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Scaling of jaw muscle size and maximal bite force in finches

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Summary

Fringillids and estrildids differ in their husking performance on hard closed-shelled seeds, which are cracked before they are eaten. The time required to husk a seed is directly related to seed hardness, and husking time is therefore expected to be related to bite force as well. We investigated whether there is a significant difference in jaw muscle mass and maximal bite force between fringillids and estrildids. The analysis shows that fringillids have relatively larger jaw muscles than estrildids and are able to produce higher bite forces than estrildids of the same body size. This difference in jaw muscle mass mainly results from a difference in jaw closing muscles. Compared with other birds, the jaw muscles of both fringillids and estrildids scale strongly positively allometric with body size. Muscle fibre length scales negatively allometric with body size, which results in relatively high muscle and bite forces. Comparison with the scarce data available for other trophic groups suggests that the scaling of jaw muscle size depends on diet and that jaw muscle size in finches is an adaptation to their feeding behaviour.

Key words: bite force, muscle, allometry, finch, fringillid, estrildid, seed, husking.

Introduction

‘Prey’ size tends to be directly proportional to the size of the ‘predator’, and larger predators take prey of wider diversity and a wider range of sizes (Wheelwright, 1985). This applies to a wide variety of animals, including granivorous birds. Large species tend to take larger food items than small species (Morris, 1955; Hespenheide, 1966; Wilson, 1971) and are able to husk large seeds faster than small species (Grant et al., 1976). Measurements of seed handling efficiency in sparrows show that large sparrows are more efficient with large seeds than are small sparrows (Pulliam, 1985). As seed size is correlated with seed hardness (Abbott et al., 1977; Van der Meij and Bout, 2000) and bite force is expected to increase with body size, these findings suggest a direct relationship between husking performance (time necessary to crack and dehusk seeds) and bite force. Direct evidence for the relationships between body size, husking performance and maximal bite force in granivorous birds is scarce. Husking performance increases in finches with a decrease in seed hardness (Van der Meij et al., in press). This suggests that with an increase in maximal bite force relative to seed hardness, husking performance will increase.

Although body size may play an important role in establishing differences in husking performance and therefore in occupying different trophic niches (Björklund and Merilä, 1993), family-specific differences in seed handling efficiency have been reported. Cardueline finches are much more efficient at handling large seeds than are emberizine sparrows, which may be related to a difference in jaw muscle mass (Benkman and Pulliam, 1988). The jaw muscles of oscines are described in several studies (Fiedler, 1951; Beecher, 1953; Classen, 1989; Nuijens and Zweers, 1997). Nuijens and Zweers (1997) suggested that there are differences in relative jaw muscle weight between estrildids and fringillids, which belong to two separate families. These two groups of finches differ in their ability to crack seeds efficiently: fringillids crack closed-shelled seeds faster than estrildids (R. G. Bout, R. Verbeek and F. W. Nuijens, manuscript submitted). The diet of fringillids consists of a wide range of seeds, including many closed-shelled dicotyledonous species (e.g. Compositae; Newton, 1967, 1972). Many estrildids feed mainly on small, soft (monocotyledonous) grass seeds (Read, 1994; Zann, 1996; Dostine et al., 2001). Some estrildid species (e.g. *Erythrura*, *Spermophaga poliogenys*), however, feed on a wide range of dicotyledonous seeds (Clement et al., 1993). This difference in diet suggests that fringillids are able to take seeds of a wider range of hardness and are able to produce higher bite forces than estrildids. One of the few attempts to measure bite force in birds directly was made by Lederer (1975). Recently, A. Herrel (personal communication) measured maximal bite forces in Galapagos finches.

The present study will try to establish the relationship between body size, jaw muscle mass and maximal bite force in two groups of finches: the estrildids and the fringillids. We will investigate whether there are significant differences in jaw muscle size and bite force between estrildids and fringillids of the same body size. Furthermore, the scaling of muscle fibre length relative to body mass is studied to investigate how muscle mass is related to muscle force (physiological cross section).

Materials and methods

Jaw muscle mass

The mass and bite force of the jaw muscles were determined in 36 species of granivorous birds: 16 species out of the family Fringillidae and 20 out of the family Estrildidae (Table 1; taxonomical names of the species follow Sibley and Monroe, 1990, 1993). For each species, one individual was used. The birds were commercially purchased and kept in separate cages (40×38×38 cm) for at least three weeks. After this period, the birds were injected with an overdose of the anaesthetic Nembutal (Sanofi Sante BV, Maassluis, The Netherlands) and dissected. Cranium length (distance between frontal nasal hinge and occiput) and bill/beak length (rictus to tip) were measured with digital callipers (Sylvac, Crissier, Switzerland). Body mass was measured with a digital balance (U3600P; Sartorius, Göttingen, Germany) twice, once at the moment the birds were purchased and the second time when the birds were sacrificed. This was done to monitor unexpected weight loss indicating sick birds. A few species were obtained freshly killed or died shortly after purchase and were only weighed once. For these birds, only muscle mass is available but no bite force data.

The nomenclature of the muscles follows Vanden Berge and Zweers (1993). Five groups of muscles were distinguished: (1) the openers of the lower jaw, musculus depressor mandibulae;

Table 1. *Body mass, total jaw muscle mass and maximal bite force at the tip of the bill*

Species	Common name	Body mass (g)	Bite force (N)	Jaw muscle mass (mg)
Estrildidae				
Amadina erythrocephala	Red-headed finch	22.7	4.0	267.2
Amadina fasciata	Cut-throat finch	18.5	5.2	183.2
Chloebia gouldia	Gouldian finch	15.2	4.1	118.6
Erythrura trichroa	Blue-faced parrotfinch	13.1	5.3	156.8
Estrilda troglodytes	Black-rumped waxbill	7.4	1.1	77.6
Hypargos niveoguttatus	Peter’s twinspot	16.1	3.1	176.8
Lagonosticta senegala	Red-billed firefinch	6.9	1.2	42.8
Lonchura fringilloides	Magpie munia	16.2	5.0	186.4
Lonchura pallida	Pale-headed munia	13.2	3.3	178.6
Lonchura punctulata	Scaly-breasted munia	12.4	3.7	129.4
Neochima modesta	Plum-headed finch	13.2	2.0	89.4
Neochmia ruficauda	Star finch	12.0	2.1	76.8
Padda oryzivora	Java sparrow	30.4	9.6	431.0
Phoephila acuticauda	Longtailed finch	18.3	2.6	141.6
Taeniopygia bichenovi	Double-barred finch	9.7	1.9	99.0
Poephila cincta	Black-throated finch	15.7	2.5	136.6
Pyrenestes sanguines	Crimson seedcracker	18.0	–	335.4
Pytilia hypogrammica	Red-faced pytilia	15.3	3.1	67.2
Taenopygia guttata	Zebra finch	22.7	3.9	176.8
Uraeginthus bengalus	Red-cheeked cordonblue	10.0	1.3	91.0
Fringillidae				
Carduelis chloris	European greenfinch	28.3	13.6	587.0
Carduelis flammea	Common redpoll	12.6	2.9	128.3
Carduelis sinica	Grey-capped greenfinch	20.0	8.1	248.4
Carduelis spinus	Eurasian siskin	13.0	3.1	174.8
Carpodacus erythrinus	Common rosefinch	21.6	6.3	310.0
Coccothraustes coccothraustes	Hawfinch	54.4	–	1454.0
Eophona migratoria	Yellow-billed grosbeak	52.0	36.1	1416.4
Fringilla coelebs	Chaffinch	19.9	–	256.0
Fringilla montifringilla	Brambling	17.0	–	278.6
Loxia curvirostra	Red crossbill	44.0	–	740.0
Mycerobas affinis	Colared grosbeak	70.0	38.4	1241.6
Pyrrhula pyrrhula	Eurasian bullfinch	20.9	4.9	284.4
Rhodopechys obsoleta	Desert finch	22.5	6.4	275.0
Serinus leucopygius	White-rumped seedeater	9.5	2.1	135.4
Serinus mozambicus	Yellow-fronted canary	12.0	2.9	175.4
Serinus sulphuratus	Brimstone canary	18.2	11.8	419.0

Table 2. *Jaw muscle mass and body mass for bird species from different families and with a wide range of body sizes*

Family	Species	Body mass (g)	Jaw muscle mass (mg)
Rheidae	*Rhea americana**	12500.0	19800.0
Anatidae	*Anas plathyrhynchos*	997.9	7176.0
Psittacidae	*Poicephalus senegalus*	148.5	4133.8
Columbidae	*Columbia livia*	537.0	1820.8
Rallidae	*Fulica atra*	450.1	1483.0
Charadriidae	*Calidris canutus*	130.9	359.4
Laridae	*Larus argentatus*	415.9	4364.8
Laridae	*Larus ridibundus*	189.1	2185.6
Paridae	*Parus major*	15.2	115.2
Passeridae	*Passer luteus*	12.7	172.2
Ploceidae	*Euplectus hordeacea*	19.3	268.2
Emberizidae	*Emberiza elegans*	16.9	90.0

*Gussekloo (2000).

(2) the closers of the lower jaw, musculus adductor mandibulae externus and musculus pseudotemporalis superficialis; (3) the openers of the upper jaw, musculus protractor pterygoidei et quadrati; (4) the closers of the upper and lower jaw, musculus pseudotemporalis profundus and musculus adductor mandibulae ossis quadrati and (5) the closers of the upper and lower jaw, musculus pterygoideus, including the musculus retractor palatini. After dissection of the muscle groups, the mass of each group was measured with a digital balance (H51; Sartorius).

To allow a first comparison between the data for the fringillids and estrildids and the scaling of jaw muscles mass within the class Aves as a whole, we also measured the jaw muscle mass of 12 bird species with body mass ranging from 12 to 12 000 g (Table 2). Furthermore, we used data from three studies that reported jaw muscle mass and body mass. Scaling exponents were calculated for the data from seven *Serinus* species (Classen, 1989), four cormorant species (Burger, 1978) and 14 anseriform species (Goodman and Fisher, 1962).

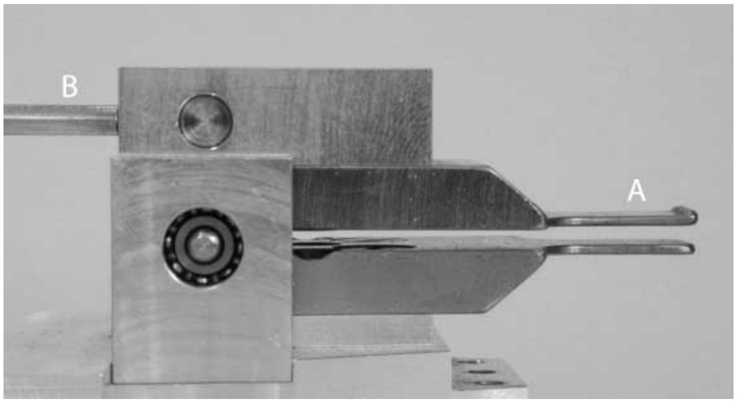

Fig. 1. Tool for bite force measurements. A: rigid metal plates that are slightly pressed together by the bills of a bird biting on the plates (notice the rounded ridge to prevent pressure of the rest of the bill). B: connection to the force transducer.

An expected value for the scaling of jaw muscle mass with body mass may be derived from the scaling of other head structures. Therefore, we used data of the head mass of eight anseriforms (Van der Leeuw, 2002) and compared the scaling of jaw muscle mass to eye (Brooke et al., 1999) and brain mass in birds (Schmidt-Nielsen, 1984).

Muscle fibre length

Muscle force is expected to scale with cross-sectional area of muscles. To evaluate the relationship between muscle mass and muscle force, the scaling of muscle fibre length with body size should be known. To determine scaling of muscle fibre length, the musculus adductor mandibulae externus from 10 Fringillidae species was preserved in alcohol. This muscle complex was chosen because it is the main jaw closer. Although there are differences in fibre length between the different jaw muscle groups (M. A. A. Van der Meij, unpublished data), the scaling of adductor fibre length is believed to be indicative for all muscle groups.

To obtain the fibre length, we used the protocol described by Herrel (1998). The collagen between the muscle fibres was gradually dissolved in nitric acid (31% HNO_3) for about 24 h and then the tissue was immersed in a 50% glycerol solution. Muscle fibres were selected at random from the dissected muscle, carefully teased from the tissue and their length measured under a Nikon microscope.

Bite force measurements

To measure the maximal bite force of the finches we used a force transducer (9000 series; Aikoh, Osaka, Japan) mounted with two flat metal plates (Fig. 1). Biting causes the upper plate to pivot around a fulcrum and to exert force on the force transducer. The birds were held by hand and trained to bite the metal plates. Most birds only used their beak tips to bite the force transducer and refused to bite at more caudal positions within the beak. The rounded ridge of the plates limited the biting area to a specific part of the beak and prevented pressure from the rest of the bill. The force transducer was set to register the peak force, which was read from the display. Before the experiments, the force transducer was calibrated by applying known forces to the plates. The accuracy of the force transducer is 0.1 N, while the measuring range of the force transducer was between 0 and 50 N. Bite force measurements were performed several times in a row on each occasion and on at least five different days to determine the maximum bite force at the tip of the bill. The maximal bite force for a bird is the highest value measured, but in all cases at least two other bite forces were recorded that differ less than 0.2 N of the maximal value.

Data analysis

The data were log transformed to normalise the variables. As the body mass of the fringillids in our sample is, on average, 1.8 times larger than the body mass of the estrildids, a comparison of bite force between the two groups should involve body mass as a covariant.

Allometric equations are of the form $Y = a\,X^{b}$ or $\log Y = \log a + b\log X$, in which Y is the dependent variable, a is the proportionality coefficient (the intercept), b is the exponent (slope of the regression line) and X is the independent variable. A difference in jaw muscle mass and/or biting force between fringillids and estrildids may result from a difference in intercept or a difference in slope. An analysis of covariance (ANCOVA) was used to test for the equality (homogeneity) of slopes for the two groups. A linear model containing the main effects as well as the interaction term is fitted through the data. The interaction term provides the test for the equality of slopes (Quinn and Keough, 2002). Statistical tests were performed in SPSS 10.0 (SPSS Inc., Chicago, IL, USA).

Results

The mean body mass, total jaw muscle mass and maximal bite force at the tip of the bill for estrildids and fringillids is given in Table 1. The total jaw muscle mass as a percentage of body mass in estrildids is lower (mean 0.99±0.33; N=20) than in fringillids (mean 1.67±0.52; N=16). The correlation between log-transformed body mass and jaw muscle mass (estrildids r=0.822; fringillids r=0.961) and between log-transformed jaw muscle mass and bite force (estrildids, r=0.825; fringillids, r=0.954) are all significant (all $P<0.001$).

Jaw muscle mass

An analysis of covariance shows that for jaw muscle mass *versus* body mass the interaction term (family × body mass) is not significant (P=0.826). The common slope for the two groups of finches is 1.29 (95% CL, 1.09–1.50) and demonstrates a positively allometric increase of jaw muscle mass with body mass in fringillids and estrildids. The intercepts for estrildids and fringillids are significantly different ($P<0.001$; Fig. 2; Table 3). Total jaw muscle mass is higher in fringillids than in estrildids.

Muscle groups

The jaw muscles can be divided into five functional groups and their proportions as percentage of total jaw muscle mass are shown in Table 4. Tested for each muscle group separately, there was no difference in the increase of muscle mass with body mass between the two families. All the interaction terms were not significant (all $P>0.28$), and the slopes for the mass of each muscle group *versus* body mass are shown in Table 4. The 95% confidence levels of the slopes for each muscle group overlap and all include the slope for total jaw muscle mass (1.29). This suggests that a common slope may describe the scaling of all muscle groups (openers and closers) with body mass. There is no significant interaction between the mass of the different muscle groups, body mass and the two families (P=0.47), and the common slope for the five muscle groups × two families was estimated to be 1.24 ($P<0.001$; Fig. 3).

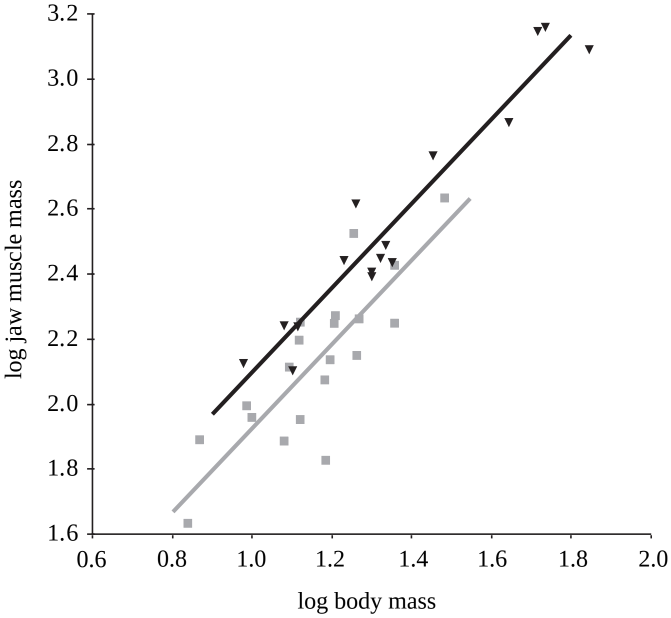

Fig. 2. Regression lines for jaw muscle mass *versus* body mass with common slope (r^2=0.890) for estrildids (grey squares; Y=0.63+1.29X) and fringillids (black triangles; Y=0.81+1.29X).

Total jaw muscle mass is higher in fringillids than in estrildids. To check whether this difference in total jaw muscle mass is the result of a single muscle group or the result of a general increase in mass of all muscle groups we tested the difference in intercepts between the two families for each

Table 3. *Parameter estimates for the line* $\log Y = \log a + b\log X$

Y	X	Family (N)	log a (±S.E.M.)	b (±S.E.M.)	log a^c (±S.E.M.)	b^c (±S.E.M.)
Jaw muscle mass	Body mass	Estrildidae (20)	0.67 (±0.24)*	1.26 (±0.21)***	0.63 (±0.03)**	1.29 (±0.10)***
		Fringillidae (16)	0.78 (±0.14)***	1.31 (±0.10)***	0.81 (±0.24)***	1.29 (±0.10)***
Maximal bite force	Body mass	Estrildidae (19)	–0.98 (±0.24)**	1.26 (±0.20)***	–1.19 (±0.03)***	1.44 (±0.13)***
		Fringillidae (12)	–1.19 (±0.21)***	1.55 (±0.15)***	–1.04 (±0.04)***	1.44 (±0.13)***
Maximal bite force	Jaw muscle mass	Estrildidae (19)	–1.36 (±0.31)***	0.87 (±0.14)***	–1.75 (±0.03)***	1.05 (±0.09)***
		Fringillidae (12)	–2.12 (±0.20)***	1.19 (±0.80)***	–1.78 (±0.03)***	1.05 (±0.09)***
Adductor fibre length	Body mass	Fringillidae (10)	–0.26 (±0.07)**	0.26 (±0.05)***	–	–

*$P\leq0.05$; **$P\leq0.01$; ***$P\leq0.001$; log a and b are estimates for estrildids or fringillids separately; log a^c is an estimate for a common slope, b^c, for estrildids and fringillids together, only done if there are no significant differences between fringillids and estrildids.

muscle complex (Fig. 3). The adductor complex ($P<0.001$), the quadrate adductors ($P=0.005$) and the pterygoid complex ($P=0.018$) are significantly heavier in the fringillids than in the estrildids relative to body mass. The mass of the protractor complex ($P=0.248$) does not differ between the two families, while the depressor complex ($P=0.046$) is minimally significant.

Bite force

As jaw muscle mass increases relative to body mass, the maximal bite force at the tip of the bill is also expected to increase with body mass (see Fig. 4). The analysis shows that the slopes for the estrildids and fringillids do not differ significantly (interaction term, $P=0.254$). Bite force increases positively allometric with body mass (slope, 1.44; 95% CL,

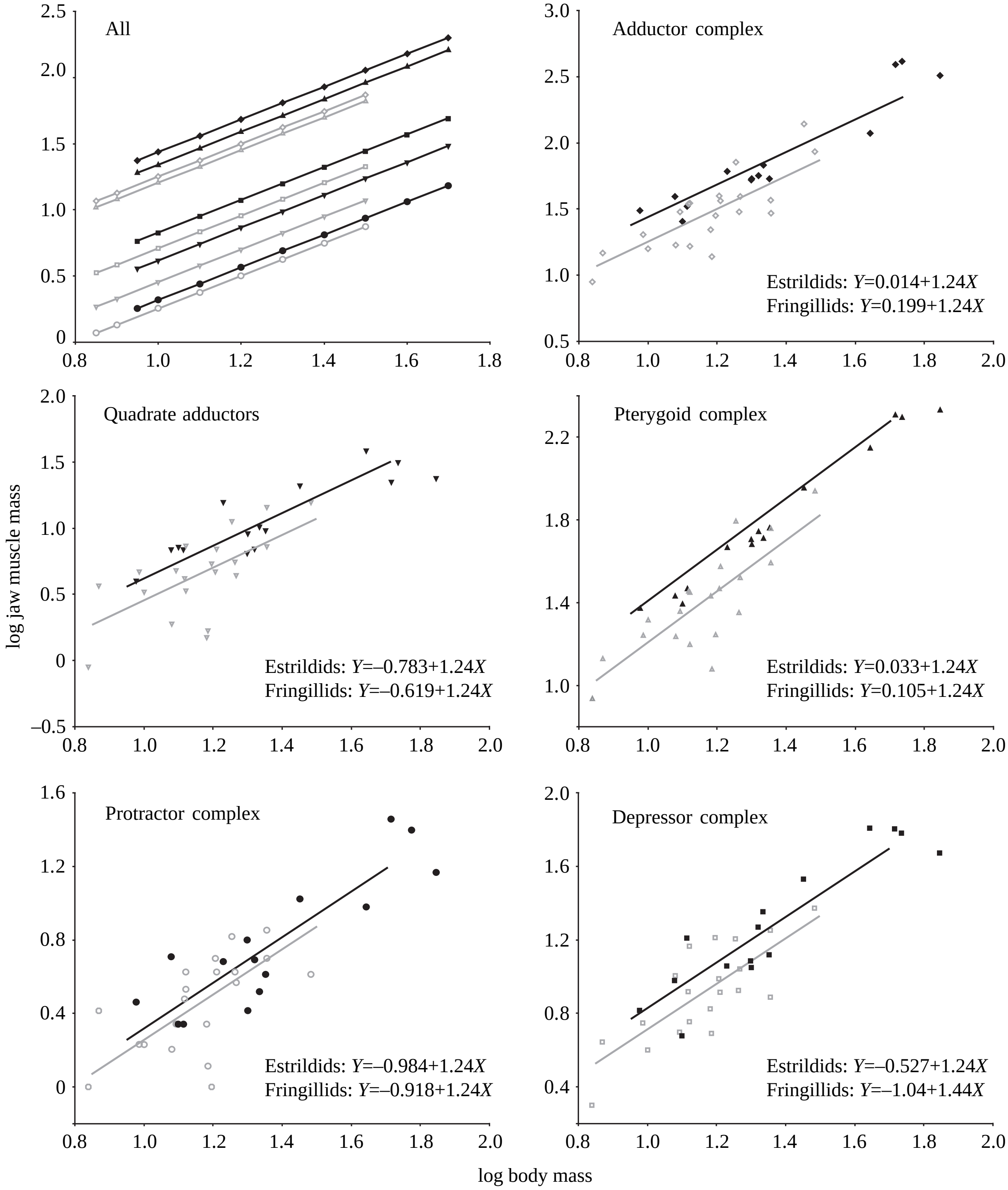

Fig. 3. Regression lines for the log-transformed mass of different jaw muscle groups *versus* log transformed body mass with common slope ($r^2=0.908$) for estrildids (grey) and fringillids (black). Markers used in separate muscle complexes graphs equals the all muscle complexes graph.

Table 4. *Mean jaw muscle mass of all jaw muscle groups as a percentage of total jaw muscle mass for Estrildidae and Fringillidae, together with the slope and the intercept of the relationship between jaw muscle mass and body mass*

Family (*N*)	Adductor complex	Quadrate adductors	Pterygoid complex	Protractor complex	Depressor complex
Estrildidae (20)	40.1 (±3.9)	7.0 (±2.2)	37.7 (±5.7)	4.4 (±1.5)	11.9 (±5.4)
Fringillidae (16)	44.2 (±6.5)	7.1 (±2.6)	34.6 (±4.2)	3.3 (±1.1)	10.8 (±3.4)
Slope (95% CL)	1.34 (1.09–1.59)	1.08 (0.72–1.44)	1.26 (1.06–1.46)	1.13 (0.80–1.46)	1.27 (1.00–1.53)
Intercept (±s.e.m.) Estrildidae	–0.12 (±0.03)	–0.06 (±0.05)	–0.06 (±0.03)	–0.86 (±0.05)	–0.56 (±0.04)
Intercept (±s.e.m.) Fringillidae	0.08 (±0.04)	–0.38 (±0.04)	0.09 (±0.02)	–0.77 (±0.04)	–0.44 (±0.04)

1.18–1.69). As for jaw muscle mass, the intercepts of the regression lines for bite force differ significantly (*P*=0.012) between estrildids and fringillids: the bite force in fringillids is 1.4 times higher than in estrildids of the same body size.

The slope for bite force *versus* jaw muscle mass is 1.05 (95% CL, 0.87–1.23; Table 3). The relationship between bite force and jaw muscle mass is similar between fringillids and estrildids. There is no significant difference in slope (ANCOVA with interaction term *P*=0.070) or intercept (*P*=0.592) between the two groups. Note that within each group there is substantial variation in bite force among species independent of jaw muscle mass (Fig. 3). The partial correlation between bite force and jaw muscle mass controlling for body size is significant in fringillids (*r*=0.754, *P*=0.007) or close to significant in estrildids (*r*=0.419, *P*=0.08). This indicates that differences in bite force among species within a single group are also related to differences in jaw muscle mass.

Muscle fibre length

To investigate the relationship between jaw muscle mass and jaw muscle force, the muscle fibre length of the adductor complex of the fringillids was determined (Table 5). The fibre length of the adductor complex scales negatively allometric with body mass (slope, 0.26; Table 6).

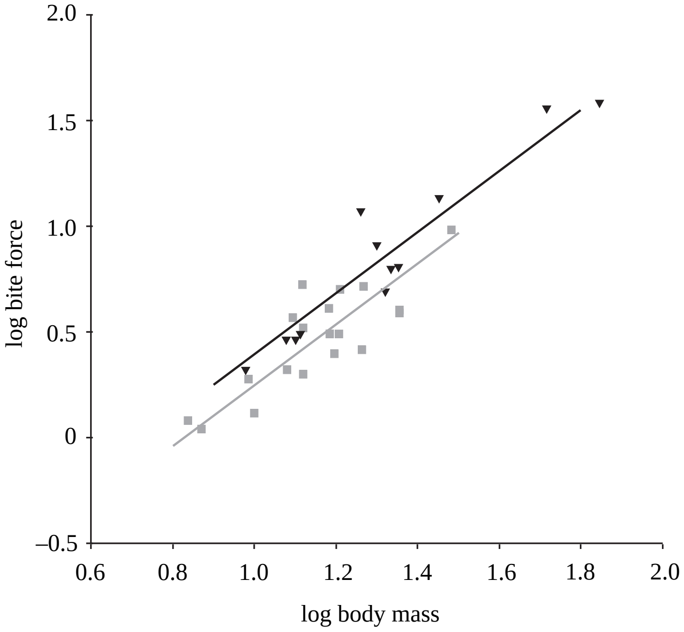

Fig. 4. Regression lines for bite force *versus* body mass with common slope (r^2=0.87) for estrildids (grey squares; y=–1.19+1.44x) and fringillids (black triangles; y=–1.04+1.44x).

Discussion

Main results

Our study shows that bite force in finches correlates positively with jaw muscle mass and body mass. The jaw muscle mass is larger in fringillids than in estrildids, and this is mainly due to a difference in jaw closing muscles. The bite force scales positively allometric against body size in both the fringillids and estrildids, but fringillids of a given body size are able to bite harder than do estrildids of similar size. The bite force also scales positively allometric against jaw muscle size, although in this relationship the two families are not statistically distinct. The muscle fibre length scales against body mass with negative allometry but proportional to linear head dimensions.

Scaling of head, jaw muscle mass and body mass in birds

A comparison with other groups of birds or an expected value is necessary to assess the scaling exponent for the relationship between jaw muscle mass and body mass in finches (1.29; 95% CL, 1.09–1.50). Data on other groups of birds are not available from the literature, but exponents were calculated for jaw muscle data from three studies that reported muscle mass and body mass (Table 6). The jaw muscle mass

Table 5. *Fibre length of the musculus adductor mandibulae externus*

Species (number of measured fibres)	Fibre length (mm; ±s.d.)
Carduelis chloris (20)	1.37 (±0.21)
Coccothraustes coccothraustes (20)	1.59 (±0.33)
Serinus leucopygius (10)	0.97 (±0.25)
Carduelis flammea (10)	0.96 (±0.27)
Carpodacus erythrinus (12)	1.10 (±0.26)
Loxia curvirostra (20)	1.42 (±0.32)
Pyrrhula pyrrhula (20)	1.11 (±0.25)
Serinus sulpuratus (21)	1.31 (±0.29)
Eophona migratoria (20)	1.59 (±0.21)
Rhodopechys obsoleta (20)	1.22 (±0.33)

Table 6. *Parameter estimates of log*Y*=a +b log(body mass) for different groups of birds*

Y	Family (*N*)	*a* (±S.E.M.)	*b* (±S.E.M.)
Jaw muscle mass	Aves (12)	1.31 (±0.25)***	0.78 (±0.11)***
	Serinus sp (7)[1]	0.84 (±0.27)*	1.31 (±0.21)**
	Phalacrocrax sp. (4)[3]	0.09 (±0.59)	1.29 (±0.19)*
	Anseriformes (14)[2]	2.25 (±0.44)***	0.45 (±0.15)**
Cranium length	Estrildinae (20)	0.85 (±0.01)**	0.28 (±0.04)***
	Fringillidae (16)	0.90 (±0.01)***	0.28 (±0.04)***
Fibre length	Fringillidae (10)	–0.26 (±0.07)**	0.26 (±0.05)**

[1]Classen (1989); [2]Goodman and Fisher (1962); [3]Burger (1978); *$P\leq0.05$; **$P\leq0.01$; ***$P\leq0.001$.

of seven *Serinus* species (Classen, 1989) scales with an exponent of 1.31, and the jaw muscle mass of four cormorant species (Burger, 1978) scales with an exponent of 1.29 (95% CL, 0.492–2.10), but the exponent for the jaw muscle mass of 14 anseriform species (Goodman and Fisher, 1962) is only 0.45 (95% CL, 0.125–0.766; Table 6).

An expected value for jaw muscle mass may be derived from the scaling of head size. Geometric scaling of jaw muscle mass with body mass would result in a scaling exponent of 1.0. However, head size and head mass seem to scale negatively allometric with body size in birds. In eight anseriform species, head mass scales with an exponent of 0.70 relative to body mass (Van der Leeuw, 2002). The two largest organs that are contained in the cranium, the eye and the brain, also show negatively allometric scaling with body size. In birds, eye mass (Brooke et al., 1999) and brain mass (Schmidt-Nielsen, 1984) scale with a factor of 0.67. From these exponents for mass, one may expect an exponent for linear dimensions of 0.67/3=0.22. This is in agreement with the exponent we found for cranium length (0.28; 95% CL, 0.20–0.36; Table 6) and muscle fibre length (0.26; 95% CL, 0.15–0.38; Table 6) in finches.

From these data on the scaling exponents of head structures, we conclude that jaw muscle mass may be expected to show negative allometry with respect to body size, when it scales proportional to other head structures. To check this expectation we measured jaw muscle mass in a small sample (*N*=12) of species from different bird families and with a wide range of body mass (Table 2). The scaling exponent for this group is 0.78 (95% CL, 0.549–1.019), which is compatible with the idea that jaw muscles generally scale proportional to head size. These results show that jaw muscle mass scales positively allometric with body mass in granivorous finches and increases much faster with body size than in other birds.

Jaw muscle size and bite force

Jaw muscles are relatively larger in fringillids than in estrildids and there are significant differences in the intercept for each complex between the fringillids and estrildids. All the jaw closers – the adductor complex, the quadrate adductors and the pterygoid muscles – differ significantly between the two groups, while the opener of the upper jaw does not differ significantly and the opener of the lower jaw is only minimally significantly different between the fringillids and estrildids. The relatively larger jaw muscle mass in the fringillids is mainly the result of the enlarged jaw closing muscles and is directly related to their larger maximal bite force.

Differences in maximal bite force may depend on differences in jaw muscle force but also on differences in the geometry of the cranial elements, the configuration of jaw muscles (lines of action) and beak length.

Muscle force scales with cross-sectional area of muscles. The length of the adductor muscle fibres scales against body mass with an exponent of 0.26, which means that cross-sectional area scales with an exponent of 1.29–0.26=1.03. This exponent is very similar to the exponent found for the relationship between bite force and jaw muscle mass. Similarly, a slope of 1.05×1.29=1.35 is expected for the relationship between bite force and body mass (compare with 1.44 found) This suggests that there are no large systematic changes in the orientation and position of muscles with respect to joints (changes in moment arms) that contribute to an increase in bite force with body size.

Differences in maximal bite force may depend on differences in the geometry of the cranial elements. A high upper bill (kinetic hinge), for instance, is often interpreted as an adaptation to large bite force because it increases the moment of the upper jaw closing muscles (Bowman, 1961; Bock, 1966). Whether there are systematic differences in skull morphology between fringillids and estrildids that contribute to differences in bite force will be investigated in a separate study. However, the contribution of differences in skull morphology may be limited. Jaw muscle mass and taxon described in this study already account for 88.5% of the variation in bite force (adjusted *R*-squared ANCOVA on log-transformed data).

Furthermore, there is no difference in the relationship between jaw muscle mass and bite force between the two groups that would indicate an effect of skull morphology on bite force independent of muscle force.

The comparison between fringillids and estrildids assumes that the beak length is the same for both groups. When beak length of the birds for which bite force is measured is analysed (ANCOVA) the beak of estrildids is 1.23 times longer than the beak of fringillids with the same body size. For the body size range of the finches in this study, this difference in relative beak length corresponds to a difference of 1–3 mm in the relative position at which the bite force was measured. As the bite force decreases with the distance to the jaw closer muscles, the lower bite force in estrildids compared with in fringillids may be the result of a longer beak. However, beak length itself is not a very accurate indicator of the position of the beak tip with respect to the jaw muscles. Morphometric analysis of the skull shows that the position of the whole beak (rictus, tip and kinetic hinge of the upper beak) may vary with respect to the jaw muscles. The length of the beak may also increase by a caudal displacement of the rictus and kinetic hinge, while the absolute position of the beak tip with respect to the jaw muscles remains the same. The small difference in beak length between fringillids and estrildids as such does therefore not explain the difference in biting force.

Jaw muscles and feeding behaviour

The large increase in biting force with body size in finches is clearly related to their ability to produce large biting forces. A similar situation may be present in cormorants. Cormorants capture fish, frogs and crustaceans, which requires a powerful bite (Burger, 1978). The feeding behaviour of anseriforms (e.g. grazing, suspension feeding), on the other hand, does not seem to require much force and their jaw muscles' size scales with an exponent of only 0.45. Jaw muscle mass increases much less with body size or head size (see above) than in the finches or cormorants.

In the present study, bite forces were measured at the tip of the beak. Seeds with hardness well within the range of the maximal bite force of the bird are positioned for cracking about halfway along the length of the beak (rictus to tip). Very hard seeds are positioned more caudally. The true maximal bite force will therefore be much higher than the force measured in this study. Unfortunately, most species would only bite the force transducer with the tip of the beak.

The forces required to crack seeds that are reported in the literature are quite high. *Geospiza fortis* eat *Opuntia* seeds that require a force of 54 N to crack (Grant et al., 1976). *Pyrenestes ostrinus* is able to feed on sedge seeds (*Scleria verrucosa*) with a hardness of 151 N (Smith, 1990). The hawfinch (*Coccothraustes coccothraustes*) is able to crack cherry stones with a hardness of up to 310 N (Sims, 1955). Such values are difficult to interpret without information on contact area (applied stress) and seem to be at odds with the values for biting force reported in the present study. The maximum bite force of the Java sparrow (*Padda oryzivora*) was calculated to be 61.3 N for safflower seeds (Van der Meij and Bout, 2000), but the bite force measured at the tip of the beak is only 9.6 N. Although the bite force increases towards rictus level, a static bite force model study (R.G.B., unpublished results) shows that maximal bite force near the rictus is, at most, two times higher than at the tip of the beak.

This apparent discrepancy between seed hardness and biting force can be resolved when the contact area between seed and bill is known. Note that the force transducers used to determine the hardness of seeds register force independent of contact area. In a pilot study, we measured contact areas between seed and force transducer during cracking of the seed shell by pressing carbon-covered seeds on paper. The maximum stresses at which safflower seeds and hemp seeds crack were 37.8±16.1 N mm^{-2} and 15.5±9.3 N mm^{-2} (N=30), respectively. To determine the contact areas between these two seed species and the rims of the beak, the seeds were pressed on the lower jaw of a number of freshly killed Java sparrows. The contact areas with the beak for safflower seeds and hemp seeds were 2.39±1.07 mm^2 and 1.02±0.68 mm^2 (N=10), respectively. The maximal bite force for the Java sparrow is estimated as twice the bite force at the tip of the beak (calculations with a static force model). The contact area between force transducer and the tip of the (upper) bill of the Java sparrow is estimated to be 0.77 mm^2, which results in a stress of 9.6/0.77=12.47 N mm^{-2}. Java sparrows are therefore able to crack safflower seeds with a measured hardness of less than 2×12.47×2.39=59.6 N and hemp seeds with a measured hardness of less than 2×12.47×1.02=25.43 N. These estimated values are in good agreement with the values determined behaviourally for safflower (Van der Meij and Bout, 2000; 61 N) and the observation that Java sparrows eat hemp readily without rejecting many seeds. Only 4% (N=100) of the hemp seeds require forces larger than 25.43 N to crack.

With an increase in the maximal bite force of finches, the birds may expand the range of their diet and, thus, husking time is expected to decrease. Husking time is directly related to seed hardness (Van der Meij et al., in press), and an increase in bite force may therefore be expected to decrease husking time.

The significant difference in maximal bite force between the fringillids and estrildids is probably also related to a difference in feeding behaviour. The diet of carduelines consists of a wide range of seeds, containing seeds of the family Compositae, like thistle and sunflower (Newton, 1967, 1972). The firetail finches (Read, 1994), the zebrafinch (Zann, 1996) and the Gouldian finch (Dostine et al., 2001), all estrildids, feed mainly on small soft grass seeds. This suggests that the fringillids are able to take seeds of a wider range of hardness than are estrildids. Why this difference between estrildids and fringillids exists is not clear. Geographically, the two families are separated. The fringillids occur in the Holarctic and Africa (Clement et al., 1993). The estrildids probably have an African origin (Mayr, 1968; Clement et al., 1993) and inhabit the tropical east through Arabia to India and most of the Oriental region, the Malay archipelago, New Guinea, Australia and the islands of the South Pacific (Clement et al., 1993). Phylogenetic analysis shows that the two groups of finches are separate, monophyletic clades (M. A. A. Van der Meij, M. A. G. de Bakker and R. G. Bout, manuscript submitted). Although little is known about the diet of finches, the information available suggests that estrildids do not explore trophic niches with hard, closed-shelled seeds. This seems to indicate that a (phylo)genetic constraint on jaw muscle size prevents estrildids from acquiring bite forces that are large enough to explore niches with hard, closed-shelled seeds.

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