

CHARACTER DISPLACEMENT BETWEEN DISTANTLY RELATED TAXA? FINCHES AND BEES IN THE GALÁPAGOS

Interspecific competition for food may result in character displacement, an evolutionary shift in the morphology of one or more interacting species (Lack 1947; Brown and Wilson 1956; Grant 1972; Slatkin 1980). The few known examples of character displacement are exclusively from taxonomically closely related species (Lack 1947; Schoener 1970; Huey and Pianka 1974; Fenschel 1975; Case 1979; Dunham et al. 1979; Fjeldså 1983). Species from widely different taxa may compete, however (Dayton 1971; Menge 1976; Brown et al. 1979; Carpenter 1979; Belovsky 1984), and character displacement between distantly related species remains a theoretical possibility.

In this report I present evidence suggesting that competition for flower nectar has resulted in character displacement between finches and bees on the Galápagos Islands. First, the evidence is threefold: the use of flower nectar by two finch species was higher on the average on three islands where flowers are present but bees are absent than on islands where bees are present; the mean body size of the two finch species is smallest on the same three islands; and in one finch population, individuals that exploited flower nectar were smaller in size than individuals that did not. Second, I discuss alternative explanations for these results. Third, on the basis of these results, I suggest how the form of character displacement between distantly related species may differ in general from that between closely related species.

DIET SHIFTS AND POSSIBLE CHARACTER DISPLACEMENT

Few pollinating insects have colonized the Galápagos Islands (Linsley 1966). A single species of bee is present, the large carpenter bee, *Xylocopa darwini*. Its distribution is restricted: it has not reached the five most northern islands of Darwin, Wolf, Pinta, Marchena, and Genovesa. *Xylocopa* is a generalist, removing pollen and nectar from quite diverse flower types. Where present, it is the most important flower visitor of Galápagos plants (Linsley et al. 1966).

Small ground finches, *Geospiza fuliginosa* and lowland forms of *G. difficilis*, also consume flower nectar on most of the islands (Smith et al. 1978; Grant and Grant 1980a; Schluter and Grant 1982, 1984b, pers. obs.). Table 1 shows that in the dry season, nectar constituted an average of 20% of the diet of the finches on Pinta, Marchena, and Genovesa, where bees are absent, and 4.4% of the diet on islands where bees are present (Mann-Whitney $U = 14$, $P < .05$). Dry-season diets are of primary interest because populations are most often food-limited at

TABLE 1
 BODY SIZE AND NECTAR USE IN *Geospiza* ON THE GALÁPAGOS ISLANDS

ISLAND	NO. SITES	% TIME NECTAR-FEEDING	NO. SECONDS OBSERVED FEEDING	BODY SIZE (mm)			BEES PRESENT	FLOWERS PRESENT
				Wing	Tarsus	N		
<i>G. difficilis</i>								
Darwin	1	0	5,045	74.4 (.3)	19.3 (.1)	39		
Wolf	1	0	17,535	72.9 (.2)	18.8 (.1)	100		
Genovesa	3	23	41,990	63.4 (.2)	16.4 (.1)	83		X
<i>G. fuliginosa</i>								
Pinta	6	10	103,990	59.8 (.2)	15.7 (.1)	62		X
Marchena	2	28	51,960	59.2 (.3)	15.5 (.1)	38		X
Fernandina	4	1	25,870	64.8 (.4)	16.9 (.2)	27	X	X
Santa Cruz	5	14	32,521	64.0 (.1)	17.0 (.1)	132	X	X
San Salvador	2	0	26,405	63.8 (.3)	17.1 (.1)	39	X	X
Española	3	0	25,365	64.7 (.3)	17.1 (.1)	37	X	X
Isabela	1	7	13,125	64.5 (.3)	17.1 (.1)	202	X	X

NOTE.—Nectar use is the proportion of foraging time spent feeding on flower nectar in the dry season. Santa Cruz data are from Smith et al. (1978) and D. J. Anderson (MS). Isabela data are from P. R. Grant (unpubl. data). Other data are from Schluter and Grant (1984b). Nectar-feeding proportions are averaged over sites, weighted by the density of birds present. Finch measurements (mean \pm SE in parentheses) are taken from museum specimens (Grant et al. 1985), males only. Flower presence indicates that flowers exploited for nectar by finches on Pinta, Marchena, or Genovesa are regularly encountered on these and other islands in the dry season.

this time (Smith et al. 1978; Grant and Grant 1980b; Schluter 1982; Schluter and Grant 1984a) and because natural selection adjusts the mean body size in relation to available foods most strongly in the dry season (Boag and Grant 1981; Price et al. 1984). High levels of nectar use by *G. fuliginosa* were recorded on one island where bees are present, Santa Cruz (Smith et al. 1978), but such high levels are not consistently reported during dry-season visits to this island (Smith et al. 1978; D. J. Anderson, MS; Schluter, unpubl. data). Studies conducted over several years show that high levels of dry-season nectar consumption are characteristic of finch populations on Pinta, Marchena, and Genovesa, where bees are absent (Smith et al. 1978; Grant and Grant 1980a; Schluter 1982; Schluter and Grant 1982). In all populations of *G. fuliginosa* and *G. difficilis* shown in table 1, the remainder of the diet consisted mainly of small seeds (Schluter 1982; Schluter and Grant 1982, 1984b).

Nectar sources used by *G. fuliginosa* and *G. difficilis* on Pinta, Marchena, and Genovesa provide additional evidence that high nectar consumption by finches is permitted in part by the absence of bees. The most important source of nectar on these three islands through the dry season is *Waltheria ovata* (Sterculiaceae), a flower exploited for nectar by *Xylocopa* on other islands (Linsley et al. 1966). The flower is small and yellow, and hence an unlikely source of nectar for birds in general; indeed, in continental regions, yellow flowers of *Waltheria* are exploited primarily by small bees and wasps (H. G. Baker and D. H. Janzen, pers. comm.). On Pinta, another major source of nectar for *G. fuliginosa* is *Passiflora suberosa* (Passifloraceae), a large, pale, yellow-green, "flat" flower similar in basic struc-

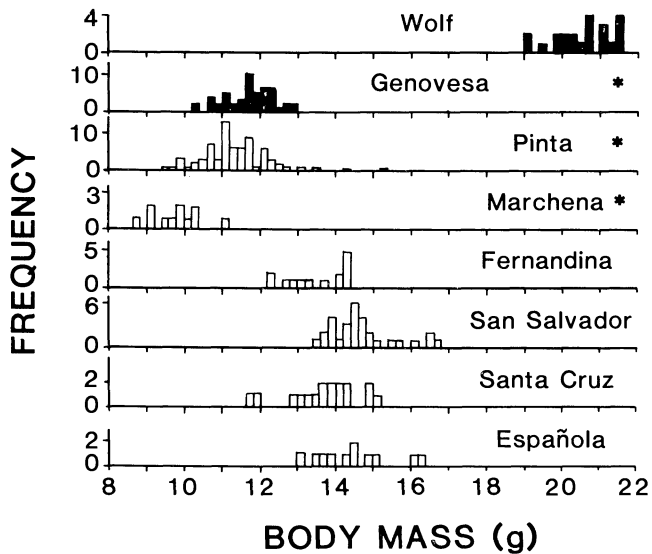


FIG. 1.—Body-mass distributions in populations of *Geospiza fuliginosa* (open) and *G. difficilis* (solid) on the Galápagos Islands. Asterisks indicate those islands where bees (*Xylocopa darwini*) are absent but nectar-producing flowers are common.

ture to *P. foetida* (see Janzen 1968). Continental *Passiflora* of such shape and color are not visited by birds (D. H. Janzen, pers. comm.). Finally, on Pinta and Marchena in the dry season, finches consume the nectar of *Castela galapageia* (Simarubaceae), a plant used extensively by *Xylocopa* on other islands (Linsley et al. 1966).

Relatively high levels of nectar consumption by finches where bees are absent is associated with small finch size. Figure 1 compares the frequency distributions of body mass in different populations of *G. fuliginosa* and *G. difficilis*. Weights are from males captured in nets from 1978 through 1981. Means for two additional measures of body size, wing length and tarsus length, are shown in table 1 for a larger sample of birds. Beak dimensions are not shown, but these are positively correlated with body dimensions (Grant et al. 1985). Both species on Pinta, Marchena, and Genovesa are smaller than on other islands (fig. 1; table 1; Grant et al. 1985). That small size and nectar use are correlated with the absence of *Xylocopa* suggests that character displacement may have occurred between finches and bees.

Evidence from *G. fuliginosa* on Marchena directly links small body size and nectar use. Flowers, mainly of *Waltheria*, were abundant in the dry season in one site on this island, and individual finches defended clumps of these against conspecifics. Birds using the site and adjacent areas were netted, measured, and individually color-banded. The diet and behavior of color-banded birds were monitored daily for the 2 subsequent weeks. Many banded birds were found to maintain territories throughout the day, though birds frequently left defended areas to feed on seeds. Table 2 compares the mean body size of banded individ-

TABLE 2
 BODY SIZE OF *Geospiza fuliginosa* INDIVIDUALS CAPTURED IN MARCHENA SITES

CATEGORY	N	TARSUS LENGTH		BODY MASS		PLUMAGE	
		mm	P	g	P	Brown	Black
A	16	15.7 (.17)		8.7 (.25)		13	3
B	6	16.9 (.49)	< .02	11.3 (.87)	< .001	4	2
C	14	16.2 (.17)	.05	9.9 (.20)	< .01	13	1

NOTE.—Category A, birds that were seen to feed on flower nectar in site 1; B, site-1 birds not seen to take nectar; C, all birds in a second location with few nectar-producing flowers. Measurements are the mean (\pm SE in parentheses). *P* values indicate the probability in pairwise *t*-tests that the means for B or C differ from that of A by chance. Also indicated are the plumage types of individuals in the samples.

uals seen taking nectar at least once, with the mean body size of banded individuals using only seeds. The nectarivores are significantly smaller.

Few nonnectarivores were seen following their capture on Marchena, probably because they are also nonterritorial and hence likely to wander. Finches were therefore netted in a second site about 4 km away. Here, nectar-producing flowers were uncommon, although I cannot rule out the possibility that some of the birds using the site were nectarivores elsewhere. Birds in this sample were also larger than the known nectar feeders (table 2).

In the above two comparisons, differences in body mass were more significant than differences in tarsus length. Regressions of body mass against tarsus length for birds in samples A and C (table 2) reveal that nectarivores weighed significantly less than nonnectarivores for a given tarsus length (ANCOVA, slopes: $F = 0.098$, $df = 1,25$, $P > .5$; intercepts: $F = 5.22$, $df = 1,26$, $P < .05$). The difference is probably caused in part by a lower food bulk in the stomachs of nectar feeders, a proximate result of diet differences, though heritable differences in body shape between nectarivores and nonnectarivores could also be present. Body mass may fluctuate with changes in diet and food supply, but dry-season diet variation is unlikely to affect other measures of body size, such as tarsus length (Boag 1983). Additionally, most traits in *Geospiza* are highly heritable (Boag and Grant 1978; Grant 1981; Boag 1983).

Size differences between nectarivores and nonnectarivores on Marchena were not simply the result of resource partitioning by age or sex. Though the sample size is small, the proportion of birds in black plumage (adult males) or brown plumage (adult females and immature birds) was not different among the categories compared (table 2; $\chi^2 = 2.16$, $df = 2$, $P > .25$).

How does nectar feeding favor smaller individuals? Results from Marchena suggest that small individuals gain little or no advantage over larger individuals in nectar-foraging rates. Rates of *Waltheria*-flower visitation by territorial *G. fuliginosa* were recorded in the dry season between 1000 and 1200 h on 3 successive days. Overall, the mean time required to visit 20 flowers did not differ significantly

among individuals (ANOVA, $F = 1.039$, $df = 12,106$, $P > .25$). The mean time to visit 20 flowers was weakly and not significantly correlated with body mass ($n = 13$, $r = .52$, $.05 < P < .10$) and tarsus length ($n = 13$, $r = .17$, $P > .10$). Therefore, smaller individuals may gain only a metabolic advantage over larger individuals. That is, a small individual meets a greater fraction of its total metabolic requirements than a larger individual while feeding on nectar, simply because its requirements are lower.

Associations between body size and a nectar-feeding habit in *G. fuliginosa* and *G. difficilis* parallel associations among avian species differing in size (see, e.g., Brown et al. 1978).

ALTERNATIVE EXPLANATIONS

A problem with any example of character displacement is that one cannot be certain whether some other factor is responsible for the pattern. I see four possible alternative explanations.

1. *Climate*.—It is unlikely that climatic differences among islands are responsible for variation in body size in *Geospiza fuliginosa* and *G. difficilis*. On the northern islands of Pinta and Marchena, *G. fuliginosa* is smallest, and hence size appears to be related to latitude in this species; however, latitudinal trends in size are not repeated in many other species sharing a similar geographic range (Grant et al. 1985). For example, *G. difficilis* populations with a body size larger than that on Genovesa occur on islands both to the north and to the south of Genovesa (Schluter and Grant 1984b). Also, Galápagos islands differing in elevation show greater climatic and vegetational differences than do islands differing in latitude (see, e.g., Wiggins and Porter 1971; Schluter 1982; Schluter and Grant 1982). Nonetheless, the smallest *G. fuliginosa* and *G. difficilis* occur on both high-elevation (Pinta) and low-elevation islands (Genovesa and Marchena).

2. *Seed characteristics of islands*.—The availability of seeds of different size and hardness on different islands strongly influences the mean size in *Geospiza* populations (Boag and Grant 1981; Price et al. 1984; Schluter and Grant 1984a). We can test the hypothesis that differences in finch size between islands with bees and those without are caused by differences in seed characteristics among the islands. Schluter and Grant (1984a) estimated the optimal mean beak size and body size for *Geospiza* populations on the basis of the size and hardness of seeds available on different islands. If seed characteristics differ between islands with bees and those without, then the optimal sizes predicted for *G. fuliginosa* and *G. difficilis* should be different in the two situations. Such differences are not observed ($t = .15$, $df = 8$, $P > .5$; see Schluter and Grant 1984a).

3. *Flower types*.—Size differences in *G. fuliginosa* and *G. difficilis* between islands with bees and those without are not the result of island differences in the types of flowers present. *Castela galapageia* and *Waltheria ovata* are two of the most important nectar sources for finches on Pinta, Marchena, and Genovesa. *Castela* is common on Santa Cruz and San Salvador, and *Waltheria* is abundant on these two islands and on Fernandina and is present on Española. Both plants

are exploited by bees on all four islands, but not extensively by finches (table 1). A third important nectar source, *Passiflora suberosa*, is to my knowledge common only on Pinta.

4. *Relative food abundance*.—The relative abundance of flower nectar and seeds within study sites may influence the average proportion of time that finches allocate to each (Schluter and Grant 1982). Unfortunately, my data are inadequate for evaluating whether variation in relative abundance of these two foods can account for body-size differences among islands. The scale and intensity of food sampling were designed to estimate the abundance of seeds and arthropods (Schluter 1982), but my methods did not adequately assess the overall flower density. Therefore, I cannot rule out this alternative hypothesis, and it remains to be rigorously tested. We do know that absolute seed abundance is not systematically low on Pinta, Marchena, and Genovesa, compared to islands where bees are present (Smith et al. 1978; Schluter and Grant 1984*b*). In addition, it is unlikely that absolute flower abundance should be highest on those islands where bees are absent; qualitative observations suggest that this is not the case.

CHARACTER DISPLACEMENT BETWEEN DISTANTLY RELATED TAXA

The data suggest that the use of flower nectar by finches on the Galápagos Islands may have been influenced by the presence or absence of bees, and that the presence or absence of bees may have influenced finch body size as a consequence. Moreover, the observation that unrelated species frequently compete for food (see, e.g., Brown et al. 1979; Carpenter 1979) indicates that character displacement between distantly related taxa may be common. It is interesting to consider whether the degree of taxonomic relatedness might influence the form of character displacement that typically occurs. What effects might degree of relatedness be expected to have?

One effect is suggested by the present study. On no islands are bees present but *G. fuliginosa* and *G. difficilis* absent; thus, the possibility of a reciprocal body-size increase in *Xylocopa* in the absence of finches cannot be tested. Such a size increase is extremely unlikely, however: whereas *G. fuliginosa* and *G. difficilis* are generalists, for which nectar is one of at least two alternative resources (seeds being the other), bees are confined to nectar. Such differences in the range of resources used are likely to be common when competitors are taxonomically dissimilar (Levins 1979). In general, one may therefore expect character displacement between distantly related taxa to more often involve asymmetrical shifts in size. Most examples of character displacement in pairs of closely related species involve shifts in both competitors (Lack 1947; Schoener 1970; Grant 1972; Fenchel 1975; Case 1979; Dunham et al. 1979; Fjeldså 1983).

The magnitude of character displacement should also be influenced by the degree of relatedness. Slatkin (1980) showed that displacement may not occur when two species have the same distribution of K (carrying capacity) over the range of possible phenotypes. Slatkin and Lawlor and Maynard Smith (1976) implied in their models that the magnitude of displacement increases as the K distributions themselves become more different. Having identical K 's implies that

in allopatry each species would use the same resources and be limited by these resources in the same way. Distantly related species are more likely to exhibit dissimilar K 's than closely related species, and thus they should exhibit large character displacement more often than closely related species.

Given that large character displacement is theoretically possible between unrelated species, it is interesting that no possible example has heretofore been suggested. This lack of examples may result because for unknown reasons character displacement is actually less common between distantly related species than between closely related species. Alternatively, the lack of examples may result from a third effect of the degree of relatedness on character displacement: unrelated species would never converge to the same approximate size in allopatry, rendering cases of character displacement between them difficult to detect.

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