

Linkage and trade-off in trophic morphology and behavioural performance of birds

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Summary

1. Bill closing behaviour involves a complex suite of tissue types, kinematics, morphological states and muscle architectural arrangements that has been under the scrutiny of natural selection for millions of years. Hence, an evolutionary shift to specialize in closing force may come at a cost to closing velocity and vice versa.

2. Using field measurements on behavioural performance and morphological data from museum specimens, we tested predictions of the force–velocity trade-off hypothesis in 18 species of North American birds with diverse phylogenetic and ecological backgrounds.

3. Linear models revealed that size and shape are excellent predictors of both bite force and closing velocity. However, taken one at a time, they each have a somewhat unique set of morphological predictors. In-lever length, mandibular depth and bill width comprise the best model of prediction for force, while a combination of out-lever length and total skull length provides the best prediction of closing velocity. Additionally, in our sample, only force is size-dependent. Hence, the predicted trade-off is revealed only after correcting bite force for head size.

4. Various modes of predation and decoupled morphological prediction models for performance suggest that specialization towards one strategy (e.g. increase force) may not necessarily come at a cost to the other.

Key-words: bill, bite force, closing velocity, ecological specialization, ecomorphology

Introduction

During speciation, certain traits may be inherited together or change together in a correlated fashion (Miles & Dunham 1993). Many instances of correlated evolution, at larger scales (e.g. clade radiation), manifest themselves in a relationship between form and function. For example, in lizards, relative toe width and number of adhesive lamellae have evolved in a correlated fashion with the ability to cling to smooth surfaces (Zani 2000). Likewise, wide gape, long legs and long distal forearm elements predict aerial flycatching and active ground foraging modes in birds (Corbin 2008; Corbin, Lowenberger & Dorkoski 2013). In trophic anatomical traits, evolutionary ecomorphological patterns are particularly clear. For example, large ground finches (*Geospiza magnirostris*) have relatively deep bills and biomechanically predictable high bite forces (Abbott, Abbott & Grant 1977; Herrel *et al.* 2005a,b; De León *et al.* 2011).

Bite force is a measurement of behavioural performance and hence serves as a linkage between ecology and morphology among a wide diversity of organisms. Obviously, biting is used as a method of obtaining and processing food: stout-billed finches with higher bite forces are faster seed huskers (van der Meij & Bout 2006) and are able to handle larger, more durable seeds (Herrel *et al.* 2005a,b). However, bite force is also an important behavioural mechanism for non-feeding behaviours including play, display, defence, acquiring mates, reinforcing copulation, etc. (see Anderson, McBrayer & Herrel 2008). For example, dominant male collared lizards (*Crotaphytus antiquus*) have higher bite forces than subordinates or submissives (Husak *et al.* 2006). Hence, it makes sense that if a tool is to be used for multiple jobs, there must be some sort of optimality problem with specialization of that tool. In other words, if organisms benefit by the specialized use (e.g. force) of a tool (the skull and associated musculature) for fitness-related behaviour, it may come at a cost to another use of that tool (e.g. closing velocity).

The biomechanics of the jaw are important to understand when studying performance related to feeding. The

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jaw has been described as a third-class lever where the in-lever spans the quadrate (an element of articulation between lower jaw and skull) to the coronoid process (attachment site of jaw-closing musculature) and the out-lever spans the quadrate to the distal tip of the lower jaw (Westneat 2003; Marshall 2008). Hence, mechanical advantage, the ratio of in-lever to out-lever, is greater when the quadrate to coronoid distance is relatively long compared to the total length of the lower jaw (Westneat 1994; Albertson *et al.* 2005; Kammerer, Grande & Westneat 2005; Marshall 2008). On the other hand, higher tip-closing velocities may be accomplished by relatively small in-lever to out-lever ratio (Albertson *et al.* 2005).

By examining two related behavioural performance measures, one can test for trade-offs. Force is necessary for crushing hard prey items, whereas velocity (a fast bite) would be needed for capturing fast-moving prey. Some data support this: labrid fishes eating slow, hard-shelled prey have greater mechanical advantage, greater bite force, but slow closing velocity, whereas fish eating fast-moving prey have higher closing speed and lower force (Westneat 1994). Also, growing snappers (*Lutjanus campechanus*) shift to harder prey items and also biomechanically shift to a slower more forceful bite (Case, Westneat & Marshall 2008). The hypothesis is applicable to bird study as well. Lederer (1975) suggested bite forces in insectivores (e.g. tyrant flycatchers) only need to be great enough to restrain a captured prey item once caught, while Holzman *et al.* (2011) suggested a result of behavioural canalization by seedeaters may preclude them from eating fast-moving insects in the future. Moreover, in *Geospiza* finches, a forceful bite and concomitant slow closing velocity (i.e. force–velocity trade-off), facilitated by high mechanical advantage and thick musculature, caps the song-note frequency ranges required to attract mates (see Herrel *et al.*

2009). Hence, it is reasonable to expect a measureable force–velocity trade-off among several species of birds. However, to our knowledge, no one has tested predictions of this hypothesis on a group of bird species from a diverse phylogenetic and ecological background. Regardless of phylogenetic affinity, species exhibiting morphology associated with high mechanical advantage should have greater bite force while species with relatively long bills and short in-levers should have greater closing velocities. In the present study, we analyse video, bite force and morphometric data from 18 common North American bird species to test that bite force and closing velocity are predicted by skull morphometrics and to test for a negative relationship (trade-off) between force and velocity.

Materials and methods

TAXON SAMPLING

Taxon sampling for this study was constrained by the species pool overlap from three different efforts: (i) closing velocity data are from videos of birds filmed at feeders during multiple seasons from August 2010 to February 2012, (ii) bite force data are from wild-caught (and released) birds in multiple seasons from June 2009 to March 2012, and (iii) morphological data come from skeletal specimens housed at the Carnegie Museum of Natural History collected by CC in 1994 and LL in 2011. We were able to collect congruent data (velocity, force and morphology for different individuals of the same species) for 12 species and partial congruency to make biomechanical predictions for an additional six species (see Fig. 1, Table 1).

VIDEO OF CLOSING VELOCITIES

Using tripod-mounted Sony CCD-TRV318 and/or Casio EX-ZR100 cameras set at 30 or 240 fps, we filmed feeders passively (between 10 min and 24 h) and actively (opportunistically for

Fig. 1. Composite phylogeny for the 18 species of North American birds used in this study. AOU common name, Latin binomial and AOU 4-letter code appear at the tips. The 4-letter code is used in subsequent figures, tables and the appendix. The composite tree (without branch lengths) was constructed using Benz, Robbins & Peterson 2006; Jonsson & Fjeldsa 2006; and Hackett *et al.* 2008 and subsequently used in analysis of phylogenetically independent contrasts.

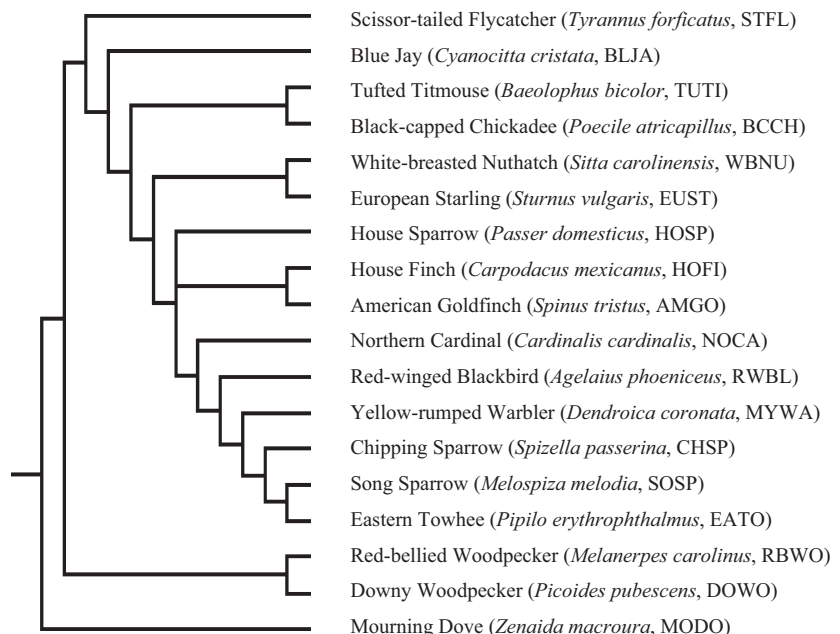


Table 1. Morphology, bite force and bill closing velocity of 18 species of North American birds. Species four-letter codes correspond to Figs 1 and 2

Species	n1	n2	n3	Closing in-lever	Coronoid process to mandible tip	Out-lever	Lower mandible height ¹	Bill length	Skull length	Bill depth	Bill width	Bite force	Closing velocity
AMGO	6	20	*	0.50	1.17	1.22	0.51	1.10	1.40	0.83	0.66	0.50	1.94
BCCH	3	20	5	0.45	1.16	1.24	0.34	1.01	1.42	0.63	0.60	0.13	2.19
BLJA	4	20	3	0.75	1.58	1.62	0.62	1.47	1.75	0.99	1.00	0.80	2.46
CHSP	3	15	*	0.42	1.16	1.22	0.38	1.05	1.41	0.68	0.59	0.13	2.14
DOWO	2	20	1	0.50	1.37	1.43	0.50	1.29	1.57	0.75	0.84	0.35	2.06
EATO	1	20	3	0.73	1.36	1.42	0.74	1.23	1.56	0.97	0.80	1.07	2.22
EUST	1	19	*	0.62	1.57	1.61	0.55	1.48	1.74	0.89	0.89	0.64	2.46
HOFI	4	18	1	0.58	1.21	1.27	0.64	1.13	1.45	0.92	0.82	0.72	1.92
HOSP	6	20	1	0.65	1.29	1.34	0.65	1.20	1.50	0.92	0.82	0.74	2.16
MODO	2	20	*	0.29	1.42	1.44	0.51	1.27	1.63	0.71	0.74	0.20	2.17
MYWA	1	17	4	0.35	1.25	1.31	0.22	1.09	1.46	0.58	0.63	-0.17	2.42
NOCA	5	20	11	0.80	1.36	1.41	0.86	1.30	1.57	1.13	0.91	1.36	2.04
RBWO	1	13	1	0.71	1.62	1.67	0.64	1.52	1.78	0.89	0.95	0.68	2.49
RWBL	2	18	*	0.64	1.42	1.48	0.65	1.36	1.64	1.02	0.75	0.94	2.08
SOSP	3	20	12	0.54	1.27	1.32	0.58	1.15	1.49	0.84	0.73	0.58	2.23
STFL	1	10	*	0.58	1.48	1.52	0.50	1.35	1.63	0.85	0.91	0.54	2.68
TUTI	3	20	8	0.52	1.27	1.34	0.42	1.12	1.50	0.79	0.72	0.46	2.03
WBNU	3	20	3	0.50	1.44	1.49	0.33	1.32	1.61	0.61	0.71	0.10	2.62

Note: Sample sizes: n1: video, n2: skull and jaw measurements, n3: bite force, *predicted bite force from morphology (see text for explanation).¹Lower mandible depth at coronoid process. All morphological measurements, bite force and closing velocity are log10-transformed. Units: morphological measurements (mm), bite force (N) and closing velocity (mm/s). Species code as in Fig. 1.

particular birds) at three sites in Pittsburgh, Pennsylvania and USA: a private residence, the Latodami Nature Center, Beechwood Farms Nature Reserve and one site on the campus of Bloomsburg University in Bloomsburg, Pennsylvania. Feeders were filled with commercially available seed mixtures and suet cakes. Both had a range of husked and unhusked seeds of various sizes. Also, we obtained video from a single scissor-tailed flycatcher (*Tyrannus forficatus*) while feeding on aerial prey items at the National Aviary in Pittsburgh. In feeder films, we identified individuals with a combination of criteria including location, species, sex, age, moult, and unique markings. Cameras were set between 10 and 15 m from the feeder to minimize parallax distortion and significant changes in the z-dimension (depth) relative to reference points. Scaling in each video was determined with a ruler (taped to the feeder), an object of known dimensions on the feeder itself, or from published species/sex averages of bill measurements (Cornell Lab of Ornithology Birds of North America online, Pyle 1997, and C. Corbin, unpublished data). We discarded data from birds with oblique views of the head, with obvious food items between the upper and lower edges of the bill, and/or where unique individuality was not certain.

The remaining video data were converted from analog to digital and/or imported directly into a computer. Sequences were trimmed, landmarked and analysed using LoggerPro, (Version 3.5, Vernier Software & Technology 2010). Depending on frame speed, landmarks in every 2nd (30 fps) or 5th (240 fps) frame were placed at the distal tips of the upper and lower rhamphotheca, the centre of the eye and another stationary point on the feeder near the bird. Closing velocity was measured as the distance (mm, derived from scaling reference) of convergence of the two bill landmarks over time (s, derived from frame rate) from open (peak (upper bill) and trough (lower bill) of sinusoidal wave) to close (convergence). The other landmarks in the video sequences were used as points of reference to account for orthogonal-axis (x, y planes only) and uniform parallel-axis excursions (e.g. movement of the head). The maximum closing value (closing velocity capacity) out of a bout of three in a

sequence was determined for each bird and then averaged across each species for analysis.

BITE FORCE

Birds were captured in mist nets and sparrow traps at Bloomsburg University. Once extracted, the birds were banded with a USGS aluminium leg band for individual identification. Bite force (N) was measured with a piezoelectric force transducer mounted to aluminium plates and to a hand-held Kistler® amplifier (see Herrel *et al.* 2005a, 2009). Birds either bit these plates voluntarily or were coaxed to bite by inserting the soft pick end of a Colgate® Wisp® toothbrush at the gape; then, the open bill was placed over the bite plates and the pick released. We attempted to obtain measurements from at least three bites per bird. For this study, the maximum (capacity) was retained, calibrated and converted to newtons (N) using a mass set and then averaged for each species. Birds were released at the place of capture. The plates and pick were sanitized with ethanol and allowed to dry between individuals. Bite forces for species not captured in the field were predicted by a linear regression with bill depth.

MORPHOLOGY

We measured skeletons housed at the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania, using either digital or dial calipers (nearest 0.05 mm). Because museum specimens were not the same individuals measured in the field, we attempted to measure the most recently curated specimens from geographically proximate locations. The measurements were as follows: closing in-lever – measured from the crista intercotylaris to the anterior point of the coronoid process; out-lever – measured from the crista intercotylaris to distal tip of the ramus; length – from coronoid to distal tip; coronoid height – the depth of the dentary at the coronoid process; bill length – measured from the nasal–frontal

hinge to tip of upper bill; skull length – its greatest length including the bill; bill depth – combined depth of upper and lower bills measured at the nasal–frontal hinge; and bill width – measured across the nasal–frontal hinge (see Nuijens & Zweers 1997 for anatomical reference). Morphological measurements were averaged for each species.

STATISTICAL ANALYSES

For purposes of normality, all data were \log_{10} -transformed prior to analysis. Because the morphological variables were not independent, we computed principal components from a covariance matrix of species means. We retained the first two orthogonal PCs for analysis; these explained *c.* 95% of the total morphological variation. In regression analyses, these were entered as morphological predictors while bite force and bill closing velocity were entered as the two response variables. In similar fashion, we tested for a negative relationship between bite force and closing velocity.

In general, behavioural and morphological traits are phylogenetically interrelated, a violation of regression assumptions. Hence, we calculated and analysed phylogenetically independent contrasts (Felsenstein 1985) of our data using the PDAP package (Midford, Garland & Maddison 2005) in Mesquite 2.75 (Maddison & Maddison 2011). For this, we constructed a composite phylogeny from existing literature (Benz, Robbins & Peterson 2006; Jonsson & Fjeldsa 2006; and Hackett *et al.* 2008; see Fig. 1). Branch lengths were set equal to one, and polytomies were assumed soft and randomly resolved with a value of 0.001. We ran contrast regressions through the origin (Garland, Harvey & Ives 1992). Analyses not run in Mesquite were run in JMP (Version 9, 2010).

Results

A total of 18 species of North American birds were examined and the averaged \log_{10} data are presented in Fig. 2 and Table 1. PC1 explained 71% of the variance and the loadings of the original variables on PC1 were all positive and of similar magnitude. We interpret this as a size axis; species with overall large skull characteristics are to the right of the origin, and species with proportionally smaller features occupy the space to the left of the origin. PC2 explained 24.4% of the variance and the loadings were of different signs and magnitudes (Table 2). Species with high mechanical advantage (long in-lever, short out-lever), tall coronoid process and short, deep bill are at the positive end of this axis while species with a low mechanical advantage, long and/or flat bill, and reduced coronoid process are at the negative end (Fig. 2).

PC1 (skull size) was positively related to bite force ($R^2 = 0.52$, $F_{17} = 17.57$, $P < 0.001$) (Fig. 2a) but not bill closing velocity ($R^2 = 0.12$, $F_{17} = 2.16$, $P = 0.16$) (Fig. 2c). PC2 (high mechanical advantage) was positively related to bite force ($R^2 = 0.45$, $F_{17} = 13.24$, $P = 0.002$) (Fig. 2b) and negatively related to closing velocity ($R^2 = 0.50$, $F_{17} = 16.08$, $P = 0.001$) (Fig. 2d). Surprisingly, while negative, the relationship between bite force and bill closing velocity was not significant ($R^2 = 0.05$, $F_{17} = 0.88$, $P = 0.36$) (Fig. 2e). Excluding species where forces were

Fig. 2. (a–f) Scatterplots and regression visualizations. The relationships (a–d) between size (PC1) and shape (PC2) morphology and behavioural performance (bite force and closing velocity) for 18 species of North American birds. Axis interpretations, corresponding to PC loadings in Table 2, are written along the PC axes. Also plotted are the relationships between velocity and bite force (e) and velocity and size-corrected bite force (f). Note that size predicts force but not velocity (a & c), hence prompting the size-correction when testing for a trade-off in behavioural performance variables. Species codes correspond to Fig. 1. Regression equations and best-fit lines (solid lines) are depicted when there is a significant relationship ($\alpha < 0.05$). The final plot (f) shows both linear and quadratic regression models (dashed line).

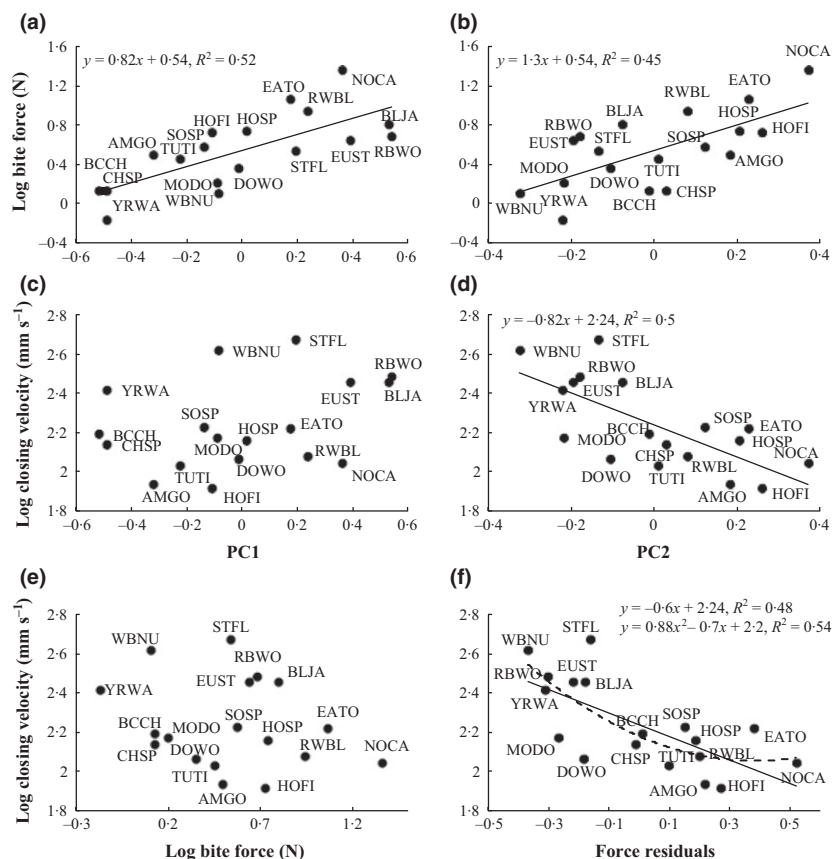


Table 2. Loadings, eigenvalues and per cent variance explained of the principal components analysis of skull measurements

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Closing in-lever	0.80	0.46	0.37	-0.06	0.06	0.00	0.00	0.00
Coronoid process to mandible tip	0.88	-0.48	-0.03	-0.02	0.01	0.03	-0.03	0.01
Out-lever	0.88	-0.47	0.03	-0.04	0.02	0.05	-0.02	-0.02
Coronoid process height	0.72	0.65	-0.21	-0.01	0.12	0.00	0.00	0.00
Bill length	0.93	-0.35	-0.04	-0.04	-0.02	-0.12	0.01	0.00
Skull length	0.88	-0.46	-0.07	-0.06	0.01	0.07	0.06	0.00
Bill depth	0.76	0.63	-0.04	-0.05	-0.16	0.02	0.00	0.00
Bill width	0.93	0.03	0.04	0.36	-0.02	0.00	0.00	0.00
Eigenvalues	0.11	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Percent variance explained	70.87	24.37	2.39	1.34	0.68	0.30	0.04	0.01

predicted from morphology (to avoid circularity) produced similar results ($R^2 = 0.05$, $F_{12} = 1.57$, $P = 0.24$).

Analyses of independent contrasts were similar in outcome. There was a significant positive correlation between the contrasts of PC1 and bite force ($R^2 = 0.74$, $F_{16} = 45.95$, $P < 0.001$), but not bill closing velocity ($R^2 = 0.11$, $F_{16} = 1.97$, $P = 0.19$). The contrasts of PC2 and bite force were positively correlated ($R^2 = 0.44$, $F_{16} = 12.52$, $P = 0.003$). There was a significant negative correlation between the contrasts of PC2 and bill closing velocity ($R^2 = 0.33$, $F_{16} = 7.94$, $P = 0.012$), but no relationship between the contrasts of bite force and bill closing velocity ($R^2 = 0.006$, $F_{16} = 0.10$, $P = 0.76$).

Discussion

In this analysis of the morphology and biting behaviour in birds from various phylogenetic and ecological backgrounds, we found significant positive relationship between skull size and bite force. This is not surprising since an overall increase in body size is related to increase bite force (Herrel, O'Reilly & Richmond 2002). Skull size, scaling isometrically with body size (Rising & Somers 1989), predicts adductor muscle mass and hence bite force (van der Meij & Bout 2004). Skull shape plays a role in bite force as well. As mechanical advantage increases in our sample, so did bite force. The coronoid process and bill depth play important roles in this interpretation. The coronoid process is an attachment site for the adductor musculature and a larger, more prominent process should facilitate higher bite forces (Nogueira, Peracchi & Monteiro 2009). Bill depth is a component of mechanical advantage in seedeaters and hence is a good predictor of bite force in *Geospiza* finches (see Herrel *et al.* 2005a,b). Also, closing velocity responded to morphological shape as predicted by biomechanical models (Albertson *et al.* 2005; see Hoese & Westneat 1996): animals with small closing in-lever to out-lever ratios exhibited relatively high closing velocities.

Surprisingly, even with strong and predictable relationships between morphology and performance, while negative, there was not a significant trade-off between closing velocity and bite force. Our results are in contrast to long-held biomechanical predictions and empirical study (see

Ritchie 1954 and references therein; see Reiser *et al.* 2013; Vogel 2013). We think there are two main, not necessarily mutually exclusive, explanations for this. First, the simplest explanation is that we did not capture maximum closing velocities for some or all of the birds in our films. Better measures of maximal closing velocity may come from singing (*sensu* Herrel *et al.* 2009) or electrically stimulated birds (*sensu* Lederer 1975). Also, our within-species sample sizes could be improved. If we assume that (i) the maximal velocities filmed in our samples closely approximate those found in even less controlled natural situations and (ii) intraspecific variability is smaller than interspecific variation (see Corbin 2008 and Corbin, Lowenberger & Dorkoski 2013), we may consider another biological possibility – velocity and force are biomechanically decoupled. Mouth-closing biomechanics (e.g. musculature, bone morphology and juxtaposition) associated with forceful or high velocity adduction may exhibit multiple modalities (see Alfaro, Bolnick & Wainwright 2005).

To entertain this idea, we explored reduced models of predictors in a stepwise fashion for each response variable. This allows us to (i) assess our interpretation of the second PC axis (albeit in least-squares space) and (ii) determine whether there is a common set of morphological predictors for bite force and velocity. We performed two *a posteriori* multiple regression analyses (forward stepwise) using the skull variables as predictors, one with bite force as the dependent variable and one with closing velocity as the dependent variable. For force, the best model (based on AIC and Mallow's Cp criteria) included the closing in-lever, coronoid height, bill depth and bill width ($R^2 = 0.987$, $P < 0.001$). However, for velocity, the best model included out-lever, coronoid height and skull length ($R^2 = 0.753$, $P < 0.001$). This decoupling suggests force, compared to closing velocity, may have a different biomechanical modality: force being more intimately tied to the size of the musculature (i.e. the regression of PC1 and bite force) and velocity more associated with the length and juxtaposition of the elements in the lever system. If this is true, then evolutionary specialization (e.g. investment in heavy musculature for high bite force) may not necessarily prevent a group from eventually exploiting a fast closing velocity (Holzman *et al.* 2011). Body

size also may be obscuring a direct trade-off between force and velocity.

The relative importance of head size as a predictor variable is confounding; it helps to explain force variation but not necessarily that of closing velocity. It seems that body size, or at least head size in our data, may be eclipsing a trade-off between the two response variables. Hence, we decided to partition (again, *a posteriori*) bite force into size and non-size components and rerun the trade-off regression, this time between velocity and a size-corrected form of bite force. First, we regressed bite force against PC1 and secondly, regressed the resulting residuals against closing velocity. This correcting manoeuvre produced the significant negative correlation expected from biomechanical models ($R^2 = 0.48$, $F_{1,17} = 14.73$, $P = 0.002$). Once the variation due to size was removed, the underlying trade-off between force and velocity becomes apparent (Fig. 2f). However, we are somewhat uncomfortable with the need to statistically remove size to uncover this pattern. Size is a central theme of ecological generalism (Sih & Christensen 2001). Relatively large predators should have increased ability to switch to other prey items as well as reduced energetic expenditure associated with handling time (MacArthur & Pianka 1966). Some selective fine-tuning of jaw morphology (at any given body size) may have significant impacts on the evolutionary ecology of species, lineages and clades. The concomitant large gape, high bite force, resulting fast husking times of larger finches (see van der Meij & Bout 2006), a relatively long in-lever, wide gape and prominent coronoid morphology in lizards (see McBrayer & Corbin 2007), and coronoid biomechanics tied to killing modes in raptors (see Sustaita 2008; Sustaita & Hertel 2010) are examples of where small changes in lower jaw configuration may foster a switch in ecological strategy. It seems that even minor variation in morphological configuration may predict fundamental ecological differences among groups of organisms. Hence, it is surprising to us that using a morphological approach to test predictions of optimal foraging is still a rare biological endeavour.

Because performance serves as the link between morphology and ecology (Bock 1966, 1994; Arnold 1983; Miles, Ricklefs & Travis 1987), it is intuitive that the evolution of ecomorphological traits also should be linked (Miles & Dunham 1993). In our analysis using phylogenetically independent contrasts, we see strikingly similar results to the analyses of tip values. During the evolutionary history of these birds, the relationships of morphology and performance have changed adaptively and in correlated fashion. On one end of the behavioural spectrum represented by these 18 species, feeding on fast-moving insects should require a bill that can quickly snap closed, while a diet of hard seeds necessitates a deep bill with high mechanical advantage.

We should note that in this analysis, we are assuming the bill is the only instrument of handling prey items, which is not true necessarily. For example, titmice

(*Baeolophus bicolor*) frequently will place a seed between their feet and peck it open (Grubb & Pravasudov 1994 and personal observations), rather than handle it using only bill and tongue. Hence, there is a chance that a bird like the titmouse may have the capacity to close their mouth much faster than what is reported here, particularly if it were feeding on flying insects. Using food items that are related to the preferred 'natural' diets of the birds (assumed in experiments of optimal foraging theory (Begon, Townsend & Harper 2006), such as insects and fruit, might produce a tighter relationship between bite force and bill closing velocity.

The morphology of muscles plays an important role in bite force and velocity. Skeletal muscle having long, parallel fibres is geared towards range-of-motion and/or velocity, whereas muscle that has short, pinnate fibres and a large cross-sectional area is geared towards force (Lieber & Bodine-Fowler 1993; Lorenz & Campello 2012). Jaw muscle mass is positively correlated with bite force in finches (van der Meij & Bout 2004) and in other systems (van der Meij & Bout 2004; Herrel *et al.* 2005a,b; Sustaita 2008). With regard to the species in this study, it would be interesting to characterize the adductor physiology and morphology (fibre type, cross-sectional area, geometric arrangement, origin/insertion mechanics, etc.) and their relationships to bite force and bill closing velocity. Additionally, most species in this analysis are ecological opportunists (see Appendix), potentially further clouding a morphological prediction of closing velocity. Hence, given time and resources, it would be interesting to flesh-out the gaps in our data with samples from one of the impressive seed-eating and flycatching radiations of the Southern Hemisphere.

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Data accessibility

Data for this study are deposited in the Dryad Digital Repository <http://doi.org/10.5061/dryad.2832v> (Corbin, Lowenberger and Gray 2014).

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Appendix

Diets and foraging guilds of 18 species of North American birds. Four-letter codes correspond to Fig. 1.

Species	Percent Animal	Examples of animal food	Percent vegetable	Examples of vegetable food	Foraging guild	References
BLJA	24.3	Beetles, grasshoppers, caterpillars	75.7	Acorns, chestnuts, corn	O	Beal (1896)
TUTI	66.57	Caterpillars, bees/wasps	33.43	Acorns, beechnuts, smaller seeds	I(b) O(n)	Beal, McAtee & Kalmbach (1916)
BCCH	70	Caterpillars, spiders, insects	30	Seeds of weeds and soft fruits	I(b) O(n)	Footte <i>et al.</i> (2010)
WBNU	28.2	Beetles and small bugs	71.8	Corn, acorns, wheat, sunflower	G(n) I(yr)	Williams & Batzli (1979)
EUST	41–58	Millipedes and beetles	41.4	Wild fruits and corn	O	Lindsey (1939), Cabe (1993)
HOSP	2	Insects	98	Grain and seeds (grass and weeds)	G	Judd (1901)
HOFI	2.4	Plant lice	97.6	Weed seeds and fruit	F(b) G(yr)	Beal (1907)
AMGO	N/A	Few insects	N/A	Primarily seeds of Compositae	O(b) G(n)	Coutlee (1963)
EATO	32	Insects and few spiders/snails	68	Mast, seeds (weeds), wild fruit	O	Greenlaw (1996)
SOSP	34	Insects and occasional spider/snail	66	Seeds (grass and weeds)	O(b) G(n)	Judd (1901)
CHSP	38	Caterpillars	62	Seeds (weeds)	O(b) G(n)	Beal & McAtee (1912)
RWBL	26.6	Beetles, grasshoppers, caterpillars	73.4	Seeds (grass and weeds)	O(b) G(n)	Beal (1900)
NOCA	28.99	Beetles, grasshoppers, caterpillars	71.01	Seeds (fruit and weeds)	O	McAtee (1908)
MYWA*	85	Wasps, ants, flies, plant lice	15	Fruit and seeds (weeds)	I(b) O(n)	Beal (1907)
STFL	96.12	Grass hoppers, beetles, caterpillars	3.88	Small fruit/berries and seeds	I	Beal (1912)
MODO	0.3	**	99.7	Seeds (grass)	G	Beckwith (1959)
RBWO	30.94	Beetles, grasshoppers, caterpillars	69.06	Fruit and acorns	I & O	Beal (1911)
DOWO	76.05	Beetles, ants, caterpillars	23.95	Fruit, poison ivy berries, acorns	I & F	Beal (1911)

*Myrtle Warbler ~ Yellow-rumped Warbler).

**Mourning Dove animal food was stated as accidentally consumed while eating seeds.

B, breeding; n, non-breeding, yr, year round, I, insectivore G, granivore O, omnivore F, frugivore.

Foraging guilds are from De Graaf, Tilghman & Anderson 1985.