nem teszi lehetővé a nyitó- és záróizmok elemzését a tekintetben, hogy mennyiben járulnak hozzá a harapás erejéhez. Jelen tanulmány egy metaanalízis a már publikált testtömeg és az állkapocs izomzat tömegének adataira vonatkozóan 10 rendből, 66 madárfaj esetében. Az állkapocs zárásához a közelítő és retractor, valamint az állkapocs nyitásához a lefelé húzó és protractor mozgásban résztvevő izmok tömegeit összegeztük és allometrikus összefüggéseket véltünk felfedezni mielőtt megvizsgáltuk volna a különböző csoportok ezen összefüggések-re gyakorolt hatásait. Az izomcsoportok és az izomcsoporthoz tartozó tömegek eltérnek a különböző madárcsoportok között. Egyes fajok, például a röpképtelen futómadarak relatív kicsi izomtömeggel rendelkeznek, ellenben a papagájok esetében egy további adduktor izom is megfigyelhető. A filogenetikailag kontrollált kapcsolatok a testtömegre és az egyes izomcsoportokra vonatkozóan rendtől függetlenül izometrikusak. Ennek ellenére a kovarianca elemzés szignifikáns kapcsolatot mutatott a rend és a testtömegadatok között. A legtöbb rend alacsony értékeket mutatott a testtömeg specifikus izomtömegre az állkapocsra vonatkozóan, ez alól kivételt csak a Passeriformes (verébalakúak) és a Psittaciformes (papagájalakúak) rendek képeztek. Ezeknek a rendeknek az esetében az értékek háromszor-négyszer nagyobbak, bár a relatív mennyisége a közelítés és visszahúzás során szerepet játszó izmoknak a Psittaciformes rendnél hasonló volt, de a közelítés tekintetében jelentősen nagyobb volt a Passeriformes rend esetében. Az elemzés eredményei rávilágítanak a fajspecifikus adatok hiányára a legtöbb madár esetében, amelyek hátrányosan befolyásolják azoknak az anatómiai jellemzőknek a megértését, amelyek meghatározzák a csőr funkcionális jellemzőit a táplálkozást illetően.

Kulcsszavak: anatómia, állkapocs, adduktor izmok, allometria, záróizmok, protraktor izmok, retractor izmok

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Introduction

Variation in bill morphology is a key aspect of feeding behaviour in birds with bill types being generally associated with the acquisition and manipulation of a particular food type. For example, competition among wading shorebirds (Charadriiformes) is often circumvented by different bill lengths and shapes that are specialised for feeding on different prey items (Ritchison 2023). Food acquisition and manipulation requires the bill to apply sufficient source to secure the food item and then to process it prior to swallowing; for example, for granivorous finches (Fringillidae, Passeriformes) typically de-husk seeds before swallowing the kernels (van der Meij & Bout 2006). Therefore, bite force is of increasing interest from evolutionary biologists because it helps to determine food selection and acquisition in birds and is important to their feeding behaviour and broader ecology (Herrel *et al.* 2005, van der Meij & Bout 2004, 2006, 2008, Sustaita & Hertel 2010, Corbin *et al.* 2015, Soons *et al.* 2015, Bright *et al.* 2016, 2019, Cooney *et al.* 2017, Navalón *et al.* 2019, Deeming *et al.* 2022).

A bite force is a consequence of the forces generated by the various jaw muscles being transmitted via the mechanical apparatus of the jaw (Bright *et al.* 2016). Deeming *et al.* (2022) reviewed patterns of bite force in birds and showed that, when controlling for phylogeny, there was a significant positive allometric relationship between total jaw muscle mass and bite force, despite considerable variation between taxa for any given body mass. Moreover, whilst bite force in birds varied with body mass, non-passerine species generated lower mass-specific bite forces compared with passerine species, which seemed to reflect smaller masses of jaw musculature, but this study was limited by the fact that it was based on a relatively small sample size of only 122 species from 14 different orders (Deeming *et al.* 2022).

The types of muscles observed in avian jaws can be categorised into four groups that are associated with closing or opening the bill (Burger 1978, Baumel *et al.* 2013, Bhattacharyya 2013). These are the adductors, which close the bill by raising the lower jaw, and the retractors, which close the bill by lowering the rostrum. Two other muscle categories are involved in opening the bill: the protractors elevate the upper jaw, and the depressors rotate the lower jaw around the quadrate bone. Many studies of the avian jaw musculature are descriptive (e.g. Burton 1974, Bhattacharyya 1994, Donatelli 2012, Quayle *et al.* 2014, Mahmoud *et al.* 2017). Different orders seem to vary in the categories of muscle present and in the levels of complexity of each muscle category (e.g. see Carril *et al.* 2015, Soons *et al.* 2015). For example, the adductor *musculus pseudotemporalis superficialis pars medialis* is present in some, but not all, New World Darwin's finches (Thraupidae; Passeriformes) and is one third of a subdivided *musculus pseudotemporalis* (Soons *et al.* 2015). By contrast, in the Old World Black-throated Finch (*Poephila cincta*, Estrildidae, Passeriformes) the *musculus pseudotemporalis* is subdivided into two (To *et al.* 2021). In *Phalacrocorax* cormorants (Phalacrocoracidae, Suliformes) the *musculus pseudotemporalis* is not subdivided (Burger 1978). Parrots (Psittaciformes) have an additional adductor, the *musculus ethmomandibularis*, which is rarely reported in other birds (Homberger 2003, 2017, Tokita 2003). Despite this variation, to date, there has been no analysis of the masses of the variety of jaw muscles in birds.

Bite force of birds can be measured directly (Carril *et al.* 2021), either determined from simulations using finite element analysis (Cost *et al.* 2020), or calculated from masses of the appropriate muscles (Sustaita 2008, Soons *et al.* 2015, Harrison 2023). Ultimately, the force of a bite is a function of the mass of jaw muscles that deliver the force to the jaw bones, yet birds seem to vary in the categories and amounts of jaw musculature (Sustaita 2008, Bhattacharyya 2013, Soons *et al.* 2015). For instance, the jaw can be closed by the action of both adductor and retractor muscles (Bhattacharyya 2013). The proportional difference in mass between these muscle groups may cause a relative difference in their bite force contribution (e.g. see Carril *et al.* 2015). Deeming *et al.* (2022) showed that the combined mass of the muscles used to close the jaw exhibited positive and negative allometric relationships with body mass for passerines and non-passerines, respectively. However, when the relationship between jaw muscle mass and bite force was modelled, there were no any notable differences between taxa; instead, there was an overall positive allometric relationship (Deeming *et al.* 2022). Deeming *et al.* (2022) suggested that perhaps the anatomical categories of the jaw musculature observed in birds might be involved in determining the magnitude of the bite force. Given the variation in bill morphology and size, and its association with food categories, the functional properties of the jaw musculature are increasingly of interest to evolutionary biologists (Bright *et al.* 2016, 2019, Navalón *et al.* 2019, Dickinson & Hartstone-Rose 2023).

This study is a meta-analysis of data collated from published reports to investigate the allometry of the relationships between body mass and the masses of each of the four jaw muscle categories. Although physiological cross-sectional area of muscle is an important determinant of force (Dickinson & Hartstone-Rose 2023), data for mass of muscles, which also strongly correlates with bite force (Deeming *et al.* 2022, Dickinson *et al.* 2022), were available for a wider range of taxa. The analysis tested the hypothesis that observations of taxonomic differences in jaw muscle morphology for birds translated into differences for their respective muscle masses. The analysis initially focussed on the allometry of each category of muscles irrespective of taxonomic order but progressed to investigate the prediction that taxonomy would be a significant factor in determining jaw muscle masses. The aim of the study was to determine whether avian jaw musculature is comparable among birds from different orders. Therefore, the masses of the adductor and retractor muscles were compared to test the prediction that there would be no difference in their relative roles in closing the jaw in different orders.

Methods

Data were collected from the peer-reviewed reports for the mass of the individual jaw muscles (mg) from one side of the jaw as described for a variety of bird species (Goodman & Fisher 1962, Burger 1978, Hull 1993, Gusseklo & Bout 2005, Sustaita 2008, pers. comm.

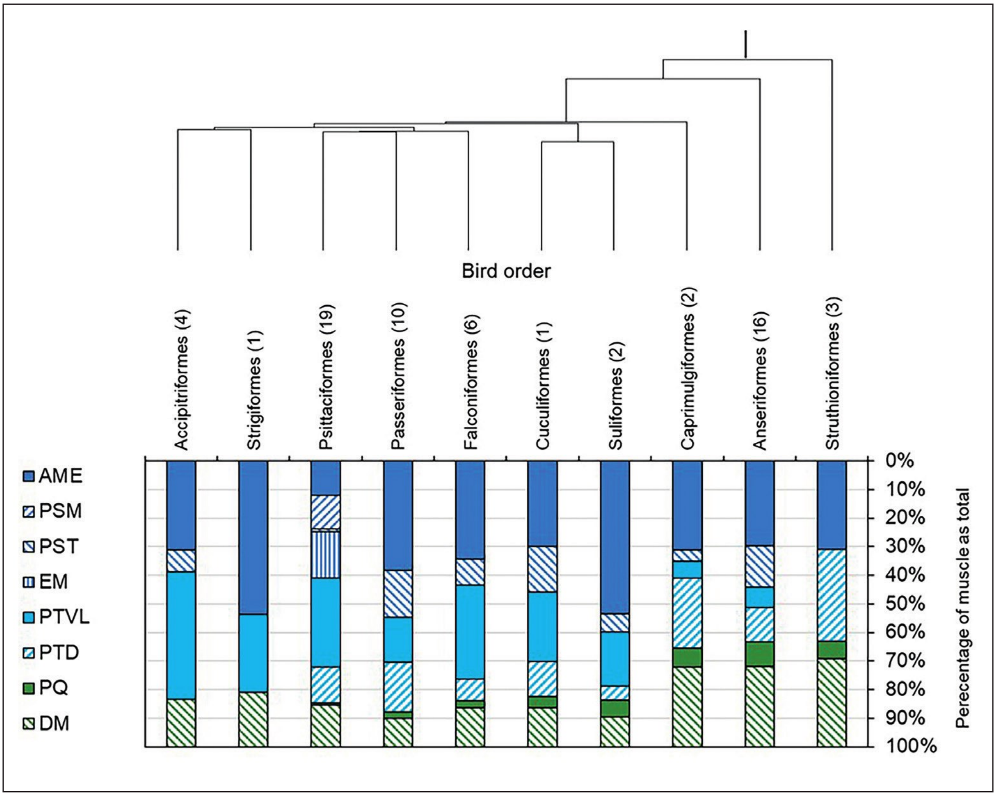

Figure 1. The percentage values of each muscle category associated with opening (green) or closing (blue) of the avian jaw expressed as a percentage of the total muscle mass. Adductors (dark blue): AME = *M. adductor mandibulae externus* complex; PSM = *M. pseudomasseter*; PST = *M. pseudotemporalis*; EM = *M. ethmomandibularis*; Retractors (light blue): PVTL = *M. pterygoideus ventralis*; PTD = *M. pterygoideus dorsalis*; Protractors (solid green): PQ = *M. protractor quadrati*. Depressors (hatched green): DM = *M. depressor mandibulae*. The degree of relatedness between the orders is shown by the phylogenetic tree was drawn up in birdtree.org using representatives of each order. The number of species represented in the order are shown in parentheses after the order name

1. ábra Az egyes izomkategóriákra vonatkozó értékek, amelyek az állkapocs nyitásában (zöld) és zárásában (kék) játszanak szerepet, százalékosan kifejezve a teljes állkapocs izomzat tömegéhez képest. Adduktorok (sötétkék): AME = *M. adductor mandibulae externus* complex; PSM = *M. pseudomasseter*; PST = *M. pseudotemporalis*; EM = *M. ethmomandibularis*; Retraktorok (világoskék): PVTL = *M. pterygoideus ventralis*; PTD = *M. pterygoideus dorsalis*; Protraktorok (középzöld): PQ = *M. protractor quadrati*. Depresszorok (sávozott zöld): DM = *M. depressor mandibulae*. Az egyes rendek közötti kapcsolat mértéke a birdtree.org által alkotott filogenetikai fán van feltüntetve. A rendhez tartozó fajok száma a rend mögött, zárójelben található

2021, Genbrugge *et al.* 2011, Carril *et al.* 2015, Soons *et al.* 2015, Demmel Ferreira *et al.* 2019, Pestoni *et al.* 2019, To *et al.* 2021, Harrison 2023). Mean body mass (g) for each species was derived from the original source or, if not measured, mean values reported by Dunning (2008) were used. In total, 66 species from 10 orders were represented in the dataset for jaw muscle masses (the number of species represented in each order is shown in *Figure 1*; see *Table 1* electronic supplementary materials). Not all muscle categories were present in all orders of birds; only 38 species sampled possessed protractor muscles.

Data were combined into the following four classifications of muscles according to their actions involved with opening or closing the jaw (Burger 1978, Bhattacharyya 2013). These were: (1) the adductors represented by the *m. adductor mandibulae externus* complex, *m. pseudotemporalis*, *m. pseudomasseter*, and, where present, *m. ethmomandibularis*; (2) The retractors represented by the *m. pterygoideus ventralis*, and *m. pterygoideus dorsalis*; (3) The protractors represented by the *m. protractor quadrati*; and (4) the depressors represented by the *m. depressor mandibulae*.

Where appropriate, data for mass were either $\log_{10}$-transformed (Fowler *et al.* 1995), or proportion data were logit-transformed (Warton & Hui 2011), prior to analysis. To account for non-independence of data points, a randomly generated phylogenetic tree of the 66 species in the dataset (see *Figure 1*, electronic supplementary materials) 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 (R Core Development Team 2021) using the packages *ape* (Paradis *et al.* 2004), *mvtnorm* (Genz & Bretz 2009) and *MASS* (Venables & Ripley 2002) as used by Deeming (2022). The models initially tested the effect of body mass on the mass of each muscle category. Further phylogenetically controlled analysis of covariance (run as a pglm) involved a reduced dataset in which orders were represented by more than two species and explored the effects of body mass as a covariate, and order as a categorical factor, on the mass of the four different muscle categories. Order

Table 1. Results of phylogenetically controlled analysis of covariance to test for the effect of order as a fixed factor and body mass as a covariate on the masses of the different categories of jaw muscles. Values are F-values with degrees of freedom in brackets and the p-value in parentheses. The coeficient of determination (R^2) and lambda (λ) value are included for each model

1. táblázat A kovariancia filogenetikailag ellenőrzött analízisének eredményei a rend, mint fix faktor és a testtömeg, mint kovariáns hatásának tesztelése a különböző állkapocs izom kategóriáinak tömegére. Az értékek F-értékek, zárójelben a szabadságfokokkal és a p-értékkel. A determinációs együttható (R^2) és a lambda (λ) értéke minden modellnél szerepel

Muscle category	LogBM	Order	Interaction	R²	λ
Adductor	559.47 [1,48] (< 0.0001)	23.61 [7,48] (< 0.0001)	4.06 [7,48] (0.0014)	0.940	<0.0001
Retractor	453.34 [1,48] (< 0.0001)	25.38 [7,48] (< 0.0001)	4.80 [7,48] (0.0004)	0.933	<0.0001
Depressor	957.34 [1,47] (< 0.0001)	17.18 [7,47] (< 0.0001)	4.05 [7,47] (0.0015)	0.959	<0.0001
Protractor	654.34 [1,25] (< 0.0001)	14.10 [4,25] (< 0.0001)	3.10 [4,25] (0.0336)	0.967	<0.0001

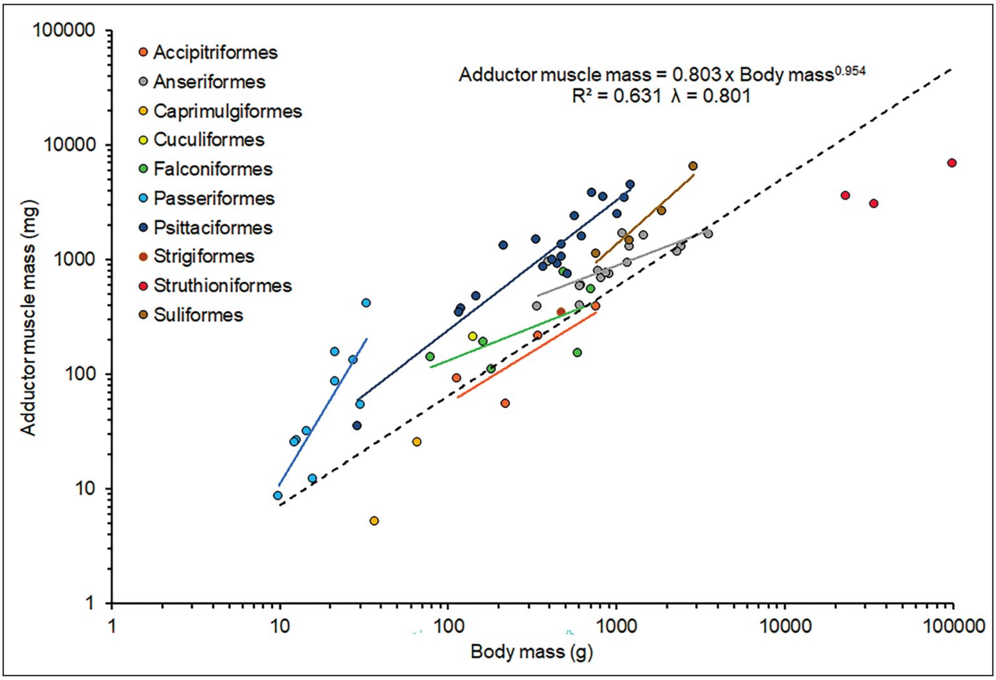

Figure 2. Relationship between body mass and the mass of the adductor muscles combined for a range of orders as indicated. Dashed line is the phylogenetically controlled relationship through all of the data points irrespective of order. Note the $\log_{10}$ scale on both axes. For slopes of coloured regression lines for each order (N > 3) see *Table 2.*

2. ábra A testtömeg és az adduktor izmok tömege közötti összefüggés az egyes rendekkel feltüntetve. A szaggatott vonal a filogenetikailag ellenőrzött kapcsolatot jelöli az összes adatponton, rendtől függetlenül. Az értékek mindkét tengelyen $\log_{10}$ skálán ábrázoltak. A színes regressziós egyenesek meredekségeihez tartozó értékek az egyes rendek esetében (N > 3) a 2. táblázatban találhatóak

was used as a factor here to explore differences between higher taxonomic groups but the analysis still had to be phylogenetically controlled because of the variation in body mass for the species represented in each of the orders, which could bias any relationship within an order. All models incorporated phylogeny as a random effect to deal with non-independence at the within-species level. Additional analysis explored the departure from isometry (slope = 1.0) by relationships between body mass and muscle masses within an order, where at least three species were represented. Comparison of slopes of all regression lines was performed using one-sample t-tests against an expected isometric slope of 1.0 (Bailey 1981). The phylogenetic signal (lambda, λ) was calculated by the analysis. A lambda value of 0 represented no evolutionary signal (no covariance in the residuals due to shared ancestry), and of 1 indicated that the observed covariance in residuals was expected under a Brownian motion model of trait evolution (Freckleton *et al.* 2002).

To compare patterns in the proportions of the adductor and retractor muscle masses, analysis of repeated samples from the same species involved phylogenetic mixed models (PMMs) using the MCMCglmm package (Hadfield 2010) as used by Deeming (2022).

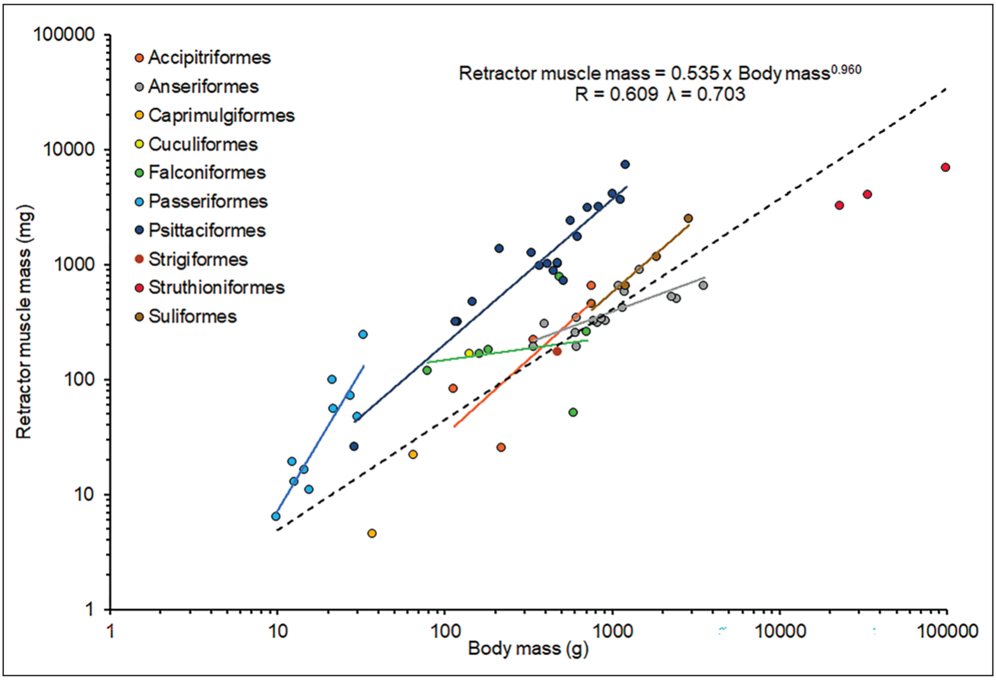

Figure 3. Relationship between body mass and the mass of the retractor muscles combined for a range of orders as indicated. Dashed line is the phylogenetically controlled relationship through all of the data points irrespective of order. Note the $\log_{10}$ scale on both axes. For slopes of coloured regression lines for each order (N > 3) see *Table 2.*

3. ábra A testtömeg és a retraktor izmok tömege közötti összefüggés az egyes rendekkel feltüntetve. A szaggatott vonal a filogenetikailag ellenőrzött kapcsolatot jelöli az összes adatponton, rendtől függetlenül. Az értékek mindkét tengelyen $\log_{10}$ skálán ábrázoltak. A színes regressziós egyenesek meredekségeihez tartozó értékek az egyes rendek esetében (N > 3) a 2. táblázatban találhatóak

This analysis included a phylogenetic covariance matrix, with species retained as a second random effect within the models (random = ~animal). The analysis ran 500,000 iterations for the MCMC models, with sampling taking place every 500 iterations after a burn-in of 10,000. Lambda (λ) was calculated by dividing the variance explained by the phylogeny by the sum of all variance components.

Results

Data on all muscle groups were not available in all orders; for instance, the *m. ethmomandibularis* and *m. pseudomasseter* were observed only in the Psittaciformes (parrots), and the *m. pseudotemporalis* was not reported in the one owl (Strigiformes) species in the dataset *(Figure 1)*. The *m. protractor quadrati* was not observed in the Accipitriformes (hawks and allies) or Strigiformes reported to date but formed almost 40% of the mass of muscles opening the jaw in Suliformes (cormorants; *Figure 1*). The proportions of the

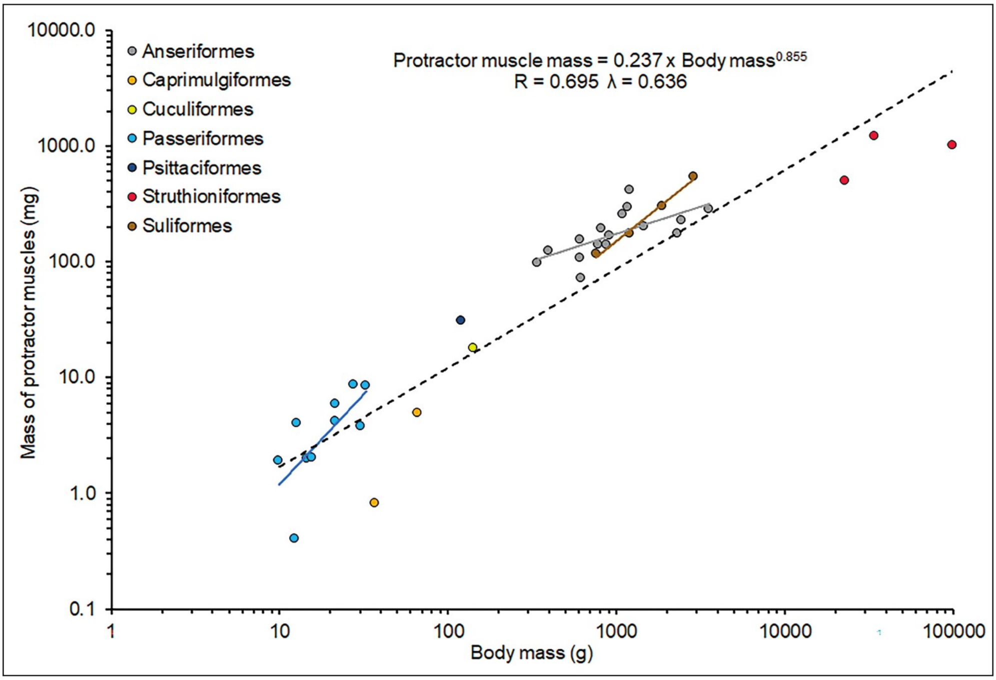

Figure 4. Relationship between body mass and the mass of the protractor muscles combined for a range of orders as indicated. Dashed line is the phylogenetically controlled relationship through all of the data points irrespective of order. Note the $\log_{10}$ scale on both axes. For slopes of coloured regression lines for each order (N > 3) see *Table 2.*

4. ábra A testtömeg és a protraktor izmok tömege közötti összefüggés az egyes rendekkel feltüntetve. A szaggatott vonal a filogenetikailag ellenőrzött kapcsolatot jelöli az összes adatponton, rendtől függetlenül. Az értékek mindkét tengelyen $\log_{10}$ skálán ábrázoltak. A színes regressziós egyenesek meredekségeihez tartozó értékek az egyes rendek esetében (N > 3) a 2. táblázatban találhatóak

individual muscle groups varied between orders and the proportions of the muscle ascribed to the four muscle categories also varied between orders *(Figure 1)*.

There were positive relationships between body mass and the masses of the combined adductor *(Figure 2)*, retractor *(Figure 3)*, protractor *(Figure 4)*, and depressor muscles *(Figure 5)*, for individual species. All of these relationships exhibited isometry when the slopes of the lines were compared against a slope of 1.0 (t_{65} = -0.496, p = 0.621; t_{65} = -0.405, p = 0.687; t_{36} = -1.517 p = 0.138; and t_{64} = -0.468, = 0.641, for the four muscle categories, respectively). The coefficient of determination values (R^2) ranged between 0.600 and 0.720 and the λ-values ranged between 0.63–0.80 for each of the relationships *(Figures 2–5)*.

A phylogenetically controlled analysis of covariance (pANCOVA) revealed a significant interaction between body mass and order that had a very low lambda value and a very high coefficient of determination *(Table 1)*. This pattern was repeated for the pANCOVA analysis for the other three muscle categories *(Figures 2–5, Table 1)*. Within individual orders of birds, the scaling relationship between body mass and jaw muscle mass was isometric in some cases, but not in others. In the Anseriformes (waterfowl), all muscle masses scaled with exponents

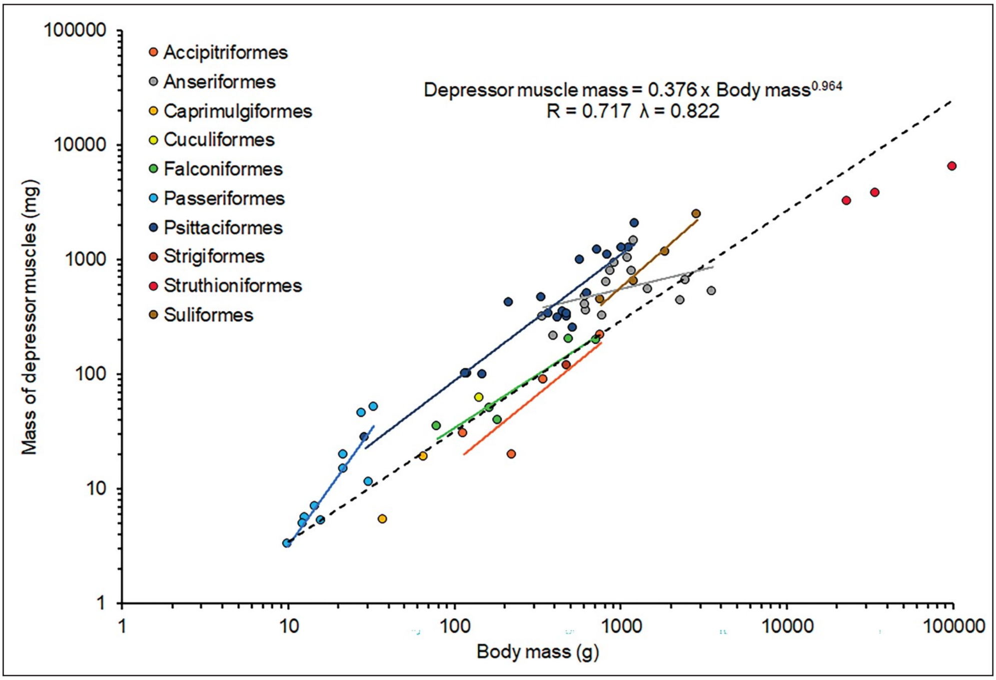

Figure 5. Relationship between body mass and the mass of the depressor muscles combined for a range of orders as indicated. Dashed line is the phylogenetically controlled relationship through all of the data points irrespective of order. Note the $\log_{10}$ scale on both axes. For slopes of coloured regression lines for each order (N > 3) see *Table 2.*

5. ábra A testtömeg és a depresszor izmok tömege közötti összefüggés az egyes rendekkel feltüntetve. A szaggatott vonal a filogenetikailag ellenőrzött kapcsolatot jelöli az összes adatponton, rendtől függetlenül. Az értékek mindkét tengelyen $\log_{10}$ skálán ábrázoltak. A színes regressziós egyenesek meredekségeihez tartozó értékek az egyes rendek esetében (N > 3) a 2. táblázatban találhatóak

significantly less than isometry would predict, with muscle groups having masses that scaled negatively allometrically *(Figures 2–5, Table 2)*. A similar negative allometric relationship was observed for retractors in the Struthioniformes (ratites; *Figures 2–5, Table 2*). These exponents reflected that neither waterfowl nor ratites are famous for their powerful bites. By contrast, the Passeriformes (perching birds), which were represented by strong biters, had significantly positively allometric relationships between the body mass and the masses of the adductors and retractors *(Figures 2–5, Table 2)*. Similarly, the retractors of Psittaciformes had an exponent that was significantly positively allometric *(Table 2)*. Other orders, such as the Accipitriformes (hawks/eagles), Suliformes, and Falconiformes (falcons) had exponents for adductors and retractors that were not significantly different from isometry *(Table 2)*.

When adductors and retractors were expressed as a proportion of the total muscle mass that close the jaw, the Struthioniformes, Caprimulgiformes (nightjars), Psittaciformes and Accipitriformes had similar proportions, but most orders had a greater proportion of adductor muscles, especially the Suliformes and Anseriformes *(Figure 6)*. After the single representatives of the Cuculiformes (cuckoos) and Strigiformes were removed from the

Table 2. Slopes (SE in parentheses) of phylogenetically controlled regression lines for $\log_{10}$-transformed values for muscle mass versus body mass for the four muscle categories for orders of birds where N > 3. Values in square brackets are t-values, degree of freedom, and p-value for each slope as tested against an isometric slope of 1.0 using a one-sampled t-test (Bailey 1981). Values in bold exhibit significant departure from isometry. A dash (-) indicates that this muscle category was not recorded in the order

2. táblázat A filogenetikailag ellenőrzött regressziós egyenesek meredeksége (zárójelben SE) az izomtömeg és a testtömeg $\log_{10}$-transzformált értékeihez képest a négy állkapocs izom kategória esetében az egyes madárrendeknél, ahol N > 3. A szögletes zárójelben szereplő értékek t-értékek, szabadságfokok és p-értékek minden meredekségre, 1,0 izometrikus meredekséggel szemben, egymintás t-próbával (Bailey 1981). A vastagon szedett értékek jelentős eltérést mutatnak az izometriától. A vízszintes vonal (-) azt jelzi, hogy ez az izomkategória nem volt elérhető az adott rendnél

	Adductors	**Retractors**	**Protractors**	**Depressors**
Accipitriformes	0.903 (0.441) [2.04, 3, 0.064]	1.313 (0.802) [1.63, 3, 0.103]	–	**1.177 (0.476)** **[2.47, 3, 0.040]**
Anseriformes	0.561 (0.127) [-3.46, 15, 0.004]	0.537 (0.116) [-3.99, 15, 0.001]	0.470 (0.140) [-3.77, 15, 0.002]	0.345 (0.186) [-3.51, 15, 0.003]
Falconiformes	0.839 (0.287) [-0.56, 5, 0.599]	0.612 (0.314) [-1.27, 5, 0.271]	–	0.932 (0.186) [-0.37, 4, 0.732]
Passeriformes	2.551 (0.273) [5.68, 9, <0.001]	2.438 (0.438) **[3.29, 9, 0.008]**	1.557 (0.541) [1.03, 9, 0.222]	**2.091 (0.278)** **[3.93, 9, 0.003]**
Psittaciformes	1.208 (0.110) [1.88, 18, 0.071]	**1.333 (0.117)** **[2.86, 18, 0.011]**	–	1.165 (0.100) [1.64, 18, 0.104]
Suliformes	1.313 (0.241) [1.30, 3, 0.151]	1.273 (0.149) [1.83, 3, 0.082]	1.163 (0.081) [2.02, 3, 0.066]	**1.308 (0.039)** **[7.99, 3, 0.001]**

dataset, phylogenetically controlled analysis showed that order had a significant effect on the logit-transformed proportions of the adductor muscles as part of the total muscle mass that close the jaw ($F_{7,56} = 6.26$, $p < 0.0001$).

When the mass of the adductor muscles was expressed relative to body mass, most of the orders had values of around 1 mg/g or less *(Figure 7)*. The two exceptions were the Passeriformes, which had almost 60% more adductor muscle than retractor muscle (3.8 versus 2.4 mg/g, respectively), and the Psittaciformes, in which the adductor and retractor muscles were of similar but comparatively higher relative masses (3.1 versus 3.2 mg/g, respectively). Phylogenetically controlled one-way ANOVA showed that there was a significant effect of order on log-transformed data for adductor muscle mass as a proportion of body mass ($F_{7,56} = 23.53$, $p < 0.0001$).

Discussion

The masses of the four functional categories of the jaw muscles of birds varied among avian orders. When order was not considered, the relationships between mass of the various muscle categories and body mass were isometric. When order was considered, it had a significant effect on the relationships between muscle masses and body mass with orders exhibiting

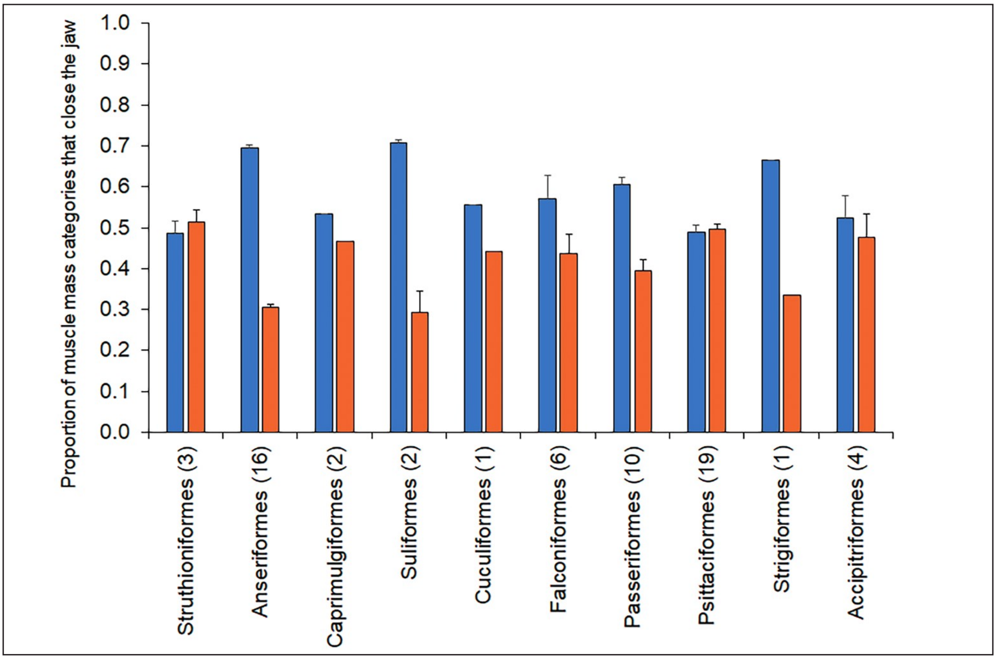

Figure 6. Mean (+SE) values for the mass of the combined adductor (blue bars) and retractor (orange bars) muscles for ten orders of birds expressed as a proportion of the total of the muscles used to close the jaw. Values in parentheses indicate the number of species represented in that order

6. ábra A testtömeg és az együttes adduktor (kék sávok) és retraktor (narancs sávok) izmok átlagértékei (+SE) a tíz madárrend esetében, az állkapocs zárásában szerepet játszó izmok összességének arányában kifejezve. A rendhez tartozó fajok száma a rend mögött, zárójelben található

significant positive or negative allometry relative to body mass. For this sample of data these relationships could be misleading because there was significant interaction between order and body mass for all four muscle categories. Most orders had low values for body mass-specific muscle mass for jaw closing with the notable exceptions of the Passeriformes and the Psittaciformes, which exhibited different patterns for the proportions of the adductor and retractor muscles.

Deeming *et al.* (2022) found that there was a significant difference between passerines and non-passerines in the allometry of jaw musculature (all muscles combined) and body mass. In the present study, for all four muscle categories, muscle mass was isometric with body mass, but the effect of order was very clear, which explains the result for all muscles combined. Deeming *et al.* (2022) had a small sample of species and this has been reduced further here because some studies report only combined values for jaw musculature rather than masses of the individual muscles. Phylogenetic relatedness influenced the isometric relationships between muscle mass and body mass, but as would be expected this effect was lost when order was included in the model. This suggests that there the high evolutionary signal reflects the higher taxonomic level rather than at the differences between individual species. This implies that when bill shape is conserved within an order (e.g. in waterfowl; Olsen 2017) this is also probably reflected in the underlying musculature.

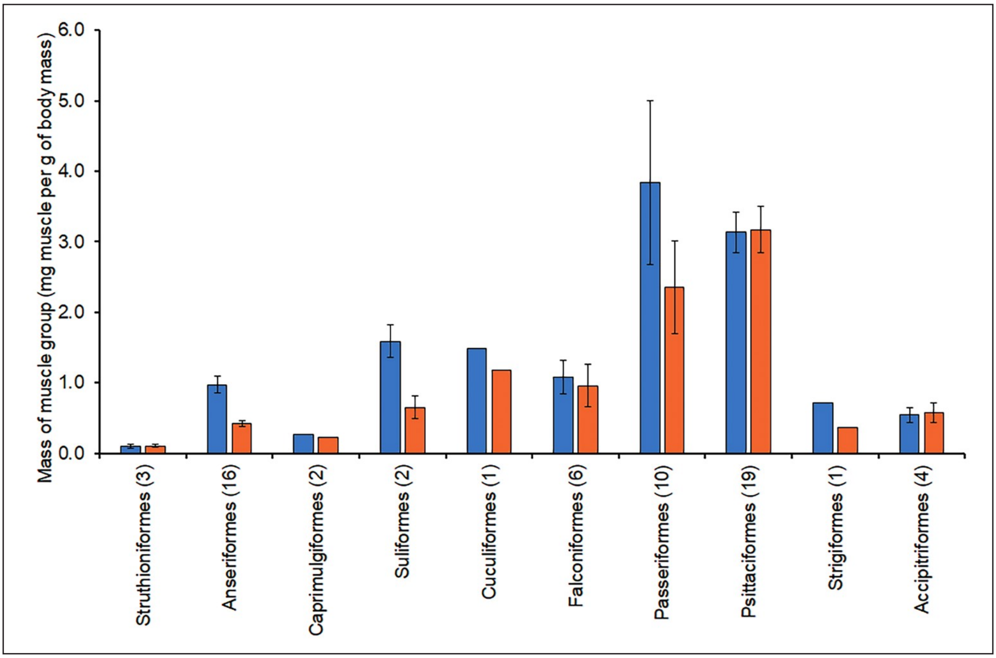

Figure 7. Mean (+SE) values for the mass of the combined adductor (blue bars) and retractor (orange bars) muscles for ten orders of birds expressed relative to the body mass of the birds (mg/g) Values in parentheses indicate the number of species represented in that order

7. ábra A testtömeg és az együttes adduktor (kék sávok) és retraktor (narancs sávok) izmok átlagértékei (+SE) a tíz madárrend esetében, a madarak testtömegéhez viszonyítva (mg/g). A rendhez tartozó fajok száma a rend mögött, zárójelben található

Although some muscle categories (e.g. the *m. adductor mandibulae externus* complex) were present in most species, there were muscle categories (e.g. the *m. pseudotemporalis*) that were absent from a few species. It was interesting that parrots have the *m. ethmomandibularis*, which seems to be a characteristic feature of parrot jaw musculature (Homberger 2003, 2017, Tokita 2003, Carril *et al.* 2015), which generates high bite forces (Cost *et al.* 2020, Pecsics *et al.* 2020, Dickinson *et al.* 2022, Harrison 2023). However, Sims (1955) also observed, but did not quantify, a *m. ethmomandibularis* in the hawfinch (*Coccothraustes coccothraustes*; Fringillidae, Passeriformes). van der Meij and Bout (2004) reported a high total jaw muscle mass for the hawfinch but did not report a bite force. The closely related Yellow-billed Grosbeak *(Eophona migratoria)* had a similar body mass and jaw muscle mass to the hawfinch and had a comparable bite force (van der Meij & Bout 2004). Given these similarities, it would be interesting to investigate whether grosbeaks also have a *m. ethmomandibularis* and the role that it plays in delivering a bite force.

The *m. pseudomasseter* seemed to be a characteristic of cockatoos (Cacatuidae) but it was not found in other parrots (Homberger 2003, 2017, Tokita 2003, Harrison 2023) or other avian taxa. It is unclear whether the development of additional muscles in parrots is a means by which their high bite forces can be generated (Cost *et al.* 2020, Dickinson *et al.* 2022, Harrison 2023), or whether this reflects how bite force can be applied by different parts of the bill as the jaw is closed. In parrots, the presence of relatively large adductor and retractor muscles suggests that the action of the jaw during feeding may require more of a balance between adduction and retraction than was observed in passerines in which, adductors were much larger. The passerines featured in the analysis reported here were mainly Darwin's finches (Thraupidae), which have very strong bite forces for their body mass (Soons *et al.* 2015). The presence of the *m. ethmomandibularis* in hawfinches (Sims 1950) suggests that some other finch species also rely more on adduction during feeding. It is unlikely that other passerine species that are less reliant on hard seeds would require larger adductor muscles, but further quantitative analysis of jaw masses in a wider range of passerine species is required to test these ideas.

It could be argued that the approach used here of treating all bellies of a muscle complex as one functional unit, is anatomically or physiologically inappropriate. However, the tendons of many jaw muscles do not originate and insert directly on bone but rather they have one end of their fibres attached to the 'tendinous' epimysium of another element of the muscle complex that may then attach to a bone. Therefore, any contraction of a part of a muscle complex will impact on the adjacent parts of the same complex and a contraction consequently has one action on the skeleton. Although muscle force was inversely related to muscle fibre length it is possible that greater forces can be delivered by having smaller bellies of jaw muscles (Deeming *et al.* 2022). However, the fine detail of how force is delivered as the jaws close is unclear from existing studies of avian jaw musculature.

Variation in the jaw musculature among birds is reflected in both skull morphology and bill shape, and all these morphological elements will influence the diet on which a bird will feed. Those passerines studied to date are characterised by their granivorous or other durophagous diets, which seem to necessitate strong bite forces delivered by robust bills (van der Meij & Bout 2004, 2006, 2008, Herrel *et al.* 2005, Soons *et al.* 2015). Other bird species that deal with food items that require less manipulation before ingestion, for instance herbivorous ratites, which feed primarily by grasping vegetation and pulling at it rather than shearing off leaves, have relatively less jaw musculature and so deliver a low bite force for their mass (Gusseklo & Bout 2005). This is also apparent in carnivorous birds of prey that often kill their prey using their talons and use the bill to tear off pieces of the carcass rather than applying a force to crush the food (Sustaita 2008, Sustaita & Hertel 2010) or, in the case of owls, swallow the prey whole (Shawyer 1994). Although falcons often rely on their bite to kill prey captured by their talons in flight, there was no obvious difference in the proportions of adductor and retractor muscles compared with the hawk species as observed in the study by Sustaita and Hertel (2010). Herbivory or carnivory may not, therefore, require a particularly strong bite force (Gusseklo & Bout 2005, Sustaita & Hertel 2010), but more research is needed on a wide range of species. It is clear, however, that mass of the jaw musculature is not a simple function of body size in birds.

The link between predominant feeding behaviour and jaw morphology is demonstrated in the Komodo Dragon *(Varanus komodoensis)*. This large lizard has a relatively weak bite force for its skull size, and the skull itself is not sufficiently strong to withstand an equivalent bite force that could be delivered by a Saltwater Crocodile *(Crocodylus porosus)* that has a similar skull size (Fry *et al.* 2009). The Komodo Dragon effectively has come to rely on a venomous bite to quell or kill prey rather than a direct killing bite and relies on strong neck muscles to tear muscle from a carcass (Fry *et al.* 2009). As interest in functional jaw morphology grows (Bright *et al.* 2016, 2019, Navalón *et al.* 2019, Dickinson & Hartstone-Rose 2022) then the interactions between muscle anatomy and size, skull, and bill morphology in the delivery of bite force will presumably of greater interest and stimulate research into a wider range of bird species that exhibit greater variety of feeding modalities.

Differing patterns of feeding behaviour and processing of food items by the bill and tongue in birds have not been fully explored in terms of the underlying musculature that delivers a bite force or serves to manipulate the food in the bill. This study shows that the jaw musculature varied between the limited sample of bird species from which data are available. Variation in bill morphology in relation to feeding is almost certainly reflected in the underlying musculature. More research of jaw musculature and architecture is needed in a wider range of feeding modalities to allow development of a better understanding of how bite forces are delivered in different bird species and how this might affect bite forces.

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