VARIABILITY IN ISLAND POPULATIONS OF THE HOUSE FINCH

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ABSTRACT.—Coefficients of variation and generalized variances are compared for nine morphological characters from five mainland and four island populations of the House Finch (*Carpodacus mexicanus*). The purpose is to test the idea that variability is reduced in isolated populations and that there is a "population variation parameter" that determines the level of variation in most characters. Variability is greater in bill characters for Guadalupe and San Benito Islands than for mainland and other island populations. There are no consistent differences among samples in variability of wing, tail, or hind-limb characters, except for a tendency toward increased tarsus-length variability in a southern Baja California population and reduced variability in this character in San Clemente Island and Guadalupe Island populations. In bill characters, increased variability is found in the most divergent populations. The results do not support the generalization that geographic (= genetic) isolation *per se* causes much of a change in variability in island populations of birds, nor is there support for the idea of a pervasive quality of the gene pool that determines the level of variability in most characters. *Received 29 June 1981, accepted 30 September 1982.*

ISLAND populations are isolated to varying degrees and, as a result, are often subject to reduced gene flow. They are also often subject to strong directional selection, especially just after colonization of a novel environment. Grant (1979) has proposed that phenotypic variation is reduced in well-isolated populations as a consequence of both diminished gene flow and strong differentiation through directional selection and random genetic drift. Soulé (1972) also identified isolation, as well as the intensity of stabilizing selection, as factors in the reduction of variability in island populations. In addition, Soulé has stated that there is strong evidence for a "population variation parameter," implying that some pervasive quality of the gene pool determines the level of variability in most characters.

I tested the ideas of an association between variability and isolation in island populations and of the similarity in variability among characters by using morphological data from island and mainland populations of the House Finch (*Carpodacus mexicanus*). "Variability" is used here to mean within-population variation as measured by the coefficient of variation or variance of log-transformed data for single characters. For multiple characters, a generalized variance is used. The House Finch is widespread in North America and occurs on the California Islands (Fig. 1). Samples from many of the islands are large enough to provide reliable measures of variability. Divergence has occurred in some characters on many of the islands (Power 1979, 1980).

METHODS

Measurements were made on specimens of House Finches in museum collections. Locality samples were those used for my earlier studies having a sample size greater than 60. Sample sizes ranged from 62 to 283, with most being in the 100–200 range. One exception is the small ($n = 27$) sample from San Benito Islands, a population that is interesting because it is phenetically intermediate between Guadalupe Island and other populations. The present analysis is of males only. There are five mainland and four island samples: (1) San Francisco Bay area, (2) Santa Barbara and Ventura counties, (3) Los Angeles and Orange counties, (4) San Diego County, (5) southern Baja California, (6) Santa Cruz Island, (7) San Clemente Island, (8) San Benito Islands, and (9) Guadalupe Island. Although some of the mainland areas are large, House Finches are not highly sedentary, and I believe there is not much risk in confusing geographic variation with intrapopulation variation.

There are nine additional samples of male House Finches in my earlier study, with sample sizes ranging from 20 to 59, plus a set of data on females. An inspection of the standard deviations of these samples (appendix tables 1–6 in my 1980 paper) shows no trends different from those reported here.

Measurements were taken according to the procedure given in Power (1979) on the following nine characters: bill length, bill depth, upper bill width, lower bill width, wing length to the longest primary

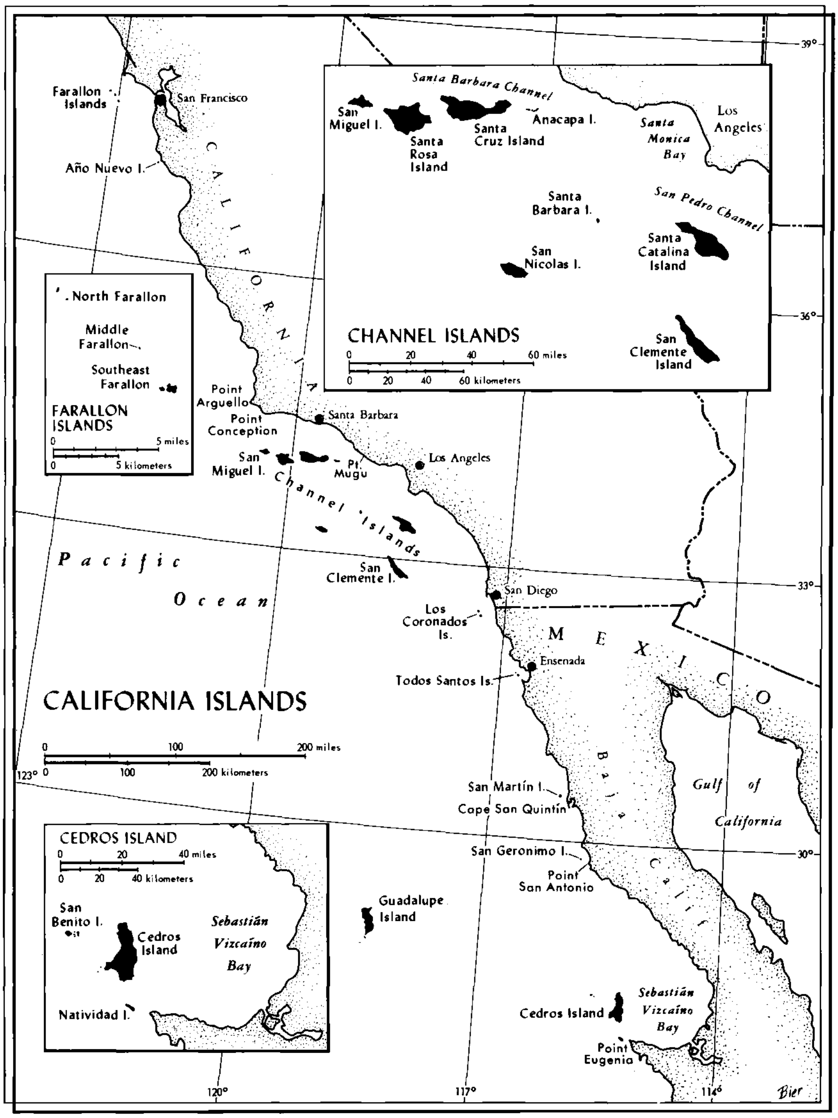

Fig. 1. Map of the California Islands. Island samples used in this study are from Santa Cruz and San Clemente (in the Channel Islands group), San Benito (near Cedros, off Baja California), and Guadalupe.

feather, wing length to the outermost secondary feather, tail length, tarsus length, and hind toe length.

Coefficients of variation (v) were calculated according to the conventional formula: $v = s/\bar{Y}$, where s is the standard deviation and $\bar{Y}$ is the mean of a sample. I multiplied v by the correction factor $[1 + (1/4n)]$ (Sokal and Braumann 1980), but the coefficients changed by insignificant amounts because of the large sample sizes. Coefficients of variation were compared graphically using variability profiles (Yablokov 1974, Sokal and Braumann 1980). I determined multivariate measures of variability by means of generalized variances (determinants of variance-covariance matrices) calculated on log-transformed data (Power 1971). Data were transformed to natural logarithms to avoid biases due to differences in means (Lewontin 1966).

RESULTS

Geographic variation.—Evolution in House Finches on the California Islands has been examined in earlier papers (Power 1979, 1980). Populations on the islands show greater geo-

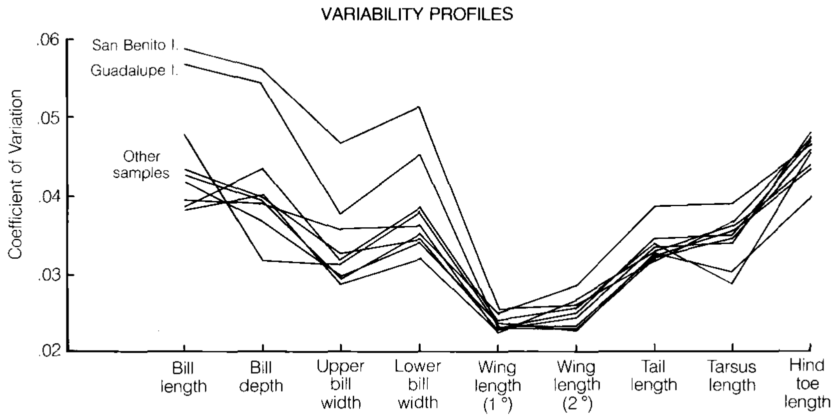

Fig. 2. Variability profiles for each sample. Guadalupe and San Benito islands samples show high variability for bill characters. Other samples tend to clump together, showing more similar variability patterns.

graphic variation than do those from the adjacent western North American mainland. Considering all characters simultaneously in a canonical variates analysis, I found that the most divergent island populations are those that are farthest from the mainland and, because of prevailing winds, are in a poor position to receive dispersing birds from the mainland or other islands. Very small islands also have some of the most divergent populations. House Finches from Guadalupe Island are the most distinct, and the population from San Benito is roughly intermediate between that on Guadalupe and those on other islands. Populations from San Clemente, Santa Barbara, Los Coronados, and San Nicolas islands are also divergent from mainland populations and have evolved in a "phenetic direction" similar to that of the most extreme populations.

Guadalupe Island House Finches are larger in every character and have proportionally larger bills (relative to cube root of body weight) than all other populations. Finches from the other islands have slightly smaller wings and tails, larger bills, and larger legs than mainland populations. Except for Guadalupe, wing and tail measurements, relative to body size (cube root of body weight), are smaller in island populations.

Univariate variability comparisons.—Coefficients of variation are plotted in Fig. 2 as variability profiles (see also Table 1). Bill characters are more variable for samples from San Benito and Guadalupe islands than for other island and mainland samples. For all other characters, island and mainland samples are much more similar to one another in variability patterns. The southern Baja California sample demonstrates a slightly elevated profile for tail length and tarsus length. The two low points for tarsus length represent San Clemente and Guadalupe island samples.

Results of tests for the homogeneity of variances of log data are shown in Table 1. [Van Valen (1978) has criticized the use of Bartlett's and F tests to test the equality of variances, because they are sensitive to nonnormality; the tests are used here simply to support the graphic analyses, which show the dominant trends I want to discuss.] That the only significant ($P < 0.05$) Chi-square values are for the bill characters and tarsus length is in agreement with the graphic analysis. In pair-wise F-tests (results not shown), variances in all bill characters from San Benito and Guadalupe Island samples were significantly different from variances from most other samples. Two samples had low variability for tarsus length; in pair-wise tests for tarsus lengths (results not shown), the San Clemente Island sample was significantly different in 5 out of 8 comparisons and the Guadalupe Island sample in 3 out of 8. In both cases one of the significant tests was with the highly variable southern Baja California sample, which was not significantly different from any other sample.

Multivariate variability comparisons.—Multivariate measures take into account both variances of single characters and covariances between pairs of characters. The covariance is an

TABLE 1. Coefficients of variation (sample sizes below) and results of Bartlett's test for homogeneity of variances of log-transformed data.[a]

	Bill length	Bill depth	Upper bill width	Lower bill width	Wing length (1°)	Wing length (2°)	Tail length	Tarsus length	Hind toe length
San Francisco Bay area	0.0432 (186)	0.0397 (175)	0.0321 (186)	0.0344 (182)	0.0228 (181)	0.0242 (179)	0.0334 (184)	0.0353 (186)	0.0432 (187)
Santa Barbara/ Ventura counties	0.0395 (67)	0.0390 (62)	0.0356 (67)	0.0359 (67)	0.0227 (67)	0.0268 (67)	0.0329 (67)	0.0354 (67)	0.0434 (67)
Los Angeles/ Orange counties	0.0387 (148)	0.0434 (143)	0.0318 (149)	0.0381 (148)	0.0233 (147)	0.0227 (146)	0.0321 (145)	0.0349 (148)	0.0477 (149)
San Diego County	0.0416 (122)	0.0365 (115)	0.0293 (123)	0.0341 (122)	0.0237 (119)	0.0256 (122)	0.0332 (121)	0.0340 (123)	0.0466 (123)
Southern Baja California	0.0423 (140)	0.0390 (131)	0.0291 (140)	0.0348 (139)	0.0246 (140)	0.0282 (139)	0.0385 (139)	0.0389 (140)	0.0462 (140)
Santa Cruz Island	0.0476 (67)	0.0315 (66)	0.0312 (68)	0.0380 (67)	0.0237 (68)	0.0248 (68)	0.0344 (67)	0.0342 (66)	0.0458 (68)
San Clemente Island	0.0380 (169)	0.0394 (168)	0.0289 (173)	0.0317 (169)	0.0225 (168)	0.0262 (168)	0.0330 (172)	0.0286 (171)	0.0452 (172)
San Benito Island	0.0584 (27)	0.0559 (24)	0.0464 (27)	0.0510 (26)	0.0249 (24)	0.0257 (22)	0.0317 (26)	0.0363 (27)	0.0487 (27)
Guadalupe Island	0.0566 (283)	0.0540 (277)	0.0372 (283)	0.0450 (282)	0.0237 (268)	0.0230 (264)	0.0325 (273)	0.0300 (283)	0.0396 (283)
Chi-square probability	59.4 <0.001	60.1 <0.001	22.8 0.004	41.9 <0.001	1.9 0.983	1.3 0.127	7.4 0.500	23.9 0.003	10.3 0.246

[a] Degrees of freedom = 8 in all cases. The procedure for Bartlett's test is given in Sokal and Rohlf (1969).

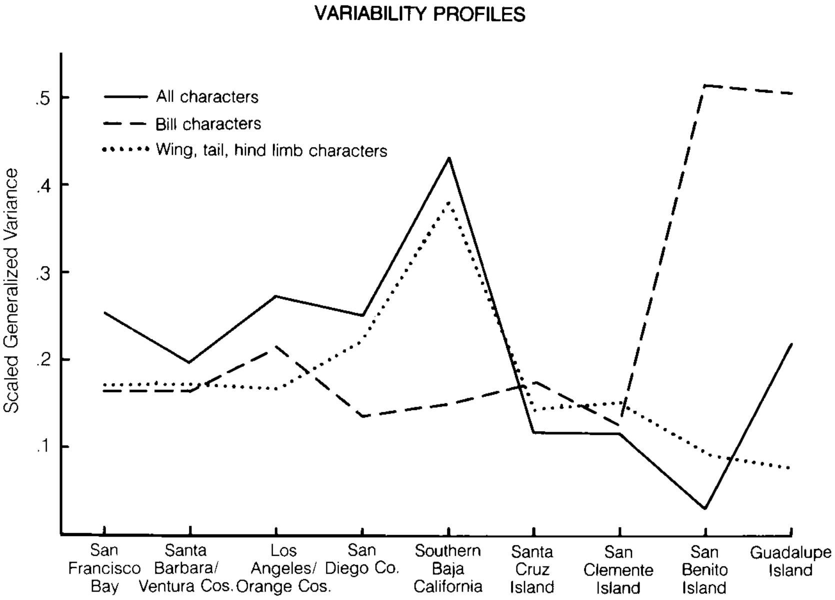

Fig. 3. Multivariate variability profiles plotting generalized variances for sets of characters against locality. High, generalized variances are found for San Benito and Guadalupe islands in bill characters. The peak for the southern Baja California sample for limb characters proved to be not quite significant (see text). Each of the three sets of determinants is scaled by a different factor (see Table 2). Thus, the lines for different character sets are not on the same scale.

important feature of phenetic variability that is often overlooked. The determinant of a variance-covariance matrix (generalized variance) is proportional to a multidimensional equal-frequency ellipsoid in a character space and may be used to assess multivariate variability (Power 1971). Three sets of variance-covariance matrices were analyzed, all calculated on log-transformed data: (1) all characters, (2) bill characters, and (3) wing, tail, and hind-limb characters.

Variability profiles appear in Fig. 3. The determinants of variance-covariance matrices and the results of overall tests of significance appear in Table 2. [Again, Van Valen (1978) warns of the sensitivity of Bartlett's test to nonnormality; the statistical tests are used as a supplement to the graphic comparison.] For all characters, the southern Baja California sample appears most variable. For wing, tail, and hind-limb characters, the southern Baja California sample emerges as the most variable, but the overall test reveals only a "nearly significant" difference. These characters appear to be responsible for the increase seen in the all-character matrices of the southern Baja California sample. For bill characters alone, both the Guadalupe and San Benito Island samples are more variable.

The results indicate, therefore, that it is the bill characters of Guadalupe and San Benito islands House Finches that are consistently more variable. This is confirmed by a series of pairwise tests of variance-covariance matrices based just on bill characters (results not shown), which indicate significant differences between the San Benito Islands sample and the other samples and between the Guadalupe Island sample and the others. San Benito and Guadalupe samples were not significantly different from one another, and there were no significant differences with other mainland and island pairs.

DISCUSSION

Variability is greater in bill characters of Guadalupe and San Benito islands populations than in those of mainland and other island populations. There are no consistent differences among samples in variability of wing, tail, and hind-limb characters, except for a tendency for tarsus length to be more variable in the southern Baja California population and less

TABLE 2. Generalized variances (determinants of variance-covariance matrices of log-transformed data), and results of Bartlett's test of significance.[a]

	All characters[b]	Bill characters[b,c]	Wing, tail, hind limb characters[b,d]
San Francisco Bay	0.253	0.171	0.172
Santa Barbara/Ventura	0.199	0.164	0.173
Los Angeles/Orange	0.273	0.213	0.169
San Diego	0.251	0.137	0.223
Southern Baja California	0.433	0.152	0.382
Santa Cruz Island	0.119	0.178	0.144
San Clemente Island	0.166	0.130	0.147
San Benito Island	0.031	0.515	0.095
Guadalupe Island	0.222	0.509	0.078
Chi-square	475.50	170.57	144.18
Degrees of freedom	360	80	120
Probability	0.001	0.001	0.079

[a] The procedure for this test is given in Morrison (1967).

[b] Values shown are actual determinants $\times 10^{27}$; [c] $\times 10^{11}$; [d] $\times 10^{15}$, hence are shown as "scaled" generalized variances in the graph.

variable in the San Clemente Island and Guadalupe Island populations.

Grant (1979) analyzed variability in morphological characters in Chaffinches (*Fringilla coelebs*) from Europe, North Africa, and certain islands in the Atlantic Ocean. He found short wings and long legs and beaks in populations from the Azores and Canary Islands. Greatest divergence in bill length was on the Canaries, the most isolated archipelago. Within-population variability decreased with isolation and with the degree of differentiation from mainland populations.

The present study agrees with Grant's insofar as the population on the most isolated island is the most divergent. The studies are at odds, however, with regard to isolation being an important factor for population variability in bill dimensions. The most divergent and the most isolated House Finch population is on Guadalupe, and this is one of the two populations having the most variable bill dimensions. Thus, there is no support for the generalization that variation is lower in isolated populations. It is clear, however, that the most divergent populations are the most variable. Factors other than isolation, such as the strength of directional selection, the underlying genetic basis of the character, and the degree of ecological release, must be important.

Soulé and Stewart (1970) have suggested that unusually high variability in a canalized, complex character, such as a bird bill, can be caused by strong directional selection affecting the expression of hidden genetic variation—a temporary release of phenotypic variation concomitant with a deterioration of canalizing selection. This would be most often observed in a genetically isolated population in a new or changing environment. Guthrie (1965), in a study of dentition of voles (*Microtus*), found that quantitative characters undergoing rapid evolution retain the same variability or become even more variable within a population. Eventually, a new adaptive peak is reached and selection becomes less directional and more stabilizing, leading to an increase in canalization of the character and a decrease in variability.

It is not easy to test the foregoing ideas using phenetic data on House Finches from the California Islands. Is the bill still under strong directional selection on Guadalupe, or has it reached a new adaptive peak? House Finches may have been on Guadalupe since the close of the Pleistocene, which may be much longer than necessary for the transient release of variability to be evident. Under any circumstances, are the bill characters under canalization? For any natural population, these kinds of questions are very difficult to answer.

One question that can be answered, however, is whether or not increasing variability is primarily a function of increasing bill size. In general, this seems not to be the case. For the four bill characters, bivariate scatter diagrams (not shown) were made of variances of log data plotted against means. Also, the determinants of variance-covariance matrices were plotted against the grand mean of the four bill-character sample means. In no case was there a *continuous* trend of increasing variability and bill size; only the bill dimensions of the Guadalupe and San Benito islands samples stood out as being both large and highly variable.

Another question that can be addressed is the relationship between variability and niche width. Morphological variability in bill size seems to be associated with niche width in certain species on islands (e.g. Van Valen 1965), but in other cases a relationship has not been demonstrated (e.g. Willson et al. 1975, Lister 1976). Rothstein (1973) provided one of the more thorough tests of the validity of the niche-variation hypothesis and found agreement in a significant number of cases. He stressed discontinuous variation through sexual dimorphism, rather than continuous variation, however, as the more adaptive system.

Measures of niche width and niche overlap for species on the California Islands are not available. One might roughly approximate the potential for competition by taking into account the number of fringillid species occurring with House Finches. Following are the number and species of fringillids, other than House Finches, reportedly breeding within historic times on the California Islands (data from Power 1972, Diamond and Jones 1980):

Santa Cruz (6: *Pheucticus melanocephalus, Carduelis psaltria, Pipilo erythrophthalmus, Aimophila ruficeps, Spizella passerina,* and *Melospiza melodia*);
San Clemente (4: *P. erythrophthalmus, Amphispiza belli, S. passerina, M. melodia*);
San Benito (1: *Passerculus sandwichensis*);
Guadalupe (2: *Junco hyemalis* and *P. erythrophthalmus*).

Clearly, there are fewer potentially competing species on the islands with greatest variability (and divergence) in bill size. Whether or not House Finches on Guadalupe or San Benito truly have a "wider niche," however, remains to be demonstrated.

A final point concerns the possibility that immigration is causing increased variability in Guadalupe and San Benito populations. In the case of Guadalupe Island, it seems unlikely that the gene pool is being enriched by immigrants from the mainland or islands farther north. Distances involved seem to me to be simply too great for immigration to be anything but an exceedingly rare event, too rare to increase variability to its present level. This may not be the case for San Benito Islands. Here, there is a possibility of immigrants from Cedros Island and the mainland of Baja California arriving more regularly. There is also the possibility that Guadalupe Island House Finches may find their way to San Benito, perhaps through human transport. Hybridization could lead to the phenetically intermediate population that we find on San Benito and to an increase in variability as well.

The second major question to be addressed deals with the population variation parameter. Soulé (1972), in his study on insular populations of the side-blotched lizard (*Uta stansburiana*) in the Gulf of California, reported what he believed to be strong evidence for some pervasive quality of a gene pool that determines the level of variation. This means that if a population is highly variable for character A, then it will be highly variable for characters B, C, and so on, relative to those same traits in another population. This is certainly not the case for the island finches reported on here. Suites of characters are obviously subject to different selection pressures on the different islands. In the present study, the pattern of variability is clearly different for limb and bill characters; bill characters are more variable in some populations than in others.

One scenario can be offered regarding the evolution of House Finches, and perhaps other species, on islands. Increased directional selection can reveal hidden genetic and phenetic variability that may then be maintained in a population owing to reduced competition and a wider range of ecological conditions. Demonstrating such effects would involve experiments and detailed ecological studies, not morphometric analyses alone. At any rate, the present data do not support the idea that isolation *per se* causes much of a change in variability or that there is an underlying population variation parameter affecting most characters.

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