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### The Taxonomic Status of the Small Ground-Finch, *Geospiza* (Aves: Emberizidae) of Genovesa Island, Galápagos, and Its Relevance to Interspecific Competition

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From their study of the feeding habits of *Geospiza difficilis* and *G. fuliginosa* on Genovesa, Pinta, and Marchena islands, Galápagos Archipelago, Schluter and Grant (1982, 1984) concluded that these species probably competed in the past. Crucial to this conclusion is the taxonomic identification of the Genovesa population, classified as *G. acutirostris*, *G. fuliginosa*, or *G. difficilis* by various authors (see below). We present morphological evidence to indicate that, contrary to its current classification as *G. difficilis*, the Genovesa population may more justifiably be placed in *G. fuliginosa*, as done by Snodgrass and Heller (1904). We also discuss the evolutionary and ecological consequences of this suggested taxonomic rearrangement.

The small ground-finch of the genus *Geospiza* living on Genovesa Island was first described by Ridgway (1894: 363; see also Ridgway 1897) as *Geospiza acutirostris*, a form "Similar to *G. parvula* (Gould) [synonymized since with *G. fuliginosa*], but bill longer, with straighter outlines, and extremely acute at tip." Rothschild and Hartert (1899) concurred with Ridgway's view. Snodgrass and Heller (1904: 316) characterized the taxon *acutirostris* as "Very similar to *G. f. fuliginosa*, but bill more acute, with straighter outlines" and ranked it as a subspecies of *G. fuliginosa* Gould, 1837. Swarth (1931: 178) felt that "The Tower [Genovesa] Island *acutirostris* is, to my notion, of the *Geospiza debilirostris* [currently considered a subspecies of *G. dif-*

*ficilis*] aggregation, but the differentiating characters are such as to make it seem desirable to treat the form as specifically distinct." Lack (1945, 1947, 1969) recognized the transfer of *G. acutirostris* to the *G. difficilis* group, but argued that its measurements overlapped widely those of *G. d. difficilis* of Pinta Island (Sharpe 1888), and combined *G. acutirostris* with the latter. Paynter and Storer (1970) followed Lack's arrangement. Harris (1973: 265) made "... no attempt ... to discuss the taxonomic status of species." Schluter (1984), Grant et al. (1985) and Grant (1987) studied the classification of Darwin's finches, found it solid, and suggested no modifications. Neither of these authors examined specifically the status of the Genovesa population. Bowman (1961, 1983) adopted Lack's classification, but noted (pers. comm.) that the "Genovesa *Geospiza* song is quite different from other *difficilis* songs as well as *fuliginosa* songs. Like *fuliginosa* it lacks the 'special basic' song of other *difficilis* populations, and this I think is very significant, indicating allegiance to *fuliginosa*. (See Bowman 1983, p. 437, fig. 62 and p. 423, fig. 48.)" It thus appears that the early authors assigned the Genovesa form to the *G. fuliginosa* group, on the basis of overall similarities, primarily in beak morphology. Swarth and Lack broke with these views when they assigned the Genovesa form to the *G. difficilis* group. We believe that they focused on a single feature, bill length, giving little

weight to other features. Modern authors adopted Lack's taxonomy, some perhaps with reservations, without reanalyzing the Genovesa issue or any of the difficult cases mentioned by Lack (1947: 18).

We studied 762 specimens, identified by museum labels as either *G. fuliginosa* or *G. difficilis*, in the Academy of Natural Sciences, Philadelphia, Pennsylvania, the American Museum of Natural History, New York, New York, the California Academy of Sciences, San Francisco, California, the Museum of Comparative Zoology, Cambridge, Massachusetts, San Francisco State University, San Francisco, California, and the U.S. National Museum of Natural History, Washington, D.C. Only adult males were considered, in order to obtain more homogeneous samples. The specimens represented 31 populations from 27 islands. Most islands had either *G. fuliginosa* or *G. difficilis*, but Pinta, Santiago, southern Isabela, and Santa Cruz islands supported both. We included 20 populations (with  $n \geq 10$ ) in the analysis. Following standard procedures (Baldwin et al. 1931), we measured bill depth, bill or culmen length, bill width, wing length, and tarsus length. We also utilized data from the literature (Lack 1945; Schluter and Grant 1982, 1984; Grant et al. 1985), and Bowman (pers. comm.). We compared the measurements of the disputed Genovesa population to those of *G. fuliginosa* and *G. difficilis* (Fig. 1A to 1F).

In five of six characters (namely bill depth, bill width, wing length, tarsus length and body mass), the Genovesa population fell within the range of variation of *G. fuliginosa*. Its affiliation was clearest in tarsus length and body mass, because it is in these features that *G. fuliginosa* differed most decisively from *G. difficilis*. The Genovesa population has an unusually long bill, which surpassed all other populations of *G. fuliginosa*. On these grounds, the Genovesa population may best be described as one of *G. fuliginosa*, of smallish dimensions, that resembles *G. difficilis* in bill length. Therefore, we suggest that the Genovesa population be transferred from *G. difficilis*, to which it is currently assigned, to *G. fuliginosa*, as first proposed by Snodgrass and Heller (1904).

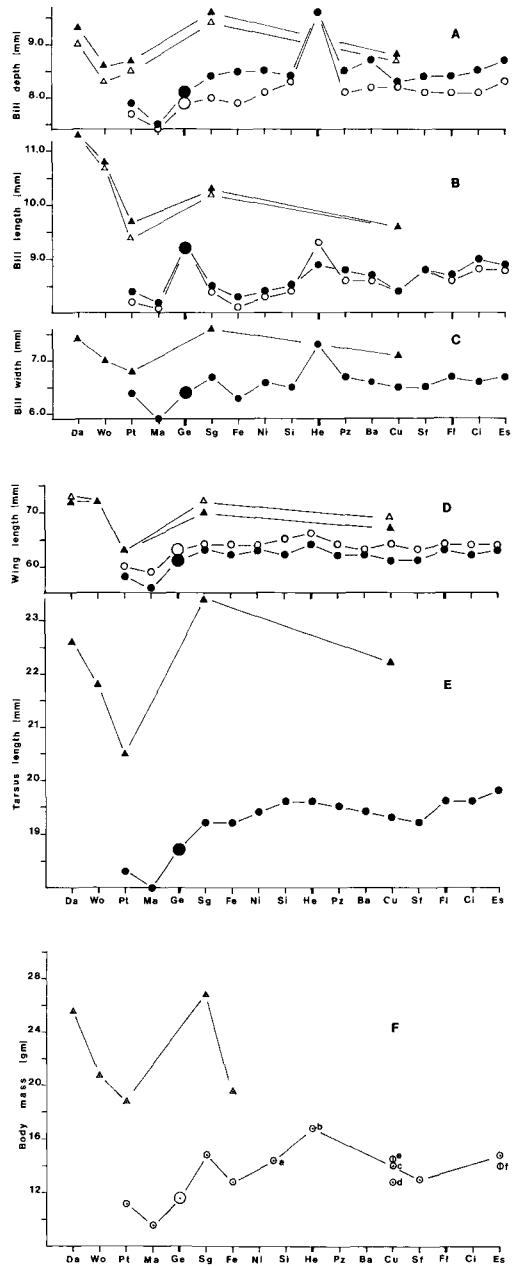


Fig. 1. Geographic variation in *Geospiza difficilis* and *G. fuliginosa*. The means of 20 populations are shown in: A, bill depth; B, bill length; C, bill width; D, wing length; E, tarsus length; F, body mass. Symbols: triangles, *G. difficilis*; ▲ our own measurements; △ from Lack (1945); △ from Grant et al. (1985); circles, *G. fuliginosa*; ● our own measurements; ○ from Lack (1945); ○ from Grant et al. (1985); note that both Lack and Grant et al. placed the Genovesa population in *G. difficilis*; ⊙ data supplied by Bowman (pers. comm.). Oversized symbols ● ○ ⊙ indicate the Genovesa population; and  $n = 11-80$  per population, except as noted below. Islands are arranged from northwest to southeast. Island names are as follows: Ba = Baltra;

Ci = San Cristóbal; Cu = Santa Cruz; Da = Darwin; Es = Espanola; Fe = Fernandina; Fl = Floreana (Santa Maria); Ge = Genovesa; He = Los Hermanos; Ma = Marchena; Ni = northern part of Isabela; Pt = Pinta; Pz = Pinzón; Sf = Santa Fé; Sg = Santiago (San Salvador); Si = southern part of Isabela; Wo = Wolf. Other abbreviations (See 1F): "a" means data refer to the whole of Isabela Island; "b,"  $n = 2$ ; "c," locality of Bahia Academia, south shore of Santa Cruz Island; "d," locality at Bahia Borrero, north shore of Santa Cruz Island "e,"  $n = 4$ ; "f,"  $n = 2$ .

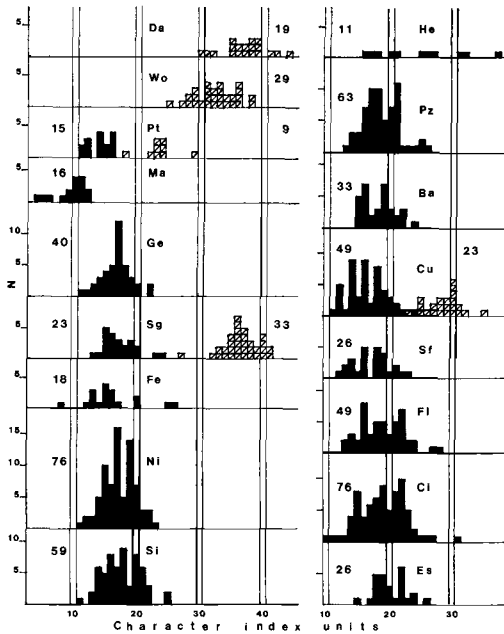


Fig. 2. Geographic variation in character index in *Geospiza fuliginosa* and *G. difficilis*. Symbols: ■ *G. fuliginosa*; ▨ *G. difficilis*. Character indices computed as explained in text;  $n$  = number of specimens; numbers next to histograms indicate sample size. The Santa Cruz population of *G. difficilis* is "no doubt" extinct (Bowman pers. comm.). Abbreviations as in Fig. 1.

The Los Hermanos population, currently assigned to *G. fuliginosa*, has large beak dimensions, body mass (Fig. 1A, 1B, 1C, 1F), and character index values (Fig. 2), as well as great variability. In our opinion, this population is a hybrid between *G. fuliginosa* and *G. fortis* (Vagvolgyi and Vagvolgyi in press).

We compared the Genovesa finches to *G. fuliginosa* and *G. difficilis* in character index (Fig. 2), computed from five characters; body mass was omitted for lack of sufficient details. The following formula was used:

$$\text{Character Index} = \frac{\text{sum of scores in 5 characters}}{2}$$

Each character was scored on a scale from 0 to 20. The *fuliginosa* character states (the small dimensions) received low scores and the *difficilis* character states (the large dimensions) received high scores. Character index values for specimens of *G. fuliginosa* ranged from 4 to 31 (not counting the values of Los Hermanos specimens); for those of *G. difficilis*, 18–44. The character indices of the disputed Genovesa specimens varied from 11 to 22 and fell in the range of *G. fuliginosa*.

Lack (1947) believed that *G. fuliginosa* and *G. difficilis* always occurred on separate islands, or in separate altitudinal zones on islands where they coexisted. He inferred from this pattern that *G. difficilis* "... has been eliminated by *G. fuliginosa* wherever the two species

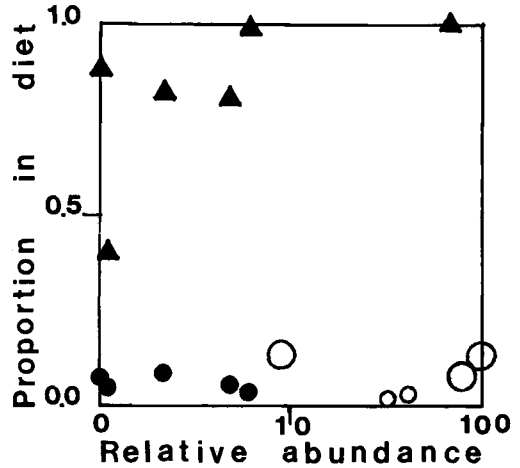


Fig. 3. The proportion in the diet of *Geospiza difficilis* and *G. fuliginosa* of invertebrates (arthropods and gastropods), plotted against their relative abundance, on Pinta, Marchena, and Genovesa islands. Redrawn from Schluter and Grant (1982: fig. 5), except that the Genovesa symbols have been changed. Schluter and Grant placed the Genovesa specimens in *G. difficilis*, and marked them with empty triangles. Symbols: ▲ *G. difficilis*, Pinta; ● *G. fuliginosa*, Pinta; ○ *G. fuliginosa*, Marchena; ○ *Geospiza* of Genovesa. Points in the diagram represent study sites; the number of specimens involved was not clearly stated.

have come in contact" (1947: 26). Abbott et al. (1977) also considered this distributional pattern as evidence for interspecific competition. However, Schluter and Grant (1982, 1984) reported that the two species overlapped altitudinally on Pinta, Santiago, and Fernandina islands without showing interspecific aggression. They ruled out present competition between them. They observed that, when sympatric, the diet of *G. fuliginosa* and *G. difficilis* was dissimilar, e.g. on Pinta. When allopatric, however, the diet of the two species was quite similar, e.g. the diet of the alleged *G. difficilis* of Genovesa resembled that of *G. fuliginosa* of Marchena (Fig. 3). Schluter and Grant concluded that in the absence of competition the Genovesa birds shifted toward the diet of the absent competitor *G. fuliginosa*, and they inferred from this pattern that the two species had competed in the past. Reviewing the case, Grant (1987: 307) asserted that the *fuliginosa*-like diet of the Genovesa finches was attributable to the "... greater profit obtained from the *fuliginosa* foods, and the absence of a population of *G. fuliginosa*" there. He also suggested (1987: 307) that "... metabolic efficiency as well as perching ability were probably major selecting factors in the evolution of small size" in the Genovesa population. He did not elaborate on these points.

Central to the competition hypothesis is the pattern of similarities and dissimilarities in the diet of the

four populations. This in turn rests upon their correct identification. There has been general agreement on the identification of the Pinta and Marchena populations of *G. fuliginosa*, and the Pinta population of *G. difficilis*; the identity of the Genovesa population, on the other hand, is contested. The competition hypothesis assumed that the Genovesa finches belonged to *G. difficilis*. However, as we have attempted to show, these finches are morphologically so similar to *G. fuliginosa* that we feel they should be assigned to that species instead. Such rearrangement would fundamentally change the dietary pattern, because the similarity in diet of the allopatric Marchena and Genovesa populations, if both belonged to *G. fuliginosa*, would clearly be attributable to their conspecificity.

Our conclusion is consistent with the results provided by the comparison of the population of Genovesa Island with those of Darwin and Wolf islands. According to the competition hypothesis, Genovesa supports *G. difficilis* which, in the absence of the competing species *G. fuliginosa*, underwent profound changes in its diet and morphology to become deceptively similar to the absent competitor. If so, comparable evolutionary events should occur on comparable islands. This was not the case, however. Although *G. difficilis* is present on Darwin and Wolf islands, and *G. fuliginosa* is absent, *G. difficilis* has not assumed any of the morphological attributes of *G. fuliginosa* on these islands. In fact, these populations are clearly dissimilar in morphology from *G. fuliginosa* (Figs. 1, 2). Unfortunately, the diet of the Darwin and Wolf populations is insufficiently known for detailed comparisons.

In essence, our hypothesis holds that the *fuliginosa*-like diet and morphology of the Genovesa population are not attributable to dietary advantages and absence of competition, rather to the ancestry of this population from *G. fuliginosa* stock. The competition hypothesis, on the other hand, holds that the *fuliginosa*-like diet and morphology of the Genovesa population are attributable to dietary advantages and release from competition; the Genovesa birds appear like *G. fuliginosa*, but evolved from *G. difficilis*. The first hypothesis is supported by two independent data sets: (1) morphological shifts did not occur in *G. difficilis* of Darwin and Wolf islands, as expected from the competition hypothesis, and (2) the song of Genovesa birds resembles *G. fuliginosa* more than it does *G. difficilis*. As far as we know, the competition hypothesis has no independent data supporting it. Studies on mate preference (Ratcliffe and Grant 1983) were inconclusive. Cytogenetic (Jo 1983) and biochemical studies (Ford et al. 1974, Yang and Patton 1981, Polans 1983, Patton 1984) yielded no information that could be used for or against either of the alternative hypotheses.

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### Homing Experiment with Leach's Storm-Petrels

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Leach's Storm-Petrels (*Oceanodroma leucorhoa*) show high rates of return to their nest sites after being experimentally released at various distances from the breeding colony (Griffin 1940, Billings 1968). Homing at speeds of up to 350 km/day and navigating distances of up to 4,800 km across unfamiliar territory, many birds actually gain mass along the way (Billings 1968). In some cases storm-petrels, which are almost never sighted over land, apparently cross land to avoid much longer all-water routes (Billings 1968). Inspired by Griffin's research at the Bowdoin Scientific Station, Kent Island, New Brunswick (44°35'N, 66°45'W), Billings tested the hypothesis of overland navigation by transporting 15 storm-petrels to the coastal town of Stephenville, Newfoundland (48°33'N, 58°36'W), which is separated from Kent Island by two major land barriers, Prince Edward Island and Nova Scotia. Billings reported return speeds nearly double those of Griffin in several different homing experiments. Given the discrepancy between their results and the fact that experiments in ecology are too rarely repeated and independently corroborated by different investigators, we report the results of a replication of Billings' Stephenville homing experiment.

Thirty-two incubating Leach's Storm-Petrels from

Kent Island were selected on the basis of nest accessibility and previous breeding experience. The birds included males and females that averaged 10.9 yr old (SD 5.2 yr) and ranged in age from a minimum of 4 yr to at least 22 yr. We estimated age by adding the number of years since the birds were first banded as breeders to the 4 yr needed to achieve reproductive maturity (Huntington and Burt 1970). Males and females did not differ in age ( $n = 20$  and  $12$ , respectively; Kruskal-Wallis Test:  $P = 0.56$ ). None had been used in Billings' experiments. For several days before the experiment, all nests were checked daily to determine when each bird had arrived to begin its incubation shift. Storm-petrels have incubation shifts that last up to 5 days (Gross 1935, C. Huntington unpubl. data) and attend their nests erratically (Boersma and Wheelwright 1979), so it was difficult to find large numbers of birds at identical stages in their incubation shifts. Consequently, we used birds that had spent varying periods of time on the nest at the start of the experiment.

The experimental procedure was similar to that of Billings (1968). Birds were removed from their nest burrows beginning at 2330, 3 July 1974. Each bird was weighed with Pesola spring scales, placed in a cloth bag, and put into a cardboard box. At 0500 the following day, the birds were transported by boat to Grand Manan Island, a distance of 9 km. Two hours later the birds were flown to Stephenville, with a brief stop in St. John, New Brunswick, to change planes. The birds were not fed in captivity. On the afternoon

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