Force–velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation?

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Summary

1. Biomechanical trade-offs have been proposed to constrain trajectories of evolutionary diversification. In songbirds, however, one such trade-off may facilitate diversification; adaptations that enhance bite force capacity are assumed to constrain vocal performance by hampering velocities of beak gape modulations required for vocal resonance tracking during song production. Resulting divergence in vocal mating signals may thus generate mating isolation between groups that eat foods of differing size and hardness.

2. We tested for a force–velocity trade-off in jaw function in Darwin's finches, by measuring bite forces and jaw movements during song production in birds on Santa Cruz Island. Bite force and speed of jaw closing varied broadly in our sample, and were negatively correlated both within and among species. Moreover, these correlations were largely independent of overall body size and phylogenetic relationships.

3. Adaptations to varying food types thus appear to drive divergence not only in beak size and bite force, but also in jaw closing velocity and vocal performance capacity. These results support a biomechanical link between adaptive divergence and mating signal divergence, the two key features that were assumed to have driven this radiation.

Key-words: bird, bite force, song, feeding

Introduction

Trajectories of ecological and evolutionary diversification are often biased by trade-offs in the development or expression of phenotypic traits (Arnold 1992; Schluter 1996). In the study of animal biomechanics, such trade-offs are generally regarded as imposing limits on organismal performance, thereby constraining diversification (Arnold 1992; Levinton & Allen 2005; Konuma & Chiba 2007). To illustrate, evolutionary specialization towards explosive locomotory movements is assumed to reduce endurance, presumably due to conflicting biomechanical and muscular requirements for speed and burst performance (Vanhooydonck *et al.* 2001; Van Damme *et al.* 2002). Speed-endurance trade-offs could then, for example, restrict the occupation of novel dietary niches as has been suggested for lacertid lizards (Vanhooydonck, Herrel & Van Damme 2007).

Our study focuses on another potential biomechanical trade-off in musculo-skeletal systems – that is between force and velocity (e.g. Westneat 1994; Paul & Gronenberg 1999; Herrel *et al.* 2002, Levinton & Allen 2005). Specialization for either force or velocity is expected to necessitate reduced performance in the other, for at least two reasons. First, muscles with high force output are typically pennate with short fibres, whereas muscles capable of rapid contraction are typically long and parallel fibered (Gans & De Vree 1987). Second, the mechanics of lever and linkage systems can either maximize force or velocity transmission, but not both simultaneously (Westneat 1994; Levinton & Allen 2005). In spite of these clear predictions, force–velocity trade-offs have only rarely been subject to explicit empirical tests, particularly at the whole-organism performance level.

Force–velocity trade-offs may hold particular significance for the evolution of foraging and song production in songbirds (Nowicki *et al.* 1992; Podos & Nowicki 2004). While singing, many birds adjust vocal tract volume, in part through modulations in beak gape distance (Westneat *et al.* 1993; Podos *et al.* 1995). These and other vocal tract adjustments actively track frequency modulations at the sound source (the syrinx), thereby enabling birds to filter vocal harmonic overtones and produce

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songs with consistently pure-tonal quality (Nowicki 1987; Nowicki & Marler 1988; Hoese *et al.* 2000; Beckers *et al.* 2003; Riede *et al.* 2006). For songs with rapid modulations in source frequencies, jaw movements need to be correspondingly rapid to maintain vocal tract resonance function. Force–velocity trade-offs, however, may constrain velocities of jaw movements, particularly for birds that have evolved the ability to bite hard, crucial when cracking hard and/or large seeds (Nowicki *et al.* 1992; Podos 1997). Indeed, birds with larger overall beaks generally show limited vocal performance, as indicated by low syllable repetition rates and narrow frequency bandwidths (Podos 1997, 2001; Podos & Nowicki 2004; Seddon 2005; Ballentine 2006, but see Slabbekoorn & Smith 2000). Given that mate choice decisions in many birds are based on variation in song structure (Searcy & Yasukawa 1996), force–velocity trade-offs may contribute to the evolution of reproductive isolation between birds adapted to different food types (Podos & Nowicki 2004).

The above scenario may have played out during the adaptive radiation of Darwin's finches of the Galápagos Islands, Ecuador. This is particularly so for the clade of ground finches (*Geospiza*), in which different species have adapted to feed on seeds of different size and hardness (Abbott *et al.* 1977; Boag & Grant 1981; Gibbs & Grant 1987; Grant 1999; Herrel *et al.* 2005a,b). We have shown previously that song parameters associated with vocal performance in Darwin's finches covary negatively with overall beak size (Podos 2001; Huber & Podos 2006). This co-variation presumably arises because high performance songs require rapid and broad jaw gape modulations that cannot be achieved by large-beaked birds with high bite force capacities (Podos *et al.* 2004; Herrel *et al.* 2005a). Divergence in song properties between groups adapted to different food types might then contribute to mating isolation, at least to the extent that the relevant song parameters are used in mate selection. Previous studies of *Geospiza* finches have shown that females choose mates largely on the basis of song parameters (Grant & Grant 1997, 1998).

Our goal was to test for a force–velocity trade-off in the jaw function of Darwin's finches. Towards this end, we measured bite force and jaw movements during singing for banded birds of known morphology. Our specific prediction was that maximal bite force would show a negative correlation with the velocity by which birds can move their jaws, and therefore with the speed and precision by which birds can maintain the resonance function of their vocal tracts. We test this prediction by examining variation among nine species and within one species that shows marked variation in overall beak size. Evidence for a trade-off between bite force and rapid gape modulations would suggest a biomechanical contribution to ecological speciation in these birds (Podos & Nowicki 2004; Podos & Hendry 2006).

Materials and methods

Field work was conducted at coastal and upland sites on Santa Cruz Island during February and March of 2003, 2005 and 2006. Birds of nine Darwin's finch species were captured in mist nets, banded with unique colour combinations, measured, tested for bite force, and then released. Morphological measurements were taken as described elsewhere (Grant 1999; Herrel *et al.* 2005a,b) and included beak length, beak width, beak depth, head length, head width, head depth, tarsus length, wing chord length, and body mass. Bite forces were measured using a Kistler force transducer set in a custom-built holder and attached to a handheld Kistler charge amplifier (see Herrel *et al.* 2005a,b). Birds were induced to bite the force transducer at the back of the jaws where seeds are typically crushed (Herrel *et al.* 2005a,b). At least three bites were recorded for each individual, of which only the strongest was retained for analysis. Gape angle during bite force measurement was kept constant by adjusting the distance between the bite plates according to the size of the bird. In total, both morphological and bite force measurements were obtained for 32 *Geospiza magnirostris*, 652 *Geospiza fortis*, 191 *Geospiza fuliginosa*, 78 *Geospiza scandens*, 61 *Platyspiza crassirostris*, 10 *Cactospiza pallida*, 3 *Camarhynchus psittacula*, 47 *Camarhynchus parvulus* and 30 *Certhidea olivacea*.

Individual birds singing in the field were filmed with a Redlake Motionmeter camera set at 250 frames per second. Only birds positioned approximately at the level of the camera were filmed. After reviewing the clips for quality (good contrast, recorded in lateral view, birds positioned perpendicular to the camera, and beak tips not obscured by vegetation), we retained between three and five song sequences for each individual for 3 *G. magnirostris*, 20 *G. fortis*, 13 *G. fuliginosa*, 7 *G. scandens*, 5 *P. crassirostris*, 7 *C. pallida*, 3 *C. psittacula*, 8 *C. parvulus*, and 9 *C. olivacea*. (See Appendix S1 Supporting Information for clip of *G. fortis* singing). The positions of the upper and lower beak tips were digitized (Fig. 1a) frame by frame and then scaled. To do so, an object of known size was placed and filmed at the location where the bird had been singing. In the few cases where this was not feasible, such as when the bird was too high in a tree, we used the beak length of the actual bird as determined from the morphological measurements (as in Podos *et al.* 2004). Scaled gape distances (between the upper and lower beak tip) were then calculated and smoothed using a fourth order zero phase shift butterworth filter with cut-off frequency set at 30 Hz (Winter 2004). Jaw movement velocity was then calculated by differentiation of the displacement profile. For each individual, only the highest instantaneous jaw opening and jaw closing velocity was retained for further analysis.

STATISTICAL ANALYSES

For interspecific analyses, we used species means of bite force, jaw closing and jaw opening velocity, gape distance and previously published data on 'vocal deviation' (Podos 2001). Vocal deviation is a composite measure of a song's trill rate and frequency bandwidth relative to a clade's upper-bound regression on these parameters (Podos 1997, 2001); lower values of vocal deviation indicate high vocal performance, and vice versa. We conducted independent contrast analyses with all branches set to unit length, as has been recommended for clades that have undergone adaptive radiations through the occupation of diverse niches (Schluter & Nagel 1995; Mooers *et al.* 1999). Additionally we ran our analyses using two sets of transformed branch lengths (Pagel and Grafen transformations; see Garland *et al.* 1999) to test whether our analyses are robust to variations in branch length. As results were similar, independent of the type of branch lengths used, we report only data for analyses with constant branch lengths. All independent contrasts were calculated using the PDAP package (Garland *et al.* 1999). Phylogenetic hypotheses were based on studies using molecular data and microsatellite DNA variation (Petren *et al.* 1999), which largely supported earlier hypotheses of branching relationships among genera. The phylogeny used for all
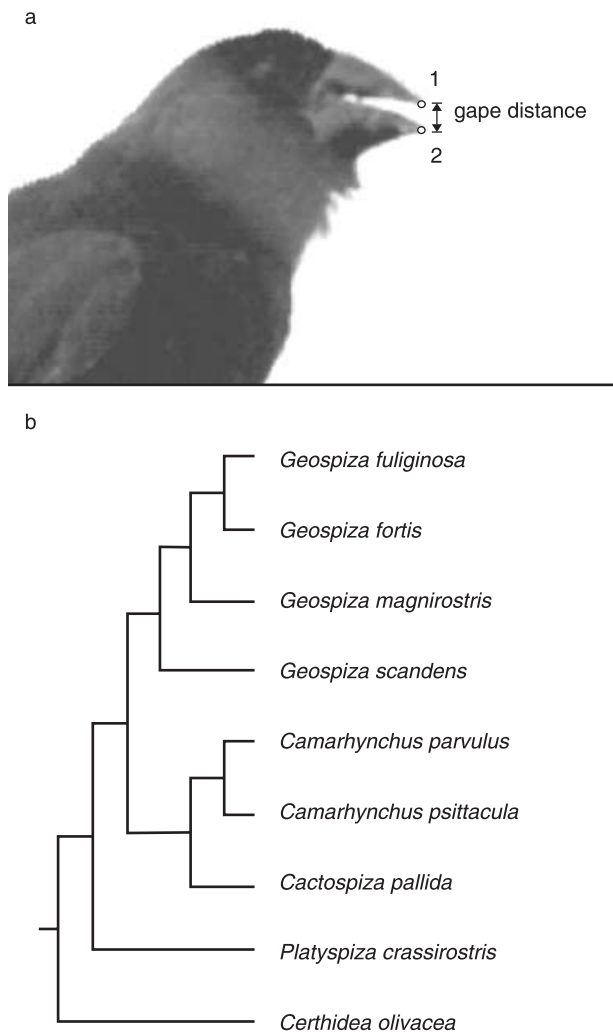
Fig. 1. (a) Frame from a high-speed video clip of a large-beaked *Geospiza fortis* singing. Landmarks digitized included the tip of the upper (1) and lower (2) beak. Based on the *XY*-coordinates of these landmarks, the gape distance and jaw movement velocity were calculated. (b) Phylogenetic relationships among the nine species of Darwin's finch included in our study based on Petren *et al*. (1999).

Fig. 2. (a) Kinematic profiles quantified from high-speed recordings in the field, showing beak movements during song production in *Geospiza magnirostris* (closed circles) and *Certhidea olivacea* (open circles) Note the greater gape distance and repetition rate in *C. olivacea* compared to *G. magnirostris* (see also Podos 2001; Podos *et al*. 2004). (b) Graph illustrating the negative relationship between the standardized contrast of bite force and the standardized contrast of jaw closing velocity (regression through the origin: $r = -0.80$; $P < 0.01$).

analyses in the present study is depicted in Fig. 1b and was obtained by pruning the tree reported in Petren *et al*. (1999) to include only the species studied here.

Intraspecific analyses focused on *G. fortis* because this species is abundant, shows unusually large variation in beak size (Hendry *et al*. 2006), bite force (Herrel *et al*. 2005a), and song parameters (Podos 2001; Huber & Podos 2006), and may even be in the early stages of speciation on Santa Cruz (Huber *et al*. 2007). For this analysis, we preferentially used jaw movement velocity data for banded birds with known bite forces. We were able to obtain such data from only nine *G. fortis*. We therefore supplemented these data by including individuals that were filmed but not previously measured ($N = 11$). In such cases, we measured beak depth on video frames and then estimated bite force based on beak depth ($r = 0.719$, Herrel *et al*. 2005a). No differences could be detected between the two data sets (ANCOVA: $F_{1,17} = 0.07$; $P = 0.80$); yet herein we report results based both for the restricted data set (with individuals of known bite forces) as well as the results for the combined data set.
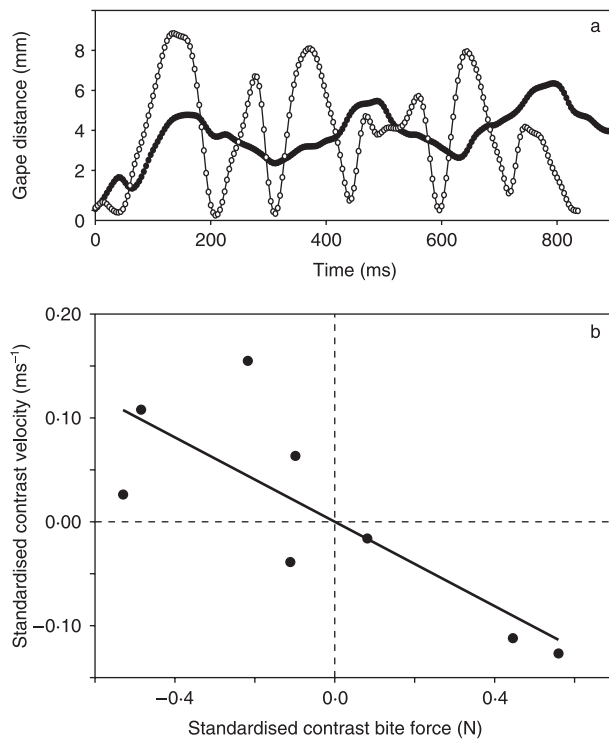
All of the measured variables might correlate with overall body size and, for this reason alone, with each other. We therefore tested, through the use of residuals, whether correlations remained after removing the effects of body size. We calculated residuals (based on standardized contrasts of the species means for interspecific analyses and individual values for intraspecific analyses) from three possible body size indicators (tarsus length, wing chord and body mass). All of these indicators yielded similar results, and so we only report the results based on tarsus length, which is measured most reliably and is least sensitive to potential short term variation in body condition.

Results

INTERSPECIFIC ANALYSIS

The nine species of Darwin's finches studied here show marked variation in jaw movement patterns. Larger-beaked species, with the large ground finch (*G. magnirostris*) at the extreme, move their jaws at low repetition rates and with small gape distances (Fig. 2a, closed circles, see also Podos 2001; Podos *et al*. 2004). Smaller-beaked species, with the warbler finch (*C. olivacea*) at the extreme, move their jaws at high repetition rates and with large gape distances (Fig. 2a, open circles). Maximal jaw closing velocity at the tip of the jaws

(averaged across individuals) ranged from 0·11 ms⁻¹ on average for the large ground finch to 0·29 ms⁻¹ on average for the warbler finch (Table 1). The range of jaw opening velocities measured was comparable (Table 1).

Jaw closing velocity correlates negatively with bite force across species in both uncorrected ($r = -0.86$; $P < 0.01$) and phylogenetically informed analyses ($r = -0.80$; $P < 0.01$; Fig. 2b), and also largely after using residuals to remove the effects of body size (uncorrected analysis: $r = -0.80$, $P < 0.01$; phylogenetically informed analysis: $r = -0.61$; $P = 0.08$). Moreover, the relationship between jaw closing velocity and bite force cannot be explained simply by absolute differences in jaw length, with longer jaws showing faster movements at the tip for a given velocity at the base. On the contrary, the species with the longest jaw (*G. magnirostris*) actually showed the slowest absolute jaw closing velocity. Our data also show that species with slow jaw closing movements had comparatively small gape distances (independent contrast analysis: $r = 0.77$, $P = 0.015$).

Jaw opening velocity was also correlated to bite force across species using phylogenetically informed analyses ($r = -0.70$; $P = 0.04$) and showed a similar but non-significant negative trend when using traditional analyses ($r = -0.59$; $P = 0.09$). When correcting for body size, however, relationships between jaw opening velocity and bite force were no longer significant (independent contrast analysis: $r = -0.42$, $P = 0.26$; traditional analysis: $r = -0.42$, $P = 0.26$) suggesting that the correlation between bite force and jaw opening velocity is due to effects of overall body size.

Our data also provide an opportunity to test the expectation that jaw closing velocity correlates positively with vocal performance (from Podos 2001). We find that species with faster jaw closing velocities tended to express lower 'vocal deviations' (independent contrast analysis $r = -0.65$, $P = 0.08$; traditional analysis: $r = -0.73$, $P = 0.04$; Fig. 3).
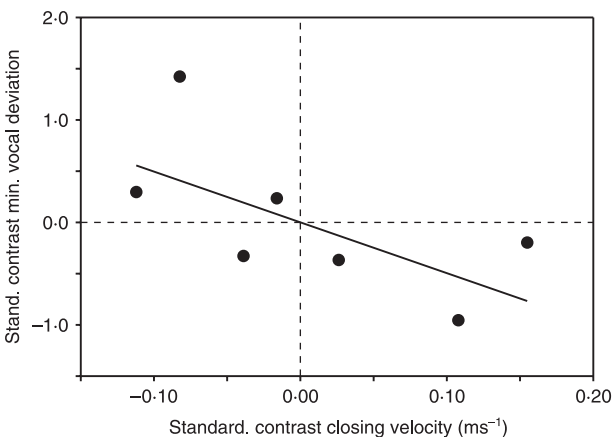

Fig. 3. Graph illustrating the negative relationship between the standardized contrast of jaw movement velocity and the standardized contrast of minimal vocal deviation (regression through the origin: $r = -0.65$, $P = 0.08$), indicating that species capable of executing high jaw movement velocities tend to sing more complex songs.

Table 1. Tarsus length, beak dimensions, bite force, gape, and jaw closing and opening velocity for 9 species of Darwin's finches

Genus	Species	Tarsus length (mm)	Beak length (mm)	Beak width (mm)	Beak depth (mm)	Maximum bite force (N)	Maximum gape (mm)	Maximum jaw closing velocity (m s⁻¹)	Maximum jaw opening velocity (m s⁻¹)
Platyspiza	crassirostris	25·47 ± 1·79 (61)	10·44 ± 0·49 (61)	9·68 ± 0·35 (61)	11·23 ± 0·54 (61)	14·5 ± 2·6 (61)	6·80 ± 2·31 (5)	0·17 ± 0·08 (5)	0·15 ± 0·08 (5)
Geospiza	fortis*	21·70 ± 1·73 (652)	11·72 ± 1·03 (652)	9·86 ± 1·04 (652)	11·26 ± 1·30 (652)	26·6 ± 6·5 (652)	10·41 ± 4·31 (20)	0·19 ± 0·06 (20)	0·20 ± 0·06 (20)
Geospiza	fuliginosa	18·32 ± 1·30 (191)	8·43 ± 0·58 (191)	6·74 ± 0·35 (191)	7·28 ± 0·73 (191)	4·7 ± 1·5 (191)	8·87 ± 3·96 (13)	0·21 ± 0·08 (13)	0·22 ± 0·09 (13)
Geospiza	magnirostris	23·15 ± 1·72 (32)	14·80 ± 0·82 (32)	13·84 ± 0·76 (32)	16·27 ± 1·16 (32)	65·5 ± 14·2 (32)	9·29 ± 3·32 (3)	0·11 ± 0·05 (3)	0·10 ± 0·04 (3)
Certhidea	olivacea	19·88 ± 1·05 (30)	7·25 ± 0·40 (30)	4·52 ± 0·41 (30)	3·76 ± 0·21 (30)	1·6 ± 0·5 (30)	11·95 ± 2·16 (9)	0·29 ± 0·08 (9)	0·22 ± 0·07 (9)
Cactospiza	pallida	23·18 ± 1·19 (10)	11·61 ± 0·88 (10)	7·46 ± 0·26 (10)	8·18 ± 0·56 (10)	9·8 ± 1·5 (10)	9·38 ± 3·04 (7)	0·23 ± 0·07 (7)	0·27 ± 0·18 (7)
Camarhynchus	parvulus	20·19 ± 2·14 (47)	7·59 ± 0·46 (47)	6·37 ± 0·27 (47)	6·92 ± 0·32 (47)	4·9 ± 1·1 (47)	9·15 ± 2·19 (8)	0·26 ± 0·11 (8)	0·23 ± 0·12 (8)
Camarhynchus	psittacula	21·45 ± 1·97 (3)	8·92 ± 0·72 (3)	7·86 ± 0·52 (3)	9·17 ± 0·88 (3)	9·3 ± 2·6 (3)	5·68 ± 2·95 (3)	0·16 ± 0·02 (3)	0·18 ± 0·05 (3)
Geospiza	scandens	20·96 ± 1·16 (78)	14·18 ± 0·74 (78)	8·12 ± 0·60 (78)	8·80 ± 0·54 (78)	7·2 ± 1·6 (78)	9·86 ± 2·45 (7)	0·24 ± 0·10 (7)	0·30 ± 0·12 (7)

Table entries are means ± SD. Sample sizes are indicated in between brackets. *note that the sample size for gape distance and jaw closing velocity for *G. fortis* is 9 for the restricted data set (see Materials and methods).
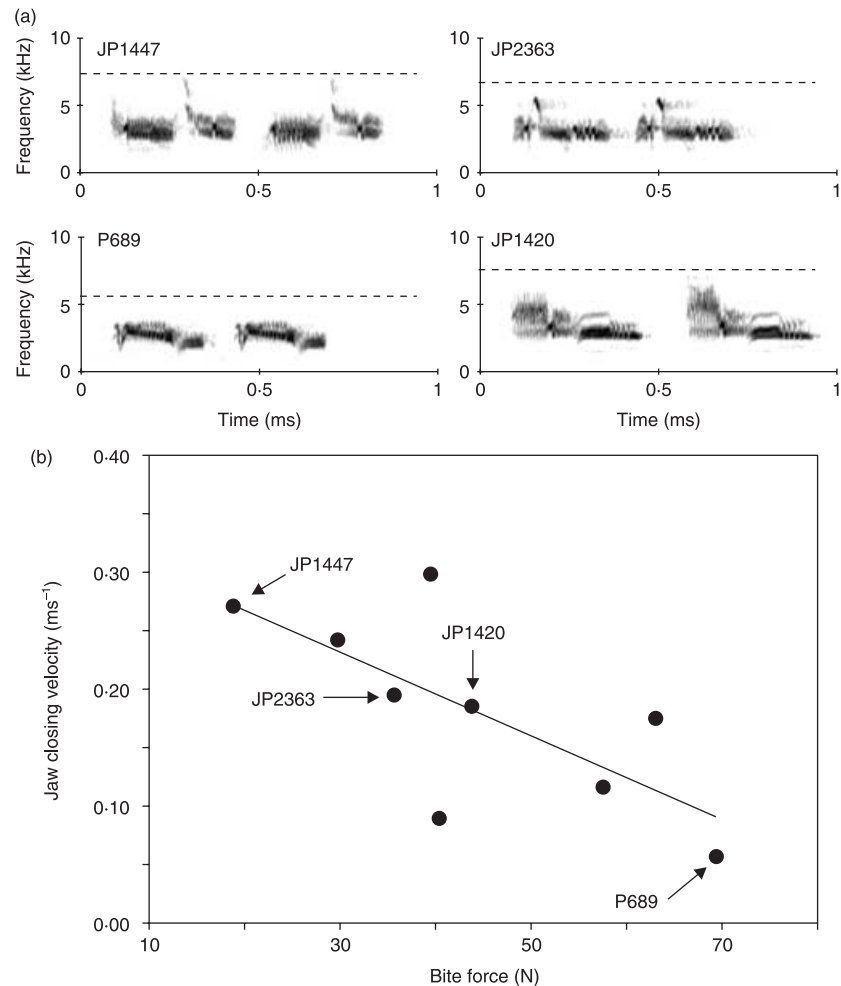
Fig. 4. (a) Representative spectrograms for four individual *G. fortis* from which bite forces and high-speed video recordings were also obtained. Animals differ in their bite forces from low to high in clockwise direction, beginning with the upper left song. Note how the song in the upper left corner is characterized by and high frequency bandwidth, a component defining song complexity (see also Podos 2001). Horizontal dashed lines indicate the upper frequency limit for each song. (b) Force–velocity trade-off at the intra-specific level (regression $r = -0.67$; $P = 0.049$) showing that *G. fortis* individuals with low bite forces move their beaks faster than do individuals with high bite forces.

INTRASPECIFIC ANALYSIS

Within *Geospiza fortis*, maximal velocity at the tip of the jaws during closing ranged from 0·06 to 0·36 ms^{-1}. As in the interspecific data, jaw closing velocity was negatively correlated with bite force (restricted data set: $r = -0.67$; $P = 0.049$; combined data: $r = -0.73$; $P < 0.001$, Fig. 4b). After using residuals to control for the effects of body size the pattern remained significant for the combined data set ($r = -0.59$; $P < 0.01$) but was no longer significant within the restricted data set ($r = -0.53$; $P = 0.14$). As with the interspecific data set, *Geospiza fortis* individuals with the slowest jaw closing movements also had the smallest gape distances (restricted data set: $r = 0.79$; $P = 0.011$; combined data set: $r = 0.62$; $P < 0.01$).

Discussion

Our data reveal a force–velocity trade-off in Darwin's finch jaw function at both inter- and intra-specific levels. Although such trade-offs are often suggested, studies explicitly testing for them have been conspicuously few (e.g. Westneat 1994; Paul & Gronenberg 1999; Herrel *et al.* 2002). Perhaps the most direct prior test of force–velocity trade-offs comes from Levinton & Allen (2005), who showed that large fiddler crab individuals have relatively low claw strength but relatively high claw closing velocity. This trade-off was attributed to differential growth of the lever arms in the system, which favours velocity but limits mechanical advantage for closing with increasing size. To our knowledge, however, no studies have tested directly for force–velocity trade-offs within and among closely related species, a crucial step in evaluating the importance of trade-offs in evolutionary diversification (Konuma & Chiba 2007).

Three potential non-mutually exclusive mechanisms that might generate force–velocity trade-offs include the intrinsic mechanics of muscle contraction, muscle architecture, and the mechanics of lever and linkage systems. For Darwin's finches, the relative contribution of these three mechanisms is presently unknown, although muscle architecture is likely important. Qualitative descriptions of jaw muscles show that Darwin's finch species with higher bite forces have more complexly pennate jaw adductors (Bowman 1961). Higher degrees of pennation may allow a muscle to generate greater forces but will impose restrictions on excursion distance and velocity (Taylor & Vinyard 2004). Consistent with this expectation, *G. fortis* individuals with the slowest jaw movement velocities also showed the smallest gape distances. Across species, mean gape distance was also correlated with mean

jaw movement velocity. Overall, these patterns support the idea that species with large bite forces and slow beak movements may indeed have more pennate jaw muscles causing them to sing at lower gapes. Analyses of the jaw adductors in these species are currently under way to test this hypothesis. Additionally, and also consistent with this hypothesis is the observation that jaw opening velocity is also lower in birds with larger bite forces. As the jaw opening muscles can evolve independently from the jaw closers, having more massive jaw closing complex composed of highly pennate muscles should impose a greater resistance to opening. The fact that the correlation between jaw opening speed and bite force is less strong and the fact that size-corrected jaw opening speed is no longer correlated to size corrected bite force suggest that this is purely a consequence of the larger jaw adductor mass against which the jaw openers have to work while opening the jaws.

In the study of adaptive radiation, patterns of morphological diversification among species are often used to infer the evolutionary mechanisms that drove the radiation (Schluter 2000). In Darwin's finches, prominent interspecific variation in beak morphology point to the importance of trophic adaptations in the evolution of this clade as a whole. This sort of inference is strengthened if it can be shown that patterns of interspecific variation are mirrored within species, that is, if relevant evolutionary mechanisms can be shown to be active at varying levels of organization within the clade. Here we can turn to *G. fortis*, which shows unusually wide variation in beak size (Grant 1999; Hendry *et al.* 2006), bite force (Herrel *et al.* 2005a), vocal performance (Podos 2001; Huber & Podos 2006), and jaw movement velocity (present study). Previous work on this species has shown that beak size is negatively correlated with vocal performance (Podos, 2001; Huber & Podos 2006). We here unite these axes of variation by showing that bite force, which is positively correlated with beak size (Herrel *et al.* 2005a), is negatively correlated with jaw movement velocity (Fig. 4). Variation and trade-offs within this single species thus parallel variation and trade-offs among species, suggesting that the correlations demonstrated here are a conserved feature of the clade.

The present results support our hypothesis of a biomechanical contribution to ecological speciation in Darwin's finches (Podos & Hendry 2006), which we now summarize and update in light of present results. Head and beak shape within and among Darwin's finch species have clearly diverged in response to ecological conditions (Abbott *et al.* 1977; Boag & Grant 1981; Gibbs & Grant 1987; Grant 1999). As a consequence, individuals and species that crack harder/larger seeds have greater bite forces, as well as larger beaks to resist the stress imposed by those forces (Price 1987; Grant 1999; Herrel *et al.* 2005a,b). As shown in the present study, trade-offs between bite force and jaw movement velocity can then impact the type of songs a bird can produce, and may thus explain the correlated evolution of finch beak morphology and song structure (Podos 2001; Huber & Podos 2006). Because song plays a central role in mating isolation between the species (Grant & Grant 1998; Grant 1999), the force–velocity trade-off confirmed here provides a possible mechanistic link between adaptive divergence in feeding niches and the evolution of mating isolation. As a caveat, we still have no experimental insights into whether song parameters as defined by vocal performance are used by Darwin's finches in mate recognition, although song parameters such as these that vary widely often do provide a basis for species or mate recognition (Nelson 1988; see also Podos & Nowicki 2004; Huber & Podos 2006, Liu *et al.* 2008). A recent study analysing the response of male *G. fortis* to songs of conspecifics from different locations on Santa Cruz island demonstrates that males attend to subtle variations in the structure of their species' songs (Podos 2007). Consequently, selection on male vocal performance capacity (sexual selection) could negatively impact the ecological scope in birds like finches which are dependent on their beaks and jaw muscles to obtain food.

The suggested biomechanical contribution to speciation might apply to other songbird radiations, with *Neospiza* buntings of the Tristan da Cunha archipelago as a case in point (Ryan *et al.* 2007). In these buntings, specialization for different foods has likely favoured evolutionary divergence in bite force capacity, which, through a negative correlation with jaw movement velocity, may explain the more rapid songs of smaller individuals (Ryan *et al.* 2007). Female preference leading to assortative mating by beak size, which we have demonstrated for Darwin's finches (Huber *et al.* 2007), may then lead to mating isolation, genetic divergence and ultimately speciation. Although we have focused on a single type of trade-off in a single clade, it seems likely that other trade-offs influencing the evolution of mating displays in other taxa may be similarly important during speciation (see Podos & Hendry 2006 for some examples). In short, we suggest that such biomechanical trade-offs may not just constrain but also promote evolutionary diversification.

Acknowledgements

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Supporting Information

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

Appendix S1. Large-beaked *Geospiza fortis* singing. Movie clip recorded at 250 frames per second and slowed down about 10 times. The movie shows a large-beaked *Geospiza fortis* singing. Note the relatively slow jaw movements and low gape angle characteristic of birds with large bite forces.

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