

to induce formation of new groups in previously unoccupied areas, attract new birds to abandoned territories, and reduce abandonment of existing territories. Preliminary results have been spectacular. Construction of artificial cavities resulted in the formation of 12 new groups in one year in a population in North Carolina that had averaged only one new group per year over the previous 10 years. In the Francis Marion National Forest in South Carolina, nearly 80% of more than 100 artificial cavities were occupied, which greatly reduced the impact of cavities destroyed by Hurricane Hugo (see also Engstrom and Evans 1990).

The Forest Service estimates it will be 20–40 years before additional suitable habitat for the woodpeckers is created by the aging of young trees. Until forests age and management practices more closely coincide with the requirements of Red-cockaded Woodpeckers, the use of artificial cavities may be the principal means to maintain the species. Ultimately, however, the long-term survival of this species depends on availability of suitable habitat that is sufficient to support self-sustaining populations.

Despite this note of cautious optimism, it is important to reemphasize that population trends are consistently downward, and emergency measures are needed now. Concerned citizens, such as readers of *The Auk*, can urge political leaders to support valid environmental issues in general and enforcement of the Endangered Species Act in particular. It is hardly radical environmentalism to insist that politicians oppose any bill that weakens this law and federal agencies responsible for enforcement. This is essential if the Red-cockaded Woodpecker is to avoid extinction. Interested citizens would do well to become involved in the Red-cockaded Woodpecker issue. The legal strategy that will determine the fate of Spotted Owls in the Northwest, and other species elsewhere in the future, is being molded with this issue of Red-cockaded Woodpeckers in the Southeast.

The Red-cockaded Woodpecker can be saved. Compromises will be required, but other USFS activities can continue. Timbering can continue, but large clearcuts and elimination of old growth must be avoided. This will not happen without political pressure and support from the public. Before the world will respond to our demands for much larger compromises elsewhere in the name of conservation, the world is watching to see if we are willing to make these small compromises on our own public land.

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## The Taxonomic Status of the Small Genovesa Ground-Finch in the Galápagos

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The Sharp-beaked Ground-Finch, *Geospiza difficilis*, is the most variable in diet and morphology of the Darwin's finches (Lack 1947; Schluter and Grant 1982,

1984; Grant 1986). It occurs in the highland zone of large central Galápagos islands, where it differs in diet from the morphologically similar Small Ground-Finch, *G. fuliginosa*, which occurs at generally lower elevations. *Geospiza difficilis* is present on low islands only where *G. fuliginosa* is absent (Genovesa, Darwin, and Wolf islands), and its feeding niche is very similar to that of the missing congener (Schluter and Grant 1982, 1984). Lack (1947) suggested that *G. fuliginosa* had competitively excluded or displaced *G. difficilis* wherever they came into contact. Our field studies support Lack's hypothesis, and we attribute

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the *fuliginosa*-like diet of *G. difficilis* on low islands to the abundance of *fuliginosa* foods and the absence of *G. fuliginosa* (Schluter and Grant 1982, 1984).

Recently, Vagvolgyi and Vagvolgyi (1989) criticized our conclusions on taxonomic grounds. They argued, from morphological study, that the Genovesa form of *G. difficilis* is actually a *G. fuliginosa*. They attributed the similarity in diet of the Genovesa finch and *G. fuliginosa* elsewhere to common ancestry rather than to niche shift and competition.

We reexamined the morphological data, and we show that while the Genovesa finch is similar to *G. fuliginosa* in general body size, its shape clearly aligns it with *G. difficilis*. We argue that shape is the more reliable index of evolutionary relationship, and we conclude that Vagvolgyi and Vagvolgyi's (1989) criticisms are unfounded. Available data on song and plumage are consistent with our morphological findings.

Vagvolgyi and Vagvolgyi (1989) did not challenge the classification of the Darwin and Wolf forms of *G. difficilis*, although they remarked that the diets are insufficiently known. However, we have demonstrated that the feeding niches of these two forms are highly *fuliginosa*-like, supporting Lack's hypothesis (Schluter and Grant 1984).

*Size and shape differences.*—Vagvolgyi and Vagvolgyi (1989) showed that the small Genovesa finch is more similar to *G. fuliginosa* than to other populations of *G. difficilis* in five of six measured traits (length, depth, and width of beak, tarsus length, wing length, and body mass; beak length is the exception). However, the six traits are not independent because they are strongly positively correlated within and among populations (Boag 1983, Grant 1983a, Grant et al. 1985), reflecting variation in general body size (Pimentel 1979). In effect, Vagvolgyi and Vagvolgyi (1989) showed the Genovesa population to be similar in size to *G. fuliginosa*, as was noted earlier by Lack (1947) and Schluter and Grant (1984).

A taxonomic judgment based solely on general size is suspect for two reasons. The first derives from evolutionary considerations. Namely, far more genetic variation in size than shape exists in finch populations (Boag 1983, Grant 1983a), and size would evolve more rapidly than shape if subject to selection (Lande 1979) or random genetic drift (Lynch 1989). Size differences are thus expected to be less informative than shape in evaluating common history. The second reason is empirical. Closely related Galápagos finch species often differ greatly in size but not shape, while more distantly related species are often similar in size but never in shape (Lack 1947, Yang and Patton 1981, Schluter 1984, Grant et al. 1985). Greater weight should therefore be given to shape differences when estimating evolutionary relationships.

We considered two multivariate procedures for handling size and shape differences when comparing finch populations. The first method calculates uncor-

related size and shape dimensions, and it weights them inversely by estimates of within-population genetic variance. This approach yielded more accurate morphology-based estimates of evolutionary relationship between Galápagos finch species (verified using electrophoretic data from Yang and Patton 1981) than did an unweighted analysis (Schluter 1984). The second approach simply removes size from consideration and assesses taxonomic affinity using the remaining shape dimensions. The second approach is the simpler, and we use it here. Genetic parameters have not been estimated for *G. fuliginosa* or *G. difficilis*, and so the first method is not yet possible.

*Multivariate reanalysis.*—We examined two sets of morphological measurements. The first consisted of eight traits measured on live males captured in mist nets: body mass, wing length, tarsus length, beak length, upper mandible depth, total beak depth, beak width, and beak length at 4 mm, as described in Abbott et al. (1977). The set included nine populations of *G. fuliginosa* (Pinta, Marchena, San Salvador, Fernandina, Tortuga, Española, Santa Fe, Santa Cruz, and Isabela [culmen depth lacking for Isabela]), five of *G. difficilis* (Pinta, Darwin, Wolf, San Salvador, and Fernandina), and the disputed Genovesa form. Sample sizes ranged from 10 to 72 individuals per population. The second set was made from museum specimens and consisted of nine beak and body dimensions of males from 18 populations of *G. fuliginosa*, 5 populations of *G. difficilis*, and the small Genovesa finch (see Grant et al. 1985 for traits and populations). Both data sets gave the same results, and we present only the results based on live individuals. Body mass was converted to cube root mass, and all traits were log-transformed before analysis.

"Beak length at 4 mm" (hereafter L@4) is the distance along the commissure of the closed beak from the tip of the upper mandible to the point where beak depth is exactly 4 mm. The trait reflects acuity of the beak tip: a large value indicates a pointed tip, while a small value indicates a rounded, blunt tip. The trait was measured only on live specimens. It was of interest because it distinguished *G. difficilis* from *G. fuliginosa* independently of other traits. Indeed, the pointed beak of *G. difficilis* inspired its name, "sharp-beaked ground finch" (Lack 1947). A plot of L@4 against the value predicted from a pooled regression onto beak length and depth shows that the small Genovesa finch is sharp-beaked (Fig. 1;  $R^2 = 0.68$ ,  $n = 14$ ,  $P = 0.003$ ). Acuity of the beak tip for a given length and depth is greater in *G. difficilis* than in *G. fuliginosa*, and the Genovesa form falls close to the *G. difficilis* line, and above the *G. fuliginosa* line.

In our multivariate analysis we calculated principal components from the pooled within-population covariance matrix (the *G. fuliginosa* among-population covariance matrix gave the same result). All traits except L@4 loaded positively onto the first component (PC1), indicating variation in general size. Mean po-

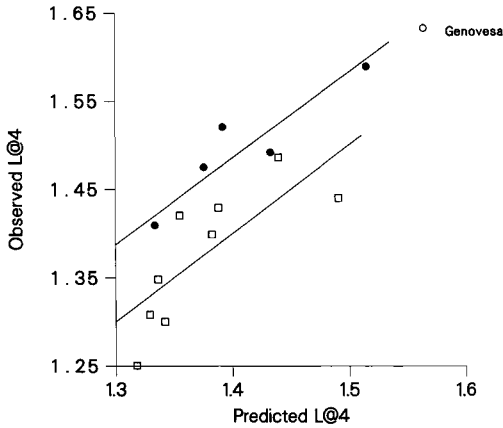


Fig. 1. Beak tip acuity ( $L@4$ ) along with values predicted from a pooled regression of  $L@4$  in populations of *G. difficilis* (●) and *G. fuliginosa* (□) onto beak length (BL) and beak depth (BD):  $L@4 = 0.79(BL) - 1.66(BD) + 2.77$ . The open circle (○) indicates the small Genovesa ground-finch.

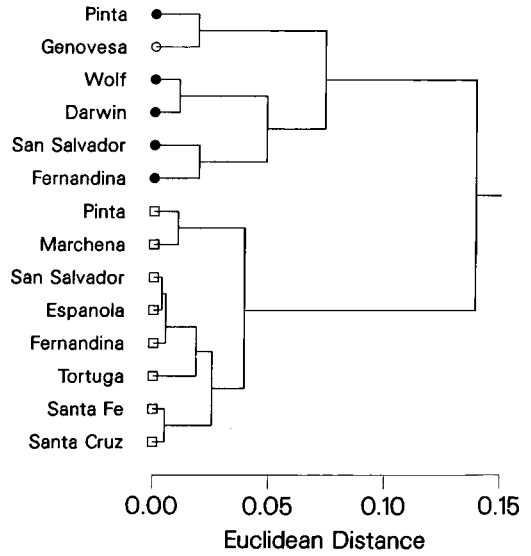


Fig. 2. UPGMA clustering of populations on the basis of beak and body shape. Symbols indicate populations of *G. difficilis* (●), *G. fuliginosa* (□), and the small Genovesa ground-finch (○). Islands are listed on the left.

sition along all but the first components was then computed for every population, representing variation in different aspects of shape. Finally, we subjected means to a UPGMA clustering algorithm (Fig. 2).

Two main clusters of populations were detected, one representing *G. fuliginosa* and the other *G. difficilis* (Fig. 2). The Genovesa finch fell clearly within the *G. difficilis* cluster. Populations of *G. difficilis* were somewhat more distinct from one another than were populations of *G. fuliginosa* (see also Grant 1983b and Schluter and Grant 1984), perhaps reflecting the greater age of the former species (Lack 1947).

We suggest that the small finch species on Genovesa is a *G. difficilis*. Without more information on phylogenetic relationships among populations we cannot be certain whether the pattern of variation in the diets on different islands represents convergence toward the absent *G. fuliginosa* or divergence in its presence. In either case, Lack's competitive explanation for the distribution and morphology of *G. difficilis* on Galápagos islands remains valid.

*Song and plumage.*—Song does not reliably classify *Geospiza* populations into species, because of dialects within species, and convergence and overlap between species (Ratcliffe 1981). Measurements of 7 song variables (length, number of figures, figure duration, interfigure interval, maximum and minimum frequency, and frequency span) indicate that most populations of *G. fuliginosa* have very similar songs (Ratcliffe 1981: fig. 12), which consist of a high-pitched, descending series of two or three notes (e.g. "TEE a chur," or "TEE chur"; Lack 1947). Songs of the two available undisputed *G. difficilis* populations (Pinta and Wolf) are distinct from *G. fuliginosa*, but they are also

different from one another—as different as the songs of different species. Cluster analysis showed that overall, the song of the small Genovesa finch ("te ZEE ah") is closer to the Pinta *G. difficilis* ("tee ZEEDE do") than to Wolf *G. difficilis* or to *G. fuliginosa* (Ratcliffe 1981). Thus, songs are consistent with the present classification of the Genovesa finch as a *G. difficilis*, although songs are not sufficient by themselves to unambiguously identify species.

In addition to advertising song, the Genovesa finch sings a high-pitched whistle that is characteristic of all *Geospiza* populations, except some *G. difficilis* (Bowman 1983: table 10). For example, *G. difficilis* on Pinta and San Salvador lack the whistle and use a "bzzz-CLINK" (special basic song, Bowman 1983) in the same behavioral context. The absence of special basic song and the presence of a whistle in the Genovesa form would appear to suggest an affinity between it and *G. fuliginosa* (Vagvolgyi and Vagvolgyi 1989). However, the trait is probably not a reliable taxonomic clue because both Darwin and Wolf forms of *G. difficilis* also have the whistle. The Darwin form lacks the special basic song, while the Wolf form uses the whistle as a modified ending to its special basic song (Bowman 1983).

Information on plumage is also consistent with the classification of the Genovesa finch as a *G. difficilis* (especially alongside the Pinta form), but a full quantitative analysis is lacking. Lack (1947) noted that the female plumage is darker in *G. difficilis* than *G. fuliginosa*, with the *G. difficilis* forms on Pinta and Genove-

sa being "less dark" than on other islands. Female *G. difficilis* also have rufous wing bars, absent in *G. fuliginosa*, but the trait occurs in very low frequency in the Genovesa and Pinta populations. The under-tail coverts in adult male *G. difficilis* are often rufous-tipped, whereas the coverts are white-tipped in *G. fuliginosa*. Lack noted considerable variation among *G. difficilis* populations in the frequency of the rufous tip: in 100% of the Darwin and Wolf specimens, 50% of those from San Salvador and Santa Cruz, and 10% of those from Pinta and Genovesa.

The small finch on Isla Genovesa, Galápagos, is similar to *G. fuliginosa* in overall body size, but in shape it is very much a *G. difficilis*. Song and plumage variables are consistent with this result. We conclude that the data best fit Lack's (1947) classification, and that the taxonomic revision proposed by Vagvolgyi and Vagvolgyi (1989) is unsupported.

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## Response to Schluter, Ratcliffe, and Grant

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Schluter, Ratcliffe, and Grant (1991) argue that the Small Genovesa Ground-Finch should be classified as *Geospiza difficilis* because the species are similar in shape, and—more so than size—shape is an independent,

reliable, and important indicator of taxonomic and evolutionary relationships.

The classification of Darwin's finches is based on size as well as shape characters. Lack (1947: 81, 88) as well as Grant and Grant (1989: 377) emphasized this: "Beak size and shape . . . have been identified as important in the evolutionary diversification [of Darwin's Finches] . . . since species differ from each other

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