



Adaptive divergence in Darwin's small ground finch (*Geospiza fuliginosa*): divergent selection along a cline

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We examine here, in a single year (2005), phenotypic divergence along a 560-m elevation gradient in Darwin's small ground finch (*Geospiza fuliginosa*) in the Galápagos Islands. In this sample, four composite measures of phenotypic traits showed significant differences along the 18-km geographical cline extending from lowlands to highlands. Compared with lowland birds, highland birds had larger and more pointed beaks, and thicker tarsi, but smaller feet and claws. Finches in an intervening agricultural zone had predominantly intermediate trait values. In a second, mark–recapture study we analyse selection on morphological traits among birds recaptured across years (2000–2005) in lowland and highland habitats. Birds were more likely to survive in the highlands and during the wet season, as well as if they had large beaks and bodies. In addition, highland birds exhibited higher survival rates if they had small feet and pointed beaks – attributes common to highland birds as a whole. Lowland birds were more likely to survive if they possessed the opposite traits. Selection therefore reinforced existing morphological divergence, which appears to reflect local adaptation to differing resources during the predominantly drought-ridden conditions that characterized the 5-year study. Alternative explanations – including genetic drift, matching habitat choice, deformation by parasites, and the effects of wear – received little or no support. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **110**, 45–59.

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INTRODUCTION

A growing number of studies have shown that adaptive divergence can manifest itself on surprisingly microgeographical scales among mainland taxa as well as among species living on small islands (Gill, 1973; Wunderle, 1981; Endler, 1995; Smith *et al.*, 1997; Blondel *et al.*, 1999; Hendry *et al.*, 2006, 2009; Kleindorfer *et al.*, 2006; Ryan *et al.*, 2007; Milá *et al.*, 2009). In many cases, such organisms could easily traverse the length of geographical clines in a fraction of a day if not limited in doing so by external forces. Such evidence of evolutionary differentiation on microgeographical scales is consistent with the ecological theory of adaptive radiation, which predicts divergence of phenotypes under conditions of differ-

ential resource use across habitats (Endler, 1977; Schluter, 1996). This theory has its direct antecedents in Charles Darwin's (1859) 'principle of divergence,' which Darwin once described as the 'key-stone' of his *Origin of Species*, along with the theory of natural selection [Darwin, 1991 (1858–1859), p. 102; letter to Joseph Hooker]. According to current refinements of this theory, trait utility among divergent phenotypes is predicted to result in differential individual fitness, with stabilizing selection occurring if mean phenotypes are close to a single fitness peak, and with divergent or disruptive selection occurring when more than one fitness peak exists (Schluter & Grant, 1984; Schluter, 2000, 2009; Benkman, 2003; Rundle & Nosil, 2005; Rundle & Price, 2009). In this article we document adaptive divergence along a 560-m elevation gradient, spanning just 18 km, in Darwin's small ground finch (*Geospiza fuliginosa* Gould), one of 14 recognized species of Galápagos finches. In addition, we examine the various biological processes that

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could be driving the observed divergence, including natural selection, genetic drift, matching habitat choice, deformation by parasites, and the effects of wear.

Darwin's finches are considered a model group of organisms for understanding evolutionary processes, including important insights into oscillating evolutionary dynamics driven by natural selection, interspecific competition, and sexual selection (reviewed by Grant, 1999; Schluter, 2000; Grant & Grant, 2008). Most long-term studies of the finches have been conducted on low, flat islands of the Galápagos Archipelago (Grant, 1999; but see Schluter & Grant, 1982). These low, flat islands are characterized by comparable environmental conditions within islands, and by large variation in environmental factors occurring across seasons and years (Grant, 1999).

Kleindorfer *et al.* (2006) reported the results of a 4-year study (2000–2004) on the foraging ecology of Darwin's small ground finch on Santa Cruz Island (864 m elevation). The relatively high elevation of Santa Cruz Island has created conditions for diverse patterns of precipitation and temperature within a single island, resulting in the establishment of seven different ecological zones (Jackson, 1993). Kleindorfer *et al.* (2006) presented evidence for adaptive phenotypic divergence among individual *G. fuliginosa* that were mist-netted and observed at the clinal extremes of their contiguous populations (arid lowlands, forest highlands). The arid zone is characterized by drought-tolerant plant species, including endemic cacti and deciduous trees and shrubs. In contrast, the moist highlands are heavily vegetated with the endemic evergreen *Scalesia* tree, epiphytes, ferns, and mosses. Birds in the lowlands had shorter beaks and larger feet, toes, and claws than birds in the highlands. This phenotypic divergence was correlated with different foraging strategies and resource use, pointing to an adaptive function.

In the first of two new studies presented here we examined phenotypic divergence across two populations of *G. fuliginosa* (lowlands, highlands) in a single year (2005), extending our previous findings for birds sampled between 2000 and 2004 at the same sites and adding, for comparison, birds living in the intervening agricultural zone. The new data from 2005 provide a test and extension of our earlier results about morphological differences along the cline, including a determination of the overall form of the cline (whether it is linear or quadratic). Depending on the morphological trait being considered, the expectation is that intermediate as well as extreme trait values may be found among finches in the agricultural zone compared with finches in the arid lowlands and forest highlands. The case for intermediate trait values rests on the fact that native resource compo-

sition and abundance are transitional in the agricultural zone, with approximately 43% of the most common native plant species being found in adjoining zones (Wiggins & Porter, 1971). In the absence of graduated resources, however, the same prediction can be made given potential interbreeding between finches from the two clinal extremes, as well as owing to immigration, or, alternatively, through genetic drift and isolation by distance – explanations we also address. Extreme values (and hence quadratic clinal trends) are also possible because the agricultural zone consists of a disturbed habitat containing many introduced trees, shrubs, and crop species. A test for clinal differences involving completely undisturbed habitat is not possible on the southern side of Santa Cruz because the agricultural zone extends across this entire portion of the island.

In a second study we examined survivorship across years (2000–2005), including in new samples collected in 2005. We previously analysed birds captured before 2005 for evidence of clinal differences in morphology (Kleindorfer *et al.*, 2006), but not for differences in survival rates. In this new study we tested for directional and stabilizing selection within different habitats. We expected to find directional selection owing to the harsh ecological circumstances that prevailed during the 5-year study period, given that harsh conditions tend to favour extreme trait values that in turn facilitate the exploitation of scarce resources (Grant, 1999; Grant & Grant, 2006). We deemed stabilizing selection, which favours birds with near-mean trait values, to be less likely. We also expected that any trends involving directional selection would differ by habitat, leading to divergent selection across habitats. Additionally, we considered matching habitat choice as a possible explanation for any observed clinal trends, as this process, which has tended to be neglected in the analysis of clinal differences, can mimic the effects of divergent selection across dissimilar habitats (Edelaar, Siepielski & Clobert, 2008; Holt & Barfield, 2008).

MATERIAL AND METHODS

MIST-NETTING AND MORPHOLOGY MEASUREMENT

Between 2000 and 2004, a total of 352 birds were mist-netted and colour banded in two habitats, which are located 18 km from one another (lowlands, $N = 172$, 50 m a.s.l.; highlands, $N = 180$, 610 m a.s.l.). Within each habitat, birds were sampled within six different study plots (100 × 200 m) separated from each other by 200 m and spanning a total distance of 2.2 km in the lowlands and 2.1 km in the highlands. Comprehensive descriptions of the study sites, mist-netting, and morphometry methods are provided in

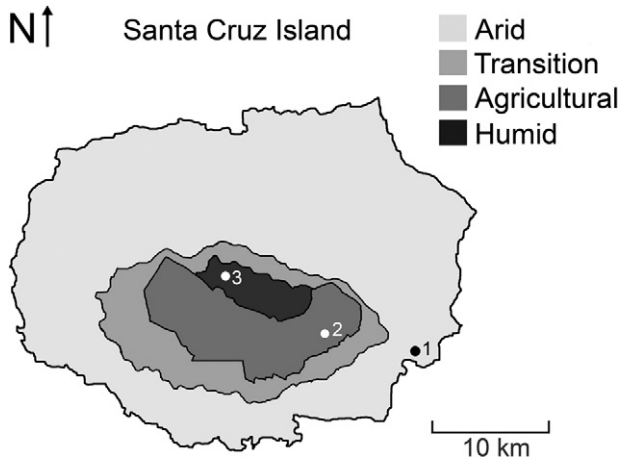


Figure 1. Map of Santa Cruz Island, Galápagos Archipelago, showing four major ecological zones and the three sites where birds were sampled: (1) El Garrapatero (arid zone), 50 m a.s.l.; (2) Cascajo (agricultural zone), 200 m a.s.l.; (3) Los Gemelos (humid zone), 610 m a.s.l.

Kleindorfer *et al.* (2006) and Kleindorfer (2007). During 2005, we increased our sampling effort to include a 100 × 200-m site in Cascajo, 8 km north-west of our lowland site (El Garrapatero) and 10 km south-east of our highland site (Los Gemelos). At 200 m elevation, this new site was located just within the south-eastern edge of the agricultural zone, a continuous band 20 km long and 5 km wide that extends across the southern side of the island at elevations between 150 and 550 m (Fig. 1). We selected our Cascajo sampling site because it possesses undisturbed transition-zone vegetation, 500 m distant from the nearest agricultural fields. From January to February 2005, we mist-netted 134 birds in our three study areas on Santa Cruz Island ($N = 44$ in the agricultural zone, $N = 41$ at the lowland site, and $N = 49$ at the highland site). For additional information about sample composition by capture episode, habitat, and sex, see Supporting information (Table S1).

Because beak, feet, claws, and overall body size all play important roles in the behavioural ecology of foraging and territorial defence (Grant & Grant, 2002; Kleindorfer *et al.*, 2006), we expected selection to act directionally on these traits under harsh conditions. At the time of mist-netting we measured 30 morphological features, including six beak, 14 body, and 10 foot and claw attributes. All measurements were taken by the same researcher (S.K.). In addition to these measurements, birds were sexed based on plumage. Among males – 68% of the sample – plumage was colour graded on a five-step scale, which provides a good indicator of age until birds reach full male plumage around the fourth year (Lack, 1947;

Grant, 1999; Kleindorfer, 2007). Ground finches can live as long as 10–15 years, and one 12-year-old male in our study was resighted in 2013 by S.K.

MARK-RECAPTURE STUDY (2000–2005)

In our mark–recapture study we analysed morphological data for birds that were banded between 2000 and 2004 (lowlands $N = 172$; highlands $N = 180$). Seventy of the 352 birds were captured again or resighted in subsequent years – 17 in the lowlands and 53 in the highlands. We spent an average of 10.6 days mist-netting birds during each of six capture occasions, 4.8 days/occasion in the lowlands and 5.8 days/occasion in the highlands. Time-varying intervals between capture occasions were used in MARK to calculate survival and recapture rates on an annualized basis (White & Burnham, 1999). Capture effort (hours spent mist-netting per day × the number of mist-nets used) was included as a predictor of recapture rates. Data are deposited in the Dryad Digital Repository (Sulloway & Kleindorfer, 2013).

STATISTICAL ANALYSES

All statistical analyses were run in SAS 9.3, PASW 19.3, or MARK. Multiple imputation was used to deal with a modest amount of missing phenotypic measurements (8%), and all statistical results, including standard errors and P -values, were adjusted to reflect the variance inflation associated with this method (for further details, see Supporting information, Appendix S1). To limit the effects of multicollinearity and over-parameterization in multivariate models, we first used principal components analysis to reduce the number of morphological covariates within each of our two study samples (2005 and 2000–2005). Based on promax rotation, extraction of five factors provided the clearest and most interpretable factor structure, and solutions for the two samples were virtually identical. Following factor extraction, composite measures were created from each PC by multiplying the z -scored value of each morphological trait by its factor loading, using only those traits with loadings of 0.50 or higher. Excluding loadings below 0.50 was intended to increase biological interpretability as well as to minimize the variance inflation associated with multiple imputation of missing data, thus reducing standard errors in modelling.

In addition to our five composite measures, we created a sixth morphological measure, for beak shape, given that selection in Darwin's finches is known to act on beak shape as well as size (Price *et al.*, 1984; Grant, 1999). This beak-shape measure consisted of the sum of two beak-length variables (culmen tip to feathers, and culmen tip to anterior

edge of the naris) divided by the sum of beak width and depth. High scores on this measure indicate birds having long, pointed beaks. We also created an omnibus measure of the clinal trend by modelling morphology as a function of habitat, using ordinal regression. We weighted standardized values for each of the six morphological measures by their respective model coefficients. Summed values for each bird were then restandardized. A high score on this omnibus measure indicates birds having long, pointed beaks, short feet and claws, and thick tarsi. This collective measure therefore represents the consistency of each bird's morphology with the clinal trend, given its habitat. We analysed all composite morphological measures, together with the omnibus six-variable measure, for the presence of linear and non-linear (quadratic) trends by habitat.

For analyses of the clinal trend among birds sampled in 2005, we generated 100 datasets by multiple imputation, using SAS PROC MI. We then assessed the relationship between morphology and habitat by means of regression, including linear and quadratic contrasts, which were adjusted for between-imputation variances by SAS PROC MIANALYZE. To determine whether any clinal differences in our sample might be attributable to cumulative wear, we correlated morphological measures with age among males, basing age on plumage.

In assessing recapture and survival rates for birds mist-netted in the lowlands and highlands between 2000 and 2005, we ran Cormack–Jolly–Seber (CJS) models in MARK. This program computes maximum-likelihood estimates, which can be modelled as functions of covariates, such as body size, beak size, and capture effort. For capture–mark–recapture data, this approach offers a distinct advantage over the more traditional method of determining selection gradients (Lande & Arnold, 1983), in that parameter estimates are unbiased for differences in recapture rates. We followed basic mark–recapture methodology and terminology (Lebreton *et al.*, 1992), and we based model selection on Akaike's Information Criterion (AIC) adjusted for small sample size and overdispersion (QAICc), including an additional variance-inflation factor arising from multiple imputation.

During the first phase of modelling in MARK, we considered appropriate starting models. These included a fully time-dependent model with habitat as a grouping variable, as well as reduced versions of this model. Because our main focus was on survival, we modelled recapture rates first (Lebreton *et al.*, 1992). The best starting model was $\phi(\cdot) p(\text{habitat} + t)$, in which survival rate (ϕ) was held constant, and recapture rate (p) was modelled as an additive effect of habitat and time (t). This model was distinctly superior to one including collecting effort instead of time as a

predictor of recapture rates. Collecting effort was not considered further in the modelling process, as its modest corrective effects were already encompassed in models having both time-dependent recapture rates and a grouping variable for $p(\text{habitat})$.

In addition to our base, or starting, model, we initially considered 11 biologically relevant covariates as candidates for inclusion in a global model. These covariates encompassed the seven effects for morphology as well as four other potential predictors of survival: (1) sex; (2) age, coded in a time-dependent manner; (3) an annualized measure of rainfall occurring within habitats during each survival interval; and (4) season – whether birds were captured during the breeding, or wet, season (January to May), as opposed to the non-breeding, or dry, season (June–December) – a period when survival is generally lower (Grant, 1999). We also modelled age and season as predictors of recapture rates. Information on rainfall was downloaded from <http://datazone.darwinfoundation.org/climate/>. In addition, we considered interactions with habitat, as well as quadratic trends in morphology, for indications of possible stabilizing or disruptive selection. Because quadratic trends typically entail smaller selection gradients than do linear trends (median $r = 0.10$ versus 0.16), our power to detect quadratic trends was only 0.54 in this study (Kingsolver *et al.*, 2001). By contrast, our power to detect the median r typically found for directional effects in selection studies was 0.91. After the exclusion of uninformative and redundant predictors, we were left with a global model for further analyses in MARK that included seven informative predictors of survival: habitat, season of capture, beak size, body size, the omnibus clinal-trend measure (itself composed of six weighted covariates), and two interaction effects (habitat \times clinal trend and habitat \times body size).

Determination of goodness of fit for our global model was conducted in two different ways. First, we used U-CARE to assess possible violations of the assumptions that underlie CJS models (Choquet *et al.*, 2009). A fully time-dependent model exhibited good fit, with only a small degree of overdispersion ($\chi^2_{17} = 18.28$, $P = 0.37$; $\hat{c} = 1.075$). In addition, we found no evidence of transience ($Z = 1.12$, $r = 0.06$, $N = 314$, $P = 0.13$, one-tailed) or trap dependence ($Z = 0.73$, $r = 0.05$, $N = 212$, $P = 0.46$, two-tailed). Additional tests for transience were conducted within different age classes and by habitat, as well as within morphological subgroups matching, and failing to match, their habitat's clinal type. These tests showed only small and non-significant trends for greater transience among younger birds, lowland birds, and birds discordant with their habitat's clinal type (for further details, see Supporting information, Appendix S2).

Given that transience and trap dependence were not significant factors in our study population, these influences were not considered further in models using MARK. Using the median- \hat{c} approach to overdispersion that is available in MARK, we determined that overdispersion in our global model was less than 1.00 (see Supporting information, Appendix S3). We therefore set \hat{c} to 1.00 (Burnham & Anderson, 2002).

Proceeding according to an information-theoretic approach, we assessed the tradeoff between precision and parsimony in CJS models using a stepwise backward-selection approach to eliminate the least important predictors from our global model, based on the smallest absolute value of β/SE for each covariate. Weak predictors were retained, however, as long as they were part of stronger interaction effects. We did not follow a stepwise process in a completely mechanical manner, as this would have eliminated a number of biologically plausible models that were included in an a-priori list of models to be run.

Beginning with a fully saturated, global CJS model having seven covariates, we examined 13 additional models that we considered as providing a possible basis for predicting recapture and survival. Models that differed from the best model by $\Delta QAIc < 2$ were considered to have substantial support as a source for making inferences, whereas models with $\Delta QAIc$ between 2 and 7 were judged to have some support and were therefore deemed competitive (Burnham & Anderson, 2002). Nevertheless, because models whose $\Delta QAIc$ is between 4 and 7 have less than 1/7th – and as little as 1/33rd – the support accorded to the top model, such competitive models provide relatively limited information for drawing biological inferences, although they are still useful for model averaging. An otherwise competitive model was judged to be non-competitive (and is indicated as such) if it was a higher-order version of another model having a QDeviance score within $2 \times \Delta K$ of the higher-order model, where ΔK is the number of additional parameters contained in the higher-order model (Burnham & Anderson, 2002; Arnold, 2010). To determine the relative importance of predictors in our 14 models as a whole, we summed QAICc (Akaike) weights for those competitive models in which each predictor appeared. Apparent survival and recapture rates were computed by model averaging.

RESULTS

MORPHOLOGY ACROSS HABITATS

Principal components analysis for birds mist-netted in 2005 produced five PCs – for body size, beak size, foot size, claw size, and tarsus thickness (see Supporting information, Table S2). These five PCs,

Table 1. Linear and quadratic clinal trends for morphological composites among Darwin's small ground finches in 2005 ($N = 134$)

Morphological composite	Linear trend by habitat	Quadratic trend by habitat	N^\dagger
	r	r	
Body size	–0.02	–0.02	124.9
Beak size	0.16 [†]	–0.05	130.0
Beak shape (pointed)	0.18*	–0.20*	134.0
Foot size	–0.31***	0.05	130.3
Claw size	–0.25**	0.11	129.7
Tarsus thickness	0.26**	0.09	134.0
Omnibus 6-variable clinal-trend measure	0.54***	–0.12	131.7

Note: For linear trends, contrast weights are –1 (lowlands), 0 (agricultural zone), and +1 (highlands). For quadratic trends, contrast weights are –1 (lowlands and highlands) and +2 (agricultural zone). P -values are adjusted for the imputation of missing data.

[†]Values of N are adjusted for the fraction of missing information, as computed by SAS's PROC MIANALYZE.

[†] $P = 0.06$.

* $P < 0.05$; adjusted for the false discovery rate (Benjamini & Hochberg, 1995), the linear and quadratic trends for beak shape are no longer significant ($P = 0.12$ and $P = 0.06$, respectively). ** $P < 0.01$. *** $P < 0.001$.

together with a variable for beak shape, comprised our six measures of morphology. Four of these six measures showed linear relationships with habitat, and an additional measure exhibited a near-significant trend (Table 1 and Fig. 2A–F). Highland birds had the largest and most pointed beaks as well as the thickest tarsi. These same birds also had the smallest feet and claws. Body size did not differ by habitat. An ordinal logistic regression model with habitat as the dependent variable showed that five of six morphological measures were significant predictors: beak size, beak shape, foot size, claw size, and tarsus thickness (Likelihood Ratio $\chi^2_6 = 45.61$, Cox and Snell $R = 0.54$, $N = 131.0$, $P < 0.0001$ – Table 1 and Fig. 3). Quadratic trends, which highlight any unique features of the agricultural zone, produced only a single finding, namely a tendency for agricultural-zone birds to have particularly blunt beaks (Table 1 and Fig. 2C). The omnibus six-variable measure of the clinal trend did not, however, exhibit a quadratic trend (Likelihood Ratio $\chi^2_1 = 1.89$, Cox and Snell $R = 0.12$, $N = 131.9$, $P = 0.17$); and a multivariate logistic regression model of morphology, with habitat modelled as a quadratic trend, also failed to reach statistical significance (Likelihood

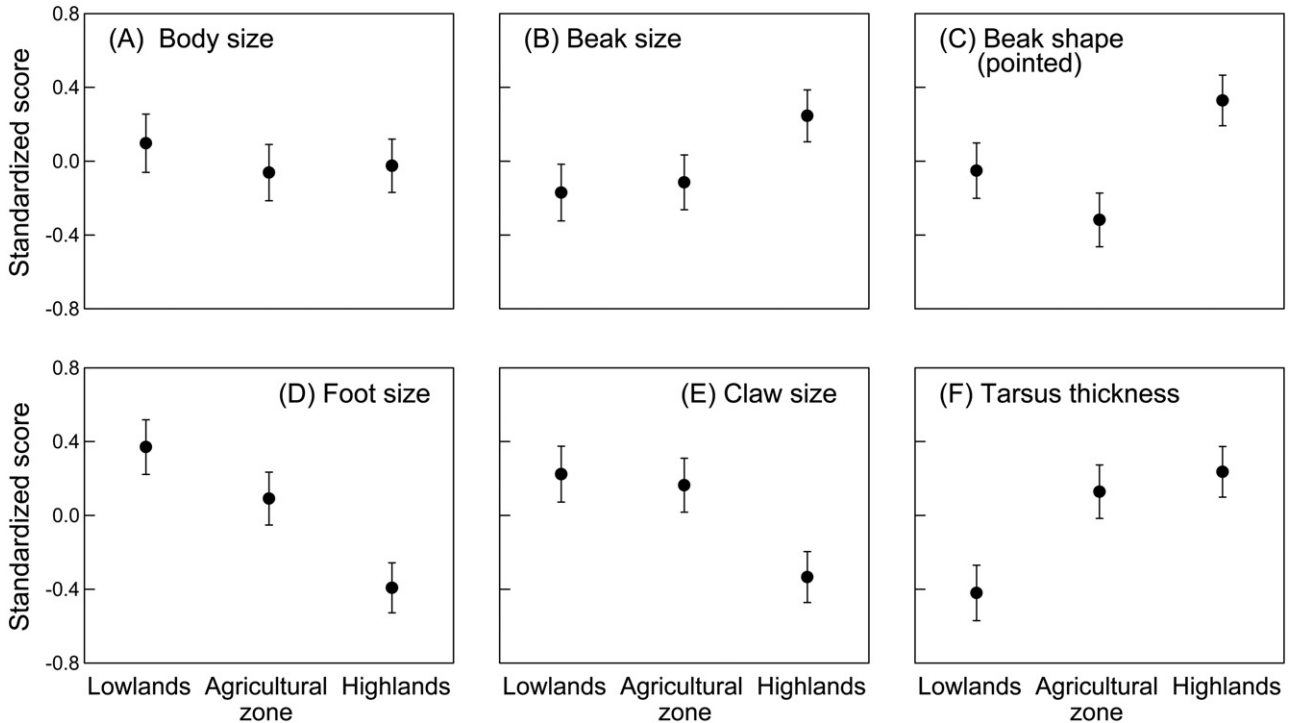


Figure 2. Means and standard errors for composite measures of (A) body size, (B) beak size, (C) beak shape, (D) foot size, (E) claw size, and (F) tarsus thickness in *G. fuliginosa* for each of three habitats (lowlands, agricultural zone, and highlands) on Santa Cruz Island in 2005 ($N = 134$). Standard errors are adjusted for the imputation of missing data. Linear trends are statistically significant for beak shape, foot size, claw size, and tarsus thickness, as is the quadratic trend for beak shape (Table 1). Similar clinal differences were previously found between lowland and highland birds sampled between 2000 and 2004 – specifically, in beak length, foot size, and claw size (Kleindorfer *et al.*, 2006).

Ratio $\chi^2_6 = 9.49$, Cox and Snell $R = 0.26$, $N = 131.2$, $P = 0.15$).

Given evidence for larger and more pointed beaks among highland birds, and for larger feet and claws among lowland birds, we conducted tests on the entire sample of birds captured between 2000 and 2005 to determine whether differences in cumulative wear by habitat might be responsible for these morphological disparities. We detected no signs that cumulative wear in the course of aging differed by habitat for any of our six composite measures of morphology (see Supporting information, Appendix S4).

MARK MODELS FOR SURVIVAL AND RECAPTURE (2000–2005)

The top CJS model consisted of our base model – $\phi(\cdot)p(\text{habitat} + t)$ – together with five covariates added to the survival side of the model, as well as a habitat \times clinal trend interaction effect (Model 1, Table 2). Apparent survival rates were highest among birds possessing large beaks and bodies as well as among birds captured in the highlands and during the wet season. Model averaging revealed that annu-

alized survival was 15% higher in the highlands than in the lowlands, and 57% higher during intervals that included the wet season (see Supporting information, Table S3).

As predicted, the habitat \times clinal-trend interaction, which was present in six of the nine competitive models ($\Delta\text{QAICc} < 7$), indicated that surviving birds tended to resemble other birds living within the same habitat. Beak shape and foot size were the two salient contributors to this interaction effect, as determined by post-hoc analyses. Each of these two morphological traits made nearly equal contributions to apparent survival, and each was an informative predictor of survival in its own right – but only in interaction with habitat. More specifically, lowland birds were more likely to survive if they had large feet and blunt beaks, whereas highland birds were more likely to survive if they had small feet and long, pointed beaks (Fig. 4). When individually predicted survival rates were examined by habitat and season, selection along the cline appeared to be distinctly directional, especially under harsh conditions (Fig. 5). In agreement with this conclusion, no evidence was found for disruptive or stabilizing selection when the square of the

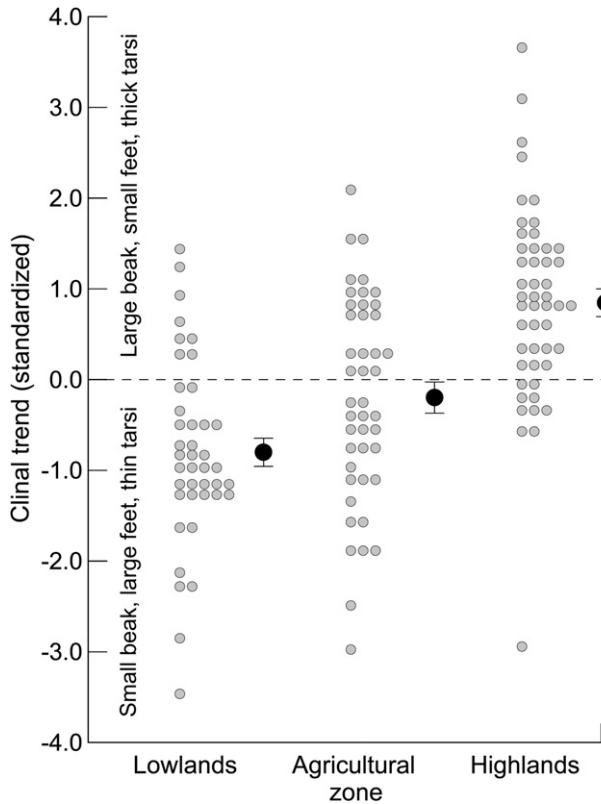


Figure 3. Density plot of the omnibus clinal-trend measure, showing the relationship between morphology and habitat in Darwin's small ground finch along an elevation gradient on Santa Cruz Island in 2005 ($r = 0.54$, $N = 131.7$, $P < 0.0001$). The omnibus measure includes five significant predictors of habitat – beak size, beak shape, foot size, claw size, and tarsus thickness. Individual cases are plotted for the first imputed dataset. Means and standard errors, adjusted for all 100 imputed datasets, are indicated to the right of each density plot.

clinal-trend measure was included in Model 1 (Table 2; $\chi^2_1 = 0.21$, $N = 421.1$, partial pseudo $r = 0.02$, $P = 0.65$). Additionally, the observed directional selection trends were consistent among different cohorts of birds (Fig. 6).

Overall, the six competitive models that included a habitat \times clinal trend interaction were 2.2 times better supported than other models. However, the effects of this interaction – considered by itself – were considerably more impressive given that most of the added explanatory power in these six models resided in the two-way interaction rather than in the two main effects that compose it. More specifically, Model 1 was 18 times better supported than a model that omitted just one variable – namely the habitat \times clinal-trend interaction ($\Delta\text{QAICc} = 5.81$, Table 2, note *).

Relative to Model 1, three other models were within 2 units of QAICc, and two of these three models

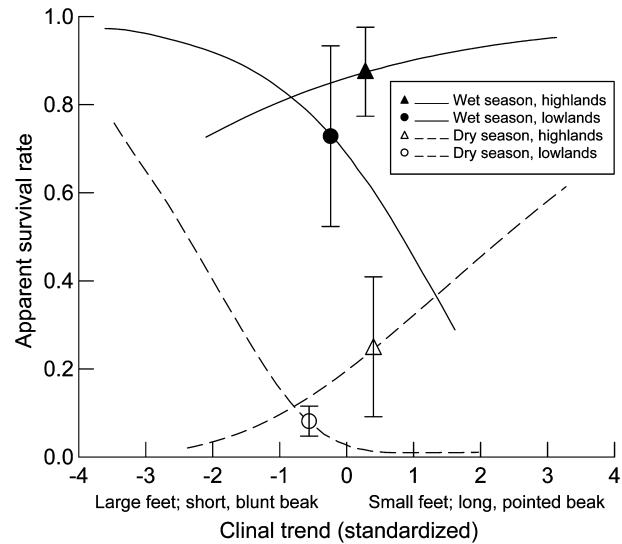


Figure 4. Apparent survival (annualized) of Darwin's small ground finch as predicted by habitat, season, and the clinal trend (Model 1, Table 2). Means and standard errors, adjusted for all 100 imputed datasets, are indicated for each subgroup. Birds in the highlands, where 3.0 times as much rainfall occurred, were 18% more likely to survive than were birds in the lowlands. Relative to the dry season, survival was 67% higher during intervals that included the wet season. In addition, birds in the lowlands were more likely to survive if they had large feet and short, blunt beaks, whereas birds in the highlands tended to survive if they had small feet and long, pointed beaks. A 1.0-SD increase in the clinal-trend measure was associated with an 8% increase in survival among highland birds and a 13% decrease in survival among lowland birds.

contained the habitat \times clinal-trend interaction effect. Nevertheless, the second-ranked model, which included a parameter for habitat \times body size, cannot be considered competitive as it achieved its low ΔQAICc score because Model 1 was nested within it. Model 4, which lacked the habitat \times clinal-trend interaction effect and the two main effects that composed it, attained competitive status through parsimony, by having only 10 parameters (and a smaller pseudo R of 0.16, compared with a pseudo R of 0.21 for Model 1). On biological grounds, however, this reduced model was not particularly plausible. More particularly, it achieved its parsimony by shifting all of the effects of habitat to the recapture side of the model, an improbable modelling scenario given that survival was strongly dependent on rainfall – as evidenced by substantially greater survival during the wet season, and also given that rainfall and survival were both higher in the highlands than in the lowlands.

Because of the relatively equal contributions made to the best-supported model by its five covariates, no

Table 2. CJS mark–recapture models estimating annualized survival (ϕ) and recapture rates (p) for Darwin’s small ground finch (2000–2005, $N = 442$)

Model*	K^\dagger	$\Delta\text{QAICc}^\ddagger$	Akaike weight		QDeviance	Model pseudo R (95% CIs) \P
			All models	Competitive models \S		
1. BASE + ϕ (season + beak + body + habitat \times clinal trend)	13	0.00	0.263	0.334	411.14	0.21 (0.12, 0.30)
2. Global model: BASE + ϕ (season + beak + body \times habitat + habitat \times clinal trend)	14	1.17**	0.146	–	410.17	0.22 (0.13, 0.31)
3. BASE + ϕ (season + body + habitat \times clinal trend)	12	1.59	0.119	0.151	414.86	0.19 (0.10, 0.28)
4. BASE + ϕ (season + beak + body)	10	1.85	0.104	0.132	419.35	0.16 (0.07, 0.26)
5. BASE + ϕ (season + body)	9	2.26	0.085	0.108	421.86	0.15 (0.05, 0.24)
6. BASE + ϕ (season + beak)	9	3.04	0.058	0.073	422.64	0.14 (0.04, 0.23)
7. BASE + ϕ (beak + habitat \times body + habitat \times clinal trend)	13	3.12	0.055	0.070	414.26	0.20 (0.10, 0.29)
8. BASE + ϕ (habitat + season + beak + body)	11	3.71**	0.041	–	419.11	0.17 (0.07, 0.26)
9. BASE + ϕ (beak + body + habitat \times clinal trend)	15	3.78	0.040	0.051	417.05	0.18 (0.09, 0.27)
10. BASE + ϕ (season + beak + habitat \times clinal trend)	12	3.82	0.039	0.049	417.10	0.18 (0.09, 0.27)
11. BASE model – $\phi(\cdot) p(\text{habitat} + t)$.	7	7.19**	0.007	–	430.96	0.00 (0.00, 0.10)

*The BASE model is Model 11 – $\phi(\cdot) p(\text{habitat} + t)$. Models with interaction effects include all associated main effects. Not listed in the main body of this table are three models whose Akaike weights in column 4 are < 0.024 ($\text{QAICc} \geq 4.79$), giving these models $< 1/10$ th the support of Model 1. These three models include only one that is competitive, namely BASE + $\phi(\text{habitat} \times \text{body} + \text{habitat} \times \text{clinal trend})$, $\Delta\text{QAICc} = 4.79$. The two non-competitive models are BASE + $\phi(\text{habitat} + \text{season} + \text{beak} + \text{body} + \text{clinal trend})$, $\Delta\text{QAICc} = 5.81$, and BASE + $\phi(\text{beak} + \text{habitat} \times \text{clinal trend})$, $\Delta\text{QAICc} = 7.64$. If the interaction effect in Model 1, which requires the inclusion of three variables (at a cost of $\Delta\text{QAICc} = 2 \times K$, or 6), is rendered more parsimoniously as a single variable – namely, as conformity to a bird’s clinal type by habitat – QDeviance is 413.99, $\Delta\text{QAICc} = -1.43$, and $K = 11$. This model becomes the top model and is superior by $\Delta\text{QAICc} \geq 3.28$ to all other models that do not include habitat \times clinal trend. Conformity to a bird’s clinal type can be expressed, parsimoniously, as clinal trend $\times (+1)$ in the highlands and clinal trend $\times (-1)$ in the lowlands.

† Number of parameters. The final recapture rate for lowland birds (p_{t5}) was fixed at zero because no lowland birds were recaptured during this episode (Supporting information, Table S3); survival during this period, however, was not necessarily zero.

‡ For the top-ranking model, $\text{QAICc} = 438.04$. For all models, \hat{c} is 1.1064, based on the fully saturated model (Model 2).

§ Akaike weights in column 5 are computed only for the nine competitive models ($\Delta\text{QAICc} < 7$). See also note **.

¶ As a measure of model effect size, pseudo R was calculated from the difference in QDeviance between each model and the BASE model [$\phi(\cdot) p(\text{habitat} + t)$], using McFadden’s version of this statistic (Veall & Zimmermann, 1994).

**Not a competitive model, because $\Delta\text{QAICc} > 7$ or because the model is a more complex version of another model having a lower QAICc score, and the higher-order model does not reduce QDeviance by at least 2.0 times the number of additional parameters (Burnham & Anderson, 2002; Arnold, 2010).

model within the overall model set received a particularly high Akaike weight. Model averaging of parameter estimates is appropriate in such cases, but weighted averages for such parameter estimates make little sense when interactions are involved because estimates vary in magnitude and direction based on the presence of the interactions. Under these circumstances it is customary to assess variable importance by summing the model weights for each

model in which a given variable appears (Burnham & Anderson, 2002).

Table 3 provides betas, SEs, partial pseudo r values, and 95% CIs for all informative parameters present in competitive models. Evaluating variable importance by the summing of Akaike weights in all nine competitive models in our study ($\Delta\text{QAICc} < 7$), the three top predictors of survival were body size (0.88), wet season (0.85), and beak size (0.71),

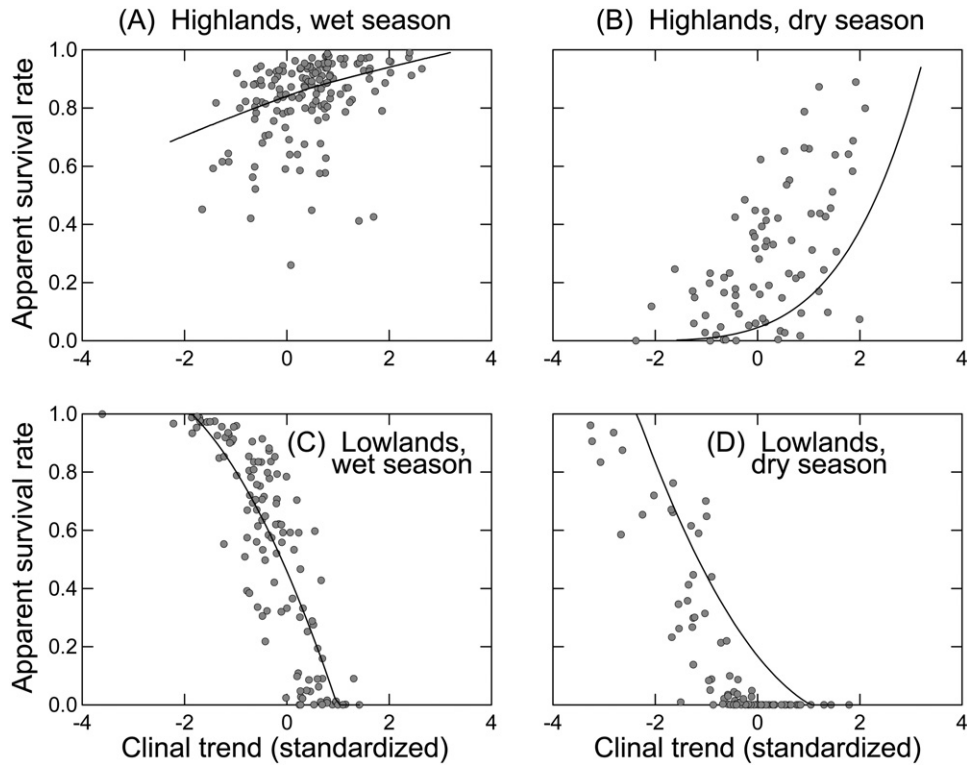


Figure 5. Apparent survival rates (annualized) in individual small ground finches, as predicted by Model 1 (Table 2) and plotted by habitat and season. Trend lines are plotted for all 100 imputed datasets. Individual cases are plotted for the first imputed dataset. The panel illustrates contrasting patterns of directional selection by habitat, especially under harsh ecological conditions – namely, those prevailing in the lowlands and during the dry season (B–D). The net result of these opposing patterns of directional selection by habitat was morphological divergence along the length of the cline.

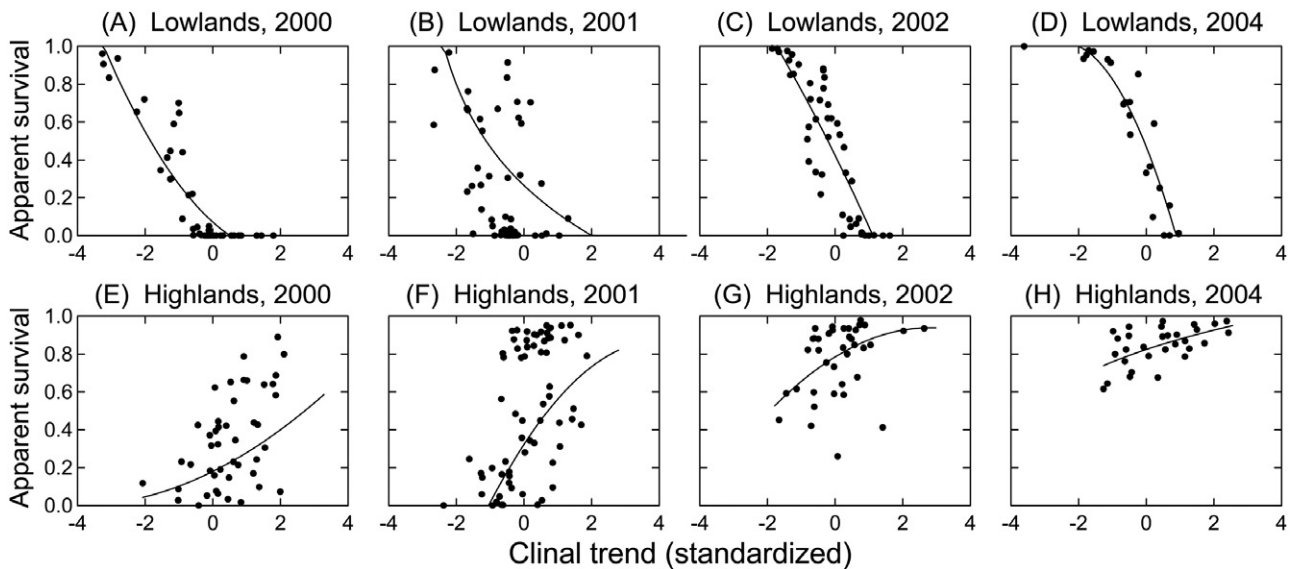


Figure 6. Apparent survival rates (annualized) in individual small ground finches, as predicted by Model 1 (Table 2) and plotted by habitat and year. Trend lines are plotted for all 100 imputed datasets. Individual cases are plotted for the first imputed dataset. Selection was consistent in direction by habitat across the four time periods (and cohorts of birds). There is no evidence of stabilizing or disruptive selection.

Table 3. Selection gradients and model-averaged parameter estimates for covariates in Table 2 models for survival (ϕ) and recapture (p) of Darwin's small ground finch (2000–2005, $N = 442$)

Variable	β /SE (95% CIs)	McFadden's partial pseudo r (95% CIs)	Model-averaged parameter estimates [cumulative Akaike weights (Σw_i)]*
ϕ (body size)	0.57/0.28 (0.03, 1.11)	0.12 (0.02, 0.21)	0.88
ϕ (season)†	2.39/0.89 (0.65, 4.12)	0.12 (0.02, 0.21)	0.85
ϕ (beak size)	0.42/0.23 (-0.03, 0.86)	0.09 (0.00, 0.19)	0.71
ϕ (habitat)†	0.91/0.56 (-0.18, 2.01)	0.08 (-0.02, 0.17)	0.69
ϕ (clinal trend)	-0.74/0.37 (-1.47, -0.02)	-0.12 (-0.21, -0.02)	0.69
ϕ (habitat \times clinal trend)	1.11/0.48 (0.16, 2.05)	0.14 (0.04, 0.23)	0.69
ϕ (habitat \times body)	-1.46/0.88 (-3.19, 0.27)	-0.08 (-0.17, 0.01)	0.10

Note: β , SE, and McFadden's partial pseudo r values are provided here for Model 1, Table 2, with the exception of statistics for ϕ (habitat \times body), which are from Model 7. In Model 7, the β for body size is 1.74, SE = 0.84 (95% CI = 0.09, 3.39), and the partial pseudo r is 0.14 (95% CI = 0.04, 0.23). Partial pseudo r values are calculated from the difference in QDeviance between each model and a reduced model, omitting the variable in question. These measures of effect size are analogous to partial correlations (selection gradients) in least-squares regression (Veall & Zimmermann, 1994).

*Five non-competitive models in Table 2 are excluded from the model-averaged results. Variables in the model set are not represented equally. For ϕ (body), $N = 7$; for ϕ (habitat), ϕ (season), ϕ (beak), ϕ (cline), and ϕ (habitat \times cline), $N = 6$; and for ϕ (habitat \times body), $N = 2$. Equalizing model n values for each parameter makes little difference in model-averaged parameter estimates because the average Akaike weight for alternative models is lower than 0.03.

†Season and habitat were dummy coded: dry (non-breeding) season = 0, wet (breeding) season = 1; lowlands = 0, highlands = 1.

followed closely by habitat, clinal trend, and the habitat \times clinal-trend interaction (all with cumulative weights of 0.69). By contrast, the habitat \times body-size interaction – which indicates that survival was more dependent on body weight in the arid lowlands than in the humid highlands – was present in only two of the nine competitive models. For this reason it received a much smaller cumulative Akaike weight (0.10). Relative to its status in Table 3 (column 3) as the single best predictor of survival, the habitat \times clinal-trend interaction in column 4 exhibited a modest reduction in importance, an outcome that reflects the manner in which Akaike model weights tend to underestimate the influence of salient interaction effects when associated main effects are small (Table 2, note *; Erikson, Wright & McIver, 1998).

Three uninformative predictors in our study (sex, age, and rainfall) bear brief comment. All three predictors displayed trends in the expected direction. Among small ground finches, sexual dimorphism is minimal, with males generally being 1–4% larger than females in most morphological traits. Females are also uniparental incubators and subject to higher mortality than males from predation by hawks and owls while attending the nest (O'Connor *et al.*, 2010). As expected, females exhibited a slightly lower rate of survival than did males, a

modest trend that was fully explained by smaller beak and body size. Because there was a substantial point-biserial correlation between habitat (lowlands versus highlands) and episode-specific measures of rainfall during the 5-year study ($r = 0.66$), and because the amount of rainfall was relatively uniform by year, rainfall contributed little to models already including habitat. Older birds were more likely to survive than younger birds, but this effect was sufficiently small that its inclusion in models added almost no explanatory power. Similarly, age as well as season failed to add meaningful explanatory power to top models when included as predictors of recapture rates.

Owing to low recapture rates (averaging 7% during the wet season, 9% in the lowlands, 21% in the highlands, and 27% during the dry season – for a mean recapture rate of 16%), our parameter estimates for apparent survival in MARK exhibited larger standard errors than would otherwise be the case, especially when survival was estimated for subgroups involving habitat and season (Fig. 4 and Table S3). In particular, mean survival estimates by season, which ranged from 0.20 during the dry season to 0.77 during the wet season ($\Delta = 0.57$), seem overly disparate given the much smaller difference in mean survival estimates observed by habitat [lowlands, 0.41; highlands, 0.56 ($\Delta = 0.15$) – Table S3]. With their

relatively large standard errors and 95% CIs, survival estimates for the four relevant subgroups should be accepted with reservation.

DISCUSSION

In comparison with most previous research on Darwin's finches, what is notable about our findings is the demonstration that selection trends can differ substantially within the same species over relatively limited geographical distances within a single island. In our study, these observed selection trends are in turn closely tied to pre-existing clinal differences, which they reinforced.

These novel findings need to be understood in the broader context of unusual weather conditions during the 5-year study (2000–2005). These years were characterized by a prolonged drought during which precipitation on Santa Cruz Island was only 51% of the 30-year mean recorded from 1970 to 1999 (Hicks & Mauchamp, 2000; Fessl, Kleindorfer & Tebbich, 2006; Kleindorfer, 2007). Such harsh conditions provide a unique window of opportunity to measure differential survival among phenotypes (Grant, 1999; Grant & Grant, 2006) and would also be expected to exert stronger selection pressures in the lowlands than the highlands, where rainfall was 3.0 times greater.

MORPHOLOGY ACROSS HABITAT (2005 STUDY)

In our 2005 study, birds from the highlands were distinguished from birds from lower altitudes by having larger and more pointed beaks, and thicker tarsi, but smaller feet and claws. The findings for foot and claw size confirm the differences detected between highland and lowland birds during the previous 4 years by Kleindorfer *et al.* (2006). In addition, Kleindorfer *et al.* (2006) found that beak length was greater among highland than lowland birds, consistent with the significant clinal trend for beak shape documented in 2005. Hence salient features of the clinal trends found in 2005 were also present in the small ground finch population on Santa Cruz during a continuous 5-year period.

These various clinal differences, including the intermediate nature of the morphological data for *G. fuliginosa* in the agricultural zone, can be explained in at least six ways by: (1) local adaptation to resources and climate; (2) gene flow; (3) genetic drift and isolation by distance; (4) environmental induction, including wear and the effects of parasites; (5) gene–environment interaction effects; and (6) matching habitat choice, a topic we address separately in our discussion of mark–recapture results. Because the observed clinal differences in beak size and shape, as well as foot size, correspond with docu-

mented differences in foraging strategies, we believe they primarily reflect adaptations to local resources. Lowland birds, for example, tend to forage on the ground, scratching in the soil with their feet as they search for seeds, and tend to pick and chip at prey with their beaks. By contrast, highland birds spend more time in the low vegetation, sliding vegetation through their long beaks to remove seeds and foraging on insects and fruits (Kleindorfer *et al.*, 2006).

The observed trend for longer beaks in highland birds may relate to the ecological niche that is currently open to the small ground finch within this zone. Prior to about 1930, this niche on Santa Cruz Island was occupied by the sharp beaked ground finch, *G. difficilis*, which largely excludes *G. fuliginosa* from the highlands on this and other islands wherever the two species coexist (Lack, 1947; Schluter & Grant, 1982). After 1930, *G. fuliginosa* probably expanded its range into the highlands as a result of growth of the agricultural zone and the subsequent extinction of *G. difficilis* on Santa Cruz (Lack, 1947; Harris, 1973). In elongated beak length, the current highland population of *G. fuliginosa* approaches the beak shape of *G. difficilis*, which, based on museum specimens, is 3.45 SD larger than beak length in *G. fuliginosa* ($t = 15.95$, d.f. = 110.5, $P < 0.0001$; Lack, 1947: tables 23 and 29).

On all islands, *G. difficilis* has a significantly longer footspan than *G. fuliginosa* (Grant, 1999), and it uses its long feet to scratch among forest litter for invertebrates (Schluter & Grant, 1982). In this study, we nevertheless found larger footspan in lowland *G. fuliginosa*, which was associated with a high level of scratching among the volcanic soil during foraging. Because highland *G. fuliginosa* do not exploit the forest litter in the same manner as *G. difficilis*, evidence of character release in *G. fuliginosa* is likely to be stronger for beak attributes than for foot size.

The predominantly intermediate nature of morphological traits among agricultural zone birds is open to two alternative interpretations that cannot be resolved here: namely, (1) that these traits are a product of interbreeding and entail no particular adaptation to the ecological resources of the agricultural zone itself; and (2) that these traits represent adaptive responses to the transitional nature of the native vegetation and physical conditions characteristic of this zone. In partial support of a selectionist interpretation, the presence of distinctly blunt beaks among agricultural zone birds relative to birds from the other two zones suggests that unique selection pressures may be associated with some aspects of this ecologically disturbed habitat (Table 1).

The hypothesis that morphological differences by habitat may have arisen by genetic drift is not supported by Galligan *et al.*'s (2012) finding that

G. fuliginosa represents a single panmictic population exhibiting relatively high levels of gene flow, and that microsatellite markers in this species exhibit no evidence of isolation by distance. We also found no evidence that clinal differences might have arisen because of differential wear (Supporting information, Appendix S4). In addition, this explanation runs counter to the observed trends for some morphological attributes, inasmuch as lowland birds, which would be expected to experience greater wear while foraging for seeds in the hard volcanic soil, had larger feet and claws than highland birds. With the exception of our various tests for wear, we do not have the appropriate means to test the hypothesis that clinal differences in *G. fuliginosa* reflect environmentally induced responses to differences in diet, temperature, and other possible influences. Cross-fostering experiments have shown that a portion of clinal differences in birds can reflect responses to environmental differences along the cline (James, 1983, 1991; Price, 2008). Nevertheless, the results of our mark-recapture study indicate that selection acted differentially at the two ends of the cline, reinforcing the clinal trend over a 5-year period. This conclusion in turn suggests that selection may have played a role in creating the trend, although we lack data for the period before 2000 to test this assertion in a formal manner.

The observed clinal differences in our own study cannot be readily explained by *Philornis downsi*, an introduced ectoparasite that causes deformation of beaks and reduction in beak and body size (Fessler *et al.*, 2006; Galligan & Kleindorfer, 2009; O'Connor *et al.*, 2010). In particular, studies have not found differences in parasitism rates on Santa Cruz by habitat (Dudaniec, Fessler & Kleindorfer, 2009; Galligan & Kleindorfer, 2009). Furthermore, the possible effects of *Philornis* would not help to explain observed differences in foot and claw size, or tarsus thickness, especially given that no clinal differences were detected in overall body size.

SELECTION TRENDS IN *G. FULIGINOSA* (2000–2005)

Based on CJS models in MARK, our findings show that selection for morphology was directional, not stabilizing or disruptive, during the 5-year period of the study, an outcome we anticipated owing to the harsh ecological conditions that prevailed during the study. We nevertheless note that the absence of agricultural zone birds from our mark-recapture analysis (2000–2005) limits our ability to generalize about the overall pattern of selection along the cline, which was assessed here only in terms of the cline's two geographical endpoints.

Some of our findings from analysis of marked and recaptured birds over a 5-year period are consistent

with previous research on Darwin's finches during periods of drought, which has shown selection favouring birds with large beaks and body size (Boag & Grant, 1981; Price *et al.*, 1984; Grant, 1999; Grant & Grant, 2008). Selection for beak depth allows birds to crush and open the largest seeds, which increasingly become the only remaining food source during droughts and which cannot readily be opened by small-beaked birds. Large body size – a correlate of large beak size – is typically a measure of good physical condition. Hence, large body size is expected to correlate with higher survival rates as long as the energetic costs associated with increasing body size do not outweigh the benefits, which can lead to disruptive selection for this attribute (Schluter, Price & Grant, 1985; Grant, 1999). In our study these two selection trends were exclusively directional, with no effects of stabilizing or disruptive selection being detected. These selection trends would be expected to generate heritable morphological differences, assuming that selection was not acting solely on the non-heritable component of physical size that is entailed in residual condition (Price, Kirkpatrick & Arnold, 1988). In previous studies of Darwin's finches, selection for beak and body size has repeatedly created heritable changes in morphology (Grant, 1999; Grant & Grant, 2008). In addition, our finding that selection reinforced an existing clinal gradient in *G. fuliginosa* over a 5-year period strongly suggests that selection facilitated adaptive divergence according to local ecological conditions.

Four alternative explanations for these selection trends include genetic drift, effects of wear, parasitism by *Philornis downsi*, and matching habitat choice. The first three of these explanations appear to be ruled out by evidence we have already presented in connection with possible sources of the clinal differences documented in 2005. Matching habitat choice is also ruled out as a probable cause of these differences, given that birds showing pronounced morphological departures from their clinal type were not more likely to emigrate from their habitats than were other, more morphologically concordant, birds (see Supporting information, Appendix S2).

Growing evidence has begun to emerge for localized adaptations in Darwin's finches within the same island. In addition to the study by Kleindorfer *et al.* (2006), Hendry *et al.* (2006) have documented the existence of disparities in beak size in *G. fortis* (the medium ground finch) over a distance of just 11 km. Disruptive selection (Hendry *et al.*, 2009) and assortative mating (Huber *et al.*, 2007) both appear to be responsible for the maintenance of local differences in beak-size bimodality in this species. These findings are consistent with the fact that gene flow was lower between beak-size morphs than within them, both

within sites and between geographically separated sites (de León *et al.*, 2010). In the same species, Vanhooydonck *et al.* (2009) have shown that wing morphology and its relationship with body mass differ in functional ways at three sites on Santa Cruz, separated by distances as small as 11 km. Together such findings provide compelling evidence that ecological differentiation can occur over surprisingly small distances among birds, despite gene flow along a cline.

Notwithstanding these recent research results for Darwin's finches, microgeographical differences in morphology are exceedingly rare among birds living on islands smaller than 10 000 km². Consistent with this generalization, there is no known case of intra-island speciation within such small islands (Coyne & Price, 2000). The few previous cases of intra-island clines that have been documented on small islands – for example, among Mascarene white-eyes (*Zosterops borbonicus*) on Réunion (2512 km²), bananaquits (*Coereba flaveola*) on Grenada (344 km²), and *Nesospiza* buntings on Inaccessible Island (13 km²) in the Tristan da Cunha archipelago – have in common steep elevation gradients associated with substantial ecological diversity (Gill, 1973; Wunderle, 1981; Ryan *et al.*, 2007). Although similar microgeographical differences along environmental and elevation gradients have been documented in mainland birds, as well as in other mainland taxa, the distances involved tend to be much greater than those cited here for small islands (Endler, 1977; Smith *et al.*, 1997; Mullen & Hoekstra, 2008; Milá *et al.*, 2009). At 1260 km² and 864 m elevation, Santa Cruz Island in the Galápagos is noteworthy for involving less than half the mean elevation gradient found in other documented instances of intra-island avian clines. Unlike the clinal trends reviewed here for Darwin's small ground finch, most other cases of intra-island clines have yielded much less information about the relative contributions of selection versus matching habitat choice, gene flow, and other potentially relevant biological processes.

CONCLUSIONS

In two related studies we have sought to contribute to the considerable challenge of documenting the adaptive nature of small morphological differences within contiguous populations that differ in habitat resources, trait utility, and consequent selection pressures. Over a 5-year period we found selection to be significantly directional and divergent at the two ends of an elevation cline, reinforcing pre-existing clinal differences. Overall, these and other recently published results for Darwin's finches illustrate a process by which microgeographical differences are being

maintained in various morphological attributes, based on their ecologically contingent utilities. Of special note in this evolutionary process is the highly localized nature of the divergent selection pressures documented here, which have occurred across a distance of only 18 km and which, for some morphological traits, appear to be responsible for the creation of clinal differences over distances as small as 8–11 km.

Although we lack relevant data to determine what other influences, including wear and matching habitat choice, may have contributed to the formation of the cline before 2000 – the year when our investigation began and by which time the cline was already established – we have shown that selection was the primary mechanism for maintaining the cline during the 5-year study (2000–2005). This finding adds to growing evidence, in Darwin's finches and other species, for adaptive divergence in the presence of considerable gene flow.

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REFERENCES

- Arnold TW. 2010.** Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* **76**: 1175–1178.
- Benjamini Y, Hochberg Y. 1995.** Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* **57**: 289–300.

- Benkman CW. 2003.** Divergent selection drives the adaptive radiation of crossbills. *Evolution* **57**: 1176–1181.
- Blondel J, Dias PC, Perret P, Maistre M, Lambrechts MM. 1999.** Selection-based biodiversity at a small spatial scale in a low dispersing insular bird. *Science* **285**: 1399–1402.
- Boag PT, Grant PR. 1981.** Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* **214**: 82–85.
- Burnham KP, Anderson DR. 2002.** *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York: Springer.
- Choquet R, Lebreton J-D, Gimenez O, Reboulet A-M, Pradel R. 2009.** U-CARE: utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* **32**: 1071–1074.
- Coyne JA, Price TD. 2000.** Little evidence for sympatric speciation in island birds. *Evolution* **54**: 2166–2171.
- Darwin CR. 1859.** *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for existence*. London: John Murray.
- Darwin CR. 1991 [1858–1859].** Burkhardt F, Smith S, eds. *The correspondence of Charles Darwin*. Vol. 7: 1858–1859. Cambridge: Cambridge University Press.
- Dudaniec RY, Fessl B, Kleindorfer S. 2009.** Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. *Biological Conservation* **139**: 325–332.
- Edelaar P, Siepielski AM, Clobert J. 2008.** Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* **62**: 2462–2472.
- Endler J. 1977.** *Geographic variation, speciation, and clines*. Princeton, NJ: Princeton University Press.
- Endler J. 1995.** Multiple-trait coevolution and environmental gradients in guppies. *Trends in Ecology and Evolution* **10**: 22–29.
- Erikson RS, Wright GC, McIver JP. 1998.** Too many variables? A comment on Bartle's model-averaging proposal. Paper delivered at the Political Methodology Conference, July 1997, Columbus, OH. Available at: <http://polmeth.wustl.edu/media/Paper/eriks97.pdf>
- Fessl B, Kleindorfer S, Tebbich S. 2006.** An experimental study on the effects of an introduced parasite in Darwin's finches. *Biological Conservation* **127**: 55–61.
- Galligan TH, Donnellan SC, Sulloway FJ, Fitch A, Bertozzi R, Kleindorfer S. 2012.** Panmixia supports divergence with gene flow in Darwin's small ground finch, *Geospiza fuliginosa*, on Santa Cruz, Galápagos Islands. *Molecular Ecology* **21**: 2106–2115.
- Galligan TH, Kleindorfer S. 2009.** Naris and beak deformation caused by the parasitic fly, *Philornis downsi* (Diptera: Muscidae), in Darwin's small ground finch, *Geospiza fuliginosa* (Passeriformes: Emberizidae). *Biological Journal of the Linnean Society* **98**: 577–585.
- Gill FB. 1973.** Intra-island variation in the Mascarene white-eye *Zosterops borbonica*. *Ornithological Monographs*, No. 12.
- Grant PR. 1999.** *Ecology and evolution of Darwin's finches*, 2nd edn. Princeton, NJ: Princeton University Press.
- Grant PR, Grant BR. 2002.** Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707–711.
- Grant PR, Grant BR. 2006.** Evolution of character displacement in Darwin's finches. *Science* **313**: 224–226.
- Grant PR, Grant BR. 2008.** *How and why species multiply: the radiation of Darwin's finches*. Princeton, NJ: Princeton University Press.
- Harris MP. 1973.** The Galapagos avifauna. *Condor* **75**: 265–278.
- Hendry A, Huber SK, de León FL, Herrel A, Podos J. 2009.** Disruptive selection in a bimodal population of Darwin's finches. *Proceedings of the Royal Society B: Biological Sciences* **276**: 753–759.
- Hendry AP, Grant PR, Grant BR, Ford HA, Brewer MJ, Podos J. 2006.** Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches. *Proceedings of the Royal Society B: Biological Sciences* **273**: 1887–1894.
- Hicks DJ, Mauchamp A. 2000.** Population structure and growth patterns of *Opuntia echios* var. *gigantea* along an elevation gradient in the Galápagos Islands. *Biotropica* **32**: 235–243.
- Holt RD, Barfield M. 2008.** Habitat selection and niche conservation. *Israel Journal of Ecology & Evolution* **54**: 295–309.
- Huber SK, de León LF, Hendry AP, Bermingham E, Podos J. 2007.** Reproductive isolation of sympatric morphs in a population of Darwin's finches (*Geospiza fortis*). *Proceedings of the Royal Society B: Biological Sciences* **274**: 1709–1714.
- Jackson M. 1993.** *Galápagos: a natural history*. Calgary: University of Calgary Press.
- James FC. 1983.** Environmental component of morphological differentiation in birds. *Science* **221**: 184–186.
- James FC. 1991.** Complementary descriptive and experimental studies of clinal variation in birds. *American Zoologist* **31**: 694–706.
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gilbert P, Beerli P. 2001.** The strength of phenotypic selection in natural populations. *American Naturalist* **157**: 245–261.
- Kleindorfer S. 2007.** The ecology of clutch size variation in Darwin's Small Ground Finch *Geospiza fuliginosa*: comparison between lowland and highland habitats. *Ibis* **149**: 730–741.
- Kleindorfer S, Chapman TW, Winkler H, Sulloway FJ. 2006.** Adaptive divergence in contiguous populations of Darwin's Small Ground Finch (*Geospiza fuliginosa*). *Evolutionary Ecology Research* **8**: 357–372.
- Lack D. 1947.** *Darwin's finches*. Cambridge: Cambridge University Press.
- Lande R, Arnold SJ. 1983.** The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR. 1992.** Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67–118.

- de León LF, Bermingham E, Podos J, Hendry AP. 2010.** Divergence with gene flow as facilitated by ecological differences: within-island variation in Darwin's finches. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 1041–1052.
- Milá B, Wayne RK, Fitze P, Smith TB. 2009.** Divergence with gene flow and fine-scale phylogeographical structure in the wedge-billed woodcreeper, *Glyphorynchus spirurus*, a Neotropical rainforest bird. *Molecular Ecology* **18**: 2979–2995.
- Mullen LM, Hoekstra HE. 2008.** Natural selection along an environmental gradient: a classic cline in mouse pigmentation. *Evolution* **62**: 1555–1570.
- O'Connor JA, Sulloway FJ, Robertson J, Kleindorfer S. 2010.** *Philornis downsi* parasitism is the primary cause of nestling mortality in the critically endangered Darwin's medium tree finch (*Camarhynchus pauper*). *Biodiversity and Conservation* **19**: 853–866.
- Price T. 2008.** *Speciation in birds*. Greenwood Village, CO: Roberts and Company.
- Price T, Kirkpatrick M, Arnold SJ. 1988.** Directional selection and the evolution of breeding date in birds. *Science* **240**: 798–799.
- Price TD, Grant PR, Gibbs HL, Boag PT. 1984.** Recurrent patterns of natural selection in a population of Darwin's finches. *Nature* **309**: 787–789.
- Rundell R, Price TD. 2009.** Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution* **24**: 394–399.
- Rundle HD, Nosil P. 2005.** Ecological speciation. *Ecology Letters* **8**: 336–352.
- Ryan PG, Bloomer P, Moloney CL, Grant TJ, Delport W. 2007.** Ecological speciation in South Atlantic finches. *Science* **315**: 1420–1423.
- Schluter D. 1996.** Ecological causes of adaptive radiation. *American Naturalist* **148** (Suppl): S40–S64.
- Schluter D. 2000.** *The ecology of adaptive radiation*. Oxford: Oxford University Press.
- Schluter D. 2009.** Evidence for ecological speciation and its alternative. *Science* **323**: 737–741.
- Schluter D, Grant PR. 1982.** The distribution of *Geospiza difficilis* in relation to *G. fuliginosa* in the Galápagos Islands: tests of three hypotheses. *Evolution* **36**: 1213–1226.
- Schluter D, Grant PR. 1984.** Determinants of morphological patterns in communities of Darwin's finches. *American Naturalist* **123**: 175–196.
- Schluter D, Price TD, Grant PR. 1985.** Ecological character displacement in Darwin's finches. *Science* **227**: 1056–1059.
- Smith TB, Wayne RK, Girman DJ, Bruford MW. 1997.** A role for ecotones in generating rainforest biodiversity. *Science* **276**: 1855–1857.
- Sulloway FJ, Kleindorfer S. 2013.** Data from: adaptive divergence in Darwin's small ground finch (*Geospiza fuliginosa*): divergent selection along a cline. *Dryad Digital Repository*. doi:10.5061/dryad.d4g94.
- Vanhooydonck B, Herrel A, Gabela A, Podos J. 2009.** Wing shape variation in the medium ground finch (*Geospiza fortis*): an ecomorphological approach. *Biological Journal of the Linnean Society* **98**: 129–138.
- Veall MR, Zimmermann KF. 1994.** Evaluating pseudo-R²s for binary probit models. *Quality & Quantity* **28**: 151–164.
- White GC, Burnham KP. 1999.** Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl): S120–S139.
- Wiggins II, Porter DM. 1971.** *Flora of the Galápagos Islands*. Stanford, CA: Stanford University Press.
- Wunderle JM, Jr. 1981.** An analysis of a morph ratio cline in the bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution* **35**: 333–344.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Sample information by capture episode and habitat for Darwin's small ground finch on Santa Cruz Island, Galápagos, Ecuador (2000–2005).

Table S2. Factor loadings calculated from principal components analysis of morphological traits in Darwin's small ground finch (N = 134) on Santa Cruz Island, Galápagos, Ecuador (2005).

Table S3. Annualized survival (ϕ) and recapture rates (p) for Darwin's small ground finch (2000–2005), based on model-averaged real parameter estimates and unconditional standard errors, using the nine competitive models in Table 2.

Appendix S1. Multiple imputation of missing data.

Appendix S2. Transience and its relationship with matching habitat choice.

Appendix S3. Overdispersion and variance inflation associated with multiple imputation of missing data.

Appendix S4. Cumulative wear by habitat.