
Adaptive divergence in contiguous populations of Darwin's Small Ground Finch (*Geospiza fuliginosa*)

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ABSTRACT

Hypothesis: The ecological theory of adaptive radiation predicts divergent morphological adaptations to different environments, and different evolutionary trait utilities in varying environments.

Organism: Darwin's Small Ground Finch (*Geospiza fuliginosa*).

Times and places: Santa Cruz Island, Galapagos Archipelago, in two study areas of different habitat type: highland forest (c. 500 m elevation) and lowland arid zone (c. 50 m elevation). The two contiguous populations of Darwin's finches were separated by a flight distance of 18 km. Data were collected from both study areas between November and March in the years 2000, 2001, 2002 and 2004.

Analytical methods: This natural experiment examined two contiguous populations for evidence of the first phase of speciation, namely adaptive divergence in morphological parameters between environments. We used mist-netting to capture and then measure birds between habitat types, and observational methods to record foraging behaviour. Foraging behaviour was recorded as a single observation per bird that was observed along transects through the study plots. Morphology data for beak and foot dimensions were analysed separately, and as principal components factor scores, and were compared between habitats and years.

Results: Birds in the lowlands of Santa Cruz Island differed significantly from birds in the highlands in foot dimensions (longer foot and claws) and beak size (shorter beak). Lowland birds spent more time foraging on the ground, and used the foraging techniques of picking and chipping at prey with their beak, and scratching the ground with their feet, whereas highland birds tended to forage in low vegetation, sliding their longer beaks through vegetation to remove seeds. This study is the first to document adaptive divergence in clinal populations of Darwin's finches. These findings highlight the role that adaptive response to ecological gradients has over relatively short distances in contiguous populations. The findings also generate testable hypotheses about species richness in lineages that show morphological differences within clines.

Keywords: allopatry, Darwin's finches, foraging, morphology, phenotypic divergence, speciation, sympatry.

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INTRODUCTION

The role of ecological factors in speciation has received increased attention in recent years (Schluter, 1996). This development stems largely from a growing number of empirical studies comparing, within taxa, the divergent morphological adaptations of related species to different environments. Such studies have addressed different evolutionary trait utilities in varying environments, whereby the adaptedness of such traits may be modified by sexual selection involving female choice (reviewed in Schluter, 2000).

Jeffries and Lawton (1984), as well as Schluter (2000), have proposed that variation in resource distribution promotes trait divergence between environments (here broadly defined as habitat, food type and foraging height). According to this ecological theory of speciation, the efficiency with which different resources are used between habitats will vary with phenotype, with stabilizing selection occurring for phenotypes that are close to the adaptive fitness peak, and with lower fitness being exhibited at atypical trait values (Schluter and Grant, 1984; Benkman, 2003). This theoretical perspective on speciation has its intellectual roots in an idea originally proposed by Charles Darwin (1859), in his *Origin of Species*, where he set forth his 'principle of divergence' in an attempt to explain sympatric speciation among continental animals and plants.

Most studies on adaptive phenotypic divergence have been conducted between species (reviewed in Schluter, 2000). Given the paucity of evidence for ecological divergence in a sympatric speciation scenario, and burdened by the fact that sympatric speciation has not received much theoretical support in Darwin's finches in particular (Lack, 1947; Grant and Grant, 1997), or in animals in general (Mayr, 1963; Coyne and Price, 2000), this study aims to provide information on the potential for morphological differentiation in contiguous populations. We do this by addressing what is usually the first phase of such a process, namely an evolutionary adaptive divergence (Benkman and Lindholm, 1991). We include detailed measures of morphology in our analysis of phenotype based on advances in the theory of ecomorphology (Leisler and Winkler, 1985, 1991). Ecomorphology addresses morphological variation within populations (and species) in relation to their ecology, and has been applied to studies on differential resource utilization among closely related species (Winkler, 1988).

We examine phenotypic differences in Darwin's Small Ground Finch (*Geospiza fuliginosa*), the most recently diverged species of Darwin's finch (Petren *et al.*, 1999), between habitats (arid lowlands versus forest highlands) in contiguous populations on Santa Cruz Island, Galapagos Archipelago, that are separated by a flight distance of 18 km. We address the question of phenotypic divergence between habitats at a low taxonomic level – that is, between populations of the same species – because the mechanisms of divergence are clearest at this level (Schluter, 2000). Morphological variation in Darwin's finches has mostly been studied between, but not within, islands (reviewed in Grant, 1999; but see Ford *et al.*, 1973). Given extreme ecological variation in breeding habitats of Darwin's finches on elevated islands of the archipelago, combined with observations of high levels of site fidelity between years in our banded population (S. Kleindorfer, unpublished), we test the hypothesis of adaptive divergence under conditions of differential resource use. We make the following predictions between habitats: (1) a significant difference in phenotype, (2) variation in food type, differences in foraging height and foraging technique, and (3) covariation between phenotype and foraging behaviour.

Previous work on the Geospizinae has shown marked annual variation in phenotype resulting from measurable selection on beak size, a heritable trait, driven by food availability

[specifically seed size and hardness (see Grant and Grant, 2002)]. Hence, we specifically analyse variation in beak morphology between habitats. In addition, we examine foot dimensions (span, toe and claw length), wing shape (curvature) and tail shape (curvature). These traits are clearly related to locomotion and aerial agility, and are considered the primary morphological traits for exploiting new resources at the level of microhabitat (Fretwell, 1969), which then sets the stage for selection on beak shape (Steelman and Danley, 2003). This perspective adheres to current theories of divergent natural selection based on differences in resource environments, demonstrating that birds exploit new habitats first by changes in prey size and food type (Diamond, 1986; Christidis *et al.*, 1988; Price, 1991; Richman and Price, 1992; Robinson and Terborgh, 1995).

MATERIALS AND METHODS

Study site and species

Morphological and behavioural data were collected on Darwin's Small Ground Finch, *Geospiza fuliginosa*, on Santa Cruz Island (0°37'S, 90°2'W), Galapagos Archipelago, over the course of six field trips: 2000 (15 January to 20 March and 3 November to 15 December), 2001 (6 January to 15 March and 20 November to 20 December), 2002 (3 January to 25 March) and 2004 (12 January to 18 March). The study was conducted in the arid lowlands and moist forest highlands of Santa Cruz (Eliasson, 1984; Jackson, 1993). The arid zone (40–200 m) is dominated by cacti *Opuntia* sp., *Croton scouleri* and the trees *Bursera graveolens*, *Pisonia floribunda* and *Piscidia carthagenensis*. The highland *Scalesia* zone (300–600 m) is an evergreen humid forest dominated by *Scalesia pedunculata* (Asteraceae). The endemic highland *Scalesia* are unique within the Asteraceae in that they grow to tree-like dimensions.

Geospiza fuliginosa is a small (13 g) passerine that occurs commonly in the lowlands and highlands of all elevated islands of the Galapagos Archipelago (Grant, 1999). It has the broadest diet of all of Darwin's finches (Bowman, 1961).

Morphological characters

A total of 324 birds were mist-netted and colour-banded in both habitat types (highlands $n = 167$, lowlands $n = 157$) during the dry season, and at the nest during incubation or early feeding in the breeding season. At this time, we measured 27 morphological features, including: (1) beak length to the base of feathers, (2) beak length from the nostril (culmen length from anterior edge of nostril opening), (3) beak width at base, (4) beak depth at base, (5) beak gape flange, (6) tarsus length, (7) vertical diameter of tarsus, (8) horizontal diameter of tarsus, (9) tail length, (10) length of outer tail feather, (11) tail gradation (outer tail length minus middle tail length), (12) wing length (the flattened wing), (13) alula, (14) ninth primary feather length, (15) eighth primary feather length, (16) primary projection, or Kipp's distance (the distance between the primary and secondary feathers), (17) mass, (18) foot span with claws, (19) foot span without claws, (20) hind toe, (21) hind claw, (22) inner toe, (23) inner claw, (24) middle toe, (25) middle claw, (26) outer toe and (27) outer claw. Foot span, toe and claw length were measured by taking an impression of the bird's right foot in plasticine that had been smoothed into a flat surface. All measurements were taken by the same researcher (S.K.).

Foraging data

Foraging data were recorded as first foraging observations (a record of the first food item ingested) to avoid statistical bias in the data (Morrison, 1984). The data were collected along 100 m transects within each quadrant of the study area over 4 weeks of the breeding season and dry season. We sampled one quadrant each week in each habitat to avoid repeated entries of individuals, with a sampling duration of 2 days per habitat type. The dominant foraging technique was recorded as: (1) bite (part of food item ingested), (2) chip (downward thrust of the beak), (3) glean (prey removal from foliage surface), (4) pick (prey removal from non-foliage surface), (5) probe (insert beak into substrate), (6) pry (hoisting of substrate), (7) scratch (scraping of ground) and (8) slide (passing of vegetation through beak). The food item consumed was recorded wherever possible as: (1) part of flower, (2) fruit, (3) seed, (4) insect and (5) foliage. Foraging height was recorded as an absolute measure in metres from the ground, but was analysed in relation to category: (1) ground (0 m), (2) 0.1–1.0 m, (3) 1.1–3.0 m, (4) 3.1–6.0 m and (5) 6.1–9.0 m. We recorded the sex of the birds based on plumage coloration (Grant and Grant, 1987). Juvenile males were distinguished from females during the breeding phase using the presence/absence of a brood patch; during the non-breeding phase, we based our sex discrimination on the initial phase of change in plumage coloration (all cases of doubt were excluded from analyses).

Factor analysis of morphology data

The morphological measurements were subjected to principal components analysis (PCA) using the statistical software package SPSS 11 for Mac OS X. Support for the factorability of the data set was found: the correlation matrix revealed many coefficients > 0.3 (Pallant, 2001). Also, the Kaiser-Meyer-Olkin value was 0.74, exceeding the recommended 0.6 (Kaiser, 1970, 1974), and Bartlett's test of sphericity (Bartlett, 1954) was statistically significant ($P < 0.001$).

Six components had eigenvalues exceeding 1, and these components cumulatively explained 60.5% of the variance. An inspection of the scree plot revealed a break after the fourth component, and using Catell's (1966) scree test it was decided that four components should be retained for further investigation. A varimax rotation with Kaiser normalization aided the interpretation of these four components, and the solution is presented in Table 1.

Principal component scores were calculated and used in subsequent analyses investigating morphological differences between birds caught in highland versus lowland habitats.

RESULTS

Morphological differences between habitats

Features associated with foot size as well as mass of the bird primarily loaded on PC1, with the exception of the hind toe measurement, which loaded on PC3 (see Table 1). Measurements taken from beaks were strongly associated with PC2, and all three wing measurements, together with tarsus and hind toe, loaded on PC3. Features associated specifically with the claws loaded primarily on PC4. We used an independent samples test to examine the factor scores in lowland versus highland habitats. Among the lowland birds, principal component scores for PC1 and PC4, but not PC2 and PC3, were significantly

Table 1. Principal component analysis factor loadings (PC1, PC2, PC3, PC4) calculated using a varimax rotation with Kaiser normalization

	PC1	PC2	PC3	PC4
Foot span with claws	0.76			
Middle toe	0.70			
Outer toe	0.66			
Foot span no claws	0.66			
Inner toe	0.59			
Mass	0.47			
Beak depth		0.77		
Beak gape flange		0.68		
Beak length feather		0.67		
Beak width		0.67		
Beak length nostril		0.36*		
Wing length			0.72	
Ninth primary			0.61	
Primary projection			0.60	
Tarsus			0.59	
Hind toe			0.49	
Inner claw				0.73
Outer claw				0.65
Middle claw				0.62
Hind claw				0.50

Note: Only loadings above 0.40 are shown, with the exception of beak length from the nostril, marked with an asterisk (*).

larger than for highland birds (variances equal, PC1: $t_{233} = 2.32$, $P = 0.02$; PC4: $t_{233} = 2.67$, $P = 0.008$). Since PC1 and PC4 were loaded strongly by foot measurements, this finding shows that lowland birds had a significantly different foot morphology than highland birds.

A two-factor analysis of variance (ANOVA) was conducted to explore the impact of sex and year on differences between habitats for PC1 and PC4. This analysis showed no significant main effect of sex (PC1: $F_{1,219} = 3.0$, $P = 0.08$; PC4: $F_{1,219} = 0.11$, $P = 0.74$) and no interaction effect for habitat \times sex (PC1: $F_{1,219} = 0.20$, $P = 0.66$; PC4: $F_{1,219} < 0.001$, $P = 0.99$). There was, however, a significant main effect of year between habitats for both principal components (PC1: $F_{3,227} = 29.71$, $P < 0.001$; PC4: $F_{3,227} = 17.11$, $P < 0.001$), but no interaction effect for habitat \times year (PC1: $F_{3,227} = 1.19$, $P = 0.31$; PC4: $F_{3,227} = 1.81$, $P = 0.15$). Foot size (PC1) generally increased over the 5 year period, whereas claw length (PC4) was diminished in 2001 and 2002 compared with the samples studied in 2000 and 2004.

Post hoc tests were conducted on year differences for PC1 and PC4 using a Tukey Honestly Significant Difference test. For PC1, the year 2000 was significantly different from all other years, and birds from 2002 were significantly different from 2004. For PC4, the year 2000 differed significantly from 2002 and 2004, and 2004 was significantly different from 2001 and 2002 (see Figs. 1 and 2).

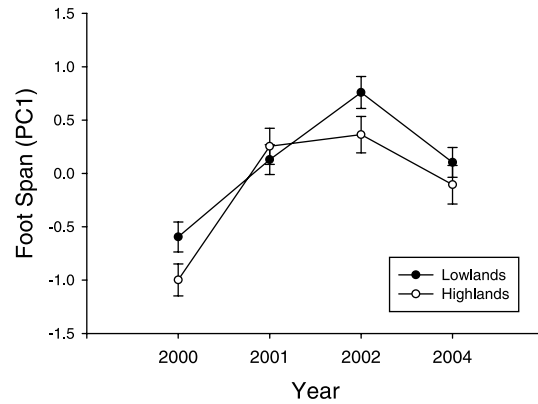


Fig. 1. Principal component scores are shown as means \pm standard errors for PC1 (foot span) (see Table 1) between years and habitats (lowlands and highlands) on Santa Cruz Island.

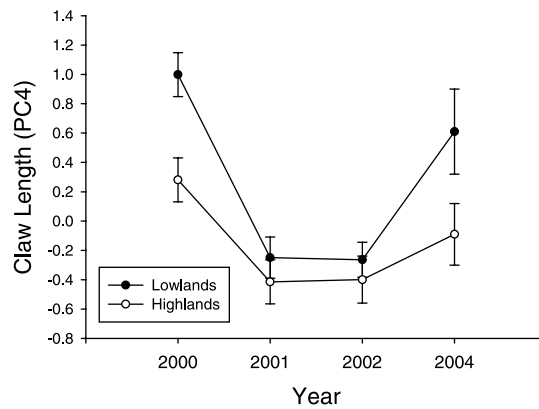


Fig. 2. Principal component scores are shown as means \pm standard errors for PC4 (claw length) (see Table 1) between years and habitats (lowlands and highlands) on Santa Cruz Island.

Beak morphology was analysed separately given its central role in studies of evolution in Darwin's finches (reviewed in Grant, 1999) (see Table 2). Using the raw measurements of beak dimensions in an independent samples test, we found a significant difference in beak length from the nostril, which was larger in the highland birds than in the lowland birds ($t_{321} = 5.27$, $P < 0.001$; the Bonferonni-adjusted alpha level is 0.008 for six planned comparisons). No other beak dimension showed a significant difference between habitats (see Table 2). Comparing beak length between years, beaks in the 2000 population were 0.27 mm larger than those in the 2004 population ($r = 0.28$), and a bird in the 2000 population was 2.4 times more likely to be above the mean in beak length compared with a bird in the 2004 population (the odds ratio). Beak length appeared to be converging between the habitats within our sampling period (see Fig. 3). A two-factor ANOVA found no significant effect on beak length of sex ($F_{1,219} = 0.03$, $P = 0.86$), year ($F_{3,227} = 1.52$, $P = 0.21$), habitat \times sex ($F_{1,219} = 0.18$, $P = 0.67$) or habitat \times year ($F_{3,227} = 0.99$, $P = 0.40$).

Table 2. Beak morphology (means \pm standard errors [SE]) is shown for the Small Ground Finch, *Geospiza fuliginosa*, in the arid lowlands (c. 50 m elevation, $n = 157$) and moist highlands (c. 500 m elevation, $n = 167$) on Santa Cruz Island, Galapagos Archipelago

	Lowlands		Highlands	
	Mean	SE	Mean	SE
Beak length (nostril)	8.33	0.04	8.65	0.05
Beak depth	7.49	0.03	7.43	0.03
Beak width	6.83	0.02	6.83	0.02
Beak gape flange	7.51	0.04	7.47	0.04

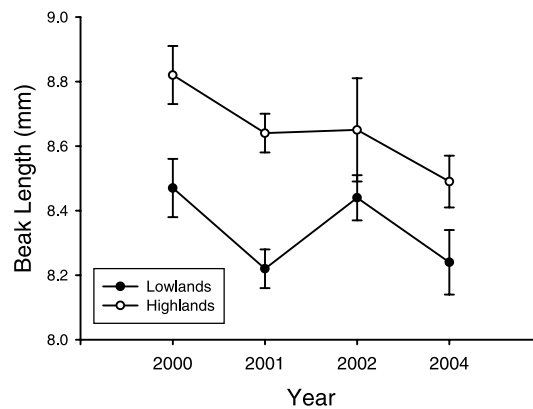


Fig. 3. Beak length (measured from the anterior edge of the nostril) is shown as means \pm standard errors between years and habitats (lowlands and highlands) on Santa Cruz Island.

Differences in diet between habitats

The diets of the highland and lowland birds spanned an identical range (see Fig. 4). Within the highlands we found no significant difference between the sexes in the proportion of food categories in their diet (highlands: 163 males and 103 females, likelihood ratio = 6.18, degrees of freedom = 6, $P = 0.40$). However, there was a significant difference between the sexes in the lowland habitat (lowlands: 179 males and 108 females, likelihood ratio = 13.79, degrees of freedom = 6, $P = 0.03$). There was also a significant difference in diet proportions between years within each habitat (highlands: $n = 266$, likelihood ratio = 97.84, degrees of freedom = 24, $P < 0.001$; lowlands: $n = 288$, likelihood ratio = 86.50, degrees of freedom = 22, $P < 0.001$) (see Fig. 4).

A chi-square test was conducted to quantify the difference in food category proportions consumed by birds between habitats, and this was done for sex and year. In all cases a significant difference was found between habitats (males: $n = 342$, likelihood ratio = 42.93, degrees of freedom = 6, $P < 0.001$; females: $n = 211$, likelihood ratio = 34.34, degrees of freedom = 6, $P < 0.001$; 2000: $n = 157$, likelihood ratio = 18.18, degrees of freedom = 5, $P = 0.003$; 2001: $n = 266$, likelihood ratio = 60.51, degrees of freedom = 6, $P < 0.001$; 2002:

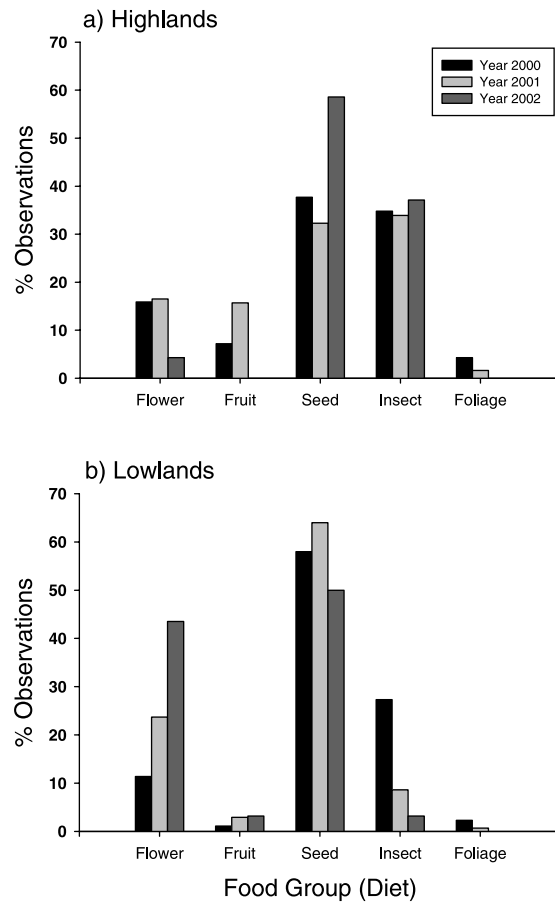


Fig. 4. Diet in Darwin's Small Ground Finch, shown as the percentage of feeding observations ($n = 565$) per food category between habitats (lowlands and highlands) on Santa Cruz Island.

$n = 132$, likelihood ratio = 52.80, degrees of freedom = 5, $P < 0.001$). What is noteworthy is that, despite the changing diets of the birds between years, a significant difference in dietary composition remained between the habitats. This consistent difference was predicted to impact on foraging technique (and associated efficiency measures for resource use) between habitat types.

Differences in foraging between habitats

The 565 observations of foraging by Small Ground Finches revealed eight separate foraging techniques (see Fig. 5). Two foraging techniques were only used by birds in the lowlands (chip and scratch), and one technique was exclusively used by birds in the highlands (slide, by which foliage is passed through the beak). There was a significant difference in foraging techniques between habitats for both males (χ^2 test, $n = 348$, likelihood ratio = 177.62, degrees of freedom = 9, $P < 0.001$) and females (χ^2 test, $n = 217$, likelihood ratio = 109.06, degrees of freedom = 7, $P < 0.001$), and between habitats with year of observation (2000:

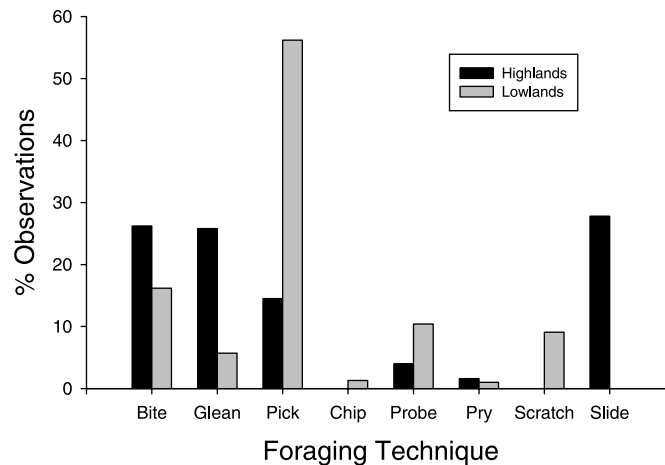


Fig. 5. The percentage of observations per foraging technique (defined in the Methods section) between habitats (lowlands and highlands) on Santa Cruz Island.

$n = 157$, likelihood ratio = 71.79, degrees of freedom = 7, $P < 0.001$; 2001: $n = 278$, likelihood ratio = 43.67, degrees of freedom = 8, $P < 0.001$; 2002: $n = 132$, likelihood ratio = 101.36, degrees of freedom = 8, $P < 0.001$). There was no significant effect of sex within each habitat (highlands: 153 males and 95 females; $\chi^2 = 10.45$, degrees of freedom = 5, $P = 0.24$; lowlands: 183 males and 112 females; $\chi^2 = 8.84$, degrees of freedom = 6, $P = 0.18$).

There was also a significant difference in foraging height between habitats ($n = 565$, $\chi^2 = 286.45$, degrees of freedom = 4, $P < 0.001$), which was upheld in a habitat comparison within each year (2000: $\chi^2 = 72.40$, degrees of freedom = 4, $P < 0.001$; 2001: $\chi^2 = 138.68$, degrees of freedom = 4, $P < 0.001$; 2002: $\chi^2 = 83.97$, degrees of freedom = 4, $P < 0.001$; see Fig. 6). Lowland birds were seen to forage on the ground most often, and highland birds just above ground level. Within each habitat we found an effect of year on foraging height. Birds shifted in the highland from infrequent to more frequent foraging in the mid-vegetation strata (3–6 m) (likelihood ratio = 16.95, degrees of freedom = 8, $P < 0.04$) (see Fig. 6). Birds in the lowlands showed a non-significant trend for a shift in foraging height between years, particularly in the height category 1–3 m – that is, the low vegetation strata (likelihood ratio = 12.27, degrees of freedom = 6, $P = 0.06$).

DISCUSSION

This study of Darwin's finches documents significant morphological differences between populations inhabiting an elevated island (Santa Cruz) that were separated by a flight distance of 18 km. These results are striking from two perspectives. First, although clinal variation is common in birds, few studies have demonstrated significant morphological differences between habitats in highly mobile organisms lacking dispersal barriers over such a short distance (but see Schaack and Chapman, 2004). Second, we found annual variation in foraging behaviour that mirrored annual shifts in morphological variation between habitats (discussed below). This extends the findings summarized by Grant and Grant (2002), who found short-term temporal morphological variation in Darwin's finches shaped by

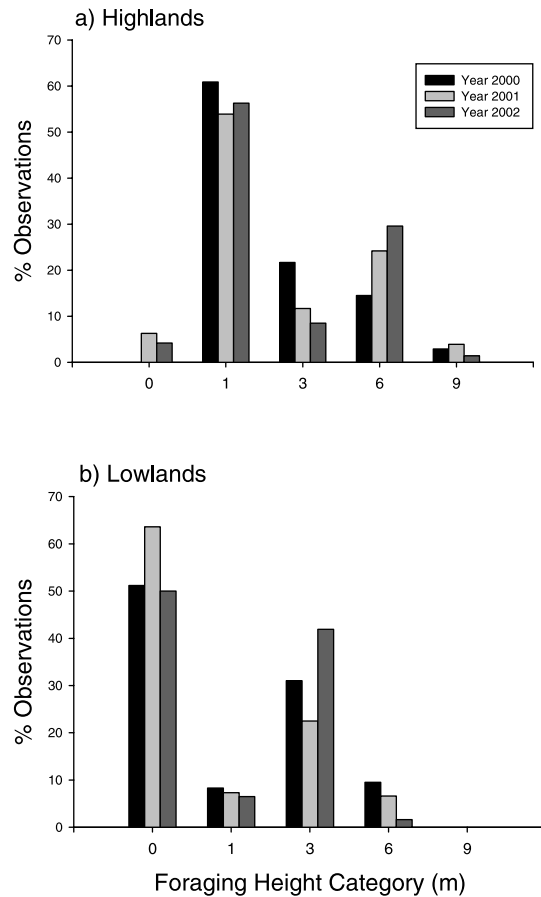


Fig. 6. The percentage of observations per category of foraging height (defined in the Methods section) between habitats (lowlands and highlands) on Santa Cruz Island.

natural selection. The results of this study point to the potential for similar processes to operate at a temporally equivalent but spatially distinct scale, driven, as we argue, by ecological differences between habitats.

We found consistent evidence for both divergence and convergence in Darwin's Small Ground Finch in relation to foraging habitat on a single island over a 5 year period. Birds in the lowlands of Santa Cruz differed significantly from birds in the highlands in foot dimensions and beak size. Compared with birds in the highlands, the lowland birds had larger feet and longer claws (see Figs. 1, 2), and shorter beak length (see Fig. 3). Over time, beak length decreased by 0.27 mm ($r = 0.28$), so that birds in the 2004 population were 2.4 times more likely than birds in the 2000 population to be below the mean (the odds ratio). Such a change points to a significant level of natural selection during this 5 year period. This variation in morphology between habitats is consistent with our findings on foraging behaviour. Although the diet in both habitats overlapped considerably (see Fig. 4), we found differences in foraging technique (see Fig. 5) and foraging height (see Fig. 6) between habitats. Birds in the lowlands spent significantly more time foraging on the ground, and

used the foraging techniques of picking (removal of prey item from a non-foliage surface), chipping (forcible pecking with the beak) and scratching (primarily involving the use of feet to scratch the ground surface) significantly more than the highland birds. In contrast, highland birds foraged mostly in the low vegetation layer (0.1–1.0 m), on low fruiting shrubs (e.g. *Rubus nevens*, introduced blackberry) or on grasses, particularly the native *Paspalum* sp. The predominant foraging techniques in the highlands were biting (especially fruit), gleaning (prey removal from a foliage surface) and sliding (a novel technique that we observed in the highlands, whereby birds slid the vegetation strip through their beaks; this technique was especially used for *Paspalum* grasses that have vertical stems laden with green seeds that stick to the finches' beaks when they slide the stem between their beaks).

In addition to consistent effects of habitat on our measures of morphology and foraging behaviour, we found marked annual variation in each of these parameters. The magnitude of annual variation between habitats was largely comparable. Between 2000 and 2002 we found an increase in foot span and a decrease in claw size, which showed a reverse pattern in 2004. It is to be noted that most previous research on morphological variation in Darwin's finches has focused on beak size, whereas foot dimensions have been somewhat neglected (but see Grant *et al.*, 1985). The magnitude of change in foot dimensions between years was comparable between habitats, while the differences between the habitats in these variables remained significant (with the exception of foot span in 2001). In contrast, beak length appeared to be converging between the two habitats (see Fig. 3), although this trend was not statistically significant. This convergence is perhaps explained by a shift in diet in the highlands in 2002, when birds significantly increased the proportion of seeds in their diet (see Fig. 4). Thus, there is evidence that diets also converged between habitats at this time. Similarly, the trend for smaller feet was supported by a shift in foraging height in both habitats between 2000 and 2002, since birds appeared to be foraging less on the ground (perhaps reducing the need for long front toes for scratching). Previous studies between islands have shown that diet is highly correlated with seed abundance in this species, and that diet is strongly associated with beak size and shape (e.g. Abbott *et al.*, 1977; Grant, 1999), and with feet, as was shown in a comparison of the long-toed insectivorous leaf-litter scratcher *G. difficilis* and the comparatively short-toed seed-eating *G. fuliginosa* on Pinta Island (Schluter, 1984).

It is notable that previous studies have failed to document breeding by the Small Ground Finch in the highlands of Santa Cruz, making it uncertain if its current pattern of highland breeding and foraging is recent or was previously overlooked (Lack, 1947; Bowman, 1961; Curio, 1969). Significant changes in species composition may have contributed to the present year-round distribution of *G. fuliginosa* in the highlands of Santa Cruz: *G. difficilis* was once common in the highlands of Santa Cruz and Floreana but was last recorded on Floreana in 1852 and has been extinct on Santa Cruz since about the 1930s (Lack, 1947; Bowman, 1961; Curio, 1969; Harris, 1973; Sulloway, 1982). *Geospiza difficilis* was long toed (Grant *et al.*, 1985) and may have hybridized with *G. fuliginosa* in the highlands of Santa Cruz. Our results, however, show that highland Small Ground Finches are shorter toed than the lowland population, where *G. difficilis* did not occur. This finding provides evidence for adaptive divergence driven by natural selection according to local conditions, as *G. fuliginosa* forages mostly in low vegetation in the highlands and not in the leaf litter, as has been observed in *G. difficilis* (Schluter, 1984). Alternatively, the differences in morphology that we found may be explained by behavioural assortment across ecotypes, if birds most suited to exploit a particular resource type dispersed to these areas (hence, the argument in this case is for selection on behaviour and

not directly on morphological traits) (Fretwell, 1969). The data available at present do not allow us to distinguish between these alternative hypotheses, but relevant evidence is discussed below.

The pattern of annual variation in morphology and foraging behaviour found in this study, which may be the result of natural selection on phenotypes or behaviour, runs the risk of being a 'just so' story (Gould and Lewontin, 1979). Although we have no direct evidence that natural selection is as swift as the data would suggest, oscillating evolutionary dynamics are a hallmark of Darwin's finches (Price and Grant, 1984; Gibbs and Grant, 1987; Grant and Grant, 1989, 2002). The well-described oscillating dynamics are driven primarily by climatic patterns and the correlated effects of rainfall on seed abundance and seed hardness. These climatic events explain shifts in heritable phenotypic traits – for example, beak size and shape – in the finches studied on the small island of Daphne Major, including during the extreme drought in 1977 followed by the El Niño-Southern Oscillation (ENSO) event of 1982–83, and another significant drought in 1986 (Boag and Grant, 1981; Boag, 1983; Price *et al.*, 1984; Grant and Grant, 1995). Each of these major climatic events pushed finch phenotypes in different directions, selecting for large beak size in 1978, more pointed beaks in the mid-1980s, and smaller beak size after 1986 (Boag and Grant, 1981; Price *et al.*, 1984; Grant and Grant, 2002). Minor oscillations have been documented for the intervening years, and for the years since then (Grant and Grant, 2002). The most recent ENSO event was in 1998, and was quite severe, though no systematic study of the finches was being conducted on Santa Cruz at that time. The data shown here may represent the tail end of selection from the extreme weather conditions in 1998, which in turn were followed by drought in 2001 (not a single egg was laid in the lowlands by the Small Ground Finch) (S. Kleindorfer, unpublished), moderate conditions in 2002 and a drought in 2004. Thus, cyclical and extreme weather conditions are well-known attributes of the Galapagos Archipelago and are known to be strong selective agents that drive phenotypic divergence (Grant, 1999).

The Small Ground Finch populations studied are contiguous: they both inhabit the island of Santa Cruz and are connected by an intervening population. Our sampling was done allopatrically at the extremes of the species' continuous elevational distribution. Hence no statements can be made about characteristics of the population between the lowland–highland gradient. The lowland and highland populations are separated by an intervening agricultural zone that harbours thousands of Small Ground Finches (these birds exploit the many introduced fruit and seed crops) (D. Wiedenfeld, personal communication). Thus, the agricultural zone *per se* is not a barrier to dispersal, and birds are seen in any particular area from the lowlands to the highlands. However, we have not detected a single bird that has dispersed between habitat types over the course of the study, with a higher level of re-sightings of banded birds (21%) in the highlands than in the lowlands (9% of banded birds have been re-sighted across years) (S. Kleindorfer, unpublished). Given phenotypic variation in diverse habitats, as shown in this study, we suggest that dispersal is not limited by a physical barrier (of which there is no obvious instance). Rather, maintenance of the observed phenotypic differences appears to be due to reduced fitness at atypical trait values relative to the adaptive fitness peak per habitat (Schluter and Grant, 1984; Benkman, 2003).

The question of reduced fitness for intermediate phenotypes between habitats remains to be investigated (Rosenzweig, 1978; Pimm, 1979), as does the possibility of positive assortative mating, with impacts on premating isolation. Song, for example, although a culturally inherited trait (Grant and Grant, 1996), may also be a morphologically referenced habitat signal,

given the relationship between beak morphology and acoustic properties of song (Podos, 2001; R. Christensen *et al.*, unpublished).

Darwin's finches continue to represent a model system for studies of adaptive divergence. It has been long established that increased environmental variation (heterogeneity) is mirrored by increased genotypic variation in populations (Levins and MacArthur, 1966). Studies of Darwin's finches conducted on environmentally variable islands – that is, elevated islands with numerous vegetation zones – provide us with the unique opportunity to study trait utility (e.g. Benkman, 2003), relative phenotypic fitness (Rosenzweig, 1978; Pimm, 1979), and assortative mating in sympatric and parapatric populations. These processes may be most pronounced on islands with the greatest habitat heterogeneity.

It should be emphasized that the theory of allopatric speciation, so well established for birds in general and for Darwin's finches in particular, is not inconsistent with the results presented here. However, our research shows that a surprising degree of adaptive morphological differentiation is possible by differing ecological zones in a relatively small island. Even if speciation by allopatry remains the rule, such impressive clinal variations have potential implications for the process of speciation. For example, the dispersal of a small number of individuals from one subpopulation rather than another to a different island, coupled with a founder effect, could quicken the pace of speciation in allopatry compared to what would be expected if dispersing individuals came from much more homogeneous subpopulations. Such a process, in effect, would 'jump start' the speciation process in sympatry (Rosenzweig, 1978; Pimm, 1979) and then conclude this process in allopatry. According to this model, species of Darwin's finches that exhibit the highest degree of adaptive morphological differentiation in sympatry, or within clines, are likely to have produced the greatest number of descendent species, an assertion that is testable. Partial support is found for this model, given our observations that Darwin's Tree Finches – a lineage with fewer descendent species than Darwin's Ground Finches – show no significant differences in morphology (specifically in *Camarhynchus parvulus*) between the same clinal populations as were studied for Darwin's Small Ground Finch (S. Kleindorfer, unpublished). Also, such clinally variant species are of interest for reasons that relate to theories of island biogeography (MacArthur and Wilson, 1967; Abbott *et al.*, 1977; Grant and Schluter, 1984). For example, by reducing the ecological opportunities available to other species, clinally variant forms ought to affect the patterns of which species are able to co-exist on the same islands. In addition, clinally variant forms ought to increase the amount of character displacement observed among ecologically competitive species inhabiting the same island. We hope to test some of these hypotheses in future research. In any event, it is clear that evolutionary processes are more active and efficacious within certain contiguous populations of Darwin's finches, on islands exhibiting ecological diversity, than has previously been appreciated.

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