CHARACTER DISPLACEMENT AND THE ADAPTIVE DIVERGENCE OF FINCHES ON ISLANDS AND CONTINENTS

DOLPH SCHLUTER

The Ecology Group, Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 2A9, Canada

Competition between species occurs frequently in many communities (Connell 1983; Schoener 1983). We are less certain that competition has had major evolutionary consequences. One such consequence is "ecological character displacement" (W. Brown and Wilson 1956; Grant 1972), defined as an effect of competition between species on morphology or other heritable traits influencing resource use.

In a typical search for character displacement, morphological differences between populations of two species occurring together in sympatry are compared with differences between the same species occurring separately in allopatry (Schoener 1970; Grant 1972, 1975; Huey and Pianka 1974; Fenchel 1975; Case 1979; Dunham et al. 1979; Arthur 1982; Fjeldså 1983; Schluter et al. 1985). Divergence is the most commonly described form of displacement (but see Abrams 1986a), when competition results in greater morphological differences between species in sympatry than allopatry. Other plausible causes of a greater difference in sympatry must be ruled out before character displacement can be tentatively concluded. Few examples of character displacement are so defined, raising doubts about the general validity of the hypothesis that interspecific competition has evolutionary effects (Grant 1972; Arthur 1982; but see Schoener 1984; Abrams 1986b).

In this report, I consider an alternative source of evidence for character displacement: the observation that morphological and ecological divergence of related species is apparently promoted by an absence of competitors from other taxa. For example, explosive adaptive divergence has occurred in many species groups of remote oceanic archipelagoes, such as the finches of the Galápagos and Hawaii (Lack 1947; Amadon 1950). A frequent explanation for this pattern is that divergence of species into novel ecological niches is difficult when the niches are already exploited by species in other taxa (fig. 1). Greater divergence in the absence of other taxa thus represents a relaxing of competitive constraints (Lack 1947; Simpson 1953; Mayr 1963; Bock 1972; Keast 1972; Stanley 1981; Grant 1986a). The process is analogous to "character release" observed in comparisons

of populations, and like its counterpart, it implies an evolutionary effect o
interspecific competition on species morphology (i.e., character displacement)

   Cases of apparent character displacement involving different amounts of diver
gence have not been investigated in detail; yet there are compelling reasons fo
doing so. One reason is that many species groups show elevated amounts o
divergence on remote archipelagoes (Lack 1947; Carson and Kaneshiro 1976
Johnson et al. 1977; Carlquist 1980; Carr and Kyhos 1981; Bowman et al. 1983
Helenurm and Ganders 1985), suggesting that character displacement might be
universal, contrary to conclusions drawn from comparisons of populations. Sec
ond, if the hypothesis that greater divergence in isolation represents characte
displacement is correct, then it would imply more far-reaching effects of competi
tion on morphological and ecological diversity than population comparisons alon
could indicate. Finally, competition among species in different taxa is an essentia
ingredient of this evolutionary hypothesis (fig. 1). In contrast, comparisons o
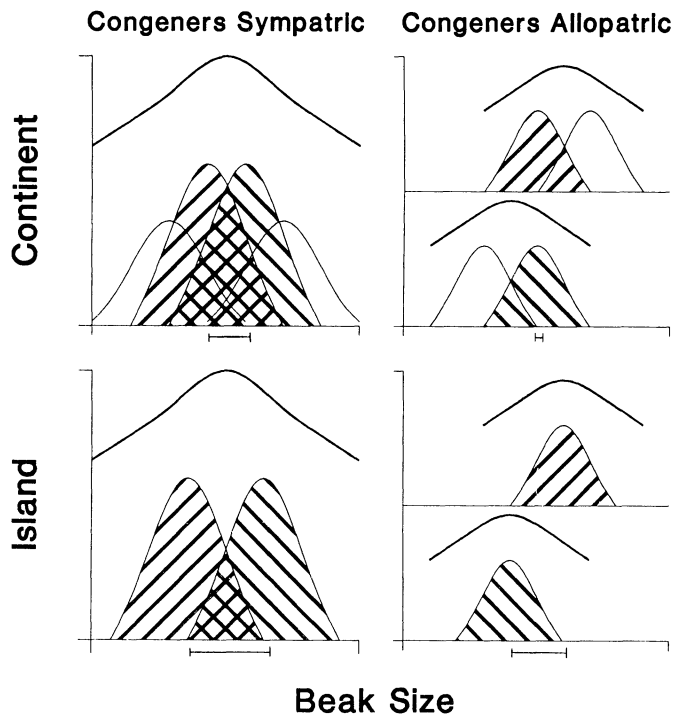

FIG. 1.—Hypothesis for an influence of interspecific competition on divergence between
related species. *Heavy upper curves*, "Carrying capacity," or total food availability, as a
function of beak size. *Cross-hatched curves*, The frequency distributions of beak sizes in two
species recently evolved from a common ancestor (congeners). *Unshaded curves*, Beak sizes
of competitor species not closely related to the other two. Line segments along the x-axes
measure the evolved difference in mean beak size between congeners in the presence
(continent) and absence (island) of competitor species. Evolved differences are greater on the
island, where species in the alternative taxon are absent. Factors promoting greater diver-
gence on islands include competition between the congeners (congeners sympatric) and
differences between locations in food (congeners allopatric).

populations in sympatry and allopatry have been largely restricted to closely related species, and evidence of character displacement among taxa is still slight (Schluter 1986a).

The hypothesis that an elevated amount of divergence on remote archipelagoes is at least in part caused by reduced competition from other taxa is widely held. I have encountered in the literature no explicit challenge to the idea (unlike almost every other hypothesis invoking interspecific competition), though James (1982) argued that divergence patterns of many continental bird groups may be no less dramatic than those of the Galápagos or Hawaii. Alternative explanations are conceivable, however, and should be ruled out before character displacement is accepted. Alternatives might be based on other ecological differences between continents and remote islands, such as the amount of predation and the diversity of resources, or on the genetic consequences stemming from reduced gene flow and small population size on islands.

Here I compare patterns of adaptive divergence in finches on islands and continents and review the evidence for an effect of interspecific competition. The pattern of divergence in the well-studied Galápagos finches is compared with that in the Hawaiian finches and those of a survey of continental finch taxa. I concentrate on the granivorous component of all finch faunas, since seeds are easily quantified and compared among situations. Divergence in beak size is emphasized because relationships between beak and seed size are established (Newton 1973; Abbott et al. 1977; Grant 1981; Schluter 1982a; Schluter and Grant 1984a; Pulliam 1985) and because the known genetic constraints on the evolution of beak and body size are few (Boag 1983; Grant 1983; Schluter and Smith 1986b).

Finches are ideal candidates for a comparison of patterns of adaptive divergence, since some information on their morphology, ecology, and genetics is available from both islands and continents. Gaps in our knowledge inevitably remain, however, and I shall indicate where further study is needed.

Species and Morphological Measurements

Galápagos.—Thirteen species of Galápagos finch (Geospizinae, Emberizidae) have evolved in situ from a common emberizine ancestor (Lack 1947; Steadman 1982; Grant 1986a). Of these, the six ground finch species (*Geospiza*) are mainly granivorous. Five morphological traits were used to describe beak and body size in the *Geospiza*: wing length, tarsus length, and beak length, depth, and width, all in millimeters. I used the measurements taken from museum specimens of adult males, as given by Grant et al. (1985), with slight modification. Beak depth here is the sum of upper and lower mandible depths given by Grant et al., equivalent to whole-beak depth measured on live specimens (e.g., Schluter and Grant 1984b). I adjusted beak width, which was measured at the anterior edge of the nares, rather than at the widest point (base of the lower mandible) as measured by Grant et al. This was done to allow a comparison with beak widths measured at the nares in the other finch groups. The adjustment was accomplished by measuring width in both ways on a sample of 10 male *Geospiza* specimens of each species and

applying the observed correction factor to measurements given by Grant et al. (1985). Specimens were measured at the American Museum of Natural History in New York.

Hawaii.—The Hawaiian honeycreepers (Drepanididae, Morony et al. 1975; or Drepanidinae, Fringillidae, AOU 1983) evolved from a common ancestor in the Carduelinae (Fringillidae; Sibley and Ahlquist 1982) into forms more varied even than the Galápagos finches (Amadon 1950; Raikow 1977). The granivorous species fall into a single genus, *Psittirostra*, of which seven members are known from skin collections. Included in this seven are the six species listed by Morony et al. (1975), plus *P. ultima*, now considered distinct from *P. cantans* (AOU 1983). One of the seven, *P. psittacea*, is frugivorous (Amadon 1950) and was therefore not included in my analysis. Three of the remaining six species are extinct, *P. kona*, *P. flaviceps*, and *P. palmeri*; the few available male specimens at the American Museum of Natural History (1–9 specimens) were measured as described above for *Geospiza*. I also measured 10 adult males of the three extant species.

Other recently extinct species of *Psittirostra* are known only from bones (Olson and James 1982). I estimated beak size in several of these species, to allow a more complete comparison of *Psittirostra* with *Geospiza*. The smallest and largest of these are *Psittirostra* "small species" and *Psittirostra* "giant Oahu species" (Olson and James 1982) with estimated beak depths of 7.0 and 22.0 mm, respectively. These estimates are based on beak measurements from bones (6.0 and 19.0 mm, respectively; H. F. James, pers. comm.), corrected for the thickness of the ramphotheca. *Psittirostra* "lesser Oahu species" were assumed to be the same size as *P. kona* (Olson and James 1982) at 18.7 mm, and *Psittirostra* "medium species" were estimated at 10.5 mm. Other extinct species such as ridge-billed and cone-billed finches were not included in my analysis; their membership in *Psittirostra* is tentative (Olson and James 1982).

Some doubt exists about whether *Psittirostra* is comparable to *Geospiza* and the continental genera (H. F. James, pers. comm.). For example, the American Ornithologists' Union (AOU 1983, 1987), after Pratt (1979, cited in AOU 1983), split *Psittirostra* into five genera united in the tribe Psittirostrini. Biochemical data are unfortunately not available to help decide the issue. For convenience, I kept the genus *Psittirostra* but also separately analyzed data for the largest subgenus, *Telespiza* (*P. cantans*, *P. ultima*, *Psittirostra* "medium species," and *Psittirostra* "small species"). Comparisons are also made between *Psittirostra* and its ancestral subfamily, Carduelinae.

Continental finch genera.—Morphology in *Psittirostra* and *Geospiza* was compared to that in a survey of continental finch genera. I restricted comparison to genera in the families Fringillidae (true finches), Emberizidae (buntings, New World sparrows, grosbeaks, etc.), Ploceidae (Old World sparrows, weavers), and Estrildidae (waxbills). No attempt was made to measure all species in any selected group of genera. Instead, I obtained lists from the literature of species present in various localities around the world. Lists were obtained from habitats ranging from tropical wet forest to tropical savanna woodland, mediterranean scrub, temperate grassland, temperate deciduous woodland, and cold desert. The result amounts to a reasonable sample of continental genera and species. Species known

not to be granivorous were excluded (e.g., *Malimbus*; Hall and Moreau 1970). Lists from a selection of habitats and geographic regions are given elsewhere (Schluter 1986*b*).

For each species, 10 male specimens from a common locality were measured as described above for *Geospiza*. Most measurements were made at the American Museum of Natural History, New York, with additional specimens measured at the Museum of Vertebrate Zoology, University of California, Berkeley, and the Cowan Vertebrate Museum at the University of British Columbia. In all, I measured 180 species from 68 continental genera (148 species in 36 genera had at least one congener measured; Appendix A). Species classification follows Morony et al. (1975).

The comparative study used species means for the five ln-transformed morphological traits. In addition, I extracted two principal components from the covariance matrix based on all species means combined (fossil *Psittirostra* excluded). The five variables contributed positively to the first component, PC1 (loadings from 0.32-0.56); hence, this is a general "size" variable. Four traits contributed to the second component, PC2: wing length and tarsus length positively, and beak depth and width negatively. Thus, PC2 is a "shape" variable, specifically, body size relative to beak stoutness. The two components accounted for most of the variance among species (76% and 15%, respectively).

Biochemical Studies

Classification of finch species into genera is based largely on morphological criteria. However, independent information of species relationships is available from electrophoretic studies of *Geospiza* (Yang and Patton 1981), and several continental genera (Avise et al. 1980; Zink 1982; Christidis 1987). I was thus able to compare morphological divergence directly to genetic distance in a few cases.

Estimates of genetic distance based on electrophoretic data are more variable than morphological distances. Standard errors (SE) for average genetic distance were computed using the bootstrap (Efron 1982). This involved resampling N loci with replacement from the data, where N is the number of loci assayed. Resampling was repeated 1000 times. For each replicate, I computed the bias-corrected Nei distance between all pairs of congeners, and their average. The bootstrap standard error is the standard deviation of these 1000 average distances. I also computed 95% confidence limits (Efron 1982), but since they were roughly equal to the average distance ± 2 SE, I present only the standard errors.

Quantitative Genetics and Natural Selection

The study of morphological divergence in finches is greatly aided by field studies of natural selection and quantitative genetics. Intrapopulation variation in the five morphological traits used here has been linked to differential survival and reproduction in two species of Galápagos *Geospiza* (Boag and Grant 1981; Price et al. 1984*a*; B. Grant 1985) and in one continental species, *Zonotrichia* (= *Melospiza*) *melodia* (Schluter and Smith 1986*a*). The latter study was actually conducted on an island (Mandarte), but the population is not greatly isolated because it is only 1-2 km from populations on adjacent islands and mainland. Heritabilities

and genetic correlations of the five morphological traits have been measured in each population (Boag 1983; Grant 1983; Schluter and Smith 1986b).

Ecological Comparisons

Finch faunas on islands (Galápagos) were also compared to those on continents (California and Kenya) in their ecological characteristics. The Galápagos studies were conducted on various *Geospiza* species on many islands over several years (see Grant 1986a). Diets were assessed through timed observation of foraging individuals in 1-ha study sites. Food supply was assessed through sampling the vegetation and the ground in quadrats located randomly in sites. Details of these methods are given elsewhere (Schluter 1982a,b). Results discussed here are from the dry season, when finch populations are limited by food supplies (Smith et al. 1978; Grant and Grant 1980; Schluter 1982b; Schluter and Grant 1984a).

Research in California was conducted in January and February 1984 in two 2-ha sites at each of two locations: the University of California Stebbins Cold Canyon Reserve (chaparral habitat), near Davis, visited 1–3 days per wk over the 2-mo period; and the University of California Boyd Deep Canyon Desert Research Center (warm desert habitat), near Palm Desert, visited for 2 wk. Research has continued at the second location (December–February 1986 and 1987; R. Repasky, unpubl. data), but the results presented here are based on 1984; the later results are similar. The study was conducted in the nonbreeding season (winter), to compare with dry-season results from the Galápagos. Granivorous species in sites were all Emberizidae (*Amphispiza bilineata*, *Spizella breweri*, *Zonotrichia leucophrys*, *Z. (Passerella) iliaca*, *Junco hyemalis*, *Pipilo fuscus*, and *P. ery-throphthalmus*). All species are resident within California, but at least two migrate to other habitats to breed (*J. hyemalis* and *Z. leucophrys*; Small 1974). Some individuals of both *Zonotrichia* species are winter visitors, breeding farther north (Small 1974).

Six locations in Kenya were visited from 1983 to 1986: (1) Bushwhackers, near Kibweze; (2) Shaba National Reserve, near Isiolo; (3) Athi Plains, adjacent to Nairobi National Park; (4) Hell's Gate National Park, near Naivasha; (5) Sokoke Forest Nature Reserve, near Malindi; and (6) Olorgesailie Prehistoric Site, in the Rift Valley near Magadi. Except for the Sokoke forest (coastal *Brachystegia* woodland), locations were similar in vegetational structure to Galápagos sites, ranging from bushed and wooded grassland to woodland and bushland. Quantitative descriptions of habitats are given elsewhere (Schluter, in press).

All six Kenyan locations were visited in the dry season (June to September) in 1985, each for a period of 3 wk. Two 2-ha sites were established at all locations except 5, where only one site was used. In the 1986 dry season, I concentrated effort in one location, Olorgesailie (6), and established three additional sites. Measurements of diet and food supply were repeated in the first (July–August) and second (September–October) halves of the 1986 season. I revisited Hell's Gate for 1 wk between these periods (late August) and took similar measurements. Four of the six locations (1, 2, 4, and 5) were also visited for 1 wk each in July 1983, but food supply was estimated in only two of them (1 and 4), and little quantitative diet information was collected. The results here are based on 1985–

1986, though the available 1983 data were similar. In combination, the above schedule permitted the study of finches at a variety of locations, while providing an estimate of annual and seasonal variability.

In all, 25 finch species from three families (Fringillidae, Ploceidae, and Estrildidae) were observed in Kenyan sites (Appendix B). All species are resident, though they may show local movements (e.g., Payne 1980), with the exception of *Quelea quelea* (Ploceidae), which is known to migrate large distances between breeding attempts (Ward 1971). This species was present in one Olorgesailie site in 1986, though it was absent there in 1985. All other species were present in both years. Details on censusing methods are given elsewhere (Schluter, in press).

Diets of continental finches were estimated by observing the fraction of time individuals spent feeding on different seed types, as described for Galápagos finches (Schluter 1982*a*,*b*). However, observations were more difficult to obtain than in the Galápagos, particularly in Kenya, because the birds were less easily approached. Thus, in Kenya I relied mainly on stomach contents from birds captured in mist nets, obtained by using an emetic, apomorphine (Schluter, in press). Finches were weighed before release. Regurgitated food items were identified with the aid of a microscope and a collection of seeds made from identified plants in sites. Roughly 500 of 700 treated finches responded, yielding an average of about 180 seeds each. At least five samples were obtained from most (20 of 25) species, and field observations were available to estimate the diets of most of the remainder; information on one species could not be obtained (*Serinus sulphuratus*). Sampling properties of diet measures (breadth and overlap) are analyzed elsewhere, and it is shown that sample sizes were sufficient to yield unbiased estimates; a fuller description of diets is also given (Schluter, in press).

Seed density was estimated in sites during visits in 1985 and 1986, using the same methods as in the Galápagos (Schluter 1982*b*). Using random numbers, 50 1-m^2 quadrats were located, and the number of seeds in the plants were counted in each. All surface seeds, litter, and soil (to 2 cm) from two 0.125-m^2 subquadrats were collected in bags. I later sifted through these samples on a broad tray, counting all seeds discovered.

Results from the above methods were supplemented with information from other field studies of continental finches (Newton 1967, 1973; Pulliam and Enders 1971; Skead 1975; Pulliam and Parker 1979; Capurro and Bucher 1982).

EVIDENCE FOR CHARACTER DISPLACEMENT

In this section, I examine patterns of divergence among finch species on islands and continents, and outline the evidence for character displacement. Alternative explanations for these patterns are discussed in the following section.

Four kinds of results suggest character displacement.

1. The amount of divergence in beak size between congeneric finches is clearly greater on islands than on continents. Variation in beak depth among congeners on continents increases with the number of species measured (fig. 2; $r = 0.68$, $N = 36$, $P < 0.0001$), but the island genera *Geospiza* and *Psittirostra* are more variable than any continental genus. *Telespiza*, the largest subgenus of *Psit-*
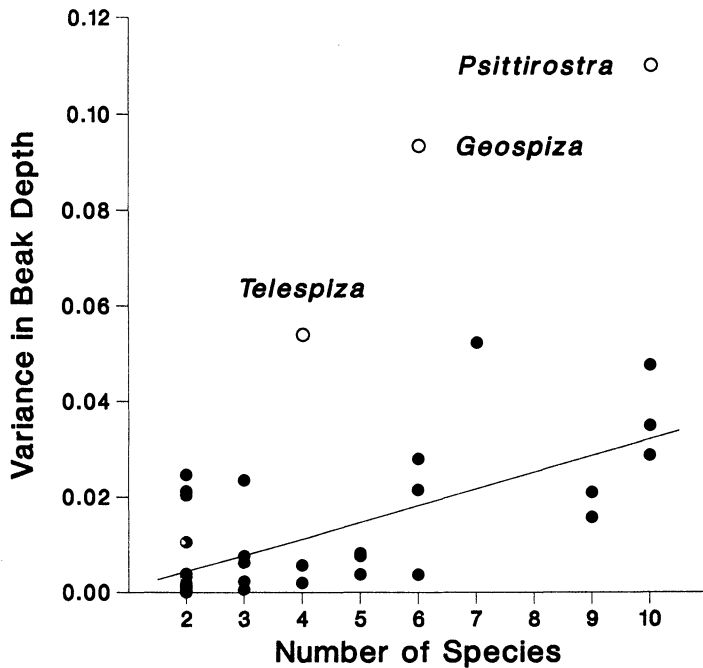
FIG. 2.—Variance in beak depth (ln-transformed) among congeneric species, as a function of the number of species measured within genera. *Dots and regression line* ($y = 0.0035x - 0.0026$), continental genera; *open circles*, island genera.

tirostra, is also more divergent in beak depth than are continental genera of similar species number. The same pattern is observed when range in beak size is used instead of variance. Beak depth and general size (PC1) are strongly correlated among species ($r = 0.95$), and PC1 gave the same result as beak depth.

Geospiza are also quite variable in shape (PC2) when compared with the continental genera measured (fig. 3). *Psittirostra* cannot be compared in full with the other genera in PC2, since we lack measurements from extinct species. However, variation in PC2 among the six extant *Psittirostra* is high relative to that of continental genera (fig. 3).

Many species of *Geospiza* and *Psittirostra* coexist on the same island, whereas continental congeners may not overlap in distribution. However, differences in degree of sympatry do not explain the different amounts of divergence on islands and continents. I examined beak-size divergence among continental congeners living in the same location and habitat, using species lists from other studies (Pulliam 1983; Schluter 1986*b*). Locations contained at most three congeneric species. Variation in beak depth among coexisting congeneric species (table 1) was not very different from that in the previous analysis (fig. 2) and remained lower on continents than on islands. Results were the same for general size, PC1, and shape, PC2 (*Psittirostra* excluded).

The greater divergence among island congeners is also not explained by the possibility that different morphological criteria were used to classify species into
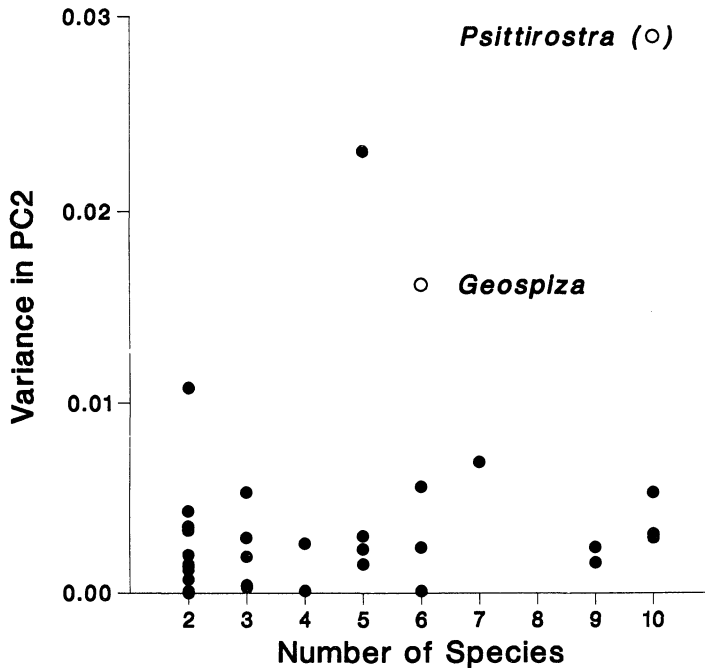
FIG. 3.—Variance in shape (PC2) among congeneric species, and the number of species measured. *Dots*, Continental genera; *open circles*, island genera. *Ammodramus* is the continental genus with unusually high variance in PC2. The *Psittirostra* value is based on an incomplete set of measurements.

genera. Indeed, biochemical data show that the average genetic distance between species of *Geospiza* is relatively low (table 2), indicating that they are more closely related to one another than are species in most continental finch genera. A close relationship among the *Geospiza* is further indicated by the youth of the Galápagos Islands (Grant 1986a) compared with the estimated age of many continental finch genera (e.g., Sibley and Ahlquist 1984). These results suggest that the greater amount of size divergence on islands relative to continents might be underestimated in figure 2; that is, the species in *Geospiza* and *Psittirostra* may have diverged morphologically to a greater extent than continental congeners, in a shorter period of time. Biochemical distances are unfortunately lacking for most finch genera, and some existing estimates are based on small numbers of loci (*Ammodramus* and *Spizella*; table 2); further comparisons of genetic distance would be useful.

In the classification used here (Morony et al. 1975), *Zonotrichia* is considered by recent authors to comprise several genera (e.g., Zink 1982). I repeated the biochemical comparison using two available genera from the latter classification (*Zonotrichia* and *Melospiza*), and the results were similar (table 2).

2. Divergence in diet is also substantially greater on islands than on continents. Variation in mean seed size among species was low in several continental genera in which data were available for three species (table 3). Variation among the three

TABLE 1

AVERAGE VARIANCE IN BEAK DEPTH (ln-TRANSFORMED) AMONG SYMPATRIC CONGENERIC SPECIES

CONTINENTAL GENERA				ISLAND GENERA	
No. of Species	No. of Genera	Average Variance	Range of Variances	Geospiza	Psittirostra
2	13	0.013	0.00–0.025	0.086	—
3	7	0.007	0.00–0.024	0.091	0.071

NOTE.—*Geospiza* values were obtained by averaging variance in beak size over pairs and triplets of species coexisting on Galápagos islands. The *Psittirostra* value is from the three-species "*Telespiza*" community on Molokai (Olson and James 1982).

TABLE 2

AVERAGE NEI'S GENETIC DISTANCE IN *GEOSPIZA* AND CONTINENTAL FINCH GENERA

Genus	No. of Species	Average Nei Distance ($\pm$ SE)	Source
Geospiza	6	0.02 (0.01)	Yang and Patton 1981
Zonotrichia	9	0.22 (0.05)	Zink 1982
(*Zonotrichia*)	5	0.12 (0.04)	Zink 1982
(*Melospiza*)	3	0.06 (0.04)	Zink 1982
Ammodramus	3	0.18 (0.09)	Avise et al. 1980
Spizella	2	0.02 (0.01)	Zink 1982
Carduelis	2	0.28	Christidis 1987
Lonchura	6	0.13	Christidis 1987
Pytilia	2	0.15	Christidis 1987
Passer	2	0.05	Christidis 1987

NOTE.—Bootstrap standard errors were computed using the original data in the source (unavailable for Christidis 1987). Genera in parentheses reflect an alternative classification of species in *Zonotrichia* (e.g., Zink 1982).

TABLE 3

DIVERGENCE IN SEED SIZE IN *GEOSPIZA* AND CONTINENTAL FINCH GENERA

Genus	No. of Species	Location	$\sigma^2 \times 100$ (beak size)	σ^2 (seed size)
Geospiza	3	Galápagos	13.0	2.92
Serinus	3	Kenya	1.5	0.23
Uraeginthus	3	Kenya	0.7	0.14
Lonchura	3	Kenya	0.5	0.73
Passer	3	Kenya	2.3	0.08
Zonotrichia	3	Arizona	0.5	0.05

NOTE.—*Geospiza* data are from the three-species granivore community on Pinta, Galápagos (Schluter 1982b). Data for Kenyan genera are based on regurgitated seeds obtained using an emetic. *Zonotrichia* data (including *Melospiza*) are from Pulliam (1983). Beak size is in ln mm. Seed size is in ln mg of the whole seed mass, except for *Zonotrichia*, where it is in ln mm^3, assumed to have the same variance as ln mg.
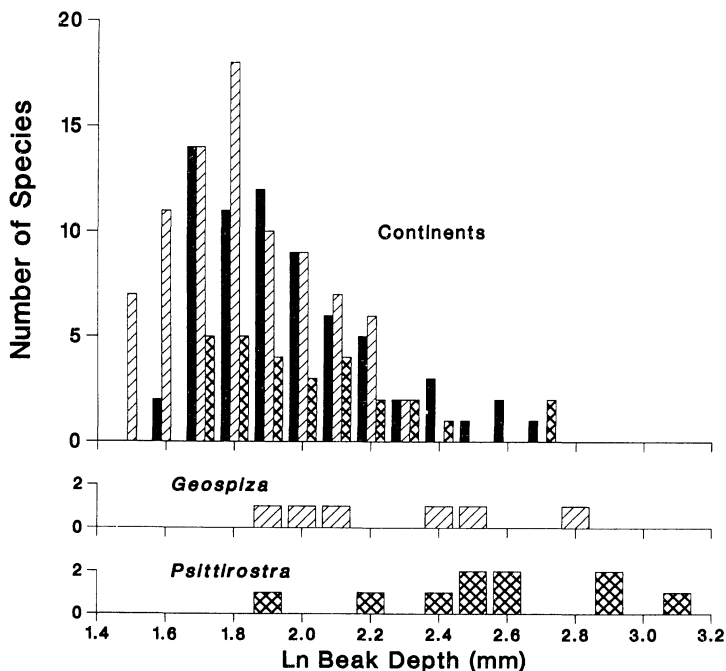
FIG. 4.—Beak-size distributions of finches on islands and continents. Continental species in subfamilies Emberizinae and Carduelinae (ancestral to *Geospiza* and *Psittirostra*, respectively) are indicated by the same shading as descendant forms. *Solid bars*, Continental species in other subfamilies.

mainly granivorous species of *Geospiza* on Isla Pinta is an order of magnitude greater. Pinta was arbitrarily chosen for this comparison; variation in mean seed size in three *Geospiza* species randomly chosen from the six (all islands combined) was similar to the Pinta value.

3. Beak-size divergence within each of the two island genera is not only greater than that within each of the continental genera, but also comparable to that in continental finches from the four families combined. The range of seed sizes consumed by finches in individual communities is often greater on islands than on continents, even though the communities on islands comprise only congeners.

Beak-size patterns in the two island genera are compared with the entire continental fauna in figure 4. The continental finches are divided into three groups, in order to compare beak sizes of the island genera with those of their ancestral subfamilies. The range of beak sizes in *Geospiza* is the same as in the Emberizinae, only slightly less than for all the continental finches, whereas range of beak sizes in *Psittirostra* matches that for the whole continental fauna. The frequency distributions of beak size are flatter for the island genera than for the continental finches, and many fewer species are present. The island faunas are also shifted to a larger mean beak size and have more large finches and fewer smaller finches than do the continental faunas.

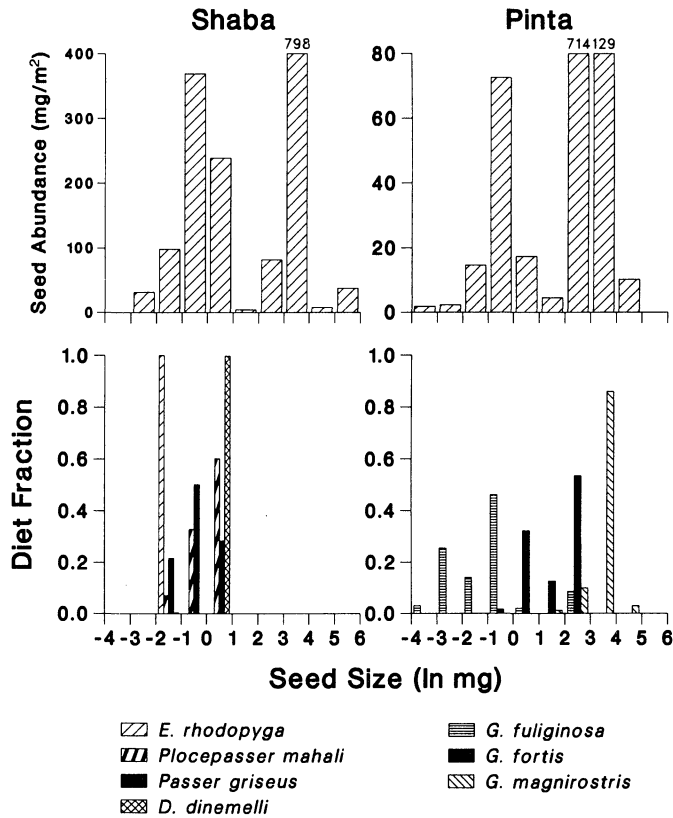The ecological significance of a high frequency of large-billed finches on islands

Fig. 5.—Availability and use of seeds by finches on Isla Pinta, Galápagos, and in Shaba National Reserve, Kenya. Pinta diets are unweighted averages of results from six sites surveyed in the nonbreeding season (Schluter 1982a). Patterns were similar within each site. Shaba results are from two sites (table 1), also in the nonbreeding season. Seed size refers to dry weight of the whole seed. Pinta species are the small-beaked ground finch (*Geospiza fuliginosa*), medium-beaked ground finch (*G. fortis*), and large-beaked ground finch (*G. magnirostris*). Shaba species are the crimson-rumped waxbill (*Estrilda rhodopyga*), grey-headed sparrow (*Passer griseus*), white-browed sparrow weaver (*Plocepasser mahali*), and white-headed buffalo weaver (*Dinemellia dinemelli*).

is revealed in comparisons of seed use between individual assemblages. In figure 5 I compare the availability and the use of seeds of different sizes in sites on Isla Pinta, Galápagos, and Shaba National Reserve, Kenya. The range of available seed sizes is similar in the two situations, but the range utilized by finches is narrower in Kenya. In particular, the largest seeds are not a component of the diet of any finch species at Shaba (fig. 5). Results are similar when other Galápagos islands or continental locations are compared (fig. 6A). On the Galápagos, the largest seed available in any site on any island was almost invariably consumed by at least one finch species, but this was rarely true in Kenya, particularly when the largest seed was over 5 mg (1–2 ln mg). Figure 6 includes results from only two of the five Olorgesailie sites (1985 data) because the data from 1986 and the other
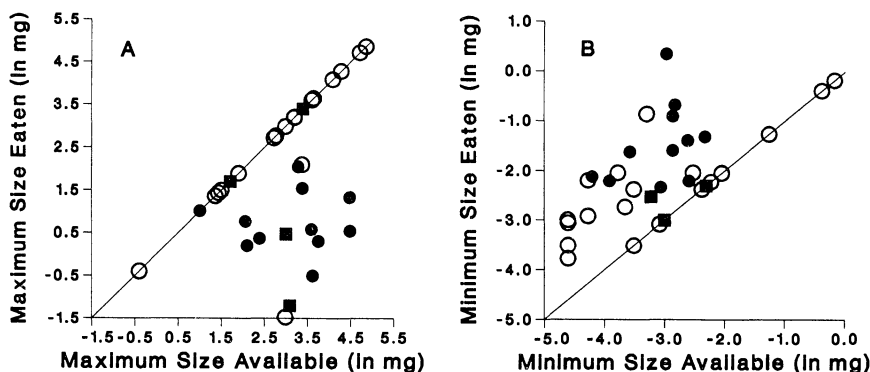
FIG. 6.—*A*, Size of the largest seed available and preferred by finches in sites in Kenya (*dots*), California (*solid squares*), and the Galápagos (*open circles*). Continental sites include only those seeds less than 4.9 ln mg, the largest seed consumed on the Galápagos. *B*, Size of smallest seed available and preferred in the same sites. Preferred seeds are those whose proportional representation in the diet is at least 1.5 times the available representation (Abbott et al. 1977; Schluter 1982*b*). Lines in each plot indicate the relation $y = x$. (The Galápagos data are from Schluter and Grant 1984*a*.)

three sites, both early and late in the dry season, are virtually identical. Fewer sites are available from California, but the results are similar to those from Kenya (fig. 6). However, one species in the chaparral site (*Pipilo fuscus*) consumes fairly large seeds (3.5 ln mg or higher; fig. 6; R. Repasky, unpubl. data).

Differences between island and continental sites in edibility of large seeds do not contribute to the differences in utilization. Comparisons in figures 5 and 6 exclude seeds in inedible families, such as ripe seeds of Labiatae, Convolvulaceae, Rubiaceae, Malvaceae, and Leguminosae (Schluter and Grant 1984*a*). Many of the large seeds available in continental sites are taxonomically similar to seeds consumed by Galápagos finches. For example, *Tribulus* (Zygophyllaceae) have large seeds, which are an important component of the diet in three *Geospiza* species (Grant 1981; B. Grant and Grant 1982; Price 1987). They are also eaten by *Psittirostra cantans* in the Hawaiian Islands (Amadon 1950). Seeds are produced in abundance throughout much of East Africa, including sites at Shaba and Olorgesailie, but they are not eaten by finches. Other abundant and widespread African seeds not eaten by finches are large seeds in the genus *Commiphora* (Burseraceae), present in sites at Bushwhackers, Shaba, and Olorgesailie; seeds in the related genus *Bursera* are eaten by Galápagos finches on all islands where they are present. *Opuntia* seeds are among the most important foods in the diet of all large finches in the Galápagos (e.g., B. Grant and Grant 1981). Seeds of *Opuntia* were also available in Sonoran Desert sites in California, but no finch consumed them.

Some other continental finch communities may possess forms consuming large seeds. For example, the hawfinch (*Coccothraustes coccothraustes*) of European temperate deciduous woodlands is able to crack large and hard seeds, such as those of wild cherry (*Prunus*; Newton 1973). However, such large species are exceptional in continental habitats, despite the ubiquity of large-seeded plants.

The ecological significance of the absence of very small billed finches from islands is unclear. The smallest Galápagos finches have a beak depth 2 mm greater than the smallest species in Kenya; yet small seeds were used by finches in both places (fig. 6B). Indeed, there is some evidence that the minimum seed size eaten is smaller in the Galápagos than in Kenya (fig. 6B; Schluter, in press). The smallest Kenyan finch species are quite specialized in their diet (Schluter, in press), and it is possible that larger minimum beak size on islands is an adaptation to a more generalized diet. This problem requires further study.

By itself, a low rate of divergence among congeneric species does not limit the range of morphologies and diets that may ultimately evolve. That continental finch communities, with a larger diversity of taxonomic groups available and a longer evolutionary history, should use a smaller range of seed sizes than many island communities supports a hypothesis that continental size-divergence patterns are constrained, possibly by competition from other taxa (i.e., character displacement).

4. Several assumptions of the hypothesis of character displacement have been tested in field studies. One assumption, that seeds limit finch numbers, is supported by comparisons of finch numbers and food supply on both islands (Smith et al. 1978; Grant and Grant 1980; Schluter 1982b; Schluter and Grant 1984a; Grant 1986b) and continents (Pulliam and Enders 1971; Newton 1973; Pulliam and Parker 1979; Capurro and Bucher 1982; Schluter, unpubl. data).

A second assumption is that competition between sympatric finch species promotes their divergence. This has been tested in Galápagos *Geospiza* by estimating carrying capacity as a function of beak size (e.g., fig. 1) and predicting beak sizes in actual populations using a model of interspecific competition for seeds (Schluter and Grant 1984a; Schluter et al. 1985). Data are not currently available to construct a similar model for continental communities. However, the presence of competition between continental finches is suggested by the fine partitioning of food and habitat (Newton 1967; Skead 1975; Pulliam and Mills 1977; Schluter, in press) and by a nonrandom ordering of species sizes within continental finch communities (Schluter 1986b).

A third assumption, that species from different taxa compete for seeds, is confirmed for ants, rodents, and possibly finches (J. Brown et al. 1986). Studies of seed removal in continental habitats show that ants and rodents are major seed consumers that may predominate over birds (Mares and Rosenzweig 1978; Gillon et al. 1983; Parmenter et al. 1984; Anderson and Ashton 1985). Rodents may be especially important to finches as competitors for large seeds. Rodents were observed to consume most species of large seeds available in the Kenya and California sites, including *Tribulus* and other seeds whose relatives are eaten by finches on the Galápagos. Other animals that consume large seeds in continental sites but are less prominent on the islands are parrots, galliform birds, and a great variety of insects.

ALTERNATIVE EXPLANATIONS

Results of the preceding section confirm that granivorous finch species on the Galápagos and Hawaii are highly divergent compared with finches on continents.

Indeed, the range of beak and seed sizes within a single island genus is comparable to or exceeds that of all continental finches combined. Similar morphological patterns in *Geospiza* and *Psittirostra*, despite different phylogenetic origins, indicate that the cause must lie in their common circumstance: remote oceanic archipelagoes. Although character displacement (fig. 1) is a reasonable explanation for these patterns, alternative hypotheses must be considered. Below, I discuss other factors that differ between islands and continents and that might explain a greater divergence on islands.

Resource Differences

By virtue of their isolation and limited size, we may expect remote islands to possess fewer plant species and habitats than continents. Study locations in Kenya possessed roughly twice the diversity of seed (and plant) species found in sites on the Galápagos Islands (Schluter, in press). A possible effect of lower resource diversity on islands is a lower diversity of niche axes along which finch species may diverge. Exaggerated divergence in beak and seed size on islands might result from a scarcity of alternative avenues (e.g., Abrams 1986a).

Though the hypothesis is plausible, little evidence indicates that resource differences can fully explain the different amounts of divergence on islands and continents. First, although the diversity of habitats is undoubtedly greater on continents than on islands (e.g., hot deserts and cold forests), low amounts of divergence on continents is evident within habitats, not just between them (table 1). Moreover, we might expect a high diversity of habitats on continents to contribute to morphological diversity in finches rather than hamper it; yet divergence is greater on islands (fig. 2).

Second, the niche axes partitioned by finches within habitats on continents do not appear to be absent from islands. Continental finches of similar size coexisting in the same habitat differ in foraging position (e.g., seeds are taken from ground or vegetation), in microhabitat (e.g., under shrubs or in open patches), or in seed type (Newton 1967; Skead 1975; Pulliam and Mills 1977; Schluter, in press). All these resources are available and exploited in the Galápagos (e.g., Schluter 1982b; Schluter and Grant 1982, 1984b). For example, estrildid finches concentrate on grains (Gramineae), whereas seeds of the Compositae are consumed mainly by fringillids (Newton 1967; Skead 1975; Schluter, unpubl. data). Both seed types are available on the Galápagos, where they are eaten by *Geospiza* (Schluter 1982a,b).

Third, microhabitat separation is not absent from islands. *Geospiza scandens* and *G. difficilis* differ from other sympatric congeneric species in both food type and foraging position (B. Grant and Grant 1981; Schluter and Grant 1982, 1984b). In this case, microhabitat differences are associated more with differences in body shape than in size (Lack 1947; Schluter and Grant 1984b). The island faunas are quite differentiated in shape compared with continental finches (fig. 3), implying that they are also relatively divergent in resources other than seed size. This argues against the hypothesis of resource differences.

Finally, the hypothesis of greater resource diversity on continents than on islands does not easily account for the smaller total range of seed sizes consumed in many continental finch assemblages (figs. 5, 6).

Predation on Continents

The Galápagos finches are not subject to a great deal of predation (Grant 1986a), and the same may have been true on Hawaii (although Olson and James [1982] reported the discovery of bones from an extinct Hawaiian bird-hawk, *Accipiter*). Potentially, predation on continents can reduce population sizes below the point at which food is limiting. However, several finch studies provide evidence that population size may be limited by food supply (see above). A more likely result of predation is competition between finch species for food in areas relatively free of predators, such as under cover (Pulliam and Mills 1977; Schluter, in press), an effect not obviously leading to a lower amount of divergence.

An alternative role for predation might be to influence the distribution of beak and body sizes on continents relative to islands. For example, predators might explain why large-beaked finches are rarer on continents, if large beak and body size make a finch particularly susceptible to predation. Few data exist to support or refute this conjecture, and study of the relation between predation and morphology is needed. Lima (1986) modeled body mass of a small bird, assuming that predation risk increased with increasing mass, but he was referring to fat stores for a bird of given size and not to the evolution of size (stature).

Though data are scarce, some arguments suggest that predation can be influential. Predation is not, however, a sufficient explanation for different amounts of divergence in beak size on islands and continents. First, many avian consumers of large seeds on continents are comparable in size to, or are larger than, a large finch (e.g., quails, small parrots, and doves). Predation has thus not constrained the evolution of bird size or avian diets in general. Second, many of the continental habitats possessing large seeds but lacking large-beaked finches are woodlands and shrublands (Schluter 1986b, in press), which provide ample cover and presumably safety from many predators.

Third, a large beak like that of *Geospiza magnirostris* (16–19-mm depth), used to crack seeds requiring up to 55-kg force (Schluter and Grant 1984a), might be a handicap when escaping predators, but only if the body is not large or powerful enough to carry it. I therefore suggest that predation is more likely to influence the ratio of beak to body size in finches than the absolute size of either trait. For example, beak depth increases with the cube root of body mass (ln-transformed) more steeply among the finch species of the Galápagos ($b = 2.11$, $N = 6$) than those of Kenya ($b = 0.89$, $N = 24$, $P = 0.025$), contributing in the former group to an ungainly appearance in some species, particularly large ones. Another possible consequence of an absence of predators on the Galápagos is greater wing loading, suggested by regressions of wing length against body mass: slope is lower in *Geospiza* ($b = 0.70$) than in Kenyan species ($b = 1.27$, $P = 0.036$), and the large *Geospiza* have relatively short wings and slow flight. Effects of predation on relative body dimensions may be common, but they have not yet been well described.

Finally, even if predation were responsible for the scarcity of large-beaked finches on continents, it would not fully explain the greater amount of divergence in island genera. If we ignore island species having a beak depth greater than 2.6 ln

mm (13.5 mm; i.e., those above the upper limit of most continental finch beaks), then variance is 0.046 among the five remaining *Geospiza* and 0.054 among the six remaining *Psittirostra* (*Telespiza* is unchanged). These values are still excessive when compared with those of continental genera of similar species number (fig. 2).

Gene Flow

Mayr (1963) and Stanley (1981) suggested that gene flow between populations could prevent substantial change by natural selection. They argued that with gene flow, selection must act in a consistent direction in order to produce change, but this is unlikely in a widespread species. The result is stasis within widespread species, and a slow rate of divergence between closely related species when both are widespread (e.g., many continental finches). This argument was not proposed as an alternative to character displacement, but it is worth considering in this context.

Evidence suggests that reduced gene flow alone does not explain the greater divergence of Galápagos and Hawaiian finches. First, it is unlikely that continental populations are subject to inordinate amounts of gene flow. Comparison of the among-population component of variance based on protein polymorphisms suggests that gene flow among populations on different Galápagos islands may be only slightly lower than in continental finch species (Barrowclough 1983). Birds in general have been estimated to have long-term effective population sizes that are quite small, on the order of 100 (Barrowclough and Shields 1984).

Second, theoretical arguments and lab experiments suggest that selection will overcome typical amounts of gene flow (Ehrlich and Raven 1969; Endler 1977; Slatkin 1978). Even where significant gene flow has been observed between certain populations and species of Galápagos finches, it did not substantially affect the outcome of selection (Grant and Price 1981; Boag and Grant 1984). Third, the argument for within-species stasis assumes that populations are subject to directional selection, whose effects are counteracted by gene flow. The only detailed study of selection patterns in a continental finch population showed that selection was either stabilizing or balanced directional (Schluter and Smith 1986*a*). Further measurements of this kind are needed, in addition to estimates of gene flow.

Finally, were gene flow between populations responsible for low divergence between species, many traits should be affected. But while continental congeners are not often greatly divergent in morphology, they may show extraordinary differences in other traits such as plumage (e.g., Lack 1947; Newton 1973).

Genetic Change and Founder Events

Divergence is one of the two main components of adaptive radiation; the other is speciation. The two components are linked in some genetic models of speciation (Mayr 1963, 1982; Carson and Templeton 1984). In these models, the genetic environment is thought to constrain evolutionary change in typical, mature populations. Founding of new populations by a small number of individuals (e.g., as on isolated islands) occasionally precipitates genetic disruption and reorganization ("revolution"), permitting rapid adaptive morphological change (divergence) and speciation. These models might explain contrasting rates of finch divergence on

islands and continents, if we hypothesize in addition that species on islands are more likely than those on continents to be formed from radical genetic events than from more-classical mechanisms.

Carson and Templeton (1984) reviewed their hypothesis that genetic changes, induced by the repeated founding of new populations by small numbers of individuals, have brought about the adaptive radiation of the Hawaiian Drosophilidae (but see Barton and Charlesworth 1984). Barrowclough (1983) suggested that the biochemical data of the Galápagos finches were consistent with a similar mechanism in that group. None of the authors has proposed that the mechanism completely explains a greater amount of divergence on the Galápagos and Hawaii, but in testing the role of competition we should evaluate such a proposal.

Evidence suggests that genetic revolutions caused by founder events are unlikely to have greatly influenced the adaptive divergence of island finches. The genetic structure demanded by models of this form of speciation seem to be lacking in finches (Price et al. 1984b). Genetic studies of *Geospiza* and *Zonotrichia* (= *Melospiza*) suggest that beak and body size are quantitative traits, influenced by many genes with small, largely additive effects, and not strongly epistatic systems involving few major genes (Boag 1983; Grant 1983; Price et al. 1984b; Schluter and Smith 1986b).

Genetic correlations between traits can constrain morphological change along certain dimensions (Lande 1979; Cheverud 1984), but these correlations are higher in *Geospiza* than in *Zonotrichia* (Schluter and Smith 1986b). Genetic variance is also higher in *Geospiza* than *Zonotrichia* (and probably other continental finches), particularly in size, a result not of genetic "instability" but of two more basic processes: relaxed stabilizing selection in *Geospiza*, and hybridization between already differentiated forms (Grant and Price 1981). Indeed, the success of occasional interspecific hybrids in *Geospiza* (Boag and Grant 1984; Grant 1986a) contradicts the hypothesis that species are separated by genetic revolutions.

Finally, a change in the seed environment in one year of the Galápagos study resulted in strong selection and a substantial evolutionary response in beak and body size in *G. fortis* (Boag and Grant 1981, 1984; Boag 1983). This result also suggests few genetic constraints on the evolution of beak size in that population.

DISCUSSION

Divergence in beak size among congeneric granivorous finches has clearly been greater on the islands of Galápagos and Hawaii than on continents. Possible causes of this pattern include character displacement: divergence on islands is facilitated by the absence of competition from unrelated species. Analysis of seed-use patterns within finch assemblages on islands and continents, as well as data on biochemical differences between species and on natural selection and the quantitative genetics of size, supports this hypothesis. Several alternative explanations were considered (resource diversity, predation, gene flow, and founder events); although each of these processes may play a role on islands and continents, little evidence indicates that they are sufficient to account for the different levels of

divergence in beak size. The available data thus suggest that character displacement is the best explanation for the pattern.

Recall that my analysis was based entirely on divergence in the granivorous component of finch communities. The study has thus not addressed the additional divergence of Galápagos and Hawaiian finches into morphological and ecological realms quite unlike any continental finch (Lack 1947; Amadon 1950; Raikow 1977; Grant 1986a). Maximum estimated genetic (Nei) distance between any two of the Galápagos Geospizinae is only 0.14, indicating that overall phenotypic divergence in the group has been unusually rapid (Yang and Patton 1981). This value compares with similar or larger genetic distances between morphologically and ecologically more similar continental emberizine finches: 0.21 between *Zonotrichia capensis* and *Z. atricapilla*; 0.31 between *Z. atricapilla* and *Z.* (= *Melospiza*) *melodia* (Zink 1982). Inclusion of the non-granivorous Galápagos and Hawaiian species would thus, I believe, strengthen the present conclusion of character displacement.

As in all previously documented cases of character displacement, these conclusions are not absolute, and further work would be very useful. I have pointed out where additional data would help clear up uncertainties, improve on estimates, and provide a fuller understanding of processes involved in the divergence of different finch groups. Valuable additional information would include better estimates of the age of taxa, measures of natural selection and the opposing rates of gene flow, theory and data on the effects of predation on body form, and levels of current competition between finches and other taxa.

That character displacement appears to be responsible for the different amounts of morphological divergence in finches on islands and continents has interesting implications for the study of community evolution. The first is that character displacement might be common. For example, numerous taxa on the Hawaiian islands consist of related species with dramatically different adaptations to alternative ecological niches, in contrast to the subdued trends within analogous taxa on continents (Carlquist 1980). Alternative explanations to character displacement would need to be investigated in all these cases, but the patterns are suggestive.

A second implication is that character displacement is often (and perhaps usually) "community-wide," occurring between species in different taxa. Ecologists are now certain that unrelated species vie for the same resources, thereby affecting each other's population dynamics (e.g., J. Brown et al. 1986). The current study indicates that such competition can, in addition, impose strong constraints on adaptation and diversification within each taxon.

Third, the realization that competition may occur between many species, possibly of diverse taxa, has implications for the detection of character displacement on continents by conventional means. If each of two species in a typical pairwise test for character displacement is actually embedded in a larger set of interacting species, then the amount of displacement between them may be small. Connell (1980) argued that a high species diversity would lower the probability of character displacement between any two species, owing to a reduction in the number of interactions. However, a high diversity of competitors does not reduce the proba-

bility of displacement between two species as much as it reduces the probability of detecting displacement, especially when locations differ in the members of the larger set of interacting species or in food supply. This problem suggests that the most sensitive test for character displacement when diversity is high is to study morphology in species isolated completely from the rest of the interacting set, as happens in the colonization of remote archipelagoes. Some of the strongest evidence for character displacement may thus ultimately be gained through comparing morphological patterns on islands and continents, as in the present study.

A fourth implication concerns the time course of community evolution. The hypothesis that divergence is facilitated by an absence of other competitors implies that the pattern of divergence between new congeners may change with time, if species accumulate through time and niches become filled. This does not mean that differences in community age provide a sufficient explanation for island-continent differences in divergence patterns; however, the diversity of competitor species, and hence the outcome of character displacement, may depend on the passage of time. A more detailed comparison between the Galápagos and Hawaii would be particularly interesting in this regard, since the Hawaiian finch group is older and more diverse overall (Sibley and Ahlquist 1982; Grant 1986a). Better estimates of the times of speciation and divergence in these two groups might allow us to study the relationship between divergence and the loss of niche opportunities.

Given the number of taxa that appear to show inordinately large amounts of adaptive divergence on isolated archipelagoes, it is curious that they have not been discussed in earlier reviews of evidence for character displacement (Grant 1972; Arthur 1982). This reflects a tendency among ecologists to define character displacement solely in terms of one pattern, a greater morphological difference between populations of two species in sympatry than between two populations in allopatry, rather than more generally as an effect of interspecific competition on the evolution of morphology and behavior. Note that the comparison of divergence patterns on islands and continents is nonetheless a "sympatry-allopatry" comparison. But instead of comparing morphology of a species in the presence and absence of a second, competitor species, we are comparing the morphologies of analogous species in the presence (continents) and absence (islands) of an entire suite of potential competitors.

Indeed, greater divergence in isolation is but one of many possible forms of character displacement. Alternative morphological trends in the presence and absence of competitors may be another. For example, several taxa of primarily herbaceous plants include species of shrubs and trees found only on isolated islands (Carlquist 1980). Conceivably, the scarcity of other shrubs and trees on those islands is partly responsible for the rapid evolution of such forms from herbs. Also, interspecific competition, by influencing the success of new populations, might influence the rate at which species themselves are formed (e.g., Sepkoski et al. 1981; Knoll 1986), though this is stretching the definition of character displacement. Evolutionary consequences of interspecific competition appear to be diverse, and to understand the importance of the process, ecologists need to investigate a greater diversity of patterns.

SUMMARY

I consider the differing amounts of adaptive divergence on continents and remote archipelagoes as a source of evidence for ecological character displacement. A classical example is the accelerated evolution of morphological differences between finch species on the Galápagos and Hawaii, thought to result from an absence of competitor taxa on the islands. I show that the amount of divergence is greater in the Galápagos and Hawaiian finches, even when only beak-size divergence in the granivorous component is considered. Studies of seed availability and use, of biochemical differences between species, and of natural selection and the quantitative genetics of size on islands and continents support the hypothesis of character displacement. Several alternative explanations are considered (greater resource diversity on continents, predation on continents, reduced gene flow, and founder events on islands), but although each may play a role, little available evidence suggests that they are sufficient to account fully for the pattern. Implications of this result are discussed, including the possibility that community-wide character displacement involving many taxa is common.

APPENDIX A

Finch genera measured from museum specimens (the number of species measured is given in parentheses).

EMBERIZIDAE
Emberiza (3), Calcarius (2), Zonotrichia (9), Ammodramus (5), Spizella (3), Amphispiza (2), Aimophila (7), Melanodera (2), Poospiza (5), Sicalis (3), Sporophila (10), Pipilo (3), Arremon (3), Coryphospingus (2), Pheucticus (2), Cardinalis (2), Saltator (2), Passerina (2)

FRINGILLIDAE
Fringilla (2), Serinus (10), Carduelis (9), Loxia (2), Coccothraustes (2)

ESTRILDIDAE
Pytilia (2), Lagonosticta (6), Uraeginthus (4), Estrilda (4), Lonchura (5)

PLOCEIDAE
Plocepasser (2), Pseudonigrita (2), Passer (3), Petronia (2), Sporopipes (2), Ploceus (6), Euplectes (6), Vidua (5)

APPENDIX B

FINCH SPECIES CENSUSED IN SITES AT THE SIX KENYA LOCATIONS:
(1) BUSHWHACKERS, (2) SHABA RESERVE, (3) ATHI PLAINS,
(4) HELL'S GATE PARK, (5) SOKOKE FOREST, AND (6) OLORGESAILIE

Common Name	Scientific Name	Locations
White-bellied canary	*Serinus flaviventrus*	6
Grosbeak canary	*S. donaldsoni*	6
Yellow-rumped seedeater	*S. atrogularis*	3
Brimstone canary	*S. sulphuratus*	4
Green-winged pytilia	*Pytilia melba*	1
Crimson-rumped waxbill	*Estrilda rhodopyga*	2,3
Common waxbill	*E. astrild*	4
Black-faced waxbill	*E. erythronotos*	6
African firefinch	*Lagonosticta rubricata*	1
Red-cheeked cordon-bleu	*Uraeginthus bengalus*	1,3
Blue-capped cordon-bleu	*U. cyanocephala*	6
Purple grenadier	*U. ianthinogaster*	4
Silverbill	*Lonchura malabarica*	6
Grey-headed silverbill	*L. griseicapilla*	6
Rufous-backed mannikin	*L. bicolor*	5
Cut-throat	*Amadina fasciata*	6
White-headed buffalo weaver	*Dinemellia dinemelli*	2
White-browed sparrow weaver	*Plocepasser mahali*	2
Grey-capped social weaver	*Pseudonigrita arnaudi*	3,6
Rufous sparrow	*Passer iagoensis*	3,4
Grey-headed sparrow	*Passer griseus*	2
Chestnut sparrow	*Passer eminibey*	6
Yellow-spotted petronia	*Petronia xanthocollis*	2,6
Vitelline masked weaver	*Ploceus velatus*	1,3,6
Red-billed quelea	*Quelea quelea*	6

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