PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2009) **276**, 753–759
doi:10.1098/rspb.2008.1321
Published online 4 November 2008

Disruptive selection in a bimodal population of Darwin's finches

Andrew P. Hendry[1,*], **Sarah K. Huber**[2,3], **Luis F. De León**[1], **Anthony Herrel**[4] **and Jeffrey Podos**[2]

[1]*Department of Biology and Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec, Canada H3A 2K6*
[2]*Department of Biology and Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003, USA*
[3]*Department of Biology, Randolph-Macon College, Ashland, VA 23005, USA*
[4]*Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA*

A key part of the ecological theory of adaptive radiation is disruptive selection during periods of sympatry. Some insight into this process might be gained by studying populations that are bimodal for dual-context traits, i.e. those showing adaptive divergence and also contributing to reproductive isolation. A population meeting these criteria is the medium ground finch (*Geospiza fortis*) of El Garrapatero, Santa Cruz Island, Galápagos. We examined patterns of selection in this population by relating individual beak sizes to interannual recaptures during a prolonged drought. Supporting the theory, disruptive selection was strong between the two beak size modes. We also found some evidence of selection against individuals with the largest and smallest beak sizes, perhaps owing to competition with other species or to gaps in the underlying resource distribution. Selection may thus simultaneously maintain the current bimodality while also constraining further divergence. Spatial and temporal variation in *G. fortis* bimodality suggests a dynamic tug of war among factors such as selection and assortative mating, which may alternatively promote or constrain divergence during adaptive radiation.

Keywords: natural selection; ecological speciation; adaptive divergence; reproductive barriers; divergent selection; incipient speciation

1. INTRODUCTION

The ecological theory of adaptive radiation hypothesizes that diversification is driven by adaptation to different ecological conditions (i.e. environments or resources). The process starts with divergent/disruptive selection causing adaptive divergence between conspecific groups that occupy different environments or use different resources (Schluter 2000). Reproductive isolation then evolves as a by-product of adaptive divergence (i.e. 'ecological speciation', Schluter 2000). Likely reproductive barriers arising in this manner include assortative mating and selection against migrants and hybrids. This basic theory has garnered considerable support from mathematical models and empirical studies, to the extent that adaptive divergence and ecological speciation are thought to play a central role in the evolution of biological diversity (Skúlason & Smith 1995; Schluter 2000; Rundle & Nosil 2005).

Recent theoretical work relevant to the above ecological theory has called particular attention to the possible importance of disruptive selection in sympatry (Dieckmann & Doebeli 1999; Rueffler *et al.* 2006; Bolnick & Fitzpatrick 2007; Doebeli *et al.* 2007; Abrams *et al.* 2008). Empirical evidence supporting this view has emerged from several different contexts. First, disruptive selection can act between competing species to accentuate their divergence, as has been recently confirmed for Darwin's finches (Grant & Grant 2006) and *Spea* tadpoles (Pfennig & Rice 2007; Pfennig *et al.* 2007). Second, disruptive selection can result from competition between hybrids and parental forms, as demonstrated in threespine stickleback (Schluter 1994, 2003). Third, disruptive selection may occur within unimodal populations that show no evidence of incipient divergence (Kingsolver *et al.* 2001), such as *Anolis* lizards (Calsbeek & Smith 2007) and most stickleback populations (Bolnick 2004; Bolnick & Lau 2008). Fourth, disruptive selection may occur in randomly mating bimodal populations, such as African *Pyrenestes* finches (Smith 1993). These studies show that disruptive selection can occur in nature, suggesting the value of further considering its role in adaptive radiation.

Additional support for the idea that disruptive selection contributes to adaptive radiation would come from evidence of its action in conspecific populations that are bimodal for traits that undergo adaptive divergence and also influence reproductive isolation. The reasons are twofold. First, such dual-context traits may catalyse progress towards speciation (Dieckmann & Doebeli 1999; Schluter 2000), and as such have been called 'magic' traits (Gavrilets 2004). Second, bimodality without complete separation of the modes suggests an intermediate stage of divergence, and might therefore reveal conditions near the tipping point between species fission or fusion. Our work focuses on a medium ground

---

*Author for correspondence (andrew.hendry@mcgill.ca).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2008.1321 or via http://journals.royalsociety.org.

Received 15 September 2008
Accepted 13 October 2008

This journal is © 2008 The Royal Society

finch (*Geospiza fortis*) population that shows bimodality in beak size, a critical dual-context trait in this taxon (Grant 1986; Podos 2001; Huber *et al.* 2007; Grant & Grant 2008). Importantly, the observed intraspecific bimodality is a small-scale version of the differences between *G. fortis* and its granivorous congeners (see below). The evolutionary forces acting within the bimodal population might therefore inform those that contributed to the initial adaptive radiation.

(a) *Darwin's finches*

The 14 recognized species of Darwin's finches in Galápagos are thought to have originated in the following manner (Lack 1947; Grant 1986; Grant & Grant 2008). At the outset, an ancestral species colonized multiple islands characterized by ecological differences, such as different seed size distributions. Resulting divergent selection among allopatric populations then caused their adaptive divergence, most notably in beak and body dimensions (Bowman 1961; Abbott *et al.* 1977; Schluter & Grant 1984; Grant & Grant 2000, 2008). Next, further dispersal among the islands brought some allopatric forms back into secondary contact (Grant 1986; Petren *et al.* 2005; Grant & Grant 2006), where several outcomes were possible. First, the allopatric divergence may have been too modest to generate major barriers to gene flow, thereby leading to fusion after secondary contact. Second, the allopatric divergence may have essentially completed speciation, and largely eliminated competition and gene flow in sympatry. Given that Darwin's finches do not show genetic incompatibilities, any such reproductive isolation would probably include ecological selection against hybrids and assortative mating based on beak/body dimensions (Ratcliffe & Grant 1983; Grant & Grant 1993, 2008; Podos 2001; Huber *et al.* 2007). Third, the allopatric divergence may have been sufficient to prevent complete fusion following secondary contact, but not to eliminate between-group competition and gene flow. In these cases, divergence and reproductive isolation might be accentuated in sympatry owing to character displacement and 'reinforcement' (Schluter *et al.* 1985; Grant & Grant 2006, 2008).

The third outcome described above is expected to involve disruptive selection that favours increasing divergence in beak dimensions. This hypothesis has recently been confirmed for interactions *between* two ground finch species (Grant & Grant 2006) and we here ask whether it also occurs *within* one of them. The relevance of this particular analysis is that sympatric interactions between partially divergent conspecific groups probably contributed to the adaptive radiation of Darwin's finches (Grant & Grant 2008). Our work focused on a *G. fortis* population (El Garrapatero, Santa Cruz Island) characterized by two modes along the morphological axes (beak and body size) that also separate this species from its smaller (*Geospiza fuliginosa*) and larger (*Geospiza magnirostris*) granivorous congeners (Foster *et al.* 2008; figure 1). The initial origins of bimodality within *G. fortis* remain uncertain, with possibilities including interspecific hybridization, allopatric divergence followed by secondary contact (as above), entirely sympatric or parapatric divergence, or phenotype-biased immigration/emigration (Huber *et al.* 2007; Grant & Grant 2008).

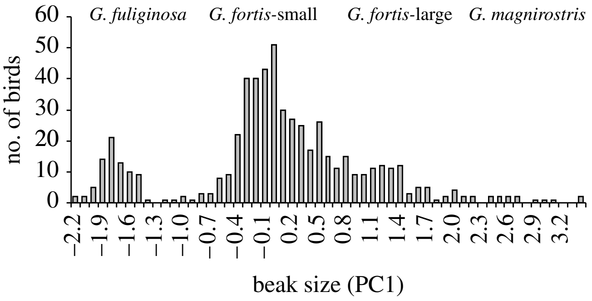

Figure 1. The frequency distribution of beak sizes for all individual *G. fuliginosa*, *G. fortis* (small and large) and *G. magnirostris* captured at El Garrapatero in 2004–2006. Beak size is represented by PC1 calculated from all the birds combined. PC1 explained 95.6% of the total variation in beak length (loading = 0.964), beak depth (0.986) and beak width (0.983). The species and mode names identify general ranges only, owing to ambiguity and possible hybrids in the areas of overlap. Although strong bimodality in beak size characterizes *G. fortis* at this site (for details see Hendry *et al.* 2006; figures 3 and 4), the numerous intermediates facilitate our test for disruptive selection.

We are interested in the factors that influence bimodality in *G. fortis*, because these factors might influence fission/fusion when partially divergent forms meet (or originate) in sympatry. In previous work, we showed that birds in the two modes show adaptive divergence and partial reproductive isolation. Specifically, they have different bite forces (Herrel *et al.* 2005), sing different songs (Huber & Podos 2006), respond differently to each other's songs (J. Podos 2006, unpublished data), mate assortatively (Huber *et al.* 2007) and show partially restricted gene flow (Huber *et al.* 2007). Birds with intermediate beak sizes are still present, however, perhaps owing to the few cross-type matings (Huber *et al.* 2007) and phenotype-biased immigration (see below). The continued maintenance of bimodality might therefore require the selective loss of individuals with intermediate beak sizes. We test for such disruptive selection by relating individual beak sizes to interannual recapture probabilities.

2. MATERIAL AND METHODS

Our study site/population differs in several ways from Daphne Major, the only other site at which selection has been estimated for *G. fortis*. El Garrapatero is part of a continuous tract of low-elevation, arid-zone forest (*Bursera graveolens* and *Cordia lutea*) and is located within 1 km of coastal-zone vegetation. Daphne Major, by contrast, is isolated and open, and does not have coastal-zone vegetation (Grant 1986). The El Garrapatero *G. fortis* population shows a wide range of beak sizes in a bimodal distribution (figure 1; Hendry *et al.* 2006), whereas Daphne Major *G. fortis* have small beak sizes in a unimodal distribution (Grant 1986). Other ground finch species at El Garrapatero include a large population of *G. fuliginosa* (figure 1), a few *G. magnirostris* (figure 1) and a few *Geospiza scandens* (J. Podos, unpublished data). Other ground finch species established at Daphne Major include *G. magnirostris* and *G. scandens* (Grant 1986; Grant & Grant 2006). We draw these contrasts to point out that selection at El Garrapatero is probably different from that at Daphne Major.

Our fieldwork at El Garrapatero took place in 2004 (28 January–27 March), 2005 (15 January–12 May) and 2006 (26 January–7 March). These 3 years saw very little

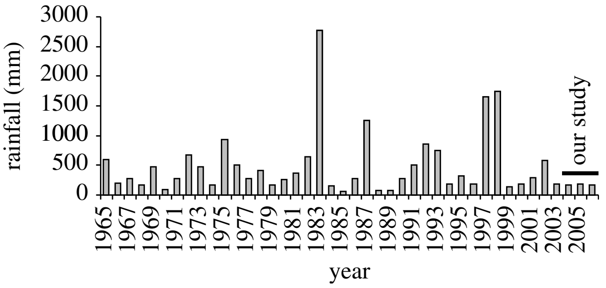

Figure 2. Total rainfall in each year of record at Academy Bay on Santa Cruz Island. The variation at this site should generally parallel that at El Garrapatero, because the two sites are nearby (approx. 10 km apart) and at roughly the same elevation on the same side of Santa Cruz (for a map see Hendry *et al.* 2006).

precipitation (figure 2), including less *total* precipitation during the 'wet' season (230 mm from January through May 2004–2006) than in any other 3-year period on record. Our study thus took place during one of the most prolonged droughts on record, resulting in very little reproduction by plants, insects and finches. These conditions are known to cause high mortality, strong selection and character displacement in Darwin's finches (Grant 1986; Grant & Grant 2002, 2006).

Mist nets were used to capture the birds, which were then banded to allow the unambiguous identification of individuals. Each time a bird was captured, we followed previous work (Grant 1986) in characterizing it as an adult or juvenile (based on beak and plumage colour) and in measuring beak length (anterior edge of nostril to tip of upper mandible), beak depth (at the nares) and beak width (base of lower mandible). All of our subsequent analyses used adult birds only, because beak size does not change appreciably after maturity (Grant 1986). The three beak dimensions were combined into a single measure of overall beak size (PC1—see §3 for details). All subsequent analyses focus on this measure because PC1 is the standard measure of overall beak size for Darwin's finches (e.g. Grant 1986; Grant & Grant 2002, 2006). Moreover, the two *G. fortis* modes and the three granivorous ground finch species (*G. fortis*, *G. fuliginosa* and *G. magnirostris*) do not differ in beak shape after controlling for beak size (Foster *et al.* 2008).

To estimate selective losses from the local population, we collected data on interannual recaptures, a commonly used method for estimating selection in birds (e.g. Smith 1993; Grant & Grant 2002; Benkman 2003; Clegg *et al.* 2008). More integrated fitness measures (e.g. lifetime reproductive success) would require multigeneration pedigrees, which could not be obtained. Regardless, previous work on *G. fortis* has confirmed that 'the most important determinant of fitness is the ability of an individual to survive to breed in many years' (Grant & Grant 2000). One of the reasons is that periodic droughts (and other factors) can eliminate reproduction and cause very high adult mortality in a given year. These were the very conditions that characterized El Garrapatero *G. fortis* during our study period (see also Huber 2008).

Birds banded in one year that were resighted or recaptured in a subsequent year clearly survived and did not emigrate (local absolute fitness = 1). Birds that were not resighted or recaptured in any subsequent year had probably died or emigrated (local absolute fitness = 0). Exceptions would occur if banded birds were present at the site but not recorded. We minimized this possibility by increasing our sampling effort from each year to the next. For example, the total number of *G. fortis* captures (including recaptures) increased from 122 in 2004 to 208 in 2005 and 237 in 2006, despite high mortality and minimal recruitment. (Note that this increasing effort prevented useful estimates of recapture probabilities from formal mark–recapture models.) Given our very large effort in 2005 and 2006, we anticipate that very few banded birds at the site went undetected.

Although most of the birds missing from one year to the next had probably died, some could simply have emigrated beyond the study site. We attempted to reduce this possibility by (i) analysing adults only, because they usually remain faithful to breeding localities (S. Huber 2004–2006, unpublished data), and (ii) conducting regular searches for banded finches beyond our main tagging area (very few were thereby discovered). At the end, however, our selection estimates necessarily conflate mortality with emigration, a situation characterizing many studies of selection in birds (e.g. Smith 1993; Benkman 2003). Fortunately, this possible conflation does not impact our main inference, because both survival and emigration represent losses from the local population. That is, birds that leave the site take their genes with them, and so no longer contribute to the next generation at the site. In short, the evolution of the local population should be similarly affected by phenotype-biased emigration and phenotype-biased mortality.

We estimated selection on beak size from 2004 to 2005, from 2005 to 2006 and from 2004 to 2006, relating local absolute fitness to PC1 in each of these 'intervals'. The standard approach to testing for disruptive selection is to fit a quadratic regression across the entire range of data (Kingsolver *et al.* 2001; Bolnick 2004; Calsbeek & Smith 2007; Bolnick & Lau 2008). This approach would not be appropriate in our study because selection was expected to be more complex. For example, selection might disfavour not only intermediates but also very large *G. fortis* (perhaps owing to competition with *G. magnirostris*; Grant & Grant 2006) or very small *G. fortis* (perhaps owing to competition with *G. fuliginosa*; Schluter *et al.* 1985). Such complicated patterns of selection would be misrepresented by a simple quadratic fit across the entire data range. We therefore first used non-parametric cubic splines (Schluter 1988) to visualize how selection changed across the range of beak sizes (for other examples see Smith (1993) and Benkman (2003)).

Our *a priori* hypothesis was selection against intermediate beak sizes, which would help to maintain the two *G. fortis* beak size modes. In addition to cubic splines, we therefore tested for statistically significant quadratic selection *between* the modes. This prediction was tested by excluding individuals more extreme than each mode and then using logistic regression to relate local relative fitness (local absolute fitness divided by local mean fitness) to PC1 and PC1^2. A positive coefficient for PC1^2 would be consistent with disruptive selection. The results of logistic regressions based on the entire data range, where disruptive selection is not necessarily expected (see above), are presented in the electronic supplementary material.

3. RESULTS

Mortality/emigration was substantial. Out of the 112 adult *G. fortis* banded and measured in 2004, 33 remained in 2005 and 19 remained in 2006. Out of the 184 adult *G. fortis* banded and measured in 2005, 41 remained

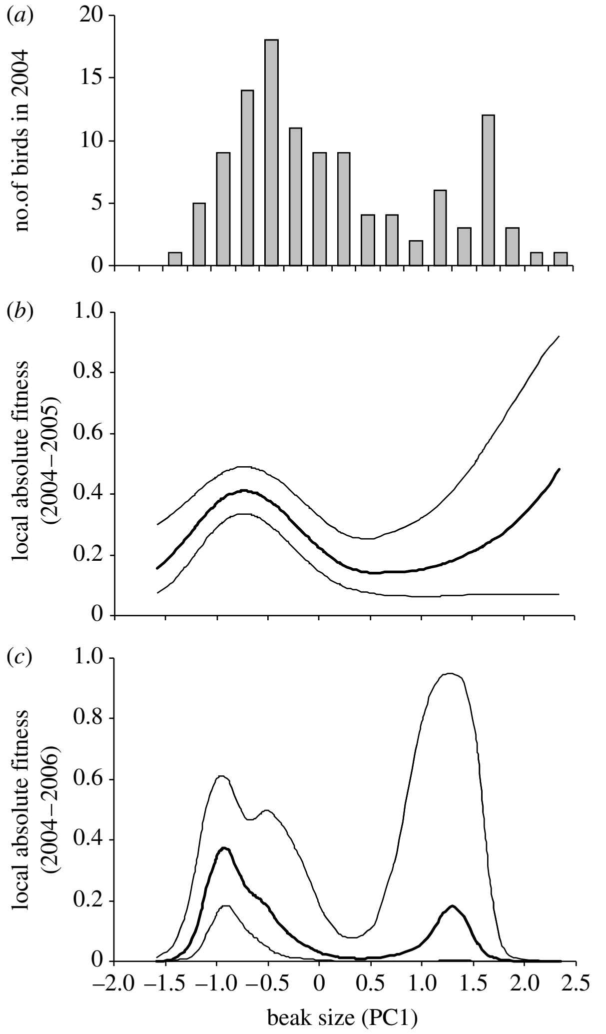

Figure 3. Selection on beak size (PC1) for El Garrapatero *G. fortis* measured and banded in 2004. (*a*) The frequency distribution of PC1 scores in banded birds at the start of the selection interval (2004). (*b*) Selection on these birds from 2004 to 2005. (*c*) Selection on them from 2004 to 2006. Selection is depicted as a cubic spline with bootstrapped 95% CIs (Schluter 1988). Cubic splines were calculated using a smoothing parameter of $\lambda = -4$ for the 2004–2005 interval and $\lambda = -8$ for the 2004–2006 interval. Note that the x-axis is not directly comparable with those in figures 1 and 4 because the PC analysis is based on different birds in each case.

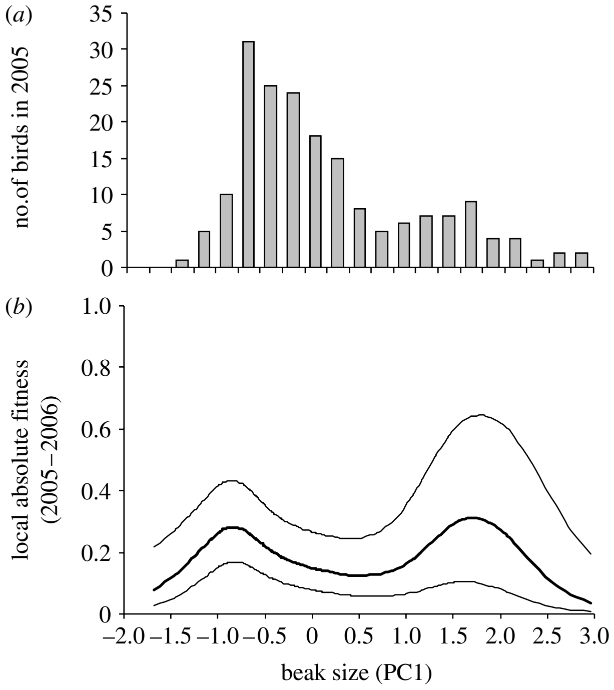

Figure 4. Selection on beak size (PC1) for El Garrapatero *G. fortis* measured and banded in 2005. (*a*) The frequency distribution of PC1 scores in banded birds at the start of the selection interval (2005). (*b*) Selection on these birds from 2005 to 2006. Selection is depicted as a cubic spline with bootstrapped 95% CIs ($\lambda = -4$). Note that the x-axis is not directly comparable with those in figures 1 and 3 because the PC analysis is based on different birds in each case.

in 2006. These high mortality/emigration rates are consistent with other studies of *G. fortis* during prolonged droughts (Grant 1986; Grant & Grant 2002, 2006). For adult *G. fortis* in the selection intervals that started in 2004, PC1 explained 84.8 per cent of the variation in beak length (loading = 0.876), beak depth (0.958) and beak width (0.926). For adult *G. fortis* in the selection interval that started in 2005, PC1 explained 90.1 per cent of the variation in beak length (loading = 0.912), beak depth (0.973) and beak width (0.962).

Mortality/emigration was highly non-random with respect to beak size. Cubic splines revealed that mortality/emigration was often the lowest for those birds closest to the large or small beak size modes (figures 3 and 4). Individuals between the modes always suffered higher mortality/emigration than did those near the modes, a pattern consistent with disruptive selection. In addition, individuals smaller than the small mode, and (sometimes) those larger than the large mode, suffered higher mortality/emigration than did those near the modes. The resulting two-peak pattern of selection would help to maintain the existing beak size modes.

Our inference of disruptive selection between the beak size modes was strengthened through quadratic regressions that excluded individuals smaller than the small mode and larger than the large mode (table 1). The quadratic term was positive in all three intervals and significant (one-tailed) in two of them (table 1). The generally lower statistical support for the intervals starting in 2004, relative to the one starting in 2005, was most likely due to the smaller sample sizes in the former. Supporting this assertion, the estimated quadratic coefficient (i.e. effect size) was higher for the intervals starting in 2004 than for the interval starting in 2005 (table 1).

4. DISCUSSION

The bimodal population of *G. fortis* at El Garrapatero shows several signatures of ecologically maintained adaptive divergence and reproductive isolation. First, the two modes differ in beak size (Hendry *et al.* 2006) and bite force capacities (Herrel *et al.* 2005), presumably owing to specialization on small/soft seeds versus large/hard seeds. Second, the two modes sing songs of different structure (Huber & Podos 2006) and respond differently to each other's songs (J. Podos 2006, unpublished data). Third, gene flow between the modes is somewhat limited (inferred from DNA microsatellites), at least partly owing to assortative mating (Huber *et al.* 2007). Here we demonstrate that bimodality might also be maintained by the selective loss of birds with intermediate beak sizes,

Table 1. Logistic regressions testing for quadratic selection between the *G. fortis* beak size modes at El Garrapatero. (Note that our hypothesis (disruptive selection on $PC1^2$) is one-tailed but *p*-values from regressions are two-tailed, so the reported *p*-values here should be halved for comparison to a two-tailed alpha of 0.05. 'Interval' gives the starting and ending years for each selection interval. 'Data range' is the range of PC1 values used for analyses, selected to represent the range where disruptive selection is expected, i.e. between the beak size modes—see figures 3 and 4. '*N* (local absolute fitness)' gives the number of marked individuals that did (1) or did not (0) remain at the study site at the end of the selection interval (i.e. response variable in the regressions). The remaining columns give the logistic regression statistics for the linear (PC1) and quadratic ($PC1^2$) terms. Disruptive selection is consistent with positive coefficients for the $PC1^2$ terms.)

		N (local absolute fitness)					
interval	data range	1	0	term	coefficient	Wald	*p*-value
2004–2005	−0.75 to 1.75	22	56	PC1	−1.159	3.84	0.050
				$PC1^2$	0.925	2.85	0.091
2004–2006	−0.75 to 1.75	12	66	PC1	−0.813	1.30	0.255
				$PC1^2$	0.632	0.89	0.345
2005–2006	−1.00 to 1.80	37	119	PC1	−0.146	2.33	0.127
				$PC1^2$	0.678	4.19	0.041

i.e. disruptive selection *between* the modes (figures 3 and 4). These phenomena all parallel those expected to be important during the radiation of ground finches in the Galápagos (Grant 1986; Grant & Grant 2008).

What are the proximate causes of the disruptive selection documented here? One possibility is that competition for shared resources reduces the success of individuals specializing on intermediate seeds, causing them to die or emigrate. Another possibility is that intermediate birds fall into a gap in the underlying resource distribution (i.e. independent of competition), such as relatively few intermediate-sized seeds. Both of these mechanisms can cause disruptive selection in theoretical models (Dieckmann & Doebeli 1999; Schluter 2000; Rueffler *et al.* 2006; Doebeli *et al.* 2007; Abrams *et al.* 2008) and have previously been implicated in the divergence of Darwin's finches (Lack 1947; Bowman 1961; Abbott *et al.* 1977; Schluter & Grant 1984; Schluter *et al.* 1985; Grant & Grant 2006). We cannot presently address how bimodality in *G. fortis* might have been driven by competition, but we can at least speculate on the role of the underlying resource distribution. In particular, spatial and temporal variation in *G. fortis* bimodality across the island is at least roughly consistent with the differences in available food types (Hendry *et al.* 2006). Disentangling the relative influences of underlying resource distributions versus competition for shared resources will be a subject of future work.

(a) *The dynamics of divergence*

Given that El Garrapatero *G. fortis* manifest multiple processes (disruptive selection and assortative mating) thought to be important during sympatric phases of adaptive radiation, why is divergence incomplete? Indeed, individuals with intermediate beak sizes are so numerous that frequency histograms are not particularly effective ways of confirming bimodality (for a discussion see Hendry *et al.* 2006). One possibility is that the current bimodality has developed only recently and will become more prominent in the future. Although this is certainly possible, it is not consistent with the observations that bimodality has periodically characterized *G. fortis* at other sites on Santa Cruz Island for at least 100 years (Hendry *et al.* 2006; Grant & Grant 2008). Recent divergence therefore does not seem to be cumulative, which suggests ongoing constraints on diversification in sympatry. Many such constraints are theoretically possible and have been discussed in detail elsewhere (e.g. Coyne & Orr 2004; Bolnick & Fitzpatrick 2007). We focus here on a subset of the constraints that are particularly intriguing in the context of our study system.

One constraint might be temporal variation in selection that hampers cumulative progress towards speciation. For example, disruptive selection might be strong during droughts but not in wet years. As a possible interspecific analogue, hybrids between *G. fortis* and *G. scandens* had low survival during dry periods but not during wet periods (Grant & Grant 1993, 1996), the latter thus precipitating their current trend towards species fusion (Grant *et al.* 2004). Something similar may have caused the loss of intraspecific bimodality in Academy Bay *G. fortis*, although the culprit here may have been the recent intensification of local human influences (Hendry *et al.* 2006).

Another constraint might be ongoing immigration of intermediate-sized birds from other locations. Such immigration could explain why substantial numbers of intermediate birds are present at El Garrapatero (figure 1) despite both strong assortative mating (Huber *et al.* 2007) and divergent selection (figures 3 and 4). It would also explain why bimodality did not appear to decrease from 2004 to 2005 despite very little local reproduction. We could not directly test this hypothesis of phenotype-biased immigration because we did not band all of the birds at our site, so new immigrants could not be confirmed. Recent work on other systems, however, is certainly drawing attention to the potential importance of phenotype-biased migration (Edelaar *et al.* 2008).

A final constraint we wish to discuss is that further adaptive divergence and reproductive isolation might actually be impeded by selection. Specifically, mortality/emigration was also high for the smallest *G. fortis* and sometimes also for the largest *G. fortis* (figures 3 and 4). Overall, then, selection in this population might be considered roughly stabilizing around each beak size mode, a situation similar to that seen in African *Pyrenestes* finches (Smith 1993). This two-peak pattern of selection might be expected if the adaptive landscape for beak size has reasonably discrete peaks corresponding to different food types (Schluter 2000). As noted above, such landscapes for Darwin's finches might be driven by gaps in the underlying resource distribution, as well as by interspecific competition (Abbott *et al.* 1977; Schluter & Grant 1984; Schluter *et al.* 1985; Grant & Grant 2006, 2008). These two possibilities cannot be discriminated at present, but it is nonetheless tempting to speculate that competition might be more important at the small end of the *G. fortis* distribution (given that *G. fuliginosa* are common; figure 1), whereas constraints of the underlying resource distribution might be more important at the large end (given that *G. magnirostris* are rare; figure 1).

(**b**) ***Food for thought***

Geospiza fortis on Santa Cruz have been collected for more than a century, revealing a spatial and temporal mosaic of bimodality (Lack 1947; Bowman 1961; Ford *et al.* 1973; Hendry *et al.* 2006; Grant & Grant 2008). At one site (Academy Bay), bimodality was historically strong but is now weak. At a second site (El Garrapatero), bimodality is currently strong. At a third site (Borrero Bay), bimodality has not been documented in the past nor the present. This spatial and temporal variation suggests a dynamic tug of war between forces promoting diversification and those constraining it. At certain times and places, promoting factors may gain the upper hand and make substantial progress towards speciation. At other times and places, constraints may gain the upper hand and reverse any such progress. We suggest that this sort of dynamic tug of war can recur during adaptive radiations. Speciation events might then represent those few cases where promoting factors, such as strong disruptive selection and assortative mating, have a sustained run of influence over constraining factors. Darwin's finches may be a promising group for observing this dynamic.

We close by noting the value of comparing morphological divergence and reproductive barriers within species versus between species, in an adaptive radiation. A selection of recent studies of vertebrates can be used to highlight a contrast emerging from such comparisons. On the one hand, adaptive divergence and reproductive barriers between species may involve dimensions (ecological, morphological and physiological) that differ from those seen between groups within species, as may be the case for *Timema* walking sticks (Nosil & Sandoval 2008). On the other hand, adaptive divergence and reproductive barriers between species may closely parallel those within species, as might be the case for *Geospiza* (see above), *Anolis* lizards (Calsbeek *et al.* 2007), threespine stickleback (Robinson 2000; Bolnick & Lau 2008) and mosquitofish (Langerhans *et al.* 2007). Or perhaps the apparent correspondence in some of these examples simply reflects the need to study more dimensions. Either way, these considerations highlight the importance of determining the conditions under which adaptive radiation can or cannot result by simply extrapolating processes seen within species.

This work was conducted in concordance with Animal Use Protocols approved by the University of Massachusetts Amherst.

Fieldwork was coordinated through the Charles Darwin Research Station and the Galápagos National Park Service. The rainfall data were provided by the Charles Darwin Research Station. Data collection in the field was assisted by E. Hilton, M. Rossi-Santos, D. Ruiz, A. Gabela, P. Kelley, M. Hendry, K. Huyghe, B. Vanhooydonck and D. Delaney. The manuscript was improved through comments from R. Calsbeek, P. Nosil and an anonymous reviewer. Financial support was provided by the National Science Foundation (J.P.—IBN 0347291), with additional funding from the Natural Sciences and Engineering Research Council of Canada (A.P.H.).

REFERENCES

Abbott, I., Abbott, L. K. & Grant, P. R. 1977 Comparative ecology of Galápagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecol. Monogr.* **47**, 151–184. (doi:10.2307/1942615)

Abrams, P. A., Rueffler, C. & Kim, G. 2008 Determinants of the strength of disruptive and/or divergent selection arising from resource competition. *Evolution* **62**, 1571–1586. (doi:10.1111/j.1558-5646.2008.00385.x)

Benkman, C. W. 2003 Divergent selection drives the adaptive radiation of crossbills. *Evolution* **57**, 1176–1181.

Bolnick, D. I. 2004 Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* **58**, 608–618.

Bolnick, D. I. & Fitzpatrick, B. M. 2007 Sympatric speciation: models and empirical evidence. *Annu. Rev. Ecol. Evol. Syst.* **38**, 459–487. (doi:10.1146/annurev.ecolsys.38.091206.095804)

Bolnick, D. I. & Lau, O. L. 2008 Predictable patterns of disruptive selection in stickleback in postglacial lakes. *Am. Nat.* **172**, 1–11. (doi:10.1086/587805)

Bowman, R. I. 1961 Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. Zool.* **58**, 1–302.

Calsbeek, R. & Smith, T. B. 2007 Experimentally replicated disruptive selection on performance traits in a Carribean lizard. *Evolution* **62**, 478–484. (doi:10.1111/j.1558-5646.2007.00282.x)

Calsbeek, R., Smith, T. B. & Bardeleben, C. 2007 Intraspecific variation in *Anolis sagrei* mirrors the adaptive radiation of Greater Antillean anoles. *Biol. J. Linn. Soc.* **90**, 189–199. (doi:10.1111/j.1095-8312.2007.00700.x)

Clegg, S. M., Frentiu, F. D., Kikkawa, J., Tavecchia, G. & Owens, I. P. F. 2008 4000 years of phenotypic change in an island bird: heterogeneity of selection over three microevolutionary timescales. *Evolution* **62**, 2393–2410. (doi:10.1111/j.1558-5646.2008.00437.x)

Coyne, J. A. & Orr, H. A. 2004 *Speciation*. Sunderland, MA: Sinauer Associates.

Dieckmann, U. & Doebeli, M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354–357. (doi:10.1038/22521)

Doebeli, M., Blok, H. J., Leimar, O. & Dieckmann, U. 2007 Multimodal pattern formation in phenotype distributions of sexual populations. *Proc. R. Soc. B* **274**, 347–357. (doi:10.1098/rspb.2006.3725)

Edelaar, P., Siepielski, A. M. & Clobert, J. 2008 Matching habitat choice causes directional gene flow: a neglected dimension in ecology and evolution. *Evolution* **62**, 2462–2472. (doi:10.1111/j.1558-5646.2008.00459.x)

Ford, H. A., Parkin, D. T. & Ewing, A. W. 1973 Divergence and evolution in Darwin's finches. *Biol. J. Linn. Soc.* **5**, 289–295. (doi:10.1111/j.1095-8312.1973.tb00707.x)

Foster, D., Podos, J. & Hendry, A. P. 2008 A geometric morphometric appraisal of beak shape in Darwin's finches. *J. Evol. Biol.* **21**, 263–275.

Gavrilets, S. 2004 *Fitness landscapes and the origin of species*. Princeton, NJ: Princeton University Press.

Grant, P. R. 1986 *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.

Grant, B. R. & Grant, P. R. 1993 Evolution of Darwin's finches caused by a rare climatic event. *Proc. R. Soc. B* **251**, 111–117. (doi:10.1098/rspb.1993.0016)

Grant, B. R. & Grant, P. R. 1996 High survival of Darwin's finch hybrids: effects of beak morphology and diet. *Ecology* 77, 500–509. (doi:10.2307/2265625)

Grant, P. R. & Grant, B. R. 2000 Non-random fitness variation in two populations of Darwin's finches. *Proc. R. Soc. B* **267**, 131–138. (doi:10.1098/rspb.2000.0977)

Grant, P. R. & Grant, B. R. 2002 Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711. (doi:10.1126/science.1070315)

Grant, P. R. & Grant, B. R. 2006 Evolution of character displacement in Darwin's finches. *Science* **313**, 224–226. (doi:10.1126/science.1128374)

Grant, P. R. & Grant, B. R. 2008 *How and why species multiply.* Princeton, NJ: Princeton University Press.

Grant, P. R., Grant, B. R., Markert, J. A., Keller, L. F. & Petren, K. 2004 Convergent evolution of Darwin's finches caused by introgressive hybridization and selection. *Evolution* **58**, 1588–1599.

Hendry, A. P., Grant, P. R., Grant, B. R., Ford, H. A., Brewer, M. J. & Podos, J. 2006 Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches. *Proc. R. Soc. B* **273**, 1887–1894. (doi:10.1098/rspb.2006.3534)

Herrel, A., Podos, J., Huber, S. K. & Hendry, A. P. 2005 Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Funct. Ecol.* **19**, 43–48. (doi:10.1111/j.0269-8463.2005.00923.x)

Huber, S. K. 2008 Effects of the introduced parasite *Philornis downsi* on nestling growth and mortality in the medium ground finch (*Geospiza fortis*). *Biol. Conserv.* **141**, 601–609. (doi:10.1016/j.biocon.2007.11.012)

Huber, S. K. & Podos, J. 2006 Beak morphology and song production covary in a population of Darwin's finches (*Geospiza fortis*). *Biol. J. Linn. Soc.* **88**, 489–498. (doi:10.1111/j.1095-8312.2006.00638.x)

Huber, S. K., De León, L. F., Hendry, A. P., Bermingham, E. & Podos, J. 2007 Reproductive isolation of sympatric morphs in a population of Darwin's finches. *Proc. R. Soc. B* **274**, 1709–1714. (doi:10.1098/rspb.2007.0224)

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P. & Beerli, P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245–261. (doi:10.1086/319193)

Lack, D. 1947 *Darwin's finches*. Cambridge, UK: Cambridge University Press.

Langerhans, R. B., Gifford, M. E. & Joseph, E. O. 2007 Ecological speciation in *Gambusia* fishes. *Evolution* **61**, 2056–2074. (doi:10.1111/j.1558-5646.2007.00171.x)

Nosil, P. & Sandoval, C. P. 2008 Ecological niche dimensionality and the evolutionary diversification of stick insects. *PLoS ONE* **3**, e1907. (doi:10.1371/journal.pone.0001907)

Petren, K., Grant, P. R., Grant, B. R. & Keller, L. F. 2005 Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. *Mol. Ecol.* **14**, 2943–2957. (doi:10.1111/j.1365-294X.2005.02632.x)

Pfennig, D. W. & Rice, A. M. 2007 An experimental test of character displacement's role in promoting postmating isolation between conspecific populations in contrasting competitive environments. *Evolution* **61**, 2433–2443. (doi:10.1111/j.1558-5646.2007.00190.x)

Pfennig, D. W., Rice, A. M. & Martin, R. A. 2007 Field and experimental evidence for competition's role in phenotypic divergence. *Evolution* **61**, 257–271. (doi:10.1111/j.1558-5646.2007.00034.x)

Podos, J. 2001 Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**, 185–188. (doi:10.1038/35051570)

Ratcliffe, L. M. & Grant, P. R. 1983 Species recognition in Darwin's finches (*Geospiza*, Gould). I. Discrimination by morphological cues. *Anim. Behav.* **31**, 1139–1153. (doi:10.1016/S0003-3472(83)80021-9)

Robinson, B. W. 2000 Trade offs in habitat-specific foraging efficiency and the nascent adaptive divergence of sticklebacks in lakes. *Behaviour* **137**, 865–888. (doi:10.1163/156853900502501)

Rueffler, C., Van Dooren, T. J. M., Leimar, O. & Abrams, P. A. 2006 Disruptive selection and then what? *Trends Ecol. Evol.* **21**, 238–245. (doi:10.1016/j.tree.2006.03.003)

Rundle, H. D. & Nosil, P. 2005 Ecological speciation. *Ecol. Lett.* **8**, 336–352. (doi:10.1111/j.1461-0248.2004.00715.x)

Schluter, D. 1988 Estimating the form of natural selection on a quantitative trait. *Evolution* **42**, 849–861. (doi:10.2307/2408904)

Schluter, D. 1994 Experimental evidence that competition promotes divergence in adaptive radiation. *Science* **266**, 798–801. (doi:10.1126/science.266.5186.798)

Schluter, D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.

Schluter, D. 2003 Frequency dependent natural selection during character displacement in sticklebacks. *Evolution* **57**, 1142–1150.

Schluter, D. & Grant, P. R. 1984 Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.* **123**, 175–196. (doi:10.1086/284196)

Schluter, D., Price, T. D. & Grant, P. R. 1985 Ecological character displacement in Darwin's finches. *Science* **227**, 1056–1059. (doi:10.1126/science.227.4690.1056)

Skúlason, S. & Smith, T. B. 1995 Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* **10**, 366–370. (doi:10.1016/S0169-5347(00)89135-1)

Smith, T. B. 1993 Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* **363**, 618–620. (doi:10.1038/363618a0)