

# Darwin's finches: Population variation and natural selection

(Galápagos/environmental heterogeneity/food selection/feeding efficiency/differential survival)

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**ABSTRACT** Van Valen's model, which relates morphological variation to ecological variation in an adaptive scheme, was investigated with individually marked and measured Darwin's finches on two adjacent Galápagos islands, Santa Cruz and Daphne Major. Results show that environmental heterogeneity is correlated with large continuous, morphological variation: variation in bill dimensions of *Geospiza fortis* is greater on Santa Cruz than on Daphne, as is environmental heterogeneity. Within populations of this species, different phenotypes distribute themselves in different habitat patches, select foods of different sizes and hardness, and exploit them with efficiencies that are phenotype-(bill size) dependent. These data constitute indirect evidence that natural selection has a controlling influence over the level of phenotypic variation exhibited by a population. Further evidence is that phenotypes did not survive equally well during the study period; on Daphne island *G. fortis* was apparently subjected to directional selection on bill tip length and *G. scandens* to normalizing selection on body weight and bill depth. Other factors which may have contributed to the establishment of a difference in variation between Santa Cruz and Daphne populations are the founder effect, genetic drift, and assortative mating. Annual climatic unpredictability is considered a source of environmental heterogeneity which, through its effect upon food supply, favors large morphological variation. It is predicted that species of large individual size are more influenced by this than are small species, and consequently exhibit greater size-corrected variation. The prediction is tested with data from six *Geospiza* species, and found to be correct.

Hubby and Lewontin (1, 2) showed that *Drosophila* populations exhibit much more genetic variation than was previously thought. Van Valen (3) presented a cogent argument for considering continuous variation within local populations to be adaptive. These two studies have stimulated, in the last 10 years, an enormous interest in the extent and significance of variation. Studies of population variation are concerned with the total amount of genotypic and phenotypic variation within a population, by how much individuals differ from each other, and how separate populations compare in these respects. Total genetic variation is usually estimated by the amount of genic heterozygosity in samples, and expressed as the average heterozygosity per individual or per locus, regardless of how that heterozygosity is distributed among individuals. This report is addressed instead to phenotypic variation in a population and to the differences between individuals. We explicitly assume, when comparing populations, that a difference in amount of phenotypic variation reflects a difference in the same direction in the underlying genetic variation. The assumption needs investigating.

Following Ludwig, Levene (4, 5), and others, Van Valen (3) devised a model which relates morphological variation to environmental heterogeneity through the agency of natural selection; the variation may be continuous or discontinuous. The model is paraphrased as follows: (1) A population exploits a relatively narrow segment of the resource space,

which is more or less uniform for each individual; or (2) A population exploits a relatively broad segment of the resource space, with each individual adapted to occupy (a) a relatively broad segment of the resource space, or (b) narrow and different segments of the resource space.

In other words a population is either a specialist, 1, or generalist, 2, and if a generalist, it is so by virtue of 'individuals' being generalist and more or less the same (2a) or specialist and different from each other (2b). Intermediates are clearly possible. The greater resource space occupied by the generalist population (2b) implies weaker stabilizing selection, as expressed by an increase in morphological variation which allows that resource space to be subdivided among individuals. Diversifying or disruptive selection can produce the same result.

The model has been tested by Van Valen (3) and others by predicting different levels of continuous variation between populations (of the same species) of known or supposed different niche widths. These predictions have met with various degrees of success. Limitations have been due to inadequate samples of measurements of the continuously varying characters (6), and to lack of detail on the ecological differences between populations, making it impossible to distinguish *a priori* between cases 2a and 2b above. Coupled with the second limitation is a weakness of the model. It does not specify the different conditions which lead to strategies 2a and 2b. But an attempt to actually invalidate the model (7) has failed (8, 9).

These difficulties can be circumvented by using an alternative approach. Instead of predicting morphological from ecological variation we predict ecological from morphological variation. We present evidence that environmental heterogeneity favors large, continuous, morphological variation in a species which behaves according to case 2b. Our results complement those of Powell, and McDonald and Ayala (10, 11), who have shown that under certain conditions environmental heterogeneity also favors large average heterozygosity in *Drosophila* populations.

## METHODS AND RESULTS

**Choice of Species.** Darwin's ground finches (*Geospiza* spp.) are ideal subjects for study. They exhibit large variation in bill dimensions (12, 13) which can be related to feeding habits and diet; *Geospiza fortis* exhibits possibly the largest relative variation of any passerine species not due to hybridization. Furthermore, bill size variation of *G. fortis* populations is significantly larger on several islands where a potential competitor species, *G. magnirostris*, is either rare or absent than where it is present at moderate to high densities (14). According to data assembled by Lack (13), *fortis* is highly variable on Santa Cruz island and much less so on Daphne Major island. We conducted fieldwork on these two islands in February to May and November to December

1973. The aim was to look for associations between bill morphology and both diet and feeding efficiency on both islands. Birds were trapped in mist nets, measured, banded with unique combinations of color bands, and released. Some were observed feeding later. Survival of banded birds into 1974 on Daphne Major was assessed in March and August by G. Wellington, P. Wellington, and T. deVries (34).

**Habitat and Patch Selection.** Santa Cruz island is large (area 90,400 ha) and high enough (864 m) to support several recognizable vegetation zones or habitats: arid (coastal), transitional, *Scaevola*, "brown", *Miconia*, and upland (12). *G. fortis* is found at times in all of these habitats, although most commonly in the lower, drier zones. If different habitat conditions select for different optimum bill sizes, a larger total population variation will be produced on a large, high island than on a small island like Daphne Major (area 32 ha) with only one habitat (see refs. 15–17 for a general discussion). In addition there is heterogeneity within the arid habitat on Santa Cruz island which may also set up selection differentials. On the northern side, areas of flat parkland dominated by grasses, chiefly *Aristida subspicata* and *Panicum fasciculatum*, are interspersed with areas of woodland, dominated by *Bursera graveolens* and *Croton scouleri* on rocky lava flows. Therefore, the arid habitat comprises qualitatively different sub-habitats or patches.

Birds were observed, netted, and measured in these two patch types in the arid zone at Borrero Bay, north Santa Cruz island. Both observations and netting results gave the same information. Medium ground finches, *G. fortis*, predominated in the woodland and small ground finches, *G. fuliginosa*, predominated in the parkland (netting results in April–May,  $N = 256$ ,  $\chi^2 = 66.8$ ,  $P < 0.001$ ). Only a single large ground finch, *G. magnirostris*, was recorded (and captured). Within the *fortis* population, birds with different bill sizes distributed themselves differently in the two patches. Individuals netted in the parkland differed from those netted in the woodland in two ways: they had a smaller total bill depth ( $t' = 2.01$ ,  $df = 44$ ,  $P \approx 0.05$ ) and a longer bill tip measured from the distal end to the arbitrarily chosen point at which the total bill depth is 4 mm ( $t' = 2.20$ ,  $df = 44$ ,  $P < 0.05$ ). Since the proportion of birds in male (black) plumage was the same in the two patches, this result is not likely to be due to segregation of the slightly dimorphic sexes into separate patches. Nor is it likely to be due to differential abrasion of the bill tip in the two patches because *fuliginosa*, feeding on the ground like *fortis*, had the same bill morphology in the two patches ( $t$  test).

In both of these bill characters, the parkland individuals of *fortis* approach the *fuliginosa* condition. Thus in a "*fuliginosa* environment," with many small grass seeds, the more *fuliginosa*-like *fortis* are commoner than in a "*fortis* environment." This fits the patch selection special case of the Van Valen model of population variation (ref. 18; see also 19 and 20). In the more heterogeneous environment of Santa Cruz island, therefore, natural selection may operate differently in the different patch types, favoring those *fortis* individuals whose bill morphologies are the most appropriate for exploiting the foods in a given patch type, thereby maintaining a large population variation. This argues for diversifying selection, without denying the possibility of relaxed stabilizing selection which Rothstein (8) has stressed. In addition, individual *fortis* with different morphologies may tend to choose different patches to exploit (20); this behavior will itself be subject to natural selection (15–17). There is some heterogeneity on Daphne island also, but perhaps the island is too small to permit this kind of resource subdivision and spe-

cialization. Correspondingly, there is less morphological variation in the *fortis* population on Daphne.

**Food Selection.** If the foregoing reasoning is correct, birds are expected to choose certain foods which they can deal with efficiently according to their bill size and shape (21), and avoid those which are difficult to exploit, perhaps after a period of trial-and-error learning (22, 23). Presumably the appropriate patches are chosen in this way too (24). Except when feeding their young, *G. fortis* feed almost entirely on seeds and fruits. Bowman (12) has already shown from gut content analysis and we have confirmed by observation (in preparation) that certain hard seeds are taken by only the large-billed members of the Santa Cruz *fortis* population. There are many more plant species producing seeds suitable for *fortis* on Santa Cruz than on Daphne (e.g., see ref. 25; confirmed by us, in preparation).

Birds banded at Borrero Bay foraged individually or in loose aggregations over large areas, and were rarely seen again after banding and release. The same difficulties were experienced to a lesser extent on the south side of Santa Cruz island at Academy Bay. Most of our information on foraging comes from the study on Daphne Major island in April 1973 where such dispersal did not occur. Exactly 100 individuals of *G. fortis* were banded on Daphne, measured, and released, and 50 were seen again there (one *magnirostris* and at least four *fuliginosa* were also present; the *magnirostris* and two *fuliginosa* were banded). There were three major feeding activities: (1) the small seeds of various herbs and shrubs (*Chamaesyce amplexicaulis*, *C. punctulata*, *Heliotropium angiospermum*) were taken from the ground or plant at a rapid rate; (2) seeds of the cactus *Opuntia echios* were extracted from dried fruits on the ground, and cracked, and the kernel was extracted; and (3) fruits were picked from *Bursera malacophylla* trees and taken to the ground up to 20 m away where the brightly colored red aril was removed and consumed. Occasionally, the seed ("stone") was cracked and the kernel extracted. Seeds of *Opuntia* and *Bursera* are moderately hard and require some effort to crack, unlike those in category 1. The average force necessary to crack the seeds was determined by a pliers device (26) to be  $5.48 \pm 0.34$  (SEM) kgf (1 kgf = 9.8 N) for *Opuntia* ( $N = 20$ ),  $4.78 \pm 0.25$  kgf for *Bursera* ( $N = 21$ ), and always less than 1.2 kgf for a variety of category 1 seeds.

The 50 banded *fortis* seen again were a random sample of the 100 banded. Of these 50, five were observed to feed on *Opuntia* seeds. They were a nonrandom sample of the 50. In culmen length, depth, and gonys width their bills were significantly larger than the remainder ( $t$  test,  $P < 0.05$  in each case). According to this result, large-billed birds select moderately hard kinds of seeds more than do small-billed birds. In contrast there was no avoidance of the larger *Bursera* berries by small-billed birds; the average bill dimensions of *Bursera* feeders are almost identical to the averages of all birds measured. But this is because some of the berry (the aril) is readily available to all birds, regardless of bill size; even the small-billed *fuliginosa* fed on *Bursera* arils.

Roughgarden (27) has shown how the total niche width of a population can be compartmentalized into a within-phenotype component and a between-phenotype component. The between-phenotype component may be as much as 32% of the total niche width of *Anolis* lizard populations in the West Indies (28). Our data show that there is a between-phenotype component in the feeding niche of the Daphne *fortis* population. Bowman's (12) data from gut content analysis show there to be this component in the Santa Cruz population. It is possibly larger in the morphologically more vari-

able Santa Cruz population, but neither study is extensive enough to permit estimation of its magnitude.

**Feeding Efficiency.** Several observations indicate that efficiency at dealing with foods (possibly modified by abundance) is the basis upon which preferences are established. Birds of different bill sizes crack seeds of a given size and hardness with different efficiency, i.e., they take different amounts of time to pick up, crack, and prepare a seed for swallowing. One line of evidence is that the average (harmonic mean) time taken to crack *Opuntia* seeds (cracking time) is inversely related to bill length ( $r = -0.91$ ,  $P < 0.05$ ), depth ( $r = -0.92$ ,  $P < 0.05$ ), and width ( $r = -0.97$ ,  $P < 0.005$ ) among *Daphne fortis* (based on 21 feeding observations of five birds).

A second piece of evidence comes from the *Bursera* feeders. Three banded individuals were observed to crack *Bursera* stones and seven banded individuals tried unsuccessfully for up to 6 min. All three bill dimensions of the successful individuals were significantly larger than those of the unsuccessful ones ( $t$  test,  $P < 0.05$  in each case). Moreover, birds in black and blackish plumage (banded and not banded) and therefore males, with slightly larger average bill dimensions than birds in brown plumage (males and females), had a higher frequency of success at cracking *Bursera* stones, 29 out of 46, than did the brown birds with five out of 35 ( $\chi^2 = 17.45$ ,  $P < 0.001$ ). Other evidence from *fortis* feeding on *Bursera* stones and *Rhynchosia minima* beans is summarized in ref. 6.

At least one advantage of having a large bill is consistently suggested by these results. Certain large and/or hard foods can be exploited more efficiently than by small-billed birds. Another consequent advantage previously suggested (29-32) is that the range of food sizes and hardnesses available to a large-billed bird is greater than that available to small-billed birds. Since *Opuntia* and *Bursera* feeders were also observed feeding often on small and soft seeds (category 1), our results also support this suggestion. In a variable population what then is the advantage, if any, of having a small bill?

One possibility is that although small seeds can be exploited by both large- and small-billed birds, they are exploited more efficiently by small-billed birds. If this is true, feeding efficiency should be negatively correlated with bill size when the seeds are small and soft. The evidence from the study of *fortis* on *Daphne* is equivocal on this point. There is a negative relationship between bill depth and average feeding rates (number of seeds consumed per minute) with category 1 seeds, but it is not significant (April  $r = -0.16$ ,  $N = 19$ ,  $P > 0.1$ ; December  $r = -0.33$ ,  $N = 6$ ,  $P > 0.1$ ). Lack of statistical significance may be due to several things, including the complicating uncontrolled factor of variations in food density. However, feeding rate of *fuliginosa* on these seeds in December is significantly, negatively related to gonyx width ( $r = -0.94$ ,  $N = 5$ ,  $P < 0.025$ ), and tends to be faster than the feeding rate of *fortis*.

Abbott *et al.* (26) have other evidence of a negative relationship between feeding rate and bill size from experiments in which rice grains were presented to *fuliginosa* of different bill sizes, but the sample sizes are very small. The second visit to *Daphne* island, in December 1973, allowed P.R.G. and J.N.M.S. to perform experiments with *fortis*. We worked independently and simultaneously, sitting about 50 m apart and timing with a stop-watch the rate of feeding of banded birds at small piles of rice grains. A rice grain, lacking a husk, is picked up by a bird and cracked. Usually one fragment remains in the bill and this is either swallowed or cracked again. The process of cracking can continue several

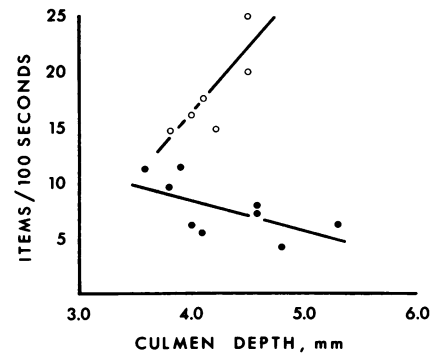


FIG. 1. The relationship between bill size and average (harmonic mean) handling time with rice grains, based on a total of 25 feeding observations (bouts) of 15 birds. For whole grains (closed circles)  $r = -0.574$ ,  $df = 7$ ,  $P \approx 0.11$ ; for fragments of rice grains (open circles)  $r = 0.796$ ,  $df = 4$ ,  $P \approx 0.06$ . Lines are fitted by the least squares method.

times with the fragments of a single grain. Each grain was recorded as a single food item by P.R.G., while each fragment was recorded as a single item by J.N.M.S. Our results, relating feeding rate to bill size, are surprisingly different (Fig. 1). To compare the two correlation coefficients we have used Hotelling's  $Z^*$  transformation as the best in the present circumstance of small sample size, although it is not entirely satisfactory (33), and we have then applied a  $t$  test. This yields a highly significant difference;  $t_s = 2.67$ ,  $df = 13$ ,  $P < 0.02$ .

The difference is due to a difference in behavior between birds of different bill sizes. Small-billed birds appeared to handle many grains, crack several but consume few fragments, whereas large-billed birds handled few grains, cracked them all and consumed many fragments. The convergence of the lines in Fig. 1 on the smallest bill size, where grains and fragments are treated similarly, may be more than just coincidence. At the other end of the bill size scale, the single banded *magnirostris* behaved like an extremely large *fortis*, just as it did with *Bursera* stones (6). It took a long time to correctly position the grain in its large beak for cracking and neglected no fragment produced, with the result that the average number of seconds devoted to a single grain (37.2) was greater than that of any of the *fortis*. Thus small-billed birds deal with rice grains quicker than do

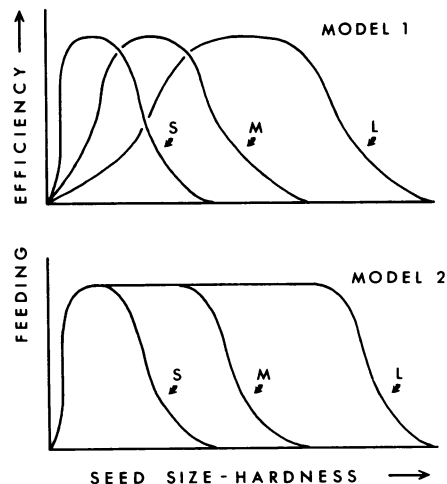


FIG. 2. Two feeding (handling) efficiency models. S, M, and L refer to birds with small, medium, and large bills. Efficiency is the reciprocal of time taken to deal with a food item.

large-billed birds, as was found for *fuliginosa* (26), but whether they are better off energetically we do not know.

An alternative possibility is that feeding (handling) efficiency with small seeds is the same for large- and small-billed birds. Bill size is positively correlated with body weight, as is total metabolic requirement, hence a large-billed bird requires a larger quantity of energy for maintenance than does a small-billed bird. A small-billed bird has an energetic advantage over a large-billed bird under the condition that only small seeds are available, providing it is not excluded by dominant large-billed birds.

The two relationships postulated for feeding efficiency and bill size are shown as alternative models in Fig. 2. It remains for further work, perhaps with captive birds, to choose between them. It should be clear from preceding remarks that they apply to both inter-specific and intra-specific comparisons. Finally note that in both models, but particularly the second, there are small ranges of seed sizes/hardnesses at which individuals of different bill sizes deal with seeds with approximately the same efficiency. The lack of significant correlations between *fortis* bill size and feeding efficiency with category 1 seeds may reflect such a range.

A final caveat. It is reasonable to interpret bill size variation in terms of variation in diet and feeding efficiency as we have done. But since bill size and body size are correlated, selection may be acting primarily on body size with consequential effects upon bill size rather than vice versa (see also ref. 18). The significance of large variation in body size is not clear, but diet is probably relevant (15–17).

## DISCUSSION

Making genetic inferences from phenotypic data is fraught with difficulties. For example, strong canalization of a trait can yield phenotypic similarity among a diverse array of genotypes in a population, whereas a lesser degree of canalization, perhaps due to drift, can yield phenotypic diversity among similar genotypes. Bearing these complications in mind we proceed to consider the establishment and maintenance of population differences in morphological variation.

**Establishment of Inter-Island Differences in Variation.** The differences in morphological variation between Santa Cruz and Daphne populations of *fortis* are associated with an ecological difference, which implies an environmental control of morphological variation. But the environment may have played no part in the establishment of the differences in variation. Daphne Major island was presumably colonized from neighboring Santa Cruz island. Genetic drift and the founder effect may have combined to reduce genetic variation in the Daphne island population. Daphne populations of both *fortis* and *G. scandens* (cactus finch) are small enough that genetic drift may be a significant factor even now (34). Sometimes, though not always, a reduction in genetic variation leads to a reduction in phenotypic variation (it can lead to an increase due to a breakdown of coadaptation). Several studies of mammals (35–37) and lizards (38, 39) have demonstrated allelic impoverishment in island populations, and this is likely to be revealed in island bird populations when biochemical methods are applied to them.

Another factor to consider is the possibility of assortative mating in one environment (Santa Cruz) and not in another (Daphne). The effect of positive assortative mating is to enhance phenotypic variation through greater genetic variance, though why it would be present in one environment only is not immediately clear. There is no published information on mating patterns among Darwin's finches. On the

basis of breeding records of captive birds and observations of mated pairs on Santa Cruz island R. I. Bowman (personal communication) believes mating to be random with respect to bill and body size. The place to examine this in detail is Academy Bay, Santa Cruz island. Preliminary analysis of our morphological data indicates that *fortis* are significantly more variable here than at Borrero Bay on the north shore of Santa Cruz (or on any other island). Ford *et al.* (40) detected bimodality in the frequency distribution of bill sizes among male *fortis* at Academy Bay. They considered the suggestion of introgressive hybridization with *magnirostris* (41) but rejected it in favor of an explanation in terms of disruptive selection arising from the occupation of two (or more) niches in which assortative mating occurs. Their argument is made more convincing by our demonstration here of different phenotypes of *fortis* segregating into different patches at Borrero Bay; this could lead to assortative mating, although we have no information on mating patterns at Borrero Bay. But the observed large variation in the *fortis* population does not require both disruptive selection and assortative mating (42, 43). Either would be sufficient. An alternative explanation is recent invasion of differentiated *fortis* (in morphology and song) from an island to the south of Santa Cruz, e.g., San Cristóbal, and a tendency towards assortative mating of the Santa Cruz and alien stocks of *fortis* now sympatric at Academy Bay. That is, incipient speciation is possibly occurring in a manner allowed for by the classical allopatric model of speciation (13).

On Daphne Major island there is no indication of assortative mating (or of recent invasion from Santa Cruz island; 34), although our data are meager. In March 1974 both members of eight breeding pairs of *fortis* were identified by their bands. The parametric correlations between morphological features of members of the pairs were not positive but negative (culmen length,  $r = -0.63$ ,  $P \approx 0.1$ ; culmen depth,  $r = -0.22$ ,  $P > 0.1$ ; gonys width,  $r = 0.33$ ,  $P > 0.1$ ). None of these are statistically significant, although the size (and sign) of the first correlation is noteworthy. Spearman's rank correlation test gives the same result. We tentatively conclude that mating is random with respect to bill morphology in this population, and take the opportunity to draw attention to the need for more information on mating patterns as well as bill-size heritabilities.

**Maintenance of Variation.** We infer a role for natural selection in the maintenance of a given level of variation in a population, and hence in the maintenance of differences in different environments, from *indirect* evidence. Mathematical models are consistent with this view (44–47). In the absence of genetic information (our ignorance is not restricted to Darwin's finches, it applies to birds in general) we are less equipped to detect selection *directly* than are *Drosophila* geneticists. Nevertheless our field study provides some indication that natural selection is currently operating on observed levels of population variation. Different phenotypes do not survive equally well.

In April and December 1973, 220 *fortis* and 60 *scandens* were banded and released on Daphne Major island. They were adults and immatures, not juveniles. There was no evidence of selection on either population between April and December, when survival was high (minimum values of 85% for *fortis* and 90% for *scandens*) and predation on the finches by short-eared owls, *Asio flammeus*, was low (four out of 49 pellets, 8%, in December contained finch remains; 34). However, between December and March 1974 selection appears to have acted on both species. *G. fortis* apparently experienced directional selection favoring individuals with

longer bill tips ( $t = 2.48$ ,  $df = 122$ ,  $P < 0.02$ ; see also section on patch selection); other traits did not show evidence of selection. This may have been associated with a higher proportion of small seeds in the environment after December than between April and December following the fruiting season of *Bursera*. Procurement of small seeds in small cracks and depressions in rocky substrate is presumably easier with a pointed bill than with a blunt bill (48). The differential loss of individuals from the population may have been due, alternatively, to emigration. We have no evidence of this (34).

*G. scandens* was apparently subject to normalizing selection. Birds surviving to March varied significantly less in body weight than did those which died ( $F = 1.89$ ,  $P < 0.05$ ). The component of the population banded in April showed the greater effect, survivors ( $N = 12$ ) being less variable in body weight ( $F = 5.21$ ,  $P < 0.02$ ) and culmen depth ( $F = 5.00$ ,  $P < 0.02$ ). Since these dimensions are correlated, selection against individuals of extreme sizes is indicated; although, not knowing the age structure of the population, we cannot rule out the possibility of a nonselective shift in the age distribution (e.g., as a result of differential loss of young and old individuals which may be particularly small and large, respectively). At this time when selection is inferred to have operated, survival was lower (minimum values of 41.6% for *fortis* and 58.6% for *scandens*) and predation by owls was higher (about 21%) than in the previous and longer time interval. A causal connection between owl predation and phenotypic shifts is possible (6), although speculative.

Kikkawa *et al.* (49) have demonstrated a similar seasonal shift in the population composition of *Zosterops lateralis* on Heron island off Australia. Socially dominant birds tended to be larger than subordinates. Survival was higher among the dominants in winter, but higher among the subordinates after the breeding season, indicating fluctuating directional selection within a year.

Superimposed upon spatial heterogeneity and seasonal variation in the Galápagos is strong annual variation in environmental conditions. There is a marked difference between "wet" and "dry" years, whose occurrence is largely unpredictable. This climatic variation must have a strong indirect effect upon population sizes and, we suggest, upon population composition through its immediate effect upon food supply. Selection may thus fluctuate, favoring different optima in different years (50, 51). We predict that the larger species are the most affected by the combined spatial and temporal heterogeneity on the Galápagos, and correspondingly show the greatest relative morphological variation. This follows from the conjecture that fluctuations of the less abundant large seeds have a potentially greater effect upon birds than fluctuations of the more abundant small seeds, if only because the numbers of large seeds are more likely to decline to and approach zero. The prediction is tested by comparing coefficients of variation of bill depth for all populations of the larger species (*G. magnirostris*, *G. fortis*, *G. controstris*, and *G. scandens*) and smaller species (*G. fuliginosa* and *G. difficilis*) of ground living geospizines. The data are taken from Table 61 in ref. 12. The result of a one-tailed Mann-Whitney U test upholds the prediction ( $U = 154.5$ ,  $z = 3.12$ ,  $P < 0.001$ ).

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