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MULTIVARIATE STUDY OF MORPHOLOGICAL VARIATION IN GALÁPAGOS AND ECUADOREAN MOCKINGBIRDS

IAN ABBOTT
AND
L. K. ABBOTT

Compared with the remarkable and well-known diversification of finches within the Galápagos Archipelago, the mockingbirds rate a poor second. They are almost as widely distributed as the finches but only one form is found on any island, in contrast to a maximum of nine finch species on some of the large, high islands (Bowman 1961). Like the finches, the mockingbirds have been well collected. This study is based on measurements made on 1,100 sexed museum specimens. However, unlike the finches, mockingbirds have never been subjected to proper morphometric study; previous workers have worked only on limited collections.

Darwin made the Galápagos mockingbirds known to science when he collected five specimens. These were described by Gould (1837), who placed them in the genus *Orpheus.* Ridgway (1890) proposed the new genus *Nesomimus* (restricted to the Galápagos) and placed all mainland forms in the genus *Mimus.* However, we prefer to treat the Galápagos mockingbirds as congeneric within mainland mockingbirds (Rothschild and Hartert 1899, Bowman and Carter 1971).

It is generally agreed that the Ecuadorean populations belong to the species *M. longicaudatus.* In contrast, there have been considerable differences in the taxonomic treatment of the Galápagos populations owing to the difficulty of deciding whether allopatric populations are specifically or only subspecifically different. Rothschild and Hartert (1899) recognized five species and six subspecies. Snodgrass and Heller (1904) rejected one of Rothschild and Hartert's subspecies and described another. Ridgway (1897) recognized the same taxa as Snodgrass and Heller but treated them as species. Swarth (1931) removed confusion over names and recognized four species and six subspecies, one of them new. The latest revisers, Davis and Miller (1960), treated all Galápagos populations as belonging to the one species (*melanotis*) and accepted nine subspecies. Their taxonomic decisions were based on whether the breast is marked with streaks, spots or blotches and on other plumage differences as well as on morphology (full summary in Table 2 of Bowman and Carter 1971). Bowman and Carter (1971) succeeded in crossing *M. parvulus* (Galápagos) with *M. longicaudatus* (Ecuador) but failed to interbreed *M. parvulus* with *M. trifasciatus* and *M. macdonaldi*, two other Galápagos populations.

Swarth (1931:105) wrote: "*Nesomimus* is a homogeneous group, obviously nearly related to the mainland genera of Mimidae, but it is not possible to designate any one form of *Nesomimus* as most closely related to a mainland species, and to trace any course of increasing divergence from this starting point or from any other." Here we take up this challenge using techniques not available to Swarth. Canonical variates analysis is used to compare morphological variation in Galápagos mockingbirds with those from the nearest mainland area, and presumed source, lowland Ecuador. Specifically, we address three questions. Which Galápagos mockingbird population(s) is/are most similar morphologically to the mainland population? Do the more isolated islands possess populations that are morphologically most unlike those on the more central islands? If any clusters (based on morphological similarities) of island populations occur, what do the islands have in common that would explain such similarity?

Morphologically distinctive populations could evolve in several ways, so long as mixing of island populations does not occur too frequently. Therefore, populations on the most isolated islands in the Archipelago should be the most distinctive. In addition, small islands should hold smaller populations than large islands, so that genetic drift could have more impact in such populations, thereby promoting morphological distinction. However, small population size carries the risk of extinction. Nevertheless, colonization of a small, empty island could involve the founder effect, which could lead to morphological differences from the source population. Large ecological differences between islands may be coupled with isolation and/or small population sizes. Selective differences in, for example, climate or food size could lead to morphological differences among various island populations.

TABLE 1. Mean values, sample sizes, and standard deviations for bill, tarsus and wing lengths of *Mimus* populations.

Population	Sex	Bill			Tarsus			Wing		
		x̄	N	s	x̄	N	s	x̄	N	s
1. San Cristóbal	M	28.83	101	0.89	37.52	102	0.84	113.5	102	2.56
	F	27.20	69	1.04	35.89	68	0.90	105.4	69	2.48
2. Española	M	37.83	61	1.45	38.54	61	0.93	124.7	61	3.10
	F	35.82	47	1.24	36.52	47	0.97	115.4	47	3.06
3. Gardner (near Española)	M	37.58	11	1.43	37.96	11	1.46	124.5	11	1.57
	F	35.44	9	0.99	36.37	9	0.62	115.3	9	2.45
4. Champion	M	33.66	9	1.37	40.80	8	0.26	123.9	9	2.76
	F	31.02	6	1.13	38.77	6	0.88	117.0	6	4.15
5. Gardner (near Santa María)	M	33.18	27	1.31	40.36	28	0.89	125.6	28	2.92
	F	31.58	19	0.97	38.11	20	0.92	118.2	20	2.67
6. Santa Fé	M	30.85	65	1.19	34.43	65	0.75	110.2	65	2.20
	F	29.94	23	0.99	32.92	25	1.16	103.9	25	3.03
7. Seymour	M	26.56	5	1.05	36.36	5	0.54	110.6	5	1.52
8. Baltra	M	26.57	15	0.51	36.06	15	0.95	111.7	15	2.76
	F	25.86	9	1.00	34.27	9	1.09	104.4	9	2.35
9. Santa Cruz	M	26.68	82	1.11	36.17	82	0.94	111.9	82	3.06
	F	25.43	60	1.10	34.32	60	0.88	103.9	60	3.28
10. Fernandina	M	25.51	19	0.99	35.72	19	1.15	110.6	19	3.75
	F	25.08	17	0.92	34.39	17	0.99	102.2	17	4.45
11. Isabela	M	25.05	68	1.16	36.58	68	1.44	109.2	68	3.90
	F	24.53	61	1.25	35.11	61	1.22	103.4	61	3.20
12. San Salvador	M	27.84	34	1.19	36.79	34	1.18	112.6	34	3.89
	F	27.45	19	1.28	36.03	19	1.31	107.5	19	4.02
13. Rábida	M	28.59	27	1.22	35.59	27	0.63	110.5	27	3.18
	F	27.86	17	0.88	34.26	17	0.90	102.0	17	3.32
14. Marchena	M	29.10	41	1.06	34.80	43	0.96	108.7	43	3.40
	F	27.84	26	0.77	33.25	28	1.05	103.6	28	2.95
15. Pinta	M	30.80	38	1.31	36.26	38	0.78	110.9	38	2.53
	F	29.27	20	1.17	34.69	21	1.03	104.0	21	2.71
16. Genovesa	M	31.53	42	1.68	35.24	42	1.23	116.0	42	3.99
	F	31.00	30	1.01	33.91	31	1.03	110.6	31	2.54
17. Wolf	M	28.81	23	1.08	34.74	23	0.98	112.3	23	2.84
	F	28.06	12	0.94	33.50	12	0.72	105.0	12	2.45
18. Darwin	M	29.79	10	1.39	35.20	11	1.17	113.9	11	2.95
	F	29.11	10	1.16	33.67	10	0.84	106.2	10	1.23
19. Ecuador	M	26.89	21	0.85	38.15	21	1.90	122.8	21	4.80
	F	26.46	11	0.80	38.28	11	1.13	118.5	11	5.03

METHODS

Three measurements were taken on each specimen. Culmen length was measured, with dividers, from the base of the skull to the tip of the bill. Tarsus length, also measured with dividers, is the distance between the tarsometatarsal joint and the base of the hallux. Wing length was taken from the carpal bend to the tip of the longest primary, with the wing pressed flat against a ruler. The first author measured all adult specimens in the collections of the California Academy of Sciences, American Museum of Natural History, Stanford University (collection on permanent loan to CAS), and British Museum of Natural History, in addition to a few from the collection of R. I. Bowman, Liverpool Museum (UK) and Philadelphia Academy of Sciences. The three measurements were considered simultaneously in a canonical variates analysis (Seal 1964), using a program slightly modified from that of Abbott (1974). Males and females were treated separately.

RESULTS

Mean values, standard deviations and sample sizes for males and females of each Galápagos population and for lowland Ecuador are listed in Table 1 (see Fig. 1 for island locations). In the multivariate analyses, 96% (males) and 97% (females) of all variation was accounted for by the first two canonical variates, which means that the third may be neglected. The first and second canonical axes are used as the

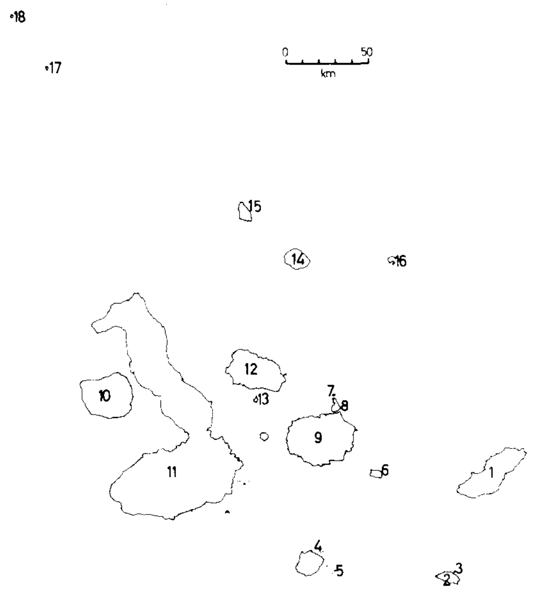

FIGURE 1. Map of Galápagos Archipelago, showing geographical position of the 18 island populations. The name of each island population is indicated in Table 1.

basis for graphically displaying the mean vectors of all populations (Figs. 2 and 3).

Males and females show the same broad trends. Five clusters represent subsets of populations that are morphologically similar and differ from other clusters to various degrees. The first cluster contains one population—the Ecuadorean mainland (19). The second consists mainly of populations from large, high, and centrally located islands. These islands are San Cristóbal (1), San Salvador (12), Santa Cruz (9), Fernandina (10), Isabela (11) and two low islands very close to Santa Cruz, Seymour (7), and Baltra (8). The third cluster contains populations from Champion

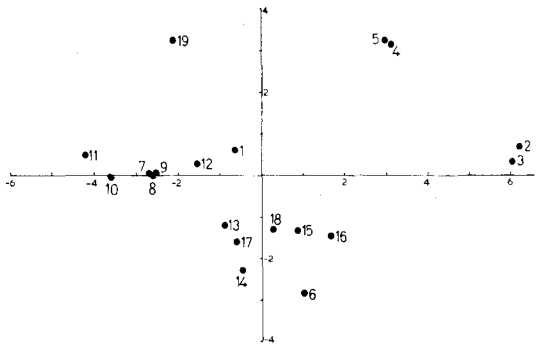

FIGURE 2. Canonical analysis of variation in three measurements of 18 Galápagos and the Ecuador populations of mockingbirds (males). See Figure 1 for geographical location of the island populations.

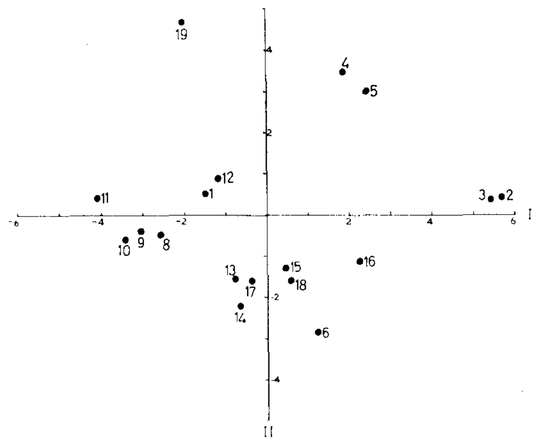

FIGURE 3. Canonical analysis of variation in three measurements of 17 Galápagos and the Ecuador populations of mockingbirds (females).

(4) and neighboring Gardner-near-Santa María (5), two small islands located SSE in the archipelago. Populations from small islands (Santa Fé [6], Rábida [13], Marchena [14], Pinta [15], Genovesa [16], Wolf [17], and Darwin [18]), predominantly those to the NW, N and NE, form the fourth cluster. The final cluster consists of populations from Española (2) and neighboring Gardner-near-Española (3), two small islands located SE of all others.

Populations on islands in the second cluster are morphologically most similar to that of the mainland. The first five islands in this cluster are all large and high, and have the most diverse habitats (Bowman 1961) and floras (Wiggins and Porter 1971). Presumably this ecological diversity is most similar to, but doubtless still less than, that of lowland mainland Ecuador.

Populations which differ most from the mainland population are on Española (2) and nearby Gardner (3), two low, arid islands in the SE part of the archipelago.

What features do the islands containing the populations in the second (1, 7, 8, 9, 10, 11) and the fourth (6, 13, 14, 15, 16, 17, 18) clusters have in common? Data are available on the distances between these islands (Admiralty Chart 1375), their areas, number of vegetation types present and flora size (Wiggins and Porter 1971). We do not have measures of population size for the mockingbirds, climate, or subtle ecological factors that the islands may have in common. Spearman rank-correlation coefficients were calculated for distance between mean vectors in cluster 2 (Figs. 2 and 3) and: (1) area ratio; (2) distance between corresponding islands; and (3) ratio of

TABLE 2. Sum-measure (arbitrary units) and island screen measure of isolation for each locality supporting mockingbird populations, in addition to sum-measure of morphological dissimilarity (arbitrary units) between all mockingbird populations.

Locality	Sum-measure of isolation	Island screen measure of isolation	Sum-measures of morphological dissimilarity	
			Male	Female
Wolf	274.7	0.01	46.5	43.3
Darwin	303.6	0.01	45.7	45.0
Pinta	179.9	0.04	48.0	43.4
Marchena	162.5	0.04	52.7	48.3
Genovesa	179.3	0.01	53.9	53.5
Fernandina	177.8	0.48	60.0	57.3
Isabela	130.3	0.69	72.4	64.7
San Salvador	133.1	0.39	45.1	45.9
Rábida	144.4	0.82	45.0	44.2
Seymour	142.7	0.35	50.9	—
Baltra	140.3	0.45	50.5	49.6
Santa Cruz	128.9	0.18	49.7	53.2
Santa Fé	150.5	0.16	60.6	57.3
Gardner (near Santa María)	175.1	0.18	79.2	67.7
Champion	167.7	0.28	79.2	68.5
San Cristóbal	177.6	0	45.5	45.4
Gardner (near Española)	195.1	0.39	95.2	82.5
Española	190.7	0.05	97.5	85.4
Lowland Ecuador	959.4	—	70.4	80.9

size of island floras. Results obtained for males were: -0.28 (not significant), 0.40 ($P < 0.05$) and -0.12 (not significant), respectively. With the females, all three coefficients (-0.13, 0.01, -0.36, respectively) were non-significant. This analysis was repeated on cluster 4. Corresponding coefficients were -0.13, -0.12, and -0.48 ($P < 0.05$) for males; and -0.24, -0.04, and -0.43 ($P < 0.05$) for females. These results are very difficult to interpret. We cannot explain why, in cluster 2, male populations show a significant correlation with distance, whereas female populations do not. The sign of the significant correlation obtained with cluster 4 suggests that islands with the most similar-sized floras have mockingbirds which are most dissimilar. Either these correlations are spurious (cluster 2) or they represent correlations with more biologically significant factors (cluster 4). Other relevant factors (such as winds, drift, and island ecology) that cannot be quantified as yet will be discussed later.

Our question as to whether the most isolated islands possess the most morphologically distinct populations was examined in two ways. Our first measure of isolation is the sum-measure index (Thornton 1967), which is calculated by measuring on a map the distance from each island supporting mockingbirds to all other islands that support them. Islands towards the periphery of the Archipelago have a high sum-measure (Table 2). The second measure, based on island screens (Levison et al. 1973), estimates the probability of colonists reaching an island from equal distances away. For example, each island is regarded as the center of a set of circles, which we arbitrarily designated with radii 50 km, 100 km, etc. Each circle intersects other islands in the Archipelago, and we measured the angles subtended by each arc that intersected islands at a distance of 50, 100 km, etc. The ratio, for each circle, of the total sum of these angles to 360° gives what we call the probability of propagules reaching the island in question from the surrounding islands which are intersected by that circle. The probabilities for the 50 km and 100 km circles are highly correlated ($r = 0.96$) so we used only the probabilities pertaining to the 50 km circles (Table 2).

The distinctiveness of each mockingbird population (Figs. 2 and 3) was assessed by measuring the distance between each mean vector and all other mean vectors (i.e., the generalized distance, Table 2). A high generalized distance signifies that a population is morphologically unlike others, and conversely for low generalized distances.

The rank correlation coefficients for analyses between the following pairs of variables were: generalized distance, all Galápagos populations plus Ecuador population versus sum-measure, 0.29 (males), 0.08 (females); generalized distance (Galápagos populations only) versus sum-measure, 0.14 (males), -0.08 (females); generalized distance (Galápagos populations only) versus island screen measure, 0.17 (males), 0.37 (females). None of these coefficients is significant. Therefore, we conclude that morphologically distinctive populations of mockingbirds are not confined to the most isolated islands. This suggests either that restriction of gene flow (as a simple correlate of distance) is not necessary for morphological distinctiveness to evolve, or that gene flow to some of the isolated islands is not infrequent. The first implies that selection pressures are strong enough and/or that drift is frequent enough to play a major part in changing morphology of populations; the second indicates that various islands will have morphologically similar populations mainly as a result of their positions relative to the wind patterns.

DISCUSSION

Lack (1947) showed that the same species of Darwin's finch frequently varied in beak morphology from island to island. He postulated that competition (dependent on the beak morphology of other finch species on the islands) was responsible for such shifts. Mockingbirds, which he did not examine, do not support this reasoning; they show just as much morphometric variation among islands as Darwin's finches, but they have no sympatric congeneric competitors anywhere in the Archipelago.

During the Pleistocene, when sea levels were about 100 m lower than at present, some of the smaller islands in the Galápagos that have mockingbirds were physically parts of larger islands. Thus, according to Admiralty Hydrographic Chart 1376, Fernandina was joined to Isabela, Rábida to San Salvador, Gardner (adjacent to Española) to Española, and Seymour and Baltra to Santa Cruz. Figures 2 and 3 indicate that only the pairs Fernandina-Isabela and Rábida-San Salvador show any marked morphological differentiation in their mockingbird populations. Such heterogeneity implicates ecological differences between islands as important.

The most morphologically distinctive populations are those on Gardner-near-Española (3), Española (2), Gardner-near-Santa María (5), and Champion (4). These islands are to the SE and S of the Archipelago and lie upwind of the prevailing winds which come from SSE-S (Alpert 1963). Alpert (1963) summarized the meager available data on average wind direction on Baltra. For eight months of the year winds blow predominantly from the SSE and in the other months from the E or SE. Thus, islands like Española and nearby Gardner are not in a good position to receive mockingbirds from the other islands: the populations on these islands are morphologically the most distinctive (Table 2, Figs. 2 and 3). Next, the satellite islands of Santa María (4, 5) are in a geographical position to receive mockingbirds, most likely from Española (2). It is noteworthy that the populations on Gardner-near-Santa María (5) and Champion (4) are morphologically more like that on Española (2) than that on geographically nearer San Cristóbal (1). The wind data could also explain why mockingbirds on Wolf, Darwin, Pinta, Marchena, and Genovesa are, although greatly isolated by distance, morphologically similar to those on San Cristóbal-Santa Cruz-San Salvador. Power (1975), in an analysis of the whole Galápagos avifauna, showed that islands to the NNW and NW had avifaunas more similar to those of the central islands than might be expected given the relatively great inter-island distances involved.

However, the position of an island relative to the prevailing wind does not totally account for the patterns in Figures 2 and 3. For example, it would not explain why the San Cristóbal (which has no island to the SE) birds are morphologically more like those of Santa Cruz than those of Española or the Santa María satellite islands. San Cristóbal, relative to the prevailing wind, is as isolated as Española or Santa María. We have also to explain why the morphological types on Española and the Santa María satellite islands are not widespread throughout the Archipelago because most of the islands lie downwind of Santa María and Española. First, the SE islands are probably the oldest (Bowman 1961) with the result that their populations may simply have had longer to diverge. The mockingbirds on Española and the Santa María outliers may be more sedentary than those elsewhere. The Española birds are known to behave differently than others, being aggressive and fearless (Bowman and Carter 1971). The absence of a morphologically distinctive San Cristóbal population suggests that this may have been one of the first islands to be colonized from mainland South America. The large size and height of this island would have prevented frequent constraints on population size as might have occurred on the smaller, drier Española and Santa María outliers. If these latter populations were derived from other islands, immigration would have been infrequent as it would have been against the prevailing wind; hence, the founder effect may have played a larger part in their evolution. Alternatively, Española and the islands near Santa María may have been colonized first from mainland South America and subsequently received no immigrants from the other islands after these were colonized.

Although the island of Santa Fé lies between the large, high islands of Santa Cruz and San Cristóbal, its mockingbirds more closely resemble those on Darwin, Wolf, Pinta, Marchena and Genovesa. These last islands (except Pinta which has a very small area of wet forest; R. I. Bowman, pers. comm.) have only coastal habitat. It is possible that selection has acted similarly on these islands, but this cannot be tested because no climatic data are available for any island except Baltra and the southern side of Santa Cruz. Of all the small low islands (excluding Gardner-near-Santa María and Champion, which have already been considered), Santa Fé and Genovesa have mockingbirds that differ most from those of the large, high islands.

Mockingbirds are apparently unable to maintain viable populations on small islets such as Daphne Major and the Plazas. However, Pinzón, which lies close to Isabela, Rábida and Santa Cruz and has an area of 18 km^2 (about the same as Genovesa), also does not support a mockingbird population. This island also lacks *Bursera* (present on nearly all islands), which provides a seed commonly eaten by mockingbirds; it is unlikely that this is the sole reason for the absence of mockingbirds. Although Pinzón is a central island it poses many biological enigmas (Thornton 1971). As mockingbirds have established themselves on the small, distant islands of Darwin and Wolf, it is likely that some ecological deficiency on Pinzón accounts for the absence of mockingbirds there. Nevertheless, movement of mockingbirds between close islands is apparently infrequent. Mockingbirds have been extinct on Santa María for over a century, but there are no records of vagrants which might precede re-establishment there. During World War II, Baltra was a military base and soldiers there exterminated the mockingbird population (Thornton 1971). Mockingbirds have not reestablished themselves during the past 30 years by crossing the 1-km strait from Santa Cruz.

In terms of subspecies, our results (Figs. 2 and 3) suggest that populations 11, 10, 7, 8, 9, 1, 12 form a loose cluster which is fairly distinct from numbers 13, 17, 14, 15, 18, 6 and 16. The first group consists of populations on either large or central islands, and the second of populations on small central and northern islands. These two groups can be treated as either comprising two subspecies of a single species or as two species. Most previous taxonomic treatments have taken population 1 as a distinct species and have recognized many of the populations in the second cluster 6 (Figs. 2 and 3) as distinct subspecies. Our analysis shows that population 1 is not morphologically distinct enough to warrant recognition as a separate species.

SUMMARY

Variation in bill, tarsus and wing length in all Galápagos populations and the closest mainland (lowland Ecuador) population of mockingbirds was examined with canonical variates analysis. Birds on the large, high islands are similar morphologically to those on the mainland. Populations most dissimilar to the Ecuadorean one are those on Española, Gardner-near-Española, and Santa Fé. Within the Archipelago, four southern islands (Gardner-near-Santa María, Champion, Española, Garder-near-Española) have the most distinctive populations. Mockingbirds on small, low islands show varying degrees of morphological divergence from those on the large, high islands. Possible evolution of the Galápagos populations is discussed in terms of genetic bottlenecks on small islands, and gene flow among populations, depending on an island's position in relation to prevailing winds.

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Department of Soil Science and Plant Nutrition, University of Western Australia, Nedlands, West Australia 6009. Accepted for publication 6 October 1977.