

EXPLORING POSSIBLE HUMAN INFLUENCES ON THE EVOLUTION OF DARWIN'S FINCHES

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Humans are an increasingly common influence on the evolution of natural populations. Potential arenas of influence include altered evolutionary trajectories within populations and modifications of the process of divergence among populations. We consider this second arena in the medium ground finch (*Geospiza fortis*) on Santa Cruz Island, Galápagos, Ecuador. Our study compared the *G. fortis* population at a relatively undisturbed site, El Garrapatero, to the population at a severely disturbed site, Academy Bay, which is immediately adjacent to the town of Puerto Ayora. The El Garrapatero population currently shows beak size bimodality that is tied to assortative mating and disruptive selection, whereas the Academy Bay population was historically bimodal but has lost this property in conjunction with a dramatic increase in local human population density. We here evaluate potential ecological-adaptive drivers of the differences in modality by quantifying relationships between morphology (beak and head dimensions), functional performance (bite force), and environmental characteristics (diet). Our main finding is that associations among these variables are generally weaker at Academy Bay than at El Garrapatero, possibly because novel foods are used at the former site irrespective of individual morphology and performance. These results are consistent with the hypothesis that the rugged adaptive landscapes promoting and maintaining diversification in nature can be smoothed by human activities, thus hindering ongoing adaptive radiation.

KEY WORDS: contemporary evolution, diversification, ecological speciation, Galápagos, adaptive radiation, human impact.

The environmental conditions experienced by natural populations are increasingly altered by human activities (Pimm et al. 1995; Vitousek et al. 1997). Potential consequences of these alterations range from extirpations–extinctions (Hughes et al. 1997; Pimm and Raven 2000; Mace et al. 2003) to a variety of other ecological and evolutionary effects (Smith and Bernatchez 2008). Some potential evolutionary effects involve changes in the mean values of presumed-adaptive traits (Reznick and Ghalambor 2001; Stockwell et al. 2003; Hendry et al. 2008), as well as the resulting

changes in individual fitness, population productivity, and the probability of persistence (Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Kinnison and Hairston Jr. 2007; Pelletier et al. 2007; Gordon et al. 2009). In the present article, we focus on a different type of evolutionary effect: the consequences of human activities for the process of evolutionary diversification.

Human activities might influence evolutionary diversification in several ways (Seehausen et al. 1997, 2008; Hendry et al. 2006; Taylor et al. 2006; Slabbekoorn and Ripmeester 2008;

Smith et al. 2008), and the different possibilities could be considered inflationary (increase diversity) or deflationary (decrease diversity). On the inflation side, humans might enhance diversification by sundering formerly continuous species ranges, thereby increasing the potential for different populations to proceed on independent evolutionary trajectories. One example might be the increased divergence between *Timema* walking-stick host races following a human-caused isolation of two host plant types (Nosil 2009). Or humans can provide new environments or resources that are distinct from existing environments or resources. If these new environments can be colonized by local individuals, new forms can evolve and become reproductively isolated from ancestral forms. A classic example is the evolution of new insect host races on introduced plants (Bush 1969; Carroll et al. 1997). On the deflation side, humans might hamper or reverse diversification by increasing contact between populations or species that then breed together and fuse into a single species. Examples include the frequent hybridization of native and introduced species (Rhymer and Simberloff 1996; Streebman et al. 2004). Or humans might alter resource distributions so as to decrease the number and distinctiveness of potential adaptive peaks. In essence, this process smoothes adaptive landscapes and reduces the divergent-disruptive selection that helps to maintain distinct populations and species. A possible example involves human-caused changes in the food resources of Darwin's finches (Hendry et al. 2006)—a possibility we further investigate in the present article.

The fusion of two diverging species back into one has been called speciation reversal (Taylor et al. 2006; Seehausen et al. 2008). We suggest that speciation reversal resulting from human-induced changes in the adaptive landscape (the last mechanism in the previous paragraph) would be most likely under three conditions. The first is when sympatric forms show adaptive divergence and reproductive isolation that is due to ecological differences, as opposed to intrinsic genetic incompatibilities. The second is when ample genetic variation is present in the adaptive traits of interest, allowing them to evolve quickly under altered selection. And the third is when adaptive divergence occurs along a resource axis (e.g., diet) that is impacted by humans. Each of these three conditions applies to Darwin's finches, and we use this group to examine how humans might impact adaptive divergence by altering adaptive landscapes.

Darwin's Finches: Beaks, Bites, Diets, and Human Impacts

Darwin's finches include 14 recognized species that radiated from a common ancestor after colonization of the Galapagos Archipelago approximately 3 million years ago (Lack 1947; Grant 1999; Grant and Grant 2008). The different species show different beak morphologies (size and shape) that are well suited

for exploiting different food resources, such as seeds of different size and hardness, fruits, insects, and nectar (Lack 1947; Bowman 1961; Abbott et al. 1977; Schluter and Grant 1984; Grant 1999; Schluter 2000; Herrel et al. 2005a,b; Foster et al. 2008; Grant and Grant 2008). This adaptive diversification is thought to have then driven the evolution of reproductive barriers between the species (Schluter 2000; Grant and Grant 2008). Among the important reproductive barriers are ecological selection against hybrids (Grant and Grant 1993, 2008) and assortative mating based on beak size and song (Ratcliffe and Grant 1983; Podos 2001; Grant and Grant 2008).

Our work focuses on a part of this radiation that is in early stages of diversification: the ground finches (*Geospiza* spp.). These species diverge at only the tips of the Darwin's finch phylogeny and they are not reciprocally monophyletic as revealed by mtDNA and microsatellite markers (Petren et al. 1999; Sato et al. 1999; Zink 2002). In addition, the different ground finch species do not show the intrinsic genetic incompatibilities that would be typical of a long period of isolation (Grant and Grant 1992, 1996, 1997, 1998; Grant et al. 2005). On Santa Cruz Island, up to four *Geospiza* species can occur in sympatry, and their foraging traits seemingly correspond to alternative fitness peaks on a diet-based adaptive landscape (Lack 1947; Bowman 1961; Abbott et al. 1977; Schluter and Grant 1984; Grant 1999; Schluter 2000; Grant and Grant 2008). *Geospiza scandens* has a long beak and is a cactus specialist, whereas the other three species have deeper-blunter beaks and are more commonly granivorous. These latter species include the small ground finch (*Geospiza fuliginosa*), which has a small beak and commonly eats small-soft seeds, the medium ground finch (*Geospiza fortis*), which has an intermediate beak and commonly eats intermediate seeds, and the large ground finch (*Geospiza magnirostris*), which has a large beak and commonly eats large-hard seeds (Abbott et al. 1977; Smith et al. 1978). These beak size differences are highly heritable both within and between species (Boag and Grant 1978; Boag 1983; Keller et al. 2001; Abzhanov et al. 2004), and the three granivorous species do not differ in beak shape after controlling for allometry (Foster et al. 2008; Campàs et al. 2010).

Geospiza fortis is our focus in the present article because multiple populations of this species show (or have shown) signs of an incipient split into two forms. At one site of our study sites, El Garrapatero, two beak size morphs (small and large) are currently present in a bimodal distribution (Hendry et al. 2006). These morphs are currently fully sympatric and differ strongly in bite force (Herrel et al. 2005a), song characteristics (Podos et al. 2004; Huber and Podos 2006; Podos 2007; Herrel et al. 2009), responses to song characteristics (Podos 2010), and mate preferences (Huber et al. 2007). Also, the two morphs experience disruptive viability selection on beak size (Hendry et al. 2009), and are differentiated at neutral genetic markers (Huber et al. 2007;

De León et al. 2010). Importantly, all of these between-morph differences in *G. fortis* are intermediate to those between *G. fortis* and its smaller (*G. fuliginosa*) and larger (*G. magnirostris*) congeners.

Although the two morphs are fully sympatric at present, their specific origin is not known. The possibilities range from (1) fully sympatric speciation, to (2) secondary contact following divergence on different islands or different places on the same island, to (3) hybridization between species (De León et al. 2010; Grant and Grant 2010). Each of these options seems plausible given that (1) Darwin's finch beaks seem an excellent candidate for the sort of "magic trait" that is so conducive to sympatric speciation (Huber et al. 2007; De León et al. 2010), (2) geographic isolation among islands has certainly been an important part of the finch radiation (Lack 1947; Grant 1999) and different *G. fortis* populations can remain isolated on secondary contact (Grant and Grant 2009), and (3) hybridization clearly contributes to the existing species (Grant and Grant 2010). Our question, however, is what maintains the two morphs in their current state of sympatry, regardless of its origin.

A contrast to the strongly bimodal population at El Garrapatero is the *G. fortis* population at Academy Bay. This population was strongly bimodal in beak size prior to the 1970s but has since lost this property (Ford et al. 1973; Hendry et al. 2006). This conclusion was reached based on quantitative analysis of original data collected using similar methods from 1964, 1968, 1973, 1988, and 1999 to the present (Hendry et al. 2006). In essence, statistical support for a bimodal distribution was strong in 1964 and 1968 but not in the subsequent samples. Hendry et al. (2006) hypothesized that the decrease in bimodality at Academy Bay was the consequence of the dramatic intensification of human activities at this site. In particular, the human population in Puerto Ayora, directly adjacent to the Academy Bay site, has increased dramatically from approximately 500 in the 1960s to more than 19,000 in 2006 (Watkins and Cruz 2007). Because the Galapagos is a national park, increases in human population density are extremely localized, and so are unlikely to exert direct influences on finch populations more than a few kilometers distant—including El Garrapatero.

Hendry et al. (2006) hypothesized that humans have altered the availability of food types at Academy Bay in ways that weaken the selective forces otherwise maintaining bimodality. In the present article, we test several predictions that derive from this hypothesis. First, beak size should be less closely associated with diet at Academy Bay than at El Garrapatero, either because the slope of the association is weaker or because variation around the association is greater. The idea here is that the food types introduced by humans at Academy Bay can be used by *G. fortis* of all beak sizes, thus reducing the need for diet specialization related to beak size. Second, and for the same reason, bite force

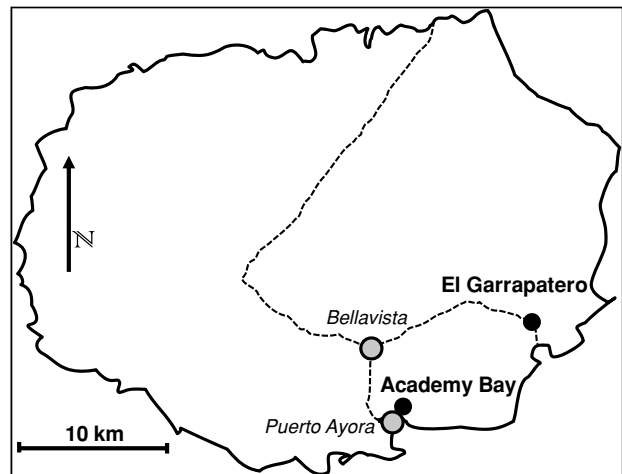


Figure 1. Study sites (black circles) and human settlements (gray circles) on Santa Cruz Island, Galapagos, Ecuador. The lines represent roads.

should be less closely associated with diet at Academy Bay than at El Garrapatero. Third, the same should be true for beak size in relation to bite force. One reason here could be a breakdown of the correlational selection that normally maintains this association: that is, individual birds no longer need to have a close match between bite force and beak size. Another reason could be that birds now have less "training" in cracking hard seeds, which might normally be necessary to develop the muscles for high bite force (i.e., plasticity). Fourth, and for the same reasons, we predict that bite force at a given beak size should be lower at Academy Bay than at El Garrapatero.

We test these predictions with a large, multiyear dataset on available foods and individual diets, bite forces, and beak dimensions at Academy Bay and El Garrapatero. This analysis is correlative and so causation is difficult to conclusively infer. Moreover, Academy Bay is the only site where a known bimodal finch population has come into contact with a rapidly expanding human population. And El Garrapatero is the only population separate from human populations that has been confirmed to be bimodal, although other such populations may exist. For these reasons, replication of the "disturbed" and "undisturbed" contexts is not possible at this time. We therefore restrict our main inferences to our specific study populations, rather than a general situation in which humans come into contact with bimodal populations.

Methods

ECOLOGICAL CONTEXT

We studied *G. fortis* at two sites on Santa Cruz Island, Galapagos, Ecuador (Fig. 1). One site, Academy Bay, is located on the south shore of the island and is contiguous with the town of Puerto Ayora. Some of the direct human influences at this site include

a high occurrence of exotic plant species and human foods, both of which finches frequently consume (see below). The other site, El Garrapatero, is located on the eastern shore of the island approximately 11 km northeast of Puerto Ayora. El Garrapatero is not adjacent to human settlements (Fig. 1) and experiences minimal direct human influences. Indirect influences do still exist in the form of browsing by feral goats and donkeys. Importantly, however, nonnative plant species and human foods are rare at El Garrapatero in comparison to Academy Bay (see below). The contrast in human influences between these two sites provides the opportunity to explore how humans might influence evolutionary diversification.

AVAILABLE RESOURCES, MORPHOLOGY, AND DIET

We surveyed the food resources available at each site using methods updated from Abbott et al. (1977). At El Garrapatero, we used GPS coordinates to randomly designate 50 different plots, each 1 m². The same number of plots was randomly designated at Academy Bay within accessible areas (in some areas the vegetation is too dense for sampling) adjoining the tourist areas of the Charles Darwin Research Station. The plots were thus approximately 700 m from the town of Puerto Ayora. For each plot, we tallied the abundance of different food items (seeds, flowers, and fruit) on each plant species in the standing vegetation. Plant species were identified with reference to published catalogues (Wiggins and Porter 1971; McMullen 1999) and by consulting herbarium specimens at the Charles Darwin Research Station. For a 10 cm² subplot within each full plot, we then tallied the abundance of seeds of each plant species on the surface of the ground. For each subplot, we also collected superficial soil samples (~45 g) that were examined under a stereoscope for additional seeds. Subplot seed counts, determined as the sum of the counts on the ground surface and in the soil samples, were extrapolated ($\times 10$) to each whole plot, and added to counts of the same items in the standing vegetation. This yielded a total count of each food type for each plot. During the above recording of plant items, we also counted and similarly tallied other potential food items, including arthropods and human items. At both Academy Bay and El Garrapatero, we sampled the same plots, but different subplots, in each of three years (2005, 2006, and 2007).

For each plant species, we measured the length, width, depth, and hardness of 10 intact seeds haphazardly collected from the ground. Hardness was estimated by cracking individual seeds with a Kistler force transducer attached to a Kistler charge amplifier (Kistler Inc., Winterthur, Switzerland). Following Abbott et al. (1977), we then estimated a weighted index of seed size-hardness for each plant species. This index (H_i) was obtained by combining mean seed depth (D) in millimeters with mean seed hardness (H) in Newtons ($H_i = \sqrt{HD}$; Abbott et al. 1977). It is intended to capture the likely efficiency with which birds of a given beak

size might handle different seeds types. That is, it should be more difficult to crack seeds that are harder and that are larger (Grant et al. 1976; Abbott et al. 1977; Boag and Grant 1984). We also categorized the seeds of each plant species into three size-hardness categories: small-easy ($H_i \leq 3.0$), intermediate ($3.0 < H_i < 11.0$), and large-hard ($H_i \geq 11.0$).

Geospiza fortis were captured in mist nets. At first capture, each bird was banded with a unique combination of three colored leg bands and a metal leg band. This allowed us to distinguish newly captured from previously captured birds, and also to individually identify free-ranging birds for feeding observations (see below). Each bird was then measured at least once for beak dimensions following Grant et al. (1985) and for head dimensions and bite force following Herrel et al. (2005a, b, 2009). Specific measurements included beak length (anterior edge of nares to anterior tip of upper mandible), beak depth (at the nares), beak width (at the base of the lower mandible), head length (from the tip of the upper mandible to the back of the head), head depth (at the deepest part of the head posterior to the orbits), and head width (the widest part posterior to the orbits). For beak traits, three measurements were taken and the median value was used for analysis. For head dimensions, only a single measurement was taken as repeat measurements were not need to improve precision (Herrel et al. 2005a). Bite force was measured at the tip and the side of the beak using a Kistler force transducer attached to a Kistler charge amplifier (Kistler Inc., Winterthur, Switzerland) (see Herrel et al. 2005a for details). All of these measurements are highly repeatable (Herrel et al. 2005a).

In each year, we recorded the number of nets set and the length of time for which they were set, which allowed us to generate rough estimates of the relative abundance of birds. Specifically, we divided the total number of *G. fortis* captured in a given site and year by the number of net hours in that site and year. We must here assume that relative capture rates are a reasonable proxy for relative abundances.

Feeding observations took place between January and April over five consecutive years: 2003 to 2007 (Table 1). Data were collected during morning and afternoon walks in which banded birds were followed and observed through binoculars until a foraging event occurred. This procedure was effective because Darwin's finches are quite tame and easily observed without disturbance at close range. For each feeding observation, we recorded the food item (e.g., plant species or "arthropod") and, if applicable, the specific plant part (e.g., seeds, fruits, leaves, or flowers). When this level of precision was not possible, we used more inclusive diet categories, including "grass" seeds (several gramineae species with small-soft seeds), "ground" (unidentified small seeds), and "human food" (Appendix S1). After a single observation of a given bird, we left it to search for other banded birds. This "point observation" method, as opposed to following individual birds

Table 1. Summary of feeding observations of individual *G. fortis* in each year at each site.

Year	Academy Bay			El Garrapatero		
	Total observations	Individual birds	Different food types	Total observations	Individual birds	Different food types
2003	52	22	10	82	16	8
2004	226	45	18	148	33	13
2005	37	19	7	241	38	11
2006	9	3	5	304	73	9
2007	1	1	1	15	2	4
Total	325	90	41	790	162	45

for extended periods of time (e.g., Abbott et al. 1977; Smith et al. 1978; Price 1987), was intended to maximize the independence of different foraging observations of individual birds. From the resulting count data, we estimated the proportion of different food types in the diets of *G. fortis* individuals. For this analysis, we included data for birds with more than one independent feeding observation.

Individual-based diet data were possible to obtain only for banded birds, and banding was only allowed in locations where tourists are not common. Thus, at Academy Bay, we could only assess individual or morph-specific diets at sites adjacent to, but not directly in, the main town. It was important, however, to obtain some information on what *G. fortis* consumed in the town itself. We therefore also performed feeding observations during walks along the main streets in Puerto Ayora. These observations are specific only to *G. fortis* as a species, rather than beak morphs or individuals

DATA ANALYSIS

Data for all years of observation were pooled for analysis because many feeding observations were needed per bird, and this depth of information required multiple years of observation. When needed to improve normality, the data were log-transformed. The software package R (<http://www.r-project.org/>) was used for all analyses, unless otherwise noted.

We first used Pearson Product Moment and Spearman’s Rank correlation coefficients to test the strength of associations among morphological traits (beak size [PC1], head size [PC1]), performance traits (bite force [tip and side]), and diet (average *Hi* for the seed types eaten, weighted by the proportion of each type eaten). We then compared these associations between the two sites by testing for significant differences between correlation coefficients (Z-test; Cohen et al. 2003). We do not here present the results for head size as these were similar to those for beak size. We also do not present the results for Spearman correlations as these were similar to those for Pearson correlations. We also classified *G. fortis* individuals into “small” and “large” beak size categories (referred to here as “morphs”). This was done using PC1 scores

based on beak dimensions (beak length, depth, and width) in a cluster analysis (e.g., Huber et al. 2007). This classification was performed for all birds pooled across both sites. We then used these data in two-way ANOVAs to test for (fixed) effects of site and beak morph category on bite force and *Hi*. We also redid these analyses replacing the dichotomous “beak morph” factor with a continuous beak size (PC1) covariate.

Given that diet is inherently multivariate and probably not best encapsulated by a single average index of seed size-hardness, we also employed permutational multivariate analysis of variance (Anderson 2001) with diet (frequencies of feeding on different food types) as the response variable. This analysis used beak morph (small or large) as a grouping variable and was based on Bray–Curtis distance matrices of proportionally scaled diets using the Adonis function (Anderson 2001). Statistical significance was obtained through 1000 permutations of the raw data. We next conducted canonical redundancy analysis (RDA) to examine the relationship between diet (response variables) and a matrix of phenotypic traits (explanatory variables). These traits included beak dimensions, head dimensions, and bite force. This analysis identifies optimal linear combinations (Thompson 1984; Ter Braak 1986; Lepš and Šmilauer 2003) of phenotypic traits that best explain the variation in diet. Statistical significance was obtained through 1000 Monte Carlo permutations.

To graphically illustrate the association between multivariate diet and morphology at each site, we performed Nonmetrical Multidimensional Scaling (NMDS) based on Bray–Curtis distances. We then used the first two NMDS axes to create a three-dimensional (3D) surface plot in the software Statistica, adding morphological traits (beak and head dimensions) and performance measures (tip and side bite force) as a vertical axis. The resulting plots helped visualize the degree to which morphological traits were associated with diet differences at each site.

Differences between the two sites in the morphological distribution of *G. fortis* could potentially influence the above analyses. For instance, the average size of birds in each morph category was larger at El Garrapatero than at Academy Bay (small morph: $t = 2.5, P = 0.01$; large morph: $t = 4.8, P < 0.001$), and this

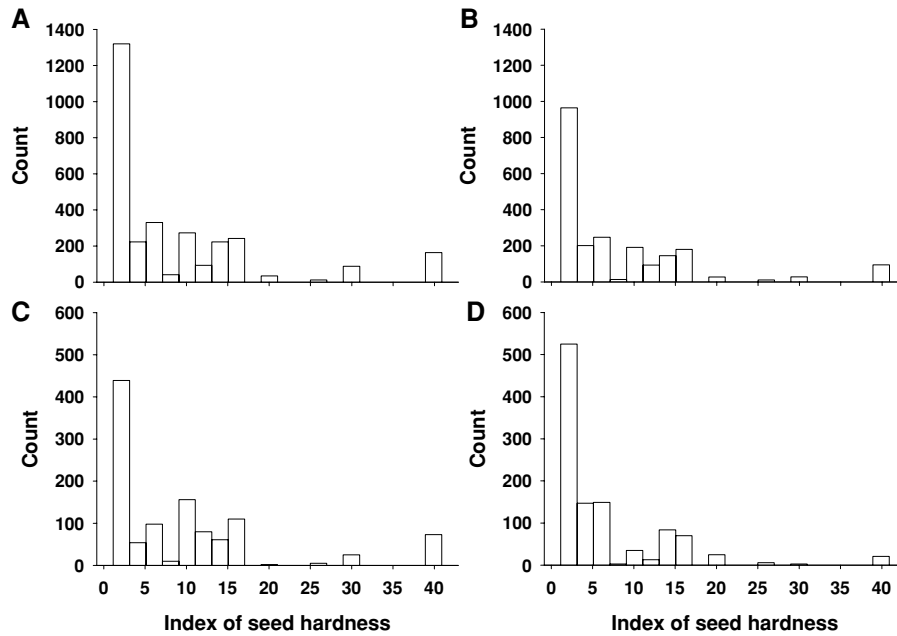


Figure 2. Distribution of available seeds of different size-hardness (*Hi*) at Academy Bay (A and C) and El Garrapatero (B and D). Seeds of all types are shown in A and B and seed types common to both sites are shown in C and D.

could influence the strength of beak-force-diet associations. To make the two sites directly comparable with respect to beak size, we therefore also “trimmed” the data by excluding extreme individuals to make the distributions more similar between the sites. After this procedure, beak size differences were no longer evident between the sites for either small ($t = 0.76, P = 0.45$) or large ($t = 11.53, P = 0.13$) morphs. We then repeated all of the above analyses using this new trimmed dataset. The untrimmed and trimmed analyses are complementary because the first quantifies the real differences between “morphs” at the two sites, whereas the latter asks what differences remain after accounting for size differences between the sites.

Results

AVAILABLE RESOURCES, DIETS, AND CAPTURE RATES

We identified a total of 44 different available food types, representing 24 different plant species (Appendix S2). Most seeds were small-soft but some large-hard seeds were also recorded (Fig. 2). If these counts were converted to biomass or energy, the relative importance of large seeds would increase. This conversion was not attempted here because all the necessary data have not been collected by previous investigators and seeds cannot currently be exported from Galapagos for analysis. Nevertheless, seed diameter is closely correlated with energy content (Schluter 1982). For this reason, and because we are interested in relative differences between sites, counts should suffice for the inferences we attempt to make.

El Garrapatero and Academy Bay differed in available food resources in several ways. First, seeds of all types combined were more than twice as abundant at Academy Bay as at El Garrapatero (Table 2; Fig. 2). Second, the overall frequency distribution of the seed size-hardness index differed between the sites for seeds of species common to both sites ($D = 0.129, P < 0.001$) and seeds of all species ($D = 0.282, P < 0.001$) (Fig. 2). In particular, relatively more small-soft seeds ($Hi < 3.0$) were present at Academy Bay (65.9%) than at El Garrapatero (57.7%). However, it is important to recognize that the differences are not large, which suggests that these natural foods are not the likely reason why bimodality differs between the sites. Third, human foods (e.g., rice, bread, and potato chips) were found only at Academy Bay (Appendix S2).

We obtained a total of 1115 point observations of 252 *G. fortis* individuals (Table 1) feeding on 28 different plant species (Appendix S1). One major difference between the two sites

Table 2. Numbers of available seed types (in plots of consistent area) across all years and both sites, categorized according to an index of seed size-hardness: small-soft ($Hi \leq 3.0$), intermediate ($3.0 < Hi < 11.0$) and large-hard ($Hi \geq 11$). The two sites differed in the frequencies of seeds in these different categories ($\chi^2 = 519.71, P < 0.01$). Percentages are given in brackets.

Seed type	Academy Bay	El Garrapatero	Total
Small-soft	27, 834 (65.9)	10, 243 (57.7)	38, 077 (63.4)
Intermediate	7722 (18.3)	4665 (26.3)	12, 387 (20.6)
Large-hard	6711 (15.9)	2856 (16.1)	9567 (15.9)
Total	42, 267 (70.4)	17, 764 (29.6)	60, 031 (100)

was that the proportion of feeding observations on “grass” (small grass seeds) and “arthropods” (consuming or searching for arthropods along branches) was at least three times higher at El Garrapatero than at Academy Bay. Another difference was that feeding observations of banded birds on human food items occurred only at Academy Bay (5.85%). In addition, for unbanded birds in the town on Puerto Ayora, we recorded 194 observations of finches feeding on human foods, including bread, cooked beans, rice, ice cream cones, and potato chips. No finches in the town were observed feeding on natural food items. Statistically, the frequency of feeding on human foods was lower at El Garrapatero than in our individual-based observations on our field site at Academy Bay (Appendix S2; $\chi^2 = 46.98$, $P < 0.001$) and in our species-level observations in the two of Puerto Ayora (Appendix S9; $\chi^2 = 336.26$, $P < 0.001$). In general, then, birds frequently exploited human food items at Academy Bay but not at El Garrapatero.

Data on capture rates in mist nets suggest that the abundance of birds is more than fourfold higher at Academy Bay (birds = 575, net-hours = 350, birds/net-hour = 1.64) than at El Garrapatero (birds = 806, net-hours = 2224, birds/net-hour = 0.36). The direction of this difference was consistent within each study year (results not shown).

BEAK SIZE AND DIET

In a simple correlation across all individuals at both sites and in all years, beak size (PC1) and the index of seed size-hardness (Hi) were positively correlated (Fig. 3). The correlations were weaker and marginally nonsignificant within each site (Fig. 3). Correlations between beak size and diet have also been found in another *G. fortis* population (Price 1987). A comparison between Academy Bay and El Garrapatero did not reveal significant differences between these correlations (Fig. 3). Analyses based on the beak morph categories suggested that (1) birds fed on larger harder seeds at El Garrapatero than at Academy Bay, and (2) that small morph birds fed on smaller softer seeds than did large morph birds at El Garrapatero but not at Academy Bay (Fig. 4A). Statistically, however, the latter of these apparent effects was not significant (Table 3). In addition, no significant effects of site, beak size, or the interaction were found in analysis of covariance (ANCOVA, Table 3).

Multivariate analysis of individual diets, as opposed to the above univariate index of seed size-hardness, was much more effective at revealing differences. In particular, the two morphs clearly have similar diets at Academy Bay but different diets at El Garrapatero (Fig. 5; Table 4). The food items with the highest scores on the axes of the multivariate space at Academy Bay were human foods, *Bursera graveolens* flowers, arthropods, *Scutia spicata* seeds, *Lantana peduncularis* seeds, and *Opuntia echios* seeds. At El Garrapatero, they were *Castela galapageia* seeds, *Commicarpus tuberosus* seeds, *Rhynchosia minima*

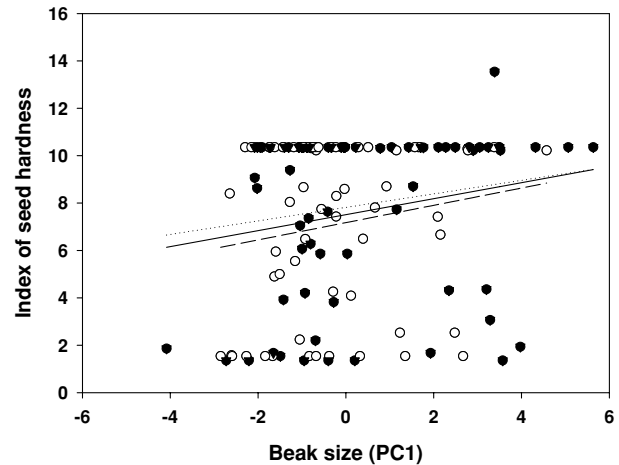


Figure 3. The average size-hardness of seeds eaten in relation to beak size. The correlation is significant when pooled across sites (solid line: $r = 0.19$, $P = 0.01$) but marginally not within El Garrapatero (dotted line and closed symbols: $r = 0.17$, $P = 0.07$) and Academy Bay (dashed line and open symbols: $r = 0.16$, $P = 0.10$). These correlations do not differ significantly between the sites ($Z = 0.04$, $P = 0.48$). The upper and lower lines with many observations correspond to abundant and accessible food items common to both sites, such as *Scutia spicata* at the upper end and grass seeds at the lower end.

flowers, grass, and *B. graveolens* seeds. Thus, part of the reason this analysis found larger differences might be because the largest differences between sites were in diet components for which no seed size-hardness data were available: human foods, flowers, arthropods, and grass.

When repeating the above analyses using the “trimmed” dataset that equalized beak sizes in the two morph categories (see Methods), the following results were obtained. First, for beak size (PC1) and diet (Hi), the correlation was not significant for both sites combined or within either site (Appendix S3). The weaker correlation for both sites with the trimmed data, relative to the untrimmed data, is probably due to the reduced range of variation in beak size in the former. Also, the strength of the correlation did not differ between sites, or was there a significant morph by site interaction in ANOVA or ANCOVA, although in both cases El Garrapatero birds ate larger harder seeds than did Academy Bay birds (Appendix S6). As in the untrimmed data, the site by morph interaction was significant in the multivariate analysis of variance (Appendix S7). Overall, then, we conclude that large and small beaked birds have different diets at El Garrapatero but not at Academy Bay, but that this difference was not captured by simple analyses of average seed size-hardness.

BITE FORCE AND DIET

In a simple correlation combining all individuals at both sites and in all years, bite force was positively correlated with seed

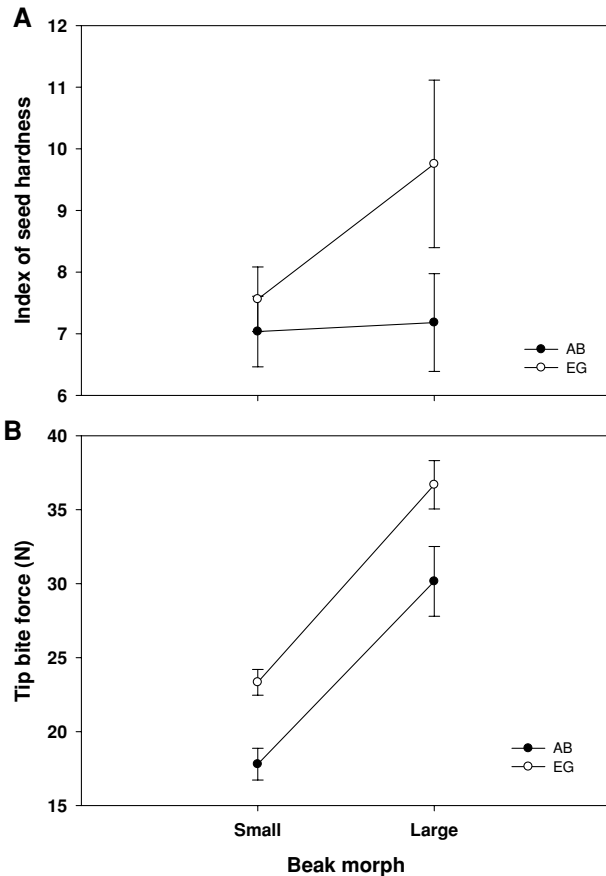


Figure 4. The relationship between beak morph category and diet and bite force. (A) The average size-hardness (H_i) of seeds consumed by *G. fortis* in each beak size category (small and large) at Academy Bay (AB) and El Garrapatero (EG). No significant differences are evident (Table 3) in a two-factor ANOVA (site and beak morph) but multivariate analyses confirm that the two morphs differ in diet at El Garrapatero but not at Academy Bay (Table 4; Fig. 5). (B) Bite force as measured at the tip of the beak is significantly different between beak morphs and sites, being higher in the large morph and at El Garrapatero (EG). Error bars indicate standard error.

size-hardness (Fig. 6), and this association was clearly stronger than the one between beak size and seed size-hardness (Fig. 3). This difference matches expectations because bite force is a composite performance trait (sensu Arnold 1983; Irschick et al. 2008) influenced by variation in both beak size and muscle mass. It should therefore be a better predictor of feeding performance than beak size alone (Bowman 1961; Herrel et al. 2005a, b; Soons et al. 2010). Bite force was also positively correlated with seed size-hardness at each site, and although the correlation appeared stronger at El Garrapatero, statistical significance was lacking in a comparison between the sites (Fig. 6). ANCOVA, however, revealed that the size-hardness of seeds consumed by finches was higher for birds with higher bite force, was higher at El Garrapatero than at Academy Bay (as above), and increased more

rapidly with bite force at El Garrapatero than at Academy Bay (Table 3).

For the trimmed data, bite force and diet correlations were positive across both sites and within each site (Appendix S4). No statistical difference in the strength of these correlations could be detected between the sites (Appendix S4). However, ANCOVA confirmed the same effects of bite force, site, and the interaction as revealed in the above analyses of the untrimmed data (Appendix S6). Overall, then, we conclude that birds with different bite forces have different diets and that these differences are greater at El Garrapatero than at Academy Bay.

BEAK SIZE AND BITE FORCE

In a simple correlation across all individuals at both sites and in all years, beak size was positively correlated with bite force (Fig. 7). Considering the sites separately, these correlations were significant for both sites and stronger at El Garrapatero than at Academy Bay (Fig. 7). In addition, ANOVA revealed that (1) small-beaked birds had lower bite force than did large-beaked birds, (2) each beak morph had lower bite force at Academy Bay than at El Garrapatero, and (3) the association between beak morph and bite force did not differ between sites (Table 3; Fig. 4B). ANCOVA found similar results for differences between beak morphs and sites, and it additionally revealed a significant interaction: the association between beak size and bite force was stronger at El Garrapatero than at Academy Bay (Table 3). Finally, multivariate analyses (RDA) showed that the strength of associations between morph-type, performance, and diet were weaker at Academy Bay than at El Garrapatero (Table 5; Fig. 8), although statistical significance might be partly influenced by the larger sample size at El Garrapatero.

In analyses of trimmed data, the beak size and bite force correlation was positive across both sites and within each site and the correlation was weaker at Academy Bay than at El Garrapatero (Appendix S5). Results for ANOVA and ANCOVA were the same as those reported above for the untrimmed data (Appendix S6). Finally, multivariate analyses (RDA) again showed that the strength of associations between beak size and bite force was weaker at Academy Bay than at El Garrapatero (Appendix S8). Overall, then, we conclude that bite forces are higher for large beaked birds than for small beaked birds, are higher at El Garrapatero than at Academy Bay, and increase more rapidly with beak size at El Garrapatero than at Academy Bay.

Discussion

CONTEXT

Previous studies of Darwin's finches have revealed that evolutionary diversification is driven by tight associations between

Table 3. Two-way analysis of variance (ANOVA) and analysis of covariance (ANCOVA) of the mean seed size-hardness (*Hi*) consumed and the bite force of individual *G. fortis* according to their beak morph/size and site (El Garrapatero and Academy Bay).

<i>Hi</i>	ANOVA			<i>Hi</i>	ANCOVA		
	df	<i>F</i>	<i>P</i>		df	<i>F</i>	<i>P</i>
Beak morph	1	1.47	0.23	Beak size	1	1.38	0.17
Site	1	16.68	<0.001	Site	1	1.11	0.27
Beak morph × site	1	0.02	0.88	Beak morph × site	1	0.54	0.81
Residual	158			Residual	216		
Tip bite force				Tip bite force			
Beak morph	1	43.65	<0.001	Beak morph	1	84.21	<0.001
Site	1	14.34	<0.001	Site	1	9.64	0.002
Beak morph × site	1	2.81	0.098	Beak morph × site	1	4.31	0.04
Residual	133			Residual	132		
Side bite force				Beak size			
Beak morph	1	42.59	<0.001	Beak morph	1	77.51	<0.001
Site	1	12.68	<0.001	Site	1	0.65	0.04
Beak morph × site	1	2.73	0.10	Beak morph × site	1	9.21	0.003
Residual	133			Residual	216		

environment (available foods and diets), performance (bite force), and morphology (beaks, heads, and bodies) (Lack 1947; Bowman 1961; Abbott et al. 1977; Schluter and Grant 1984; Grant 1999; Herrel et al. 2005a; Grant and Grant 2008). An illustrative example will set the stage for the incorporation of our results into this story. If a group of finches starts feeding on larger harder seeds, they should be selected for stronger bite forces, which are achieved through larger jaw muscles, which select for larger beaks to resist the resulting stresses (Herrel et al. 2010; Soons et al. 2010). Spinoff effects are larger heads and bodies (Herrel et al. 2005b). This correlated variation should be present among species and populations and also within populations—the latter at least partly because broad resource distributions and competition should generate selection for individual specialization (Bolnick et al. 2007).

In natural populations of Darwin’s finches, we thus expect strong associations between diet, morphology, and performance. We also expect that morphology and performance distributions will match the distribution of available food types. Supporting the first expectation, strong associations have been reported between diet, morphology, and bite force both within and among Darwin’s finch species and populations (Lack 1947; Bowman 1961; Price 1987; Herrel et al. 2005a, b). Supporting the second expectation, the Darwin’s finch species found at a given site have beak characteristics that are well suited for the locally available food types (Schluter and Grant 1984). Given that these resource-based promoters of diversification are ecological, they might be sensitive to environmental change wrought by humans.

PRIMARY CONCLUSIONS

In the population, where human influences are relatively minor (El Garrapatero), we found that environment–morphology–performance associations were generally present. In particular, the birds in this population manifest positive associations between diet, beak size, and bite force. In addition, these characteristics show a bimodal distribution (Hendry et al. 2006) that is associated with low gene flow between the morphs (De León et al. 2010). This partial split within *G. fortis* appears to be maintained by assortative mating that limits the production of intermediate forms (Huber et al. 2007), and viability selection against intermediates that are produced (Hendry et al. 2009). The specific source of viability selection is unknown but might relate to a relative scarcity of intermediate seeds (Fig. 2) or to strong competition for those seeds.

In the population, where human influences are stronger (Academy Bay), we found that aspects of the environment (diet)–morphology (beaks)–performance (bites) associations are diminished—and that bite force is lower for a given beak size. In short, this population may be experiencing a breakdown of the associations that drive diversification in this group. This finding is consistent with the idea that the adaptive landscape for beak size has flattened at this site. The expected result should be a reduction in disruptive selection (intermediate birds might no longer show a disadvantage), which might ultimately reduce assortative mating between the morphs (given that assortative mating by beak size is not perfect, an increase in the number of intermediates will lead to more large and small birds mating with intermediates). Although selection and mating have not yet been studied for Academy Bay

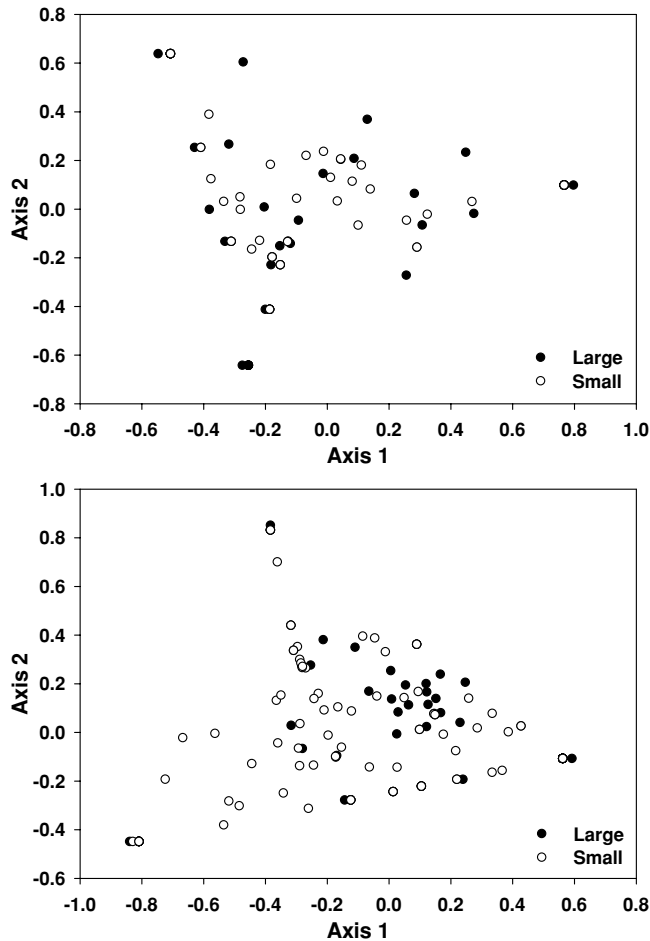


Figure 5. Nonmetrical multidimensional scaling (NMDS) plot of the diets of individual small (open circles) and large (filled circles) beak size morphs of *G. fortis* at Academy Bay (Upper panel) and El Garrapatero (Lower panel). The data represent diets as derived from specific plant items and the morphs are significant at El Garrapatero but not at Academy Bay (Table 4). Some of the point coordinates were slightly modified to avoid overlap and so make them more visible.

G. fortis, the population does show the anticipated evolutionary outcome of these changes: bimodality has weakened (Hendry et al. 2009) and genetic differentiation is low (De León et al. 2010). In short, the historical divergence noted for Academy Bay *G. fortis* (Ford et al. 1973) appears to have reversed, perhaps because environmental conditions have changed with the dramatic increase in local human population density.

The breakdown of environment–phenotype–performance associations at Academy Bay could reflect a combination of genetic and plastic effects. Genetic effects likely predominate for beak morphology given its very high heritability (Boag 1983; Keller et al. 2001; Abzhanov et al. 2004). The same might be true for head size and bite force given their strong correlation with beak size (Herrel et al. 2005a, b). However, plastic effects might also

Table 4. Permutational multivariate analysis of variance using matrices of distances between individuals in the proportions of different food types consumed. These matrices were calculated using Bray–Curtis distances. The table first shows results for an interaction between beak size (morph) and location (site), and then shows results for a comparison of the two morphs within each site: Academy Bay (AB) and El Garrapatero (EG).

ANOVA based on plant items				
	df	<i>F</i>	<i>R</i> ²	<i>P</i>
Morph × site	1	2.460	0.009	0.013
AB morph	1	1.220	0.014	0.27
EG morph	1	2.972	0.018	0.006
Residual	246			

play a role for head size and bite force. For instance, increased feeding on hard seeds might lead to the development of larger jaw abductor muscles, which would then lead to higher bite force and a larger head (Bowman 1961; van der Meij and Bout 2004; Herrel et al. 2005b). We considered the potential for such training effects by comparing the bite force of fully grown young birds (1–3 years of age) with that of older birds (> 3 years of age), expecting that older birds would have more training. Here, correlation analyses revealed that birds of similar age and morphology (beak size) have

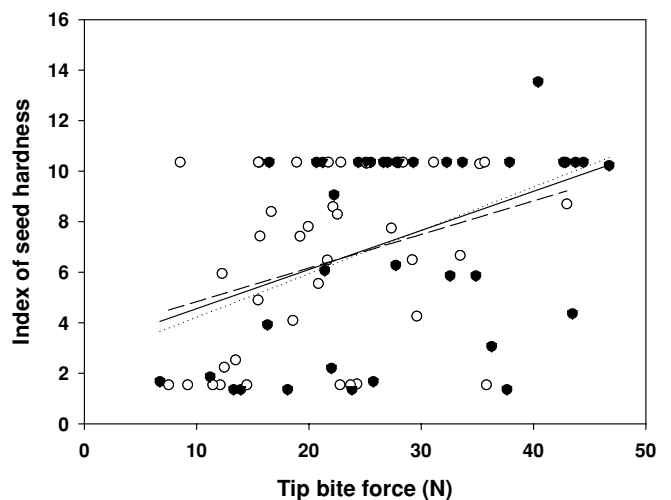


Figure 6. The average size-hardness of seeds eaten in relation to bite force at the tip of the beak. The correlation is significant when pooled across sites (solid line: $r = 0.41$, $P < 0.001$) and within El Garrapatero (dotted line and closed symbols: $r = 0.45$, $P = 0.002$) and Academy Bay (dashed line and open symbols: $r = 0.32$, $P = 0.02$). These correlations do not differ significantly between the sites ($Z = 0.62$, $P = 0.27$). The upper and lower lines with many observations correspond to abundant and accessible food items common to both sites, such as *Scutia spicata* at the upper end and grass seeds at the lower end. Similar correlations were obtained using side bite force instead of tip bite force (results not shown).

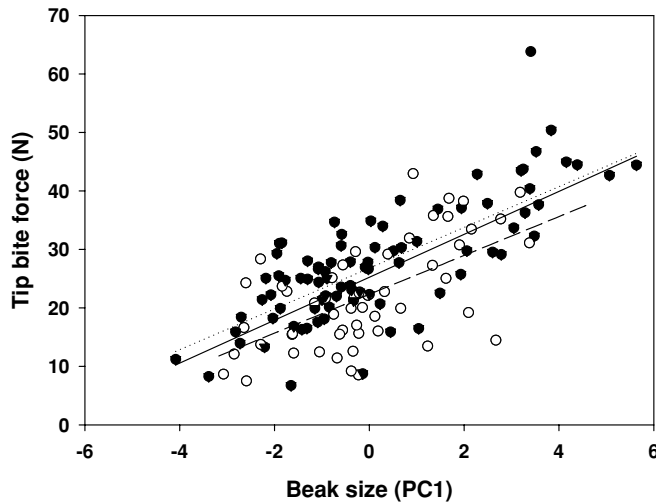


Figure 7. Bite force at the beak tip in relation to beak size. The correlation is significant when pooled across sites (solid line: $r = 0.70$, $P < 0.001$), within El Garrapatero (dotted line and closed symbols: $r = 0.78$, $P = 0.001$) and within Academy Bay (dashed line and open symbols: $r = 0.63$, $P < 0.001$). These correlations do not differ significantly between the sites ($Z = -1.61$, $P = 0.09$). Similar correlations were obtained using side bite force instead of tip bite force (results not shown).

a weaker association (juveniles: $Z = -3.46$, $P < 0.001$; adults: $Z = -6.03$, $P < 0.001$) between beak size and bite force at Academy Bay (juveniles: $r = 0.07$, $P = 0.85$; adults: $r = 0.60$, $P < 0.001$) than at El Garrapatero (juveniles: $r = 0.59$, $P = 0.41$; adults: $r = 0.78$, $P < 0.001$). Thus, although training does seem to influence bite force, standardizing for one aspect of training (age) did not change the difference between sites. Other effects of plasticity could, of course, remain unaccounted for.

Our hypothesis that the decrease in bimodality at Academy Bay is the result of human disturbance requires that these finches consume foods that have been introduced into the environment by humans. Data on available seeds show some differences between the sites (Fig. 2) but not of a magnitude that would be expected to cause the difference in bimodality. Instead, our data showed that finches do feed on human foods at Academy Bay but not at El Garrapatero (Appendix S1). Moreover, our intensive surveys of individually banded birds underestimates the true fre-

quency with which Academy Bay finches consume human foods, in part because we were not allowed to band birds in areas visited by tourists. However, surveys of unbanded birds confirmed that *G. fortis* frequently consumes human foods but not natural foods in Puerto Ayora itself (see Results). In addition, large numbers of *G. fortis* routinely feed on rice at human-maintained “feeders” within 100 m of our study site (Hendry et al. 2006). Importantly, both large and small *G. fortis* can consume these human foods because they do not require a particular beak size or bite force—in contrast to the situation for many natural foods (Grant 1999).

ALTERNATIVE HYPOTHESES

Our main hypothesis is that human influences on the distribution of food resources for finches have caused the collapse of historically strong bimodality in Academy Bay *G. fortis*. However, because our study is correlative (manipulations are not permitted) and unreplicated (this is the only known situation where human population increase has occurred alongside a bimodal population), alternative hypotheses are hard to rule out. But we can perhaps cast doubt upon them.

Some alternatives relate to the general inference that humans are the cause of the decrease in bimodality, regardless of the specifics as to how this happened. One alternative is changes in “immigration,” which implies that intermediate-sized immigrants have recently become proportionally more common at Academy Bay but not at El Garrapatero. We have no reason to suspect that this might be the case—and it would not explain the reduced environment–morphology–performance correlations at Academy Bay. Moreover, even if it has occurred it could be the result of human influences. Another alternative is increased “hybridization” between beak morphs at Academy Bay but not at El Garrapatero. This is certainly possible; however, mate choice in Darwin’s finches is closely linked to beak size and the resulting songs (Ratcliffe and Grant 1983; Grant 1999; Podos 2001; Podos et al. 2004), and so changes in assortative mating would likely be a downstream effect of changes in beak size. And, again, this would not explain the reduced environment–morphology–performance correlations—and it too could be the result of human influences. A third alternative is that some environmental factor unrelated to

Table 5. Permutation tests for canonical redundancy analysis (RDA) of the contribution of morphology/performance to the difference in diet between the two *G. fortis* beak-size morphs at each site

Test	df	Variance	F	Permutations	P
Academy Bay	3	3.16	1.33	1000	0.09
Residual	84				
El Garrapatero	3	2.8	1.39	1000	0.03
Residual	158				

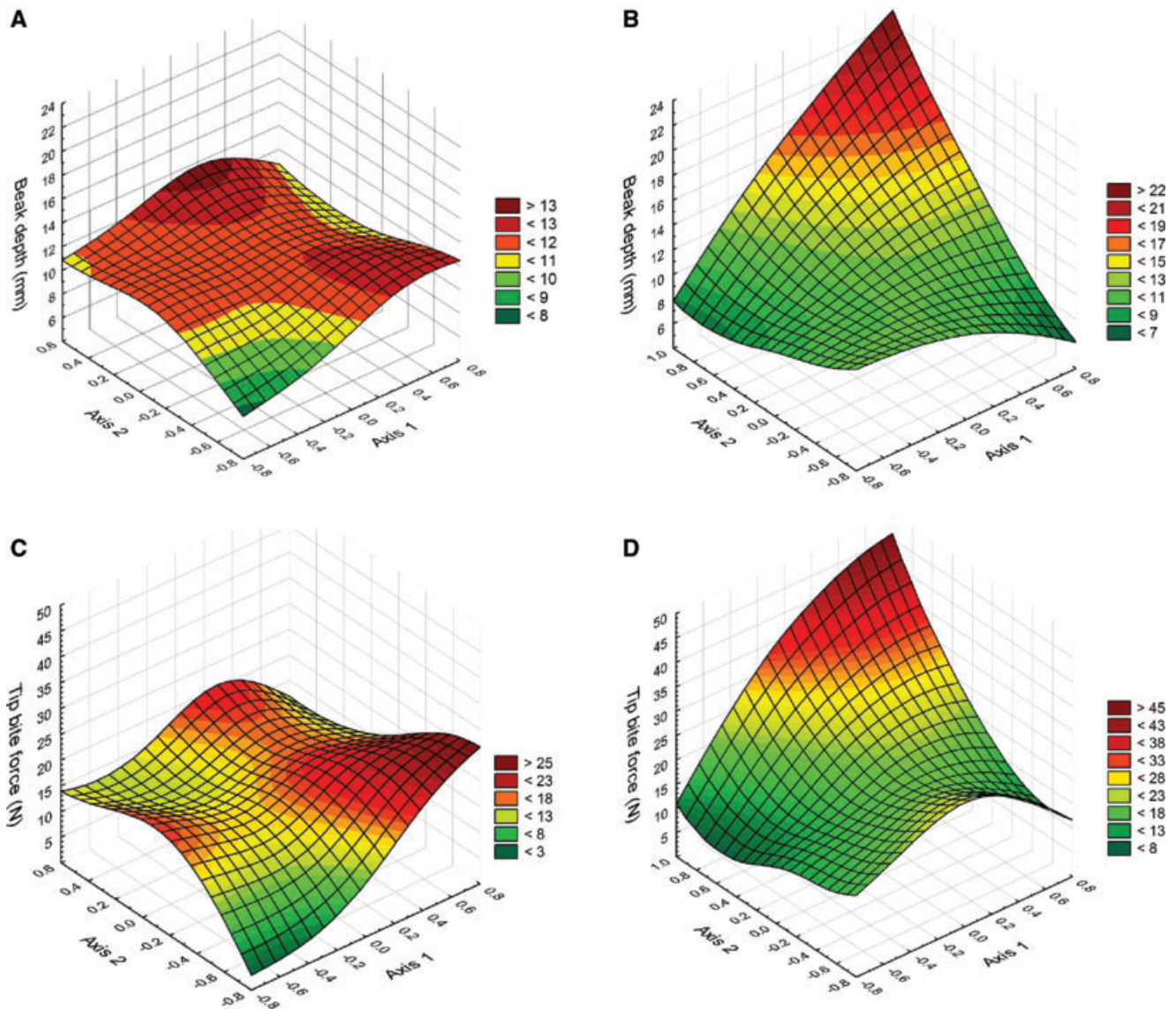


Figure 8. Nonmetrical multidimensional scaling (NMDS) 3-D surface plots of mean beak depth (A,B) and tip bite force (C,D) at Academy Bay (A, C) and El Garrapatero (B, D) against the first two diet axes. We show these two particular variables as they are expected to be particularly important in the way that finches interact with their diets. The results show that birds exploiting different food items have different traits at each site, but the association is stronger at El Garrapatero than at Academy Bay. Similar results are obtained for the rest of the measured morphological traits (results not shown).

local human activities has changed at Academy Bay but not El Garrapatero. However, the most obvious environmental variables (rainfall) would vary more through time (Grant and Grant 2002) that between the two sites. Thus, conclusions that humans are the primary driver, and that this is in some way related to feeding ecology, seem robust.

Other alternatives relate to the specific human-mediated driver of the decrease in bimodality. We have argued that humans have altered the underlying resource distribution available to finches. An alternative is that human activities have caused a relaxation of competition, which has smoothed the adaptive land-

scape without altering the shape of the underlying resource distribution. For instance, human activities at Academy Bay could reduce competition among finches by increasing their mortality rate for other reasons (e.g., parasites or cats). However, our capture-per-unit effort data suggest that finch abundance is more than fourfold higher at Academy Bay than at El Garrapatero, potentially maintaining competition and thereby pointing again to the importance of the underlying resource distribution. We cannot conclusively distinguish between these alternatives with our correlative data but both still invoke human-induced changes in the adaptive landscape experienced by finches.

Summary and Implications

The ongoing and increasing human influence in Galapagos appears to negatively impact at least one part of the adaptive radiation of Darwin's finches. We specifically argue that the introduction of new food types at Academy Bay is eroding the diet-based disruptive selection that is thought to have previously maintained beak size bimodality in *G. fortis*. In contrast, the relative scarcity of human influences at a nearby site (El Garrapatero) has allowed the two beak morphs to remain bimodal, preserving their correlated ecological, performance, and genetic divergence.

Human impacts might also be possible at other locations in Galapagos. On Santa Cruz Island, for instance, introduced agricultural plants are widely cultivated around Bellavista (Fig. 1), and some of these (and other) plants have become invasive (Mauchamp 1997; Tye 2001). Moreover, settlements on the islands of San Cristobal and Isabela are also increasing dramatically in human population density (Watkins and Cruz 2007). Perhaps *G. fortis* in these other areas will be similarly impacted—although the extent to which they were historically bimodal is not known. It is also possible that such effects could influence separation among the recognized finch species, given their lack of intrinsic genetic incompatibilities and the corresponding importance of reproductive barriers based on ecological selection against hybrids (Grant and Grant 1989, 1993). If that selection is removed owing to environmental change, the species could converge. As a telling example, severe El Niño conditions eliminated selection against hybrids between *G. fortis* and *G. scandens* on Daphne Major Island, which caused ongoing merging of the two species (Grant and Grant 2002; Grant et al. 2004). Perhaps the increased availability of human foods and introduced plants could cause analogous effects in the future.

Our findings suggest at least three broader implications for the conservation of biological diversity from the perspective of adaptively divergent and reproductively isolated groups. First, we have illustrated yet another way in which evolutionary processes can be influenced by human disturbances (Smith and Bernatchez 2008). Second, our results highlight the importance of conserving the processes that generate and maintain biodiversity, rather than just the product of those processes (Moritz 2002). Third, we have raised the spectre of new conservation concerns in Galapagos, a hot spot for both biodiversity (Myers et al. 2000) and evolution (Davis et al. 2008; Grivet et al. 2008). A region so important to our original understanding of evolutionary processes could now prove important for understanding how humans alter those processes and thereby modify future evolutionary trajectories.

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Supporting Information

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

Appendix S1. Sampled food resources at our two study sites on Santa Cruz Island.

Appendix S2. Common specific feeding categories (food items) consumed by *G. fortis* on Santa Cruz Island.

Appendix S3. The average size-hardness of seeds eaten in relation to beak size in the trimmed dataset.

Appendix S4. The average size-hardness of seeds eaten in relation to bite force at the tip of the beak in the trimmed data.

Appendix S5. Bite force at the beak tip in relation to beak size in the trimmed data.

Appendix S6. Analysis of “trimmed data” from Table 3.

Appendix S7. Analysis of “trimmed data” from Table 4: Permutational multivariate analysis of variance using matrices of distances between individuals in the frequencies of different food types consumed.

Appendix S8. Analysis of “trimmed data” from Figure 5: Permutation tests for Canonical Redundancy Analysis (RDA) of the contribution of morphology/performance to the difference in diet between the two *G. fortis* beak-size morphs at each site.

Appendix S9. Frequency of *G. fortis* feeding in “human food” at Academy Bay.

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