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Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape

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Summary

1. Previous studies of the Medium Ground Finch, *Geospiza fortis*, have documented that selection is most severe under drought conditions, which generally favour beaks that are comparatively deep and narrow. Deep beaks are presumed to enhance a bird's ability to crack hard seeds, and narrow beaks have been proposed to enhance a bird's efficiency in manipulating seeds.

2. In the present study, we make the first direct measurements of bite force in Darwin's finches. We used 147 *G. fortis* from Isla Santa Cruz, Galápagos, to document the influence of beak, head and body dimensions on bite force.

3. Among the various beak dimensions, depth, width and shape were all significant predictors of bite force. Among the various head dimensions, width was the best predictor of bite force. Generally low predictive values of multiple regression models including all morphological variables, as well as positive allometric scaling of bite force on head width, suggest an important additional role for variation in muscle architecture or jaw biomechanics in bite force generation.

Key-words: Birds, bite force, feeding, Galápagos, morphology, performance

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Introduction

Darwin's finches of the Galápagos Islands are well known for the diversity they express in beak form and function (Lack 1947; Bowman 1961; Grant 1999). Long-term field studies have provided strong evidence that beak morphology evolves rapidly and precisely in response to changing ecological conditions, such as food type, food availability and interspecific competition (Boag & Grant 1981; Schluter & Grant 1984; Gibbs & Grant 1987; Grant 1999; Grant & Grant 2002). These relationships have been particularly well documented for the Medium Ground Finch (*Geospiza fortis*) on Isla Daphne Major. In that population, ecological changes during a drought – reduced availability and increased average hardness of seeds – resulted in disproportionately higher survival of birds with large bodies and beaks (Boag & Grant 1981). Because body size and beak morphology are highly heritable (Boag 1983), these traits evolved to be larger in the subsequent generation (Grant & Grant 1995).

Multiple regression analyses for this selective episode further revealed that beak depth was a primary target of selection. Specifically, selection gradients (selection acting directly on a trait independent of correlations with other traits) for beak depth typically exceeded those for other beak and body dimensions (Price *et al*. 1984; Grant & Grant 1995). This finding is consistent with the observation that birds with deeper beaks eat larger seeds that are more difficult to crack (Abbott, Abbott & Grant 1977; Grant 1981). Unexpectedly, selection gradients for beak width under drought conditions were consistently negative, indicating that wider beaks (controlling for other beak and body dimensions) were somehow disadvantageous for survival. A proposed explanation for this last finding is that wide beaks may be less effective than narrow beaks for the specialized twisting motions used by *G. fortis* as they feed on fruits of *Tribulus cistoides* (Price *et al*. 1984; Grant 1999). Despite this direct selection for narrower beaks, the population evolved wider beaks in the subsequent generation, presumably because of the strong positive correlation between beak depth and beak width, coupled with stronger positive selection on the former than negative selection on the latter (Price *et al*. 1984; Grant & Grant 1995). Accordingly,

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selection differentials (which include direct selection on each trait plus indirect selection owing to correlations with other traits) were positive for beak width (Price *et al*. 1984; Grant & Grant 1995; Grant 1999).

Our goal was to further explore relationships between morphology, performance and selection by quantifying *G. fortis* bite force in relation to beak and head dimensions. Studies conducted previously were based on observations of seed selection in relation to seed hardness (Bowman 1961; Abbott *et al*. 1977; Grant 1981). Abbott *et al*. (1977), for example, found that *Geospiza* species pairs with the greatest average difference in beak depth also had the greatest average difference in the hardness of seeds eaten. Similarly, beak size and seed hardness were correlated within a population of *G. fortis* (Price 1987). These results provide strong indirect evidence that larger beaks can exert stronger forces on seeds. However, the actual bite force of Darwin's finches has never been quantified, leaving some ambiguity as to the contribution of various beak dimensions to the force that birds might apply to a seed. Moreover, it remains entirely unknown how well morphological traits such as beak dimensions can predict bite force across individuals.

We used custom-designed force transducers to take direct measurements of bite force from individual *G. fortis*. This method provides a novel approach for testing hypotheses about relationships between morphology, performance and selection, thus complementing inferences based on feeding observations (Grant 1981). We used multiple regression analyses to quantify the joint and independent influence of beak, head and body size parameters on bite force. We predicted that the relative strength of these parameters as predictors of bite force would mirror observed relationships between morphology and selection (Price *et al*. 1984; Grant & Grant 1995). For example, if the survival advantage during a drought that is conferred by a deeper beak is based on (or correlated with) bite force, beak depth should be a particularly strong predictor of bite force.

However, beak size does not by itself confer a particular bite force or crushing ability, because the beak is not a force-generating structure. Rather, the beak transmits forces generated by the jaw-closing muscles, which are positioned at the back of the head (Bowman 1961). Variation in bite force should therefore be associated with variation in head dimensions. In particular, we predicted that bite force would be positively correlated with head width and depth, as in other vertebrate taxa (e.g. Herrel *et al*. 1999; Aguirre *et al*. 2002), because of the extra space available for larger jaw muscles (Bowman 1961) and yet, if intrinsic variation in muscle structure or jaw mechanics are important in generating bite force, perhaps head dimensions will not be particularly strong predictors of bite force variation.

Materials and methods

Field work was conducted at coastal and upland sites on Santa Cruz Island, Galápagos, during February and March 2003. Finches were captured with mist nets and then banded, measured, tested for bite force and released ($N = 147$). Morphological measurements included beak depth, beak width, beak length, tarsus length, wing chord, body mass, head width, head length and head depth. The first six measurements were taken as in Grant (1999). Head width was measured at the widest part of the head, just posterior to the eyes. Head depth was measured at the deepest part of the head, again just posterior to the eyes. Total head length was measured from the back of the head to the tip of the upper beak. Morphological measurements were highly repeatable (intraclass correlation coefficients ranging from 0·95 to 0·97) as has been found in previous studies (see, e.g., Grant 1999).

Bite forces were measured with a Kistler piezoelectric force transducer (type 9203, Kistler Inc., Switzerland; ± 500 N) mounted in a custom-built holder, and connected to a portable Kistler charge amplifier (type 5059A). A detailed description of this setup is available in Herrel *et al*. (1999) and Aguirre *et al*. (2002). The bite plates were moved farther apart when testing larger animals to ensure that all birds were biting at equivalent gape angles, and were thus tested under mechanically similar conditions. Bite plates were positioned at two-thirds of the length of the lower beak back from the tip, i.e. at the point of greatest curvature of the upper rim of the lower beak. This is the beak location where birds generally crack hard seeds, as indicated by extensive field observations (e.g. see Fig. 1). The birds were eager to bite when taken from the nets, and most produced bites spontaneously. All bites were scored while being measured and at least three 'good' bites were recorded for each individual. Bite force measurements were highly repeatable within individuals across the three trials (intraclass correlation coefficient: 0·95; $F_{143,286} = 57{\cdot}39$; $P < 0{\cdot}0001$). The strongest bite was used in subsequent analyses as an estimate of maximal bite force.

We quantified relationships between bite force and head and beak dimensions by regressing $\log_{10}$-transformed bite force against each $\log_{10}$-transformed head and beak dimension individually (i.e. simple reduced major axis regressions). R^2-values provide an

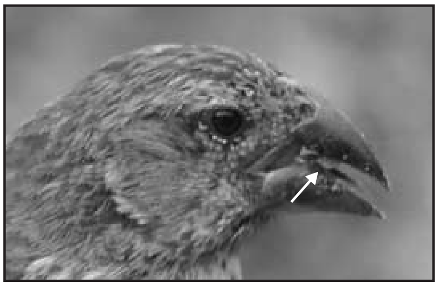

Fig. 1. Photograph taken in the field by A.P. Hendry showing a *G. fortis* on Santa Cruz crushing a seed. Birds were induced to bite the transducer at this position on beak when measuring bite force.

Table 1. Variation in morphology and bite force in the Medium Ground Finch (*Geospiza fortis*) on Santa Cruz Island ($N = 147$)

	Minimum	Maximum	Mean	Standard deviation
Tarsus length (mm)	15·3	25·3	20·8	1·8
Wing chord (mm)	61·0	81·5	69·4	3·9
Mass (g)	14·0	32·0	21·3	3·3
Beak length (mm)	9·6	14·6	11·5	0·9
Beak depth (mm)	9·4	14·9	11·4	1·2
Beak width (mm)	8·3	12·5	9·9	0·9
Head length (mm)	29·5	37·4	32·7	1·5
Head width (mm)	14·4	18·5	16·0	0·9
Head depth (mm)	12·9	18·6	15·5	1·2
Bite force (N)	7·2	47·1	17·4	7·0

Table 2. Simple linear regressions of log$_{10}$ beak and head dimensions against log$_{10}$ wing chord

Independent	R^2	P	Slope
Log$_{10}$ beak length	0·27	<0·001	0·73*
Log$_{10}$ beak width	0·38	<0·001	1·00
Log$_{10}$ beak depth	0·30	<0·001	0·99
Log$_{10}$ head length	0·24	<0·001	0·78*
Log$_{10}$ head width	0·10	<0·001	0·48*
Log$_{10}$ head depth	0·24	<0·001	0·67*
Log$_{10}$ bite force	0·25	<0·001	3·29*

*Significantly ($\alpha = 0{\cdot}01$) different from the predicted slope of 1 for linear dimensions or 2 for bite force.

index of the strength of each morphological parameter as a predictor of bite force. To simultaneously test for the effects of body, head and beak dimensions, we performed a single multiple regression including all log$_{10}$-transformed morphological traits as independent variables and log$_{10}$-transformed bite force as the dependent variable. Because head dimensions, beak dimensions and bite force all covary positively with body size (see Appendix 1), we performed a second analysis that statistically 'removed' the effects of body size, thus isolating the influences of head and beak dimensions *per se*. For this size-free analysis, we regressed each log$_{10}$-transformed head dimension, beak dimension or bite force against the log$_{10}$-transformed values for three different measures of body size: wing chord, tarsus length and body mass. We also used the first principal component from an analysis with all body size indicators (tarsus length, wing chord, mass).

Residuals from the regressions against wing chord were used in three analyses. First, we explored scaling relationships by regressing residual bite force against each residual beak and head dimension separately (i.e. simple linear regressions). The slopes from these regressions can be used to test the null hypothesis that bite force scales isometrically with body, beak and head dimensions. Slopes of 2·0 are expected under isometry because doubling a linear dimension will quadruple the cross-sectional area (Schmidt-Nielsen 1984). Deviations from isometry would suggest additional mechanisms for force production beyond those conferred by scaling, e.g. changes in muscle architecture and jaw biomechanics. Second, we tested for the effects of various morphological parameters by entering all residual beak and head dimensions into a multiple regression, with residual bite force as the dependent variable. Third, we tested whether two aspects of beak shape – beak depth for a given beak width, and vice versa – influence bite force. For this analysis, we regressed the log$_{10}$-transformed beak depth (width) against log$_{10}$-transformed beak width (depth) and extracted the residuals. These residuals were then regressed against the residual ('size free') bite force. All analyses were performed using SPSS V10 (SPSS Inc., Chicago, USA).

Results

As previously demonstrated (e.g. Grant *et al*. 1985), we found that *G. fortis* on Santa Cruz are unusually variable in body size and beak dimensions (Table 1). We also found high variation in maximum bite force, which ranged from just over 7 N to almost 50 N (Table 1). This variation makes *G. fortis* an excellent study species for exploring relationships between morphology and bite force. All head and beak dimensions were correlated significantly and positively with all body size measures (PC1, body mass, tarsus length and wing chord; $P < 0{\cdot}01$ for all traits; see Table 2 for correlations with wing chord; see also Appendix 1). In fact, all conclusions held regardless of whether wing chord, tarsus length, body mass or PC1 was used as the surrogate for body size. We therefore limit our presentation to wing chord results only. Beak width and beak depth increased isometrically with body size, whereas beak length and head dimensions scaled with significant negative allometry (Table 2). These results differ noticeably from those reported by Boag (1984) who reported strong positive allometries for beak width and beak depth for a different population of *G. fortis* on Santa Cruz (see Table 7 in Boag 1984). In contrast to beak dimensions, all head dimensions scaled with negative allometry, indicating they increased in size less than expected with increasing body size. Bite force, on the other hand, scaled with significant positive allometry (slope > 2, Table 2). Regressions of bite force as a function of each beak and head dimension were positive and highly significant (all $P < 0{\cdot}001$; Fig. 2). A step-wise multiple regression with all traits retained a highly significant model ($r^2 = 0{\cdot}549$; $P < 0{\cdot}001$) that included beak depth, beak width and body mass. Standardized partial regression coefficients revealed that beak width ($\beta = 0{\cdot}328$) and beak depth ($\beta = 0{\cdot}320$) explain more of the variation than did body mass ($\beta = 0{\cdot}157$).

After removing the effect of overall body size, beak and head dimensions retained their positive and significant correlations with residual bite force (Table 3; Appendix 2). Inspection of r^2 values indicated that residual beak depth ($r^2 = 0{\cdot}38$) and residual beak

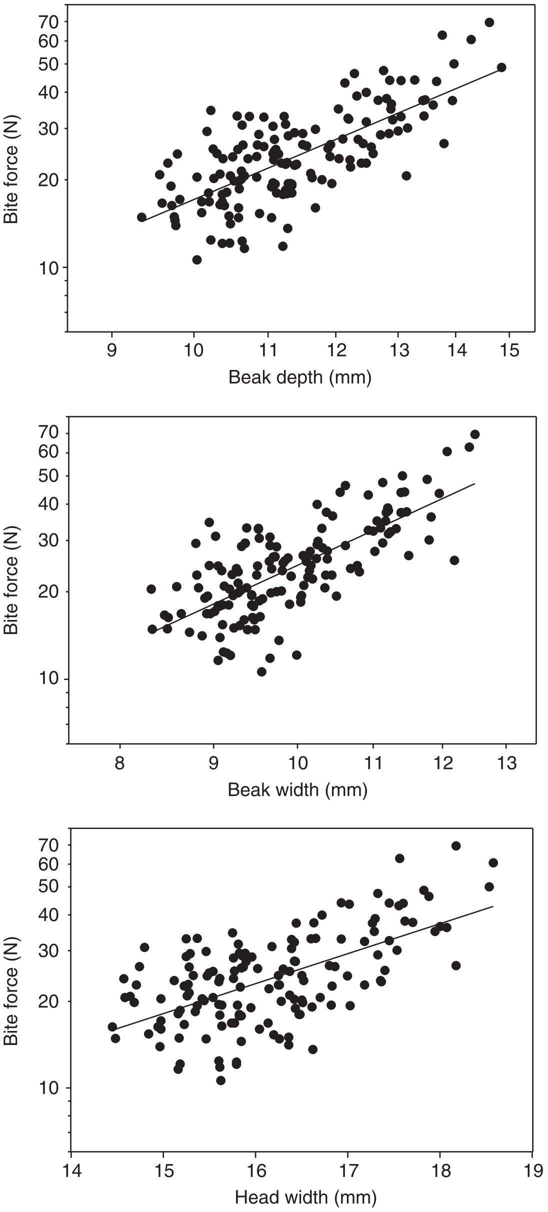

Fig. 2. The relationship between beak dimensions, head width and bite force in *G. fortis* from Santa Cruz Island, Galápagos. Both beak depth and beak width are significantly correlated with, and are good predictors of, bite force. The bottom graph shows that individuals with wider heads bite harder than those with narrower heads. Wider heads presumably allow for more jaw-closing muscles. Note that both the *x*- and *y*-axes are on a logarithmic scale.

Table 3. Simple linear regressions of residual beak and head shape variables against residual bite force

Independent	R^2	P	Slope
Residual beak length	0·22	<0·001	2·18
Residual beak width	0·36	<0·001	2·67*
Residual beak depth	0·38	<0·001	2·29
Residual head length	0·11	<0·001	2·64
Residual head width	0·24	<0·001	3·09*
Residual head depth	0·08	0·001	1·30

*Significantly different from the predicted slope of 2 at α = 0·05.

width (r^2 = 0·36) were the strongest predictors of bite force. Among the head dimensions, residual head width was by far the best predictor of bite force (r^2 = 0·24).

A stepwise multiple regression with all size-free traits retained a significant model with only two parameters, residual beak depth and residual beak width (r^2 = 0·405; P < 0·001). The standardized partial regression coefficients for beak depth and beak width were 0·361 and 0·303, respectively, suggesting that bite force has a slightly stronger association with the former than the latter. When entering residual head dimensions only (i.e. excluding beak dimensions), a significant model was retained with residual head width as the only variable (r^2 = 0·24; P < 0·001).

Analyses based on beak shape (i.e. residuals from beak depth *vs* beak width regressions) revealed that bite force was slightly greater for birds that had deeper beaks for a given width (r^2 = 0·04; $F_{1,145}$ = 6·196; P = 0·014) but was not associated with beak width for a given beak depth (r^2 = 0·002; $F_{1,145}$ = 0·236; P = 0·63).

Discussion

We found that bite force was positively correlated with several beak dimensions, especially depth and width (Fig. 2, Table 3). This association between beak dimensions and bite force supports previous studies that have shown strong positive selection on beak depth as available seeds become fewer and harder (Boag & Grant 1981; Price *et al.* 1984; Grant & Grant 1995). It is intuitively satisfying that selection should act directly on a beak dimension that is strongly related to bite force and, presumably, seed-crushing ability. We also found that head width was the only good predictor of bite force among the various head dimensions. We interpret the importance of head width as follows: because the major jaw closing muscles (the m. adductor exeternus complex) are situated at the back of the head, lateral to the lower jaw (Bowman 1961), a wider head probably indicates the presence of bulkier jaw muscles, which can generate correspondingly greater forces.

Given the unequivocal conclusions of previous studies (see Grant 1999 for an overview), we were surprised to find that head and beak dimensions explained only a moderate amount of the variation in bite force. Despite the high repeatabilities of our measurements, our best multiple regression model had an r^2 value of only 0·55, indicating that 45% of the variation in bite force could not be explained by the variables we measured. After controlling for body size, morphological traits explained only 40% of the variation. These results point to probable variation among individuals in the properties of the jaw adductor muscles themselves. Moreover, this variation may be related to more than just differences in total muscle mass, as revealed by the strong positive allometry (significantly greater than 2) in the regressions of bite force on head dimensions. Both lines of evidence suggest the presence of intrinsic changes in muscle geometry or physiology. This conclusion is further supported by previous interspecific comparisons among Darwin's finches, which indicate distinct changes in the position and the degree of pennation in the external jaw adductors (Bowman 1961). Measurements of jaw muscle masses, degree of pennation and orientation are needed to address this further.

An additional novel conclusion from our work is that beak width is nearly as good a predictor of bite force as is beak depth (Fig. 2, Table 3). In particular, the stepwise multiple regressions revealed that individuals that bite harder have both wider and deeper beaks for a given body size. The positive correlation of beak width with bite force may at first appear to contradict previous studies showing negative selection on beak width during a drought (Price *et al.* 1984). However, the difference between studies may simply reflect differences in food availability. Observational studies on Daphne Major have shown that *G. fortis* individuals with big beaks tend to eat relatively hard seeds, such as *Tribulus* (Grant 1999), which are very common (Abbott *et al.* 1977; Smith *et al.* 1978). When doing so, these birds employ a twisting motion, in which the upper and lower bills are moved laterally across the seed surface (Grant 1981). Application of torsion on the mericarp, rather than a direct crushing effort, presumably reduces the actual force needed to crack the seed. Price *et al.* (1984) proposed that relatively narrow beaks might be particularly well suited for specialized twisting motions, because of increased versatility and precision. As *Tribulus* seeds are much less abundant at our sampling sites on Santa Cruz (Abbott *et al.* 1977; Smith *et al.* 1978; A. P. Hendry, unpublished data), it seems possible that selection in this population would not favour narrow beaks through the mechanism proposed by Price *et al.* (1984).

However, our data do indicate that beak depth is somewhat more important than beak width in resisting reaction forces during seed crushing. This suggestion is supported by two lines of evidence. First, bite force scales isometrically with beak depth (slope = 2) but shows significant positive allometry with beak width (slope > 2; Table 3). This shows that as bite force increases, beak width increases at a slower than expected rate. It is important here to realize that changes in beak shape are a *consequence* of the force regime and thus beak dimensions that are essential to maintain the structural integrity of the beak are expected to track the changes in bite force. Second, we find that birds that have relatively deep beaks for a given width bite significantly harder. Birds with wide beaks for a given depth, on the other hand, do not bite harder (see Results).

In conclusion, our data illustrate the importance of distinguishing force generating structures (i.e. muscles) from force-transmitting structures (i.e. the beak) when interpreting selection and its effects on feeding performance. Although morphological traits such as beak and head dimensions are significantly correlated with bite force in *G. fortis*, a considerable part of the variation in bite force cannot be explained by simple morphological indicators. Beak dimensions are correlated with bite force because the beak transmits the forces from the jaw closing muscles to the food item. Thus, the shape of the beak needs to be such that it withstands reaction forces exerted by the food item. Our data show that *G. fortis* head and beak dimensions may respond very differently to selection for increased crushing performance. Although beak dimensions such as depth and width are significant predictors of the magnitude and directions of forces generated during seed crushing, more detailed biomechanical analysis are needed to determine the precise morphological basis of the variation in bite performance in *G. fortis*.

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Appendix 1.

Correlation matrix (Pearson correlations) based on the raw log10-transformed data

	BL	BD	BW	HW	HL	HD	TARS	WING	Bite
Beak length (BL)	1	0·768	0·745	0·631	0·710	0·479	0·271	0·518	0·607
		0·000	0·000	0·000	0·000	0·000	0·001	0·000	0·000
Beak depth (BD)	0·768	1	0·886	0·765	0·653	0·627	0·300	0·547	0·719
	0·000		0·000	0·000	0·000	0·000	0·000	0·000	0·000
Beak width (BW)	0·745	0·886	1	0·762	0·680	0·679	0·390	0·620	0·722
	0·000	0·000		0·000	0·000	0·000	0·000	0·000	0·000
Head width (HW)	0·631	0·765	0·762	1	0·590	0·554	0·258	0·471	0·610
	0·000	0·000	0·000		0·000	0·000	0·002	0·000	0·000
Head length (HL)	0·710	0·653	0·680	0·590	1	0·544	0·336	0·486	0·497
	0·000	0·000	0·000	0·000		0·000	0·000	0·000	0·000
Head depth (HD)	0·479	0·627	0·679	0·554	0·544	1	0·472	0·489	0·459
	0·000	0·000	0·000	0·000	0·000		0·000	0·000	0·000
Tarsus length (TARS)	0·271	0·300	0·390	0·258	0·336	0·472	1	0·398	0·348
	0·001	0·000	0·000	0·002	0·000	0·000		0·000	0·000
Wing chord (WING)	0·518	0·547	0·620	0·471	0·486	0·489	0·398	1	0·504
	0·000	0·000	0·000	0·000	0·000	0·000	0·000		0·000
Bite force (BITE)	0·607	0·719	0·722	0·610	0·497	0·459	0·348	0·504	1
	0·000	0·000	0·000	0·000	0·000	0·000	0·000	0·000	

Appendix 2.

Correlation matrix (Pearson correlations) using the residual data for all traits (based on regressions on wing chord)

	rBL	rBD	rBW	rHW	rHL	rHD	rBITE
Residual BL	1	0·676	0·632	0·513	0·614	0·303	0·468
		0·000	0·000	0·000	0·000	0·000	0·000
Residual BD	0·676	1	0·833	0·687	0·530	0·493	0·614
	0·000		0·000	0·000	0·000	0·000	0·000
Residual BW	0·632	0·833	1	0·678	0·552	0·550	0·604
	0·000	0·000		0·000	0·000	0·000	0·000
Residual HW	0·513	0·687	0·678	1	0·468	0·421	0·490
	0·000	0·000	0·000		0·000	0·000	0·000
Residual HL	0·614	0·530	0·552	0·468	1	0·402	0·334
	0·000	0·000	0·000	0·000		0·000	0·000
Residual HD	0·303	0·493	0·550	0·421	0·402	1	0·282
	0·000	0·000	0·000	0·000	0·000		0·001
Residual BITE	0·468	0·614	0·604	0·490	0·334	0·282	1·000
	0·000	0·000	0·000	0·000	0·000	0·001	