

# Evolution of bite force in Darwin's finches: a key role for head width

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## Abstract

Studies of Darwin's finches of the Galápagos Islands have provided pivotal insights into the interplay of ecological variation, natural selection, and morphological evolution. Here we document, across nine Darwin's finch species, correlations between morphological variation and bite force capacity. We find that bite force correlates strongly with beak depth and width but only weakly or not at all with beak length, a result that is consistent with prior demonstrations of natural selection on finch beak morphology. We also find that bite force is predicted even more strongly by head width, which exceeds all beak dimensions in predictive strength. To explain this result we suggest that head width determines the maximum size, and thus maximum force generation capacity of finch jaw adductor muscles. We suggest that head width is functionally relevant and may be a previously unrecognized locus of natural selection in these birds, because of its close relationship to bite force capacity.

## Introduction

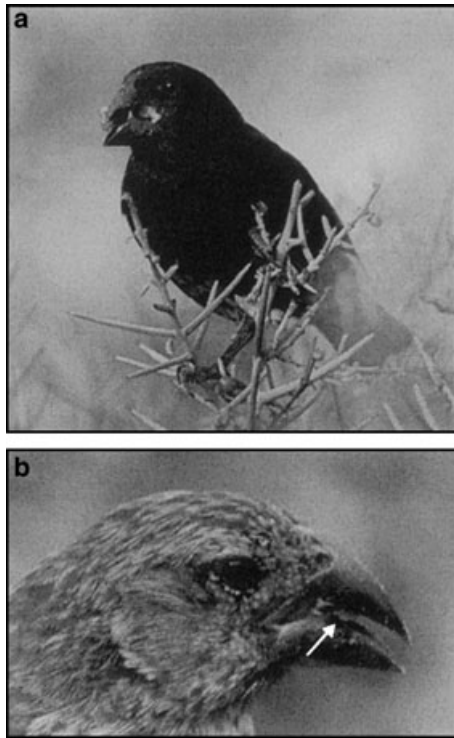
Adaptive radiation in vertebrates often features prominent diversification in feeding habits and in the form and function of the feeding apparatus (e.g. Simpson, 1953; Liem, 1973; Schluter, 2000; Streebman & Danley, 2003). The evolutionary mechanisms underlying this divergence have been particularly well documented in studies of Darwin's finches of the Galápagos Islands, Ecuador (Lack, 1947; Grant, 1999; Grant & Grant, 2002a,b). Research on these birds has shown that beak morphology evolves via natural selection as a response to variation in food type, food availability, and interspecific competition for food (Schluter *et al.*, 1985; Grant & Grant, 1987, 2002a,b; Grant, 1999). Measures of beak morphology, however, ultimately provide only a limited window into feeding performance, i.e. an animal's ability to eat different kinds of foods. This is because the avian feeding apparatus comprises multiple structural components including skeletal, muscular, and

neural systems, all of which work together to ensure its proper function.

Consider *Geospiza* ground finches that crush food items in their beaks (Fig. 1). Food-crushing ability is determined most directly by bite force, which in vertebrates depends largely on the strength of the jaw adductor muscles (Bowman, 1961; Herrel *et al.*, 2001, 2002; Van der Meij & Bout, 2004). These muscles, situated at the back of the head, generate crushing forces that are transferred to food by means of the upper and lower beak (Bowman, 1961; Van der Meij & Bout, 2004). Beak morphology in *Geospiza* finches is expected to evolve in concert with jaw adductor strength, in order to avoid structural failure because of increased food reaction forces, and also to limit costs associated with developing unnecessarily strong beaks. But beak morphology may be subject to additional selection pressures not associated with food crushing (e.g. probing, food manipulation, or preening), and beak dimensions might thus evolve as a compromise between bite force capacity and these other tasks.

The fitness consequences of beak size and shape in *Geospiza* finches have been well documented in field studies of natural selection (Grant & Grant, 1995, 2002a,b). The influence of variation in beak size and

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**Fig. 1** (a) Field photograph by A.P. Hendry of a *G. fortis* individual crushing a *Scutia spicata* seed. (b) Field photograph by A.P. Hendry of another *G. fortis* individual, illustrating the location where the seeds are crushed (arrow). Bite forces were measured unilaterally at this location on the beak for all species.

shape on seed crushing ability, however, has been inferred indirectly from correlations among beak dimensions, seed selection, and measurements of seed hardness (Abbott *et al.*, 1977; Grant, 1981, 1999; Schluter & Grant, 1984). Here we document, using *in vivo* measures of maximal bite force capacity, the functional relationship between bite force capacity (i.e. seed crushing ability) and beak dimensions across nine Darwin's finch species. Our method allows us to document directly the degree to which variation in beak dimensions can predict bite force. We also test whether variation in head dimensions is correlated with bite force across species. Previous studies in other vertebrates including lizards, turtles, and fishes have shown that head dimensions correlate closely with bite force, presumably because of a positive relationship between head size and the size of the jaw adductor muscles (Bowman, 1961; Herrel *et al.*, 2001, 2002; Van der Meij & Bout, 2004). Moreover, previous morphological analyses of jaw adductor muscles in Darwin's and other finches have suggested strong correlations between head dimensions and jaw adductor mass (Bowman, 1961; Van der Meij & Bout, 2004), and between jaw adductor mass and bite force (Van der Meij & Bout, 2004).

## Materials and methods

### Samples

We collected morphological and bite force data from nine species of Darwin's finches. Field work was conducted at coastal and upland sites on Santa Cruz Island during February and March 2003. Birds were captured in mist nets, measured, tested for bite force, banded with unique colour combinations to prevent subsequent remeasurement, and released. Morphological measurements were taken according to previous work and included: beak length, beak depth, beak width, tarsus length, wing chord length and body mass (see Grant, 1999). Beak 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). In addition we measured head length from the tip of the upper beak to the back of the head; head width at the widest part of the head, just posterior to the orbits; and head depth at the deepest part of the head, again just posterior to the orbits (see also Herrel *et al.*, in press). Species means were calculated and  $\text{Log}_{10}$  transformed before further analysis. The number of individuals measured were as follows: *Geospiza magnirostris*,  $n = 11$ ; *G. fortis*,  $n = 137$ ; *G. fuliginosa*,  $n = 65$ ; *G. scandens*,  $n = 24$ ; *Platyspiza crassirostris*,  $n = 28$ ; *Cactospiza pallida*,  $n = 5$ ; *Camarhynchus psittacula*,  $n = 2$ ; *C. parvulus*,  $n = 24$ ; *Certhidea olivacea*,  $n = 30$ .

### Bite forces

Bite force was measured using a piezo-electric force transducer (Kistler Inc., Winterthur, Switzerland) mounted in a custom-designed holder and connected to a portable charge amplifier (Kistler Inc., see Herrel *et al.*, 2001, 2002, in press). By biting the free end of the holder, forces are transferred across the fulcrum to the transducer and registered using a portable charge amplifier. Birds were induced to bite the transducer at a position closely corresponding to that used to crack seeds, as determined by the analysis of photographs and films showing birds crushing seeds in the field (Fig. 1). Most birds were eager to bite spontaneously upon capture. Remaining birds were encouraged to bite the transducer with a gentle tap on the side of the beak, which readily induced defensive bites. Three independent bite force measurements were taken for each individual, the maximum of which was retained for subsequent analyses as a measure of maximal bite force. Bite forces were highly repeatable across the three measurements [intraclass correlation coefficient for the most variable species (*G. fortis*)  $r = 0.95$ ;  $F_{143,286} = 57.39$ ;  $P < 0.001$ ;  $n = 144$ ]. Species means were calculated and  $\text{Log}_{10}$  transformed before further analysis. Regressions for each morphological trait and bite force gave similar results when regressed on wing chord, tarsus length, or body mass. Here we report only results based on wing chord residuals.

## Analyses

In order to account for the possible influence of body size on bite force, we calculated residuals of all morphological and performance traits across three indices of body size: wing chord, tarsus length, and body mass. We conducted regression analyses on these size-corrected data as well as on the raw data. Regressions were calculated in a phylogenetic context using independent contrast analysis, which takes into account the statistical nonindependence of species samples and allows to test for evolutionary correlations among morphological and performance traits. Independent contrast analyses used a punctuational or speciation assumption of evolutionary change, with all branch lengths set to unit length, as has been recommended for clades that have undergone adaptive radiations through the occupation of diverse niches (Mooers *et al.*, 1999). Phylogenetic hypotheses were based on a study using microsatellite DNA variation (Petren *et al.*, 1999), which largely supported earlier hypotheses of branching relations among genera (Grant, 1999) (see Fig. 3a). All independent contrasts were calculated using the PDAP software package (Garland *et al.*, 1992). We also conducted regression analyses without correcting for phylogenetic relationships in order to test the influence on our results of potential uncertainty with the microsatellite DNA-derived phylogeny (Burns *et al.*, 2002; Zink, 2002).

## Results

Means and SDs for morphological and bite force traits are presented in Table 1. For both size-corrected and raw data, we identified strong and positive correlations between bite force and two beak dimensions: beak depth and beak width (Table 2 and 3; Fig. 2). Beak length, however, is weakly or not correlated with bite force across species (Table 2 and 3). Our analyses also revealed a strong and previously unrecognized relationship between head dimensions and bite force (Table 2 and 3; Fig. 2).

A stepwise multiple regression analysis that included all residual morphological measures and wing chord (as an indicator of body size) as independent variables, with residual bite force as the dependent variable, retained a highly significant model ( $r = 0.98$ ) with head width and beak depth as the only significant predictor variables. Standardized partial regression coefficients revealed that head width was a far better predictor of bite force than was beak depth (head width: 0.72; beak depth: 0.32). Among all morphological variables examined, and taking into account phylogenetic nonindependence of species, head width was thus the best predictor of bite force among species (Table 4). The fit of the regression of residual head width on residual bite force was remarkably high, at  $r = 0.96$  ( $P < 0.001$ , Fig. 3b). Moreover, the slope of the head width regression was

**Table 1** Mean values  $\pm$  SD of morphological and bite force traits for the nine species of Darwin's finches sampled.

	Beak length (mm)	Beak depth (mm)	Beak width (mm)	Head length (mm)	Head depth (mm)	Head width (mm)	Bite force (N)	Tarsus length (mm)	Wing chord (mm)	Body mass (g)
<i>Certhidea olivacea</i> (30)	7.41 $\pm$ 0.44	3.90 $\pm$ 0.21	4.40 $\pm$ 0.29	27.24 $\pm$ 1.42	10.64 $\pm$ 1.15	12.53 $\pm$ 0.57	1.67 $\pm$ 0.58	19.88 $\pm$ 1.05	52.66 $\pm$ 2.44	9.88 $\pm$ 0.61
<i>Cactospiza pallida</i> (5)	12.16 $\pm$ 0.55	7.99 $\pm$ 0.32	7.34 $\pm$ 0.14	34.64 $\pm$ 0.51	13.40 $\pm$ 1.70	15.52 $\pm$ 0.84	10.59 $\pm$ 1.66	23.18 $\pm$ 1.19	70.60 $\pm$ 1.98	22.50 $\pm$ 1.32
<i>Camarhynchus parvulus</i> (24)	7.56 $\pm$ 0.50	7.03 $\pm$ 0.34	6.42 $\pm$ 0.20	26.36 $\pm$ 0.81	12.28 $\pm$ 1.33	13.89 $\pm$ 0.50	4.59 $\pm$ 1.14	20.19 $\pm$ 2.14	62.75 $\pm$ 1.62	12.63 $\pm$ 0.97
<i>Camarhynchus psittacula</i> (2)	8.78 $\pm$ 0.85	8.71 $\pm$ 1.15	7.53 $\pm$ 0.55	27.51 $\pm$ 4.40	14.05 $\pm$ 2.21	14.83 $\pm$ 0.43	10.06 $\pm$ 2.83	21.45 $\pm$ 1.97	65.25 $\pm$ 4.60	17.00 $\pm$ 0.00
<i>Geospiza fortis</i> (147)	11.52 $\pm$ 0.95	11.36 $\pm$ 1.19	9.92 $\pm$ 0.98	32.49 $\pm$ 2.21	15.46 $\pm$ 1.25	15.87 $\pm$ 1.13	17.40 $\pm$ 6.96	20.80 $\pm$ 1.73	69.59 $\pm$ 4.03	21.46 $\pm$ 3.46
<i>Geospiza fuliginosa</i> (65)	8.28 $\pm$ 0.58	7.31 $\pm$ 0.60	6.84 $\pm$ 0.31	27.74 $\pm$ 1.15	12.43 $\pm$ 1.10	13.91 $\pm$ 3.35	5.26 $\pm$ 1.30	18.32 $\pm$ 1.30	60.97 $\pm$ 2.68	14.13 $\pm$ 1.91
<i>Geospiza magnirostris</i> (11)	15.07 $\pm$ 0.79	16.39 $\pm$ 1.04	13.98 $\pm$ 0.51	37.17 $\pm$ 1.77	18.97 $\pm$ 0.57	19.58 $\pm$ 1.04	70.77 $\pm$ 15.28	23.15 $\pm$ 1.72	77.55 $\pm$ 4.77	32.77 $\pm$ 2.04
<i>Geospiza scandens</i> (24)	13.85 $\pm$ 0.77	8.91 $\pm$ 0.55	8.32 $\pm$ 0.45	36.30 $\pm$ 2.50	14.01 $\pm$ 1.05	15.31 $\pm$ 0.84	7.76 $\pm$ 1.69	20.96 $\pm$ 1.16	68.52 $\pm$ 4.00	21.56 $\pm$ 2.36
<i>Platyspiza crassirostris</i> (28)	10.24 $\pm$ 0.44	11.15 $\pm$ 0.50	9.68 $\pm$ 0.32	31.60 $\pm$ 3.80	16.29 $\pm$ 0.75	17.08 $\pm$ 1.24	15.56 $\pm$ 2.82	25.47 $\pm$ 1.79	81.88 $\pm$ 2.09	31.30 $\pm$ 2.72

Sample sizes for each species are indicated in between brackets next to species names.

**Table 2** Regressions of bite force as the dependent variable vs. head and beak and body dimensions.

Variable	<i>r</i>	<i>P</i> -value	Slope
Beak length	0.78	0.012	3.10
<b>Beak depth</b>	0.97	0.000	2.53
<b>Beak width</b>	0.98	0.000	3.13
Head length	0.71	0.032	5.58
<b>Head depth</b>	0.98	0.000	5.92
<b>Head width</b>	0.98	0.000	7.82
Wing chord	0.86	0.003	6.79
Tarsus length	0.62	0.077	6.52
Body mass	0.90	0.001	2.32

Bold variables indicate variables correlating strongly with residual bite force. Analyses with other size indicators (e.g. tarsus length, body mass) gave similar results.

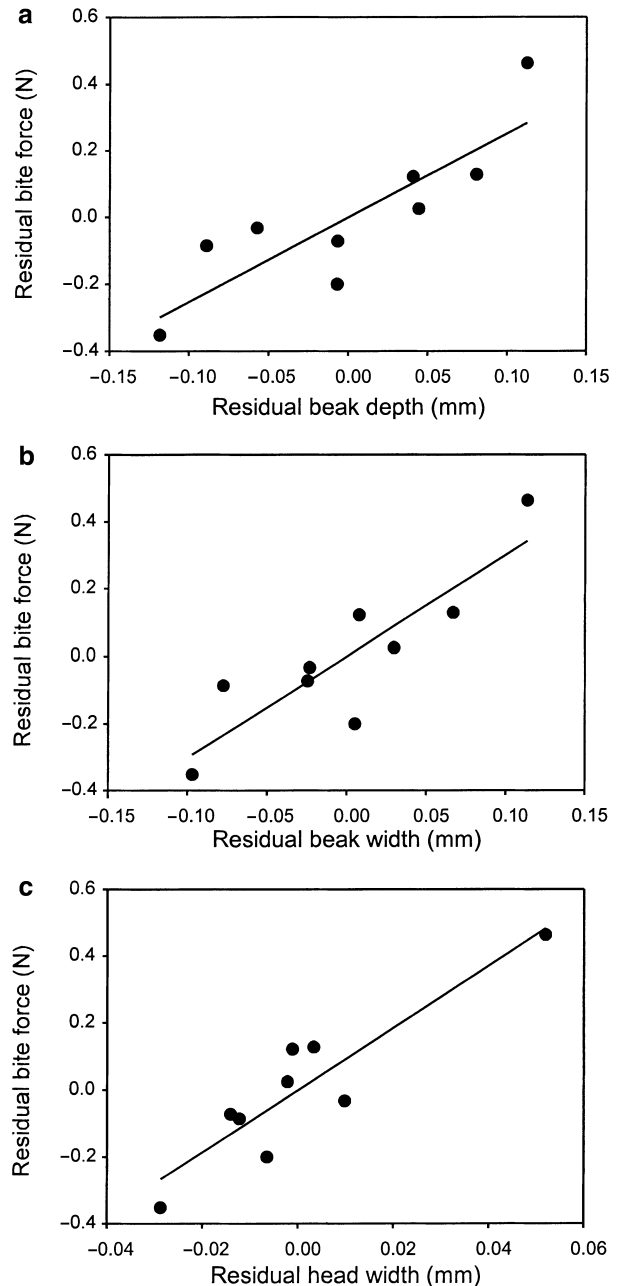
**Table 3** Regressions of residual bite force as the dependent variable vs. residual head and beak dimensions, not corrected for phylogenetic nonindependence.

Variable	<i>r</i>	<i>P</i> -value	Slope
Residual beak length	0.46	0.21	1.35
<b>Residual beak depth</b>	0.88	0.002	2.61
<b>Residual beak width</b>	0.91	0.001	3.14
Residual head length	0.31	0.42	1.71
<b>Residual head depth</b>	0.91	0.001	6.53
<b>Residual head width</b>	0.91	0.001	9.34
Residual tarsus length	0.33	0.39	-3.14
Residual body mass	0.53	0.14	2.90

Residual data are based on regressions on wing chord. Bold variables indicate variables correlating strongly with residual bite force. Analyses with residuals based on regressions on other size indicators (e.g. tarsus length, body mass) gave similar results.

comparatively high (Tables 3 and 4), which suggests that even small changes in residual head width would have major consequences for the evolution of bite force capacity.

Because residual beak and head dimensions were correlated, we calculated an indicator of beak shape – residuals from a regression of beak depth on beak width; hereafter referred to as beak depth/beak width – that was not correlated with residual head width ( $r = -0.44$ ,  $P = 0.28$ ). A new stepwise multiple regression that included all residual morphological measures, wing chord and this new indicator of beak shape retained a highly significant model ( $r = 0.99$ ) that included only head width and beak depth/width. Inspection of the standardized partial regression coefficients again indicates that head width is the best predictor of bite force (head width: 1.15; beak depth/width: 0.31). This new analysis suggests that head width and beak shape (depth relative to width) are better predictors of bite force in Darwin's finches than are simple measures of beak size *per se* (i.e. depth and width).



**Fig. 2** Relationships between residual beak depth (a), residual beak width (b), residual head width (c) and residual bite forces in Darwin's finches. Circles represent residuals extracted from the regression of  $\text{Log}_{10}$  transformed species means of morphological variables and bite force against  $\text{Log}_{10}$  transformed wing chord.

## Discussion

Our results provide direct evidence that beak width and depth are correlated with bite force in Darwin's finches (see also Herrel *et al.*, in press for within species

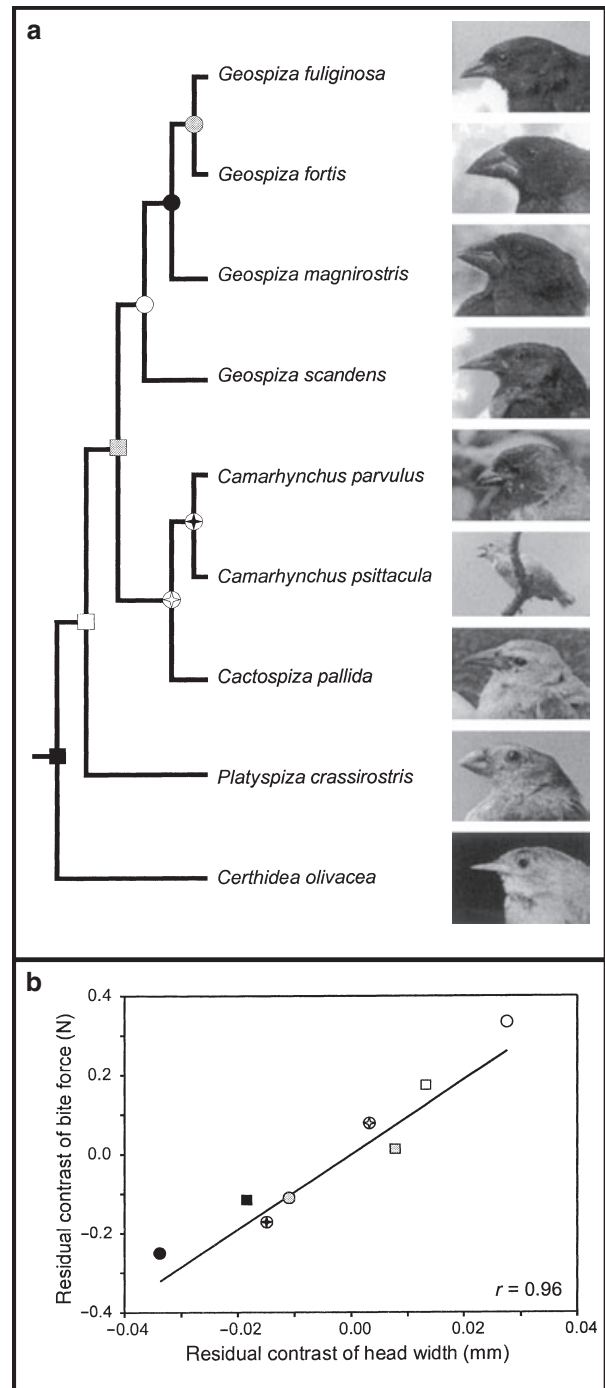
**Table 4** Regressions of residual independent contrasts of bite force as the dependent variable vs. the residual independent contrasts of head and beak dimensions.

Variable	<i>r</i>	<i>P</i> -value	Slope
Residual contrast of beak length	0.42	0.30	1.38
<b>Residual contrast of beak depth</b>	<b>0.90</b>	<b>0.003</b>	<b>3.33</b>
<b>Residual contrast of beak width</b>	<b>0.93</b>	<b>0.001</b>	<b>3.83</b>
Residual contrast of head length	0.26	0.53	1.66
<b>Residual contrast of head depth</b>	<b>0.92</b>	<b>0.001</b>	<b>6.08</b>
<b>Residual contrast of head width</b>	<b>0.96</b>	<b>0.000</b>	<b>9.2</b>
Residual contrast of tarsus length	0.39	0.35	11.71
Residual contrast of body mass	0.76	0.03	4.56

Residual contrast data are based on regressions on the contrasts of wing chord. All regressions were forced through the origin. Bold variables indicate variables correlating strongly with residual bite force.

correlates). This is consistent with previous studies that suggested performance and fitness advantages for birds with deep and wide beaks in cracking hard seeds (Grant, 1981; Grant & Grant, 1995). These data thus support the hypothesis that evolutionary increases in bite force in Darwin's finches have gone hand in hand with overall increases in beak depth and width. We also find that beak length is not associated with bite force (Table 1). As has been noted previously, beak length appears to be associated more closely with changes in requirements for food manipulation (Price *et al.*, 1984; Grant, 1999).

Our results are also consistent with models of jaw biomechanics in finches and other vertebrates. The jaw adductors are positioned at the back of the head, posterior to the orbits. Any evolutionary changes in head dimensions at this location will likely drive changes in the size or position of the jaw adductors and hence influence bite force capacity (Bowman, 1961; Van der Meij & Bout, 2004). In an analysis of jaw musculature in Darwin's finches, Bowman found that as head size increases across species, the size of jaw adductor muscles also increases (Bowman, 1961). Evolutionary changes in relative head depth are also likely associated with changes in the orientation of the jaw adductor muscles relative to the lower jaw (e.g. more vertical orientation of the adductor externus complex, see Figure 6 in Bowman, 1961), and changes in relative head width most likely affect the maximum allowable volume, and thus the cross-sectional area of the jaw adductors (see also Figure 21 in Bowman, 1961). Both of these changes in the jaw adductor muscles should have strong and positive effects on bite force potential. It would be useful to test further this hypothesis using additional biomechanical approaches (e.g. dissections, electromyography), although some of these approaches will not be possible given these birds' protected status. Still, recent experimental data on a wide range of estrildid and fringilid finches demonstrate that bite force generation capacity is



**Fig. 3** (a) Phylogeny depicting the relationships among the species examined in this study. Photographs to the right illustrate the heads and beaks of each species. Nodes are coded by symbols. (b) Graph showing the relation between the residual contrast of head width and the residual contrast of bite force ( $r = 0.96$ ). Symbols represent nodes in the phylogeny indicated in (a).

closely related to the size of the jaw adductors (Van der Meij & Bout, 2004), thus further supporting our hypothesis.

Our finding that head width is the strongest predictor of bite force across the Darwin's finches has interesting implications for the evolution of beak dimensions in these birds. In particular, our results suggest that evolutionary adjustments to bite force could be achieved through changes in head shape that are somewhat independent of beak size and shape, i.e. that head and beak dimensions may be partially decoupled in their evolution. This is important because beak size and shape also play a crucial role in food manipulation, drinking, preening, etc. (Grant, 1981, 1999). During the finch radiation, partial decoupling of selection on the beak and head may have facilitated the evolution of the considerable variability in beak dimensions observed within some species (Grant, 1999). As finches evolved stronger bite forces, corresponding changes in beak strength and thus beak dimensions were likely required to avoid structural failure (i.e. beak fracture) in the face of the forces generated during biting. This appears to be most strongly reflected in beak shape expressed as the depth of a beak for a given width.

Studies of phenotype-environment associations in Darwin's finches have provided some of the most compelling evidence for the adaptive nature of vertebrate radiations (Simpson, 1953; Schluter & Grant, 1984; Schluter, 2000). However, it is increasingly recognized that adaptive radiation is also contingent upon evolutionary changes in trait utility, i.e. the mechanisms that underlie phenotype-environment correlations (Schluter, 2000). Darwin's finches have served as a key model system in documenting one aspect of trait utility – the fitness consequences of morphological variation (Grant & Grant, 1995). Here we illustrate that an examination of ecologically relevant performance traits such as bite force, which provide a bridge between morphology and fitness (see Arnold, 1983; Wainwright & Reilly, 1994) may provide a means to identify potential pathways of evolutionary diversification.

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## References

- Abbott, I., Abbott, L.K. & Grant, P.R. 1977. Comparative ecology of Galapagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecol. Mon.* **47**: 151–184.
- Arnold, S.J. 1983. Morphology, performance and fitness. *Am. Zool.* **23**: 347–361.
- Bowman, R.I. 1961. Morphological differentiation and adaptation in the Galapagos Finches. *Univ. Calif. Publ. Zool.* **58**: 1–302.
- Burns, K.J., Hackett, S.J. & Klein, N.K. 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution* **56**: 1240–1252.
- Garland, T. Jr., Harvey, P.H. & Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**: 18–32.
- Gibbs, H.L. & Grant, P.R. 1987. Oscillating selection in Darwin's finches. *Nature* **327**: 511–513.
- Grant, P.R. 1981. The feeding of Darwin's finches on *Tribulus cistoides* (L.) seeds. *Anim. Behav.* **29**: 785–793.
- Grant, P.R. 1999. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton, NY.
- Grant, P.R. & Grant, B.R. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49**: 241–251.
- Grant, P.R. & Grant, B.R. 2002a. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707–711.
- Grant, P.R. & Grant, B.R. 2002b. Adaptive radiation of Darwin's finches. *Am. Sci.* **90**: 130–139.
- Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. 2001. The implications of bite performance for diet in two species of lacertid lizards. *Can. J. Zool.* **79**: 662–670.
- Herrel, A., O'Reilly, J.C. & Richmond, A.M. 2002. Evolution of bite performance in turtles. *J. Evol. Biol.* **15**: 1083–1094.
- Herrel, A., Podos, J., Huber, S.K. & Hendry, A.P. in press. Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Funct. Ecol.*, in press.
- Lack, D. 1947. *Darwin's Finches*. Cambridge University Press, Cambridge.
- Liem, K.F. 1973. Evolutionary strategies and morphological innovations – cichlid pharyngeal jaws. *Syst. Zool.* **22**: 425–441.
- Mooers, A.O., Vamosi, S.M., Schluter, D. 1999. Using phylogenies to test macroevolutionary hypotheses of trait evolution in Cranes (Gruinae). *Am. Nat.* **154**: 249–259.
- Petren, K., Grant, B.R. & Grant, P.R. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length variation. *Proc. R. Soc. Lond. Ser. B* **266**: 321–329.
- Price, T.D., Grant, P.R., Gibbs, H.L. & Boag, P.T. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. *Nature* **309**: 787–789.
- Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Schluter, D. & Grant, P.R. 1984. Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.* **123**: 175–196.
- Schluter, D., Price, T.D. & Grant, P.R. 1985. Ecological character displacement in Darwin's finches. *Science* **227**: 1056–1059.
- Simpson, G.G. 1953. *The Major Features of Evolution*. Columbia University Press, New York.
- Streelman, J.T. & Danley, P.D. 2003. The stages of vertebrate evolutionary radiation. *T. R. E. E.* **18**: 126–131.

Van der Meij, M.A.A. & Bout, R.G. 2004. Scaling of jaw muscle size and maximal bite force in finches. *J. Exp. Biol.* **207**: 2745–2753.

Wainwright, P.C. & Reilly, S.M. (1994) *Ecological Morphology*. The University of Chicago Press, Chicago, IL.

Zink, R.M. 2002. A new perspective on the evolutionary history of Darwin's finches. *Auk* **119**: 864–871.

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