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Ecological Character Displacement in Darwin's Finches

Abstract. *Character displacement resulting from interspecific competition has been extremely difficult to demonstrate. The problem was addressed with a study of Darwin's ground finches (*Geospiza*). Beak sizes of populations of* G. fortis *and* G. fuliginosa *in sympatry and allopatry were compared by a procedure that controls for any possible effects on morphology of variation among locations in food supply. The results provide strong evidence for character displacement. Measurement of natural selection in a population of* G. fortis *on an island (Daphne) lacking a resident population of* G. fuliginosa *shows how exploitation of* G. fuliginosa *foods affects the differential survival of* G. fortis *phenotypes.*

Ecological character displacement occurs when morphological differences between coexisting species are enhanced as a result of competitive interactions between them (*1*). Despite the wide range of conditions under which character displacement is predicted by coevolutionary models (*2, 3*) there are few good examples of its occurrence in nature (*4, 5*). Most evidence suggesting ecological displacement derives from a comparison of differences between species in locations of sympatry and allopatry. The main assumption used in inferring character displacement from such comparisons is that there are no other factors influencing morphological differences between locations—for example, differences in food supply. This assumption may often be false.

Darwin's finches provide one of the most familiar examples of apparent character displacement (*6*) (Fig. 1). *Geospiza fortis* and *G. fuliginosa* are sympatric on most Galápagos islands (for example, Santa Cruz), where they are very different in beak and body size. Their beak sizes are intermediate where they occur alone, on the islands of Daphne Major (*G. fortis*) and Los Hermanos (*G. fuliginosa*).

We reexamine this example of apparent character displacement by two approaches: (i) we compare the morphology of the species in sympatry and allopatry, controlling for any differences that might arise because of variation in food supply, and (ii) we use observations of selection pressures on one species in allopatry to show how the differential survival of phenotypes is affected by the use of foods exploited elsewhere by the second species. The results support the original interpretation of character displacement (*6*).

Detailed studies on the Galápagos show that seed supply strongly determines the distribution and survival of finch phenotypes (*7–11*). We can investigate the possibility that morphological differences in allopatry and sympatry result simply from variation in food supply (*12*) by quantitatively describing food characteristics of individual islands in terms relevant to the differential survival of finch phenotypes (*13*). The resulting "adaptive landscapes" (*14*) permit predictions of mean beak sizes for *G. fuliginosa* and *G. fortis* on different islands on the assumption that morphology is determined by food supply alone (*15*). Greater morphological differences in sympatry than expected from food supply would constitute evidence for character displacement.

The procedure for quantifying an island's food supply as an adaptive landscape (*13*) involves the estimation of expected density of a solitary finch population on an island as a function of mean beak depth. First, we identify those seeds that would be included in the diet of a finch population with a given mean beak depth by noting all edible seeds on a given island with size greater than a specific lower bound and with hardness softer than a specific upper bound. The size-hardness limits, determined from empirical data on 21 *Geospiza* populations, are both increasing functions of mean beak depth (*13*). Second, we compute the summed density of seeds on the island that fall between these two limits (*13*). Third, we estimate the number of individual finches which may be supported by that density of seeds, using an empirical relation between the density of finches in individual populations on islands and the available standing crop of the seeds they eat (*13*). These three steps are repeated for 0.05-mm increments of mean beak depth between 5.5 and 15 mm. The resulting curves describe expected population density on each island over the range of beak sizes spanned by actual populations of *G. fuliginosa* and *G. fortis* (*16*).

This procedure was used to calculate expected finch density as a function of beak size on eight Galápagos islands where both *G. fortis* and *G. fuliginosa* are present (Pinta, Marchena, San Salvador, Fernandina, Rábida, Plazas, Santa Fe, and Santa Cruz) as well as the single-species islands of Daphne and Los Hermanos. Almost all seed supply data were collected during visits in the dry season (June to January) when food supply limits finch density (*8, 9*). The exception is Plazas, where seed supply data are available for only the wet season (March). The essential features of expected density curves are not sensitive to seasonal or annual variation in food supply, as shown by analysis where repeated measurements of seed data are available (*17*).

Expected population density curves for Santa Cruz, Daphne, and Los Hermanos (Fig. 1) show two important features: first, there are distinct local maxima (peaks) in expected density and, second, a given island often has more than one maximum—that is, the distributions are polymodal.

Polymodality results from wide gaps in the frequency distribution of seed size and hardness classes on an island. A finch population with mean beak size directly under a given maximum has a higher expected density than a slightly smaller species because it is able to crack and consume one or more seed types that are too hard for a smaller finch to deal with. A finch population with a mean beak size to the right of this peak has lower expected density than a population at the peak because it includes no additional hard seeds in its diet, and it may include fewer smaller seeds. A population of larger finches has a lower expected density than a population of smaller finches when supported by the same biomass of seeds (*13*).

Expected density curves are important

because, by the operation of natural selection, and in the absence of other interacting species, mean morphology in a population is expected to shift, with the consequence that population size is approximately maximized (*3*). There is indeed a general correspondence between mean beak sizes of finch species observed on an island and the positions predicted from peaks in expected density (*13*) (Fig. 1). Since peaks in expected density are determined solely by food, the associated beak sizes provide a standard against which actual beak sizes on different islands can be compared. Additional effects of interactions between particular species may be detected as discrepancies between observed and predicted beak sizes.

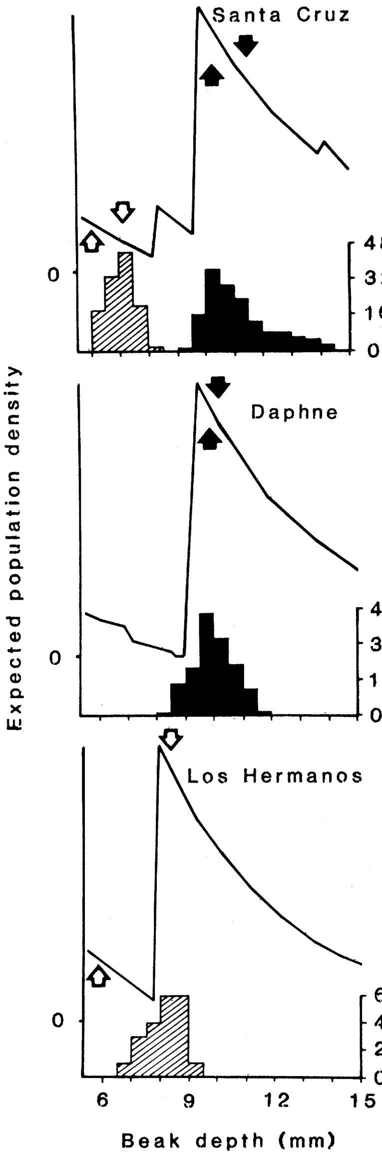

Fig. 1. Apparent character displacement in Darwin's finches, discovered by Lack (*6*). Beak depth histograms are for adult male *Geospiza fuliginosa* (dashed) and *G. fortis* (solid). Note greater difference in sympatry (Santa Cruz) than in allopatry (Daphne, Los Hermanos). Curves above histograms indicate expected population density of a ground finch species as a function of mean beak depth. Arrows indicate predicted (upward) and observed (downward) sizes for *G. fuliginosa* (pale) and *G. fortis* (dark).

In Fig. 2, mean beak sizes of populations of *G. fuliginosa* and *G. fortis* are compared with the sizes predicted by density curves (*18*). The relatively small mean size of *G. fortis* observed on Daphne is close to the size predicted from the peak in the density curve on this island (Fig. 1). In contrast, sympatric populations of *G. fortis* are displaced from the positions predicted by the nearest peak on each island (Fig. 2) (*19*). On Los Hermanos, *G. fuliginosa* is large in relation to the size predicted from the density curve. But in this case a shift has occurred from one peak to the next: while *G. fuliginosa* populations on other islands are associated with comparable peaks in expected density at small beak size, the Los Hermanos population lies under a second peak that occurs at substantially larger mean beak size (Fig. 1) (*19*). The results support hypotheses of character displacement for both species.

A study of natural selection in the allopatric population of *G. fortis* on Daphne illuminates the mechanism of displacements. This population experienced a severe drought in 1977, when 85 percent of all individuals died (*10*). A large sample of adults (n = 642) had been banded and measured before the drought. Using a regression technique (*20*) we are able to quantify the relative fitnesses of individuals as a function of their size during this period of mortality. The results show significant disruptive selection on the population (*21*). Most individuals that survived the drought exploited the large seeds, *Opuntia echios* and *Tribulus cistoides*, which determine the second peak in expected population density on the island (Fig. 1). However, at least six individuals that were not able to crack these seeds nevertheless survived by exploiting the few remaining small seeds in the environment (*22*). The six small individuals which survived were all females and formed a large proportion (20 percent) of all surviving females. Their presence in the 1978 breeding population affected the mean morphology of offspring subsequently produced (*23*). Thus, the disruptive selection can be attributed to the use by members of the Daphne population of both the *G. fortis* and *G. fuliginosa* niches, as defined by the two peaks in the expected density curve; note the close correspondence between the expected density and individual fitness curves in Fig. 3.

These observations help us interpret evolutionary shifts in *G. fortis*. Mean morphological size in a *G. fortis* population can be thought of as arising from a trade-off between feeding rates on small soft seeds and large hard seeds. The trade-off is affected by the presence of *G. fuliginosa*, which reduces the availability in the dry season of small soft seeds to *G. fortis*. Those individuals too small to crack the large seeds responsible for the *G. fortis* peak compete directly with the more efficient *G. fuliginosa* for the smaller seeds. Disproportionate mortality in these *G. fortis* individuals therefore leads to a large mean size on islands where *G. fuliginosa* is present. Selection

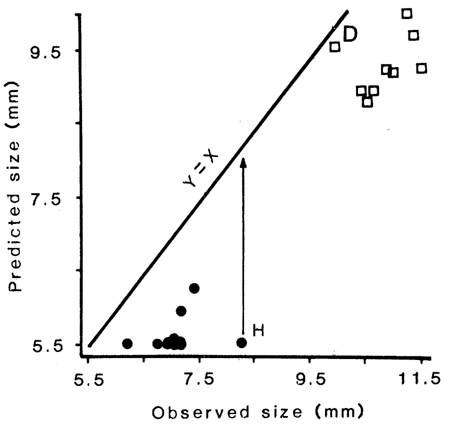

Fig. 2. Observed mean beak sizes for adult males in populations of *G. fuliginosa* (○) and *G. fortis* (☐) compared with the mean beak sizes predicted from peaks in expected population density. Allopatric populations are Los Hermanos (H) and Daphne (D). The arrowhead indicates the observed size of *G. fuliginosa* on Los Hermanos in relation to the second peak in expected density on this island (Fig. 1).

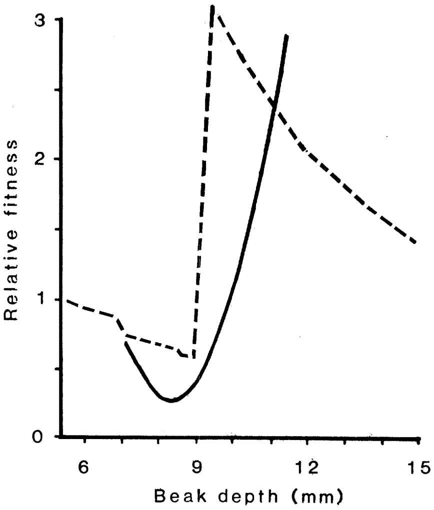

Fig. 3. Relative fitness of individual *G. fortis* on Daphne associated with mortality during a drought showing disruptive selection (solid curve) (*22*). The dashed curve indicates expected population density (Fig. 1).

may have also favored *G. fortis* individuals with beak size slightly larger than the minimum size at which the large hard seeds can be cracked, for reasons of improved handling efficiency (*9, 11, 24–26*).

Our observations on *G. fortis* in sympatry are not as detailed as those on Daphne but are consistent with the above explanation. Because of their greater size, *G. fortis* in sympatry are more efficient at consuming the large seeds responsible for peak position than are *G. fortis* on Daphne, and they less frequently abandon individual seeds without having successfully cracked them (*11, 25, 27*). Also their annual consumption of small seeds is lower than it is on Daphne (*7, 9, 25*).

The difference between mean beak size in the *G. fuliginosa* population on Los Hermanos and the beak size predicted by the second peak in expected density is very small (arrowhead in Fig. 2) (*19*). This situation is analogous to that on Daphne and is correlated with a similar absence of a smaller competitor for the small soft seeds. Thus, but for a small difference in the position of this second peak, the populations of *G. fuliginosa* on Los Hermanos and *G. fortis* on Daphne are morphologically and ecologically identical.

Size shifts in *G. fuliginosa* may also be explained by competition with *G. fortis*. Populations of *G. fuliginosa* in sympatry consume small soft seeds in the dry season (*9, 28*). Mean beak size in sympatry relative to the associated peak in expected density (Fig. 2) is thus probably largely a consequence of selection for efficient exploitation of these small seeds. In contrast, the allopatric population on Los Hermanos has a large beak size corresponding to a position determined by moderately large seeds (notably *Cenchrus*), consumed in sympatry by *G. fortis* (*9, 25*).

To summarize, previous work has shown that morphological patterns in Darwin's finches correspond reasonably well with those expected from the distribution of peaks in expected density curves (*13*). It also provided evidence of interspecific competitive effects. These effects could be the result of character displacement, an evolutionary process, or competitive exclusion, an ecological process. Our study carries the investigation a step further. First, we compare the sizes of particular species in sympatry and allopatry with the sizes predicted by peaks in the density curves. In agreement with an hypothesis of character displacement, *G. fortis* and *G. fuliginosa* were found to vary in their proximity to peaks according to whether they were sympatric or allopatric. Second, a study of marked *G. fortis* on an island lacking *G. fuliginosa* illustrates the connection between feeding and selection pressures associated with morphology. This approach to the study of character displacement should be useful, especially if the magnitude of a given displacement is small and therefore difficult to detect by the usual simple comparison of morphologies in sympatry and allopatry (*4, 29*). Indeed, applied to other systems the approach may show character displacement to be more common than is presently realized.

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16. Although empirical data from actual populations are used to generate expected population density curves, the shape of the curve for any island, given the seeds there, is independent of the number of species present and their mean beak sizes. Hence the problem of circularity [P. R. Grant and I. Abbott, *Evolution* **34**, 332 (1980)] is avoided. To confirm this we repeated the procedure and generated curves without using the empirical data for *G. fuliginosa* and *G. fortis* on Santa Cruz, Daphne, and Los Hermanos, the islands compared in Fig. 1. The positions of the maximums in the expected density curves for all the islands, including these three islands, did not change.
17. Expected densities for given beak depths vary with season or year to some extent, but the shape of the expected density curve is generally invariant. For example, all six Daphne curves, derived from seed data collected in January and June of 1979 to 1981, were virtually identical, despite large seasonal and annual fluctuations in primary production and standing crop of seeds (*8, 10*). Wet season curves for Pinta, Marchena, Santa Cruz, and Los Hermanos were also similar to the corresponding dry season curves. In no case did the predicted optimum beak depth for either finch species depend on the choice of density curve.
18. Predicted beak size for each population is the beak size associated with the peak immediately to the left of the actual mean. The leftward criterion is necessary because a peak to the right of the observed mean beak size is determined by seeds which are not exploited by the population because of their hardness. With this criterion it was possible to associate 15 of the 16 sympatric populations of *G. fortis* and *G. fuliginosa* unambiguously with a particular peak (*13*) (Fig. 1). On Fernandina beak size in *G. fortis* did not correspond to any nearby peak, possibly because of insufficient seed sampling, and this island was excluded from further consideration. Predicted beak size for the two allopatric populations is the beak size associated with the peak to the left of the largest mean for the same species in sympatry.
19. The difference between observed and predicted beak size for *G. fortis* on Daphne (0.46 mm) is significantly less than the difference on other islands: 1.7 mm ± 0.11, standard error; Dixon's outlier test [R. R. Sokal and F. J. Rohlf, *Biometry* (Freeman, San Francisco, ed. 2, 1981), p. 413], one-tailed, $n = 9$, $r_{11} = 0.57$, $P < 0.05$. *Geospiza fuliginosa* on Los Hermanos is also close to the second peak on that island (0.20 mm), but it is significantly further away from the first peak (2.7 mm) than other *G. fuliginosa* populations (1.4 mm ± 0.08, $n = 12$, $r_{21} = 0.65$, $P < 0.01$). In addition, 54 of 121 male Daphne *G. fortis* were smaller than the predicted mean size on that island (Fig. 1). This compares with 12 of 454 for *G. fortis* on other islands combined [$\chi^2(1) = 110.2$, $P < 0.0001$].
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21. A regression analysis of relative fitness of individuals (w, being 0 for those that died and 6.6 for those that survived) on beak depth and the square of beak depth was carried out to obtain coefficients of selection (*20*). The regression equation $w = 21.49 - 5.13x + 0.31x^2$ ($n = 642$, $F = 27.7$, $P < 0.001$). The coefficient of directional selection was $\beta = 0.75 \pm 0.11$ standard error ($P < 0.001$) and of disruptive selection $\gamma = 0.62 \pm 0.21$ ($P < 0.01$). This selection event, and in particular the directional selection, is discussed in (*10*).
22. The smallest individuals on the island are unable to crack the hard seeds (*10, 11, 24*). Forty-six individuals were followed continuously for 30 to 90 minutes during a dry period in 1980. The proportion of time spent feeding on hard seeds was correlated with beak depth (Spearman's $r = 0.64$, $P < 0.001$). Some small individuals have never been seen to crack hard seeds, although some have occasionally attempted to do so and failed [(*24*); T. D. Price, in preparation].
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27. For example, Daphne *G. fortis* males took 34.0 seconds (1.3 seconds, standard error) to crack and consume *Opuntia* seeds ($n = 45$ observations) whereas the species on San Salvador took 16.0 seconds ±2.0 ($n = 6$). Daphne *G. fortis* rejected on average 75 percent of *Tribulus cistoides* seeds (*24*) whereas *G. fortis* on Pinta, Marchena, and San Salvador were rarely or never observed to reject the large hard seeds

determining the peak position on these islands (*Lantana*, ripe *Rhynchosia*, and *Opuntia*). On Daphne 42 percent of *G. fortis* that tried to crack *Bursera* stones were successful (*11*), whereas on Pinta 77 percent were successful (*25*).
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30. We thank P. T. Boag for providing some data and P. T. Boag, B. R. Grant, R. Lande, T. W. Schoener, and J. N. M. Smith for comments and advice. Supported by NSF grants DEB 79-21119 and DEB 82-12515 to P.R.G.

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Regulation of Extravascular Coagulation by Microvascular Permeability

Abstract. *Extravascular coagulation is a prominent feature of such important pathological processes as cellular immunity and neoplasia and has been thought to result from procoagulants associated with the inflammatory or tumor cells peculiar to these entities. It was found that increased microvascular permeability alone is sufficient to induce equivalent extravascular coagulation in several normal tissues. The results indicate that saturating levels of procoagulant are present even in normal tissues and that microvascular permeability is a rate-limiting step in extravascular coagulation.*

Interest in the clotting system has focused on intravascular coagulation—the thrombotic and embolic processes that are intimately associated with atherosclerosis, myocardial infarction, and cerebrovascular disease (*1*). However, extravascular coagulation is a prominent feature of many important pathological entities, including cell-mediated immunity and neoplasia (*2*). Thus, fibrin is deposited locally in delayed hypersensitivity reactions and in solid tumors. This fibrin is derived from plasma fibrinogen that has extravasated from blood vessels, clotted, and become cross-linked in the tissue space (*3*). The biological significance of extravascular coagulation in these and other disease processes is only now beginning to be investigated. It is known that extravascular deposits of fibrin, by forming a water-trapping gel, cause the induration characteristic of delayed hypersensitivity and contribute to brain damage in autoimmune encephalitis (*4*). In addition, extravascular clotting and associated fibrinolysis have been implicated in depressing the immune response, in enhanced vessel permeability, and in tumor growth, angiogenesis, desmoplasia, and metastasis (*2, 5*).

How is extravascular coagulation regulated? Much attention has been devoted to the characterization of cellular procoagulants that can initiate or promote clotting, particularly macrophage and tumor cell membrane-associated molecules that act at various steps in the coagulation pathway (*2, 6*). However, one potential control point that has received little or no attention is the availability in the extravascular space of plasma clotting factors, particularly fibrinogen. Under conditions of normal low vascular permeability, levels of extravascular fibrinogen are negligible, bordering on the limit of detection (*3*). If significant extravascular fibrin is to be deposited, therefore, tissue fibrinogen and probably other plasma clotting factors must first be increased. Increased vascular permeability to plasma proteins regularly parallels extravascular coagulation in both cellular immunity and malignant tumors (*2*).

We therefore investigated the relation of blood vessel permeability to extravascular coagulation in several normal tissues. Adult Hartley guinea pigs were injected intravenously with ^{125}I-labeled guinea pig fibrinogen (GPF) and immediately thereafter were challenged locally with histamine, bradykinin, or a tumor-secreted vascular permeability mediator (VPM) (*7*), all agents that transiently increase venule permeability. Twenty minutes later the quantity and nature of locally accumulated [^{125}I]GPF were determined (*3, 8, 9*).

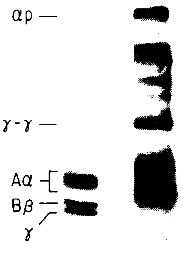

Fig. 1. Autoradiogram of reduced sodium dodecyl sulfate–polyacrylamide gel of [^{125}I]GPF (track 1) and of urea residue from skin taken 20 minutes after injection of histamine (track 2). Injected guinea pig fibrinogen shows, as expected, Aα (doublet), Bβ, and γ chains. [^{125}I]GPF circulating in plasma showed an identical pattern. Prominent bands corresponding to γ-chain dimers (γ-γ; molecular weight, ~93K), and high molecular weight α-chain polymers (αp; >200K), are present in gels from the histamine skin test site—indicative of cross-linked fibrin. A variety of uncharacterized fibrinogen-fibrin breakdown products are also represented in the latter gel.

Intradermal injection of histamine led to a dose-dependent increase in [^{125}I]GPF accumulation greatly exceeding that of uninjected or saline-injected skin (Table 1). Thus 1 μg of histamine led to the accumulation of 118 μl of platelet poor plasma (PPP), equivalent to 394 μg of fibrinogen, per gram of skin. Moreover, most [^{125}I]GPF extravasated at histamine injection sites was not extractable with aqueous buffer or with 3*M* urea and thus had acquired properties of cross-linked fibrin (*2, 3, 9*). Neither [^{125}I]GPF accumulation nor clotting was increased further when guinea pig brain tissue factor (*10*) or thrombin (0.2 U) was included in the histamine injections, suggesting that the amount of procoagulant activity present in normal skin was sufficient and not rate-limiting. Similar results were obtained when bradykinin or VPM was used to enhance skin vessel permeability or when the effects of local histamine were studied in the eye (Table 1) or the peritoneal wall.

Local anticoagulation achieved by including clotting inhibitors in histamine-containing eye drops (Table 1) or in injections of the skin with histamine strikingly inhibited the amount and fraction of extravasated [^{125}I]GPF that was insoluble in urea. Similar results were obtained when animals were treated systemically with heparin.

Conclusive evidence for the cross-linked nature of the fibrin deposited in histamine skin test sites was obtained from autoradiograms of sodium dodecyl sulfate–polyacrylamide gels subjected to electrophoresis (Fig. 1) (*11*). The autoradiograms showed extensive γ-γ dimerization and α-chain polymerization, characteristic of cross-linked fibrin (*1, 3, 9*). Thus the fibrin deposited in skin as the result of locally increased microvascular permeability had the same biochemical characteristics as that found in solid tumors and in skin undergoing delayed hypersensitivity reactions (*3*).

The extravascular localization of tissue fibrin was further defined by immunohistochemistry and electron microscopy of histamine skin test sites (Fig. 2). Fibrin was concentrated in focal deposits centered about individual fixed connective tissue cells, fibrocytes, and histiocytes. The fibrin, which transmis-