ALTITUDINAL VARIATION IN A RESIDENT AND A MIGRANT PASSERINE ON JAMAICA

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THE body size of many bird species varies with altitude. Such variation may be clinal or discontinuous, and is often the basis for subspecific differentiation. Altitudinal variation has been described on continents (Traylor 1950; Moreau 1957; Hamilton 1958, 1961; James 1970; Power 1970) and the very large island of New Guinea (Rand 1936; Mayr 1940). During a study of forest birds on the relatively small island of Jamaica (11,740 sq km), unsuspected altitudinal variation in body size was detected in one species, the resident Bananaquit, *Coereba flaveola,* one of seven species (four resident and three migrant) that were mist-netted commonly between sea level and 1,100 m. Some evidence, based on very small samples, showed similar altitudinal variation in the migrant Black-and-White Warbler, *Mniotilta varia.* The purpose of this paper is to present this information and to relate it to what is known of variation in these species on the continent.

METHODS

Birds were caught in mist nets at four trapping sites, chosen to include the most important habitats within about 5 km of the capital, Kingston. The lowest site (154 m above sea level) was Port Henderson Hill, a tract of arid secondary scrub on limestone on the south coast, and the highest, Green Hills (1,077 m), was in montane forest on the windward (northern) side of the western end of the Blue Mountain range. The other two sites, Mona (185 m) and Irish Town (769 m), were respectively semirural and rural areas approximately intermediate in climate and location between the two extreme sites. Data from a few birds caught in other places have been included with those from the nearest regular trapping site.

Wing length was measured to the nearest 0.5 mm with a stopped rule, the wing being held in its natural position without being flattened or straightened. Bill length (exposed culmen) was measured to the nearest 0.1 mm with vernier calipers, and weight was measured to the nearest 0.25 g with a Pesola spring balance.

Mean weights before 10:00 averaged 4 percent less than later weights; all weights in this paper are "morning" weights, those taken after 10:00 having been corrected by subtracting 4 percent. Subcutaneous fat was estimated on a scale of 0 (none) to 3 (fat mounded) in each of four parts of the body: furculum (tracheal pit), axilla, abdomen, and rump. Museum specimens were measured in the same way as live birds, except that the wing was straightened and flattened. Possible shrinkage of skins does not affect the results, as no direct comparisons are made between absolute measurements of skins and of live birds.

Trapping was carried out between October 1970 and April 1971. Skins measured were from the collections of the British Museum (Natural History) and the United States National Museum.

TABLE 1

ALTITUDINAL VARIATION IN BANANAQUITS[1]

Altitude x	Number measured	Mean y	CV[2]	Regression equation: $y = m.x + c$			Correlation coefficient
				m	SE of m	c	
Jamaica							
Wing length							
1077	44	57.11	4.79				
769	60	57.10	3.84				
185	47	55.79	4.70				
154	89	55.59	4.13				
All	240	56.29	4.45	0.0018	0.0004	55.398	0.278[3]
Bill length							
1077	45	12.49	4.44				
769	60	12.01	4.43				
185	41	12.27	3.97				
154	84	11.88	4.40				
All	230	12.10	4.72	0.0004	0.0001	11.912	0.257[3]
Weight							
1077	44	8.72	8.80				
769	66	8.37	7.32				
185	36	8.44	5.81				
154	102	8.05	9.28				
All	248	8.31	8.30	0.0005	0.0001	8.066	0.284[3]
South and Central America							
Wing length							
Males only	64	57.00	5.30	0.0022	0.0003	55.136	0.668[4]
Males below 1,000 m	38	55.91	4.22	0.0022	0.0013	55.250	0.263
Females only	25	54.10	5.44	0.0004	0.0009	53.848	0.082
All	89	56.15	5.87	0.0019	0.0003	54.614	0.515
Bill length							
Males only	58	12.59	9.95	0.0008	0.0002	11.877	0.508[4]
Males below 1,000 m	34	12.28	7.83	0.0006	0.0006	12.086	0.180
Females only	25	11.88	5.58	0.0004	0.0002	11.609	0.346
All	83	12.38	9.32	0.0008	0.0002	11.736	0.496[3]

[1] Measurements in mm, weight in g, altitude in m.

[2] CV = coefficient of variation.

[3] $P < 0.01$.

[4] $P < 0.001$.

RESULTS

Bananaquits.—The means and coefficients of variation of the weights and measurements of the adult Bananaquits caught at each trapping site, and the equations of the calculated regressions of these on altitude, are given in Table 1. Wing length, bill length, and weight were all positively correlated with altitude. Square root and logarithmic transformations of altitude did not improve the predictive power of the regression, nor did multiple regressions on altitude and mean annual rainfall, because altitude and rainfall are highly correlated ($r = 0.98$).

The amount of visible subcutaneous fat did not differ significantly between sites (mean fat scores 4.4 Port Henderson, 3.7 Mona, 3.0 Irish Town, 3.5 Green Hills).

TABLE 2

ALTITUDINAL VARIATION IN WING LENGTH IN BLACK-AND-WHITE WARBLERS IN JAMAICA[1]

				Regression equation: $y = m.x + c$; correlation coefficient (r)			
Altitude	Number measured	Mean	SE of mean	m	SE of m	c	r
Females							
1077	2	69.75	0.25	0.00233	0.00079	66.536	0.506[2]
769	10	68.10	0.41				
185	10	67.35	0.35				
154	5	66.30	0.92				
Males							
1077	2	71.13	0.43	0.00281	0.00099	68.220	0.634[3]
769	4	71.00	0.41				
185	3	69.00	0.58				
154	5	68.30	0.75				

[1] Measurements in mm, altitude in m.

[2] $P < 0.01$.

[3] $P < 0.02$.

Black-and-White Warblers.—In this species, unlike the Bananaquit, the sexes can be distinguished by plumage characters. Only wing length is correlated with altitude (Table 2), and this correlation is found in both sexes, altitude accounting for more of the variation in wing length in males (40 percent) than in females (26 percent). When both sexes are taken together, altitude accounts for only 23 percent of the variation in wing length. Males averaged about 1.9 mm longer in the wing than females ($P < 0.001$, t-test).

DISCUSSION

Bananaquits.—The usual evolutionary interpretation of altitudinal variation in size, and the one adopted here, is that the size of the bird is adapted to the climate in which it lives. This relationship has been expressed by Bergmann's rule, which states that the members of a polytypic species that live in the cooler parts of the species' range are larger than those in the warmer parts. Although this relationship is well-established empirically for birds, its physiological basis has been challenged (Scholander 1955; McNab 1971), and some notable anomalies have been described. Still no better explanation has been put forward that would apply to the size cline described here. McNab (1971) suggested that latitudinal variation in body size is due to similar trends in prey species or to the presence or absence of competitors of similar body size. In the present case there is no evidence for the former, and the latter, which is ruled out here by the absence of any

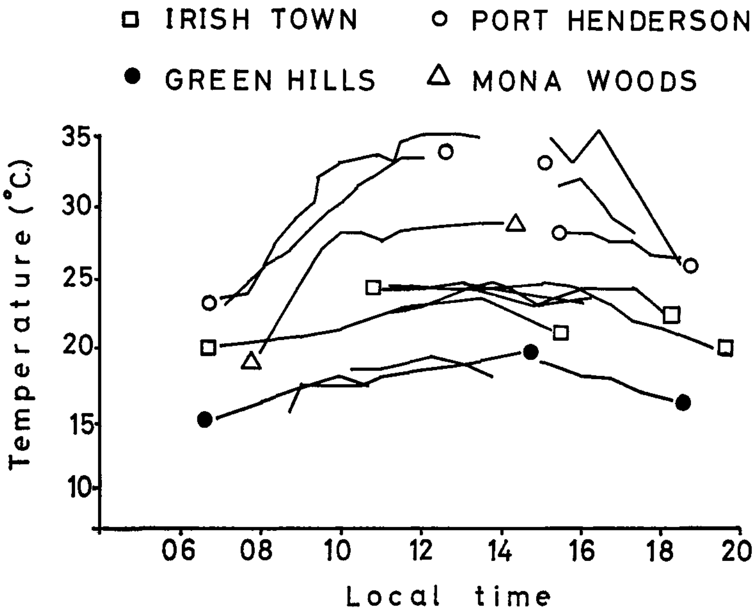

Figure 1. Diurnal changes in temperature at each trapping site in Jamaica. Each line represents 1 day's records. Records were made as opportunity offered and therefore may not be strictly representative.

such competitor, would in any case account only for a discontinuous, rather than a clinal, variation in body size.

An additional factor that might select for smaller body size in the hotter parts of Jamaica is the restriction of feeding time by high ambient temperatures. Temperatures increased very rapidly between dawn and about 10:00 at the two lowest sites, whereas at the two higher ones they increased much more gradually to a low peak in midafternoon (Figure 1). Birds in the latter two areas can probably feed throughout the day without encountering thermoregulation problems, whereas in the lowlands, heat stress may well depress feeding activity after about 10:00. The effect of high ambient temperature in depressing feeding activity has been shown in the House Sparrow, *Passer domesticus*, by Kendeigh (1969).

Comparison with mainland populations.—If this interpretation of the variation in body size is valid for Bananaquits, populations elsewhere subject to similar environmental gradients should show parallel variation. To test this, I measured skins collected in other parts of the species' range in continental South and Central America. Table 1 and Figure 2 show the regressions of these measurements on altitude, and Figure 2 also shows the regression line calculated for live Jamaican birds. Three features of these

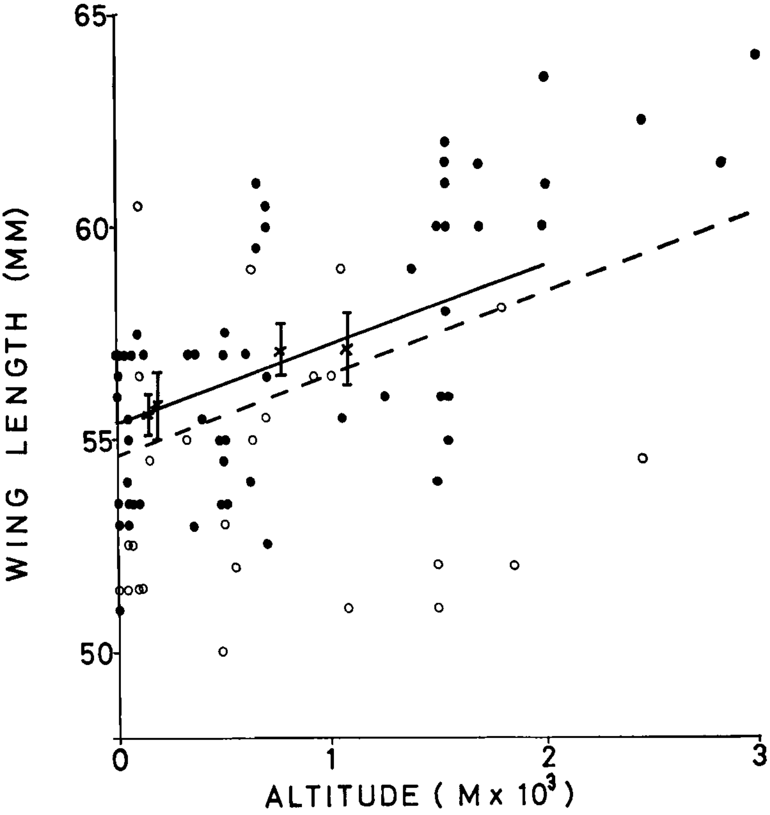

Figure 2. Regressions of adult Bananaquit wing length on altitude. Circles: mainland specimens (solid: males, hollow: females). Cross and vertical bar: mean and 95 percent confidence intervals for each trapping site in Jamaica. Solid line: regression of all Jamaican birds. Dashed line: regression of mainland males. (For regression equations, see Table 1.)

relationships deserve mention: 1) The slopes of the two regression lines are similar ($P > 0.1$, t-test). 2) On the mainland only males show a significant relation between wing length and altitude. 3) Altitude apparently has little effect on either wing or bill length at elevations below 1,000 m on the continent. This is confirmed by a regression on altitude of the measurements of specimens collected below 1,000 m, which is not significant ($P > 0.1$). It also probably explains why females show no altitudinal variation, as most were collected below 1,000 m and none above 1,800 m.

Both on Jamaica and on the continent, the increase in wing length is slightly less than 2 mm for every 1,000 m increase in altitude. Although

TABLE 3

ALTITUDINAL DISTRIBUTION OF AGE OF SEX CLASSES OF BLACK-AND-WHITE WARBLERS

Altitude	Ad ♂	Im ♂	♂ of unknown age	Ad ♀	Im ♀	♀ of unknown age
1077	2	0	0	0	0	2
769	3	2	0	2	0	14
185	1	0	1	1	1	10
154	2	3	0	0	1	5

this may seem too small a difference to be of adaptive significance, it is only slightly less than that reported by Moreau (1957) in African white-eyes Zosteropidae (2.3 mm per 1,000), and is thus equally likely to be adaptive.

The amount of variation explained by the regression is very small (8 percent Jamaica, 25 percent mainland). Much of the variation in the Jamaican sample is probably attributable to sexual dimorphism; the sexes cannot be distinguished by plumage characters, but museum specimens show that males are longer-winged than females. Sexual dimorphism can be eliminated as a complicating factor in the mainland specimens (unless any were wrongly sexed), in which the regression for males alone accounts for 45 percent of the variation whereas the regression of both sexes together accounts for only 25 percent.

Other island populations.—The only other island on which Bananaquits from different altitudes have been measured is Trinidad (measurements supplied by D. W. Snow). The regression of wing length on altitude is not significant, probably because the maximum altitude on Trinidad is only 950 m and so the variety of habitats is less than on Jamaica (maximum elevation 2,280 m) and the mainland.

The Bananaquit is one of the most variable of species; Lowery and Monroe (1968) recognized 41 subspecies. It is therefore not surprising that it should show significant variation in body size, but it is perhaps unexpected that the altitudinal component of this variation is strong enough to be recognizable despite the influences of the many other factors that might affect body size. On the mainland of South and Central America, birds showing altitudinal variation (i.e. those collected at elevations of 1,000 m or more) are currently placed in seven different subspecies, based mainly on plumage characters and only partly on size.

Black-and-White-Warblers.—It is possible that the altitudinal variation in wing length shown by this species is a result of young birds settling at lower altitudes than adults in the winter. Too few birds could be aged accurately to eliminate this possibility, and Table 3, though based on small samples, suggests that birds of different ages might select different altitudes. However the data do raise the possibility that altitudinal variation may exist in adults, and the point will therefore be discussed further.

Of the three migrant warblers that occurred regularly at all the trapping sites in Jamaica, and in which altitudinal variation might have been detected, only the Black-and-White Warbler showed such variation. This may be because only one population of each of the other two warblers (Common Yellowthroat, *Geothlypis trichas*, and American Redstart, *Setophaga ruticilla*) winters in Jamaica, whereas several populations of the Black-and-White Warbler winter together in Jamaica. Although no geographical variation has been described in this species, my data suggest that such variation may exist. It is also to be expected on the grounds that the Black-and-White Warbler has the most extensive breeding range, covering about 34 degrees of latitude, of any North American warbler. Each of the five species with the next largest breeding ranges (Orange-crowned, Yellow, and Wilson's Warblers, *Vermivora celata*, *Dendroica petechia*, and *Wilsonia pusilla*, Common Yellowthroat, and American Redstart) is separated into at least two subspecies (twelve in *Geothlypis*) in the A.O.U. Check-list (1957). Further study of variation in the wing length of Black-and-White Warblers in relation to environmental gradients would be expected to reveal a pattern at least as marked as that in Jamaica.

Altitudinal variation in other island birds.—Altitudinal variation has been reported from only three other islands. Snow and Snow (1963) found that species of *Manacus* and *Turdus* on Trinidad were lighter and shorter-winged in the lowlands than in the mountains, but their samples were too small to test these differences. Altitudinal variation in size is also shown by the birds of New Guinea which, with an area of over 881,000 sq km, is nearly eight times the size of Jamaica and is more nearly a continent than an island. Of the bird species Rand (1936) studied in the New Guinea archipelago, 33 percent showed a positive correlation between wing length and altitude (compared, for example, with 45 percent in Bolivia (Traylor 1950)). Two of the species in which altitudinal variation was most marked —a cockatoo, *Cacatua galerita,* and a honeyeater, *Foulehaio carunculata*— Mayr (1940) described as examples of random geographical variation in size, but later (1942) he reinterpreted the variation in *Cacatua* in ecological terms, birds on low hot islands (with two exceptions) being smaller than those on large humid ones. Recently Gill (1973) found altitudinal variation in wing length in the white-eye, *Zosterops borbonica,* on Reunion Island, and interpreted the variation in terms of thermoregulation. Altitudinal variation in size may prove to be a widespread phenomenon in island birds when it is more thoroughly investigated.

ACKNOWLEDGMENTS

This work formed part of a study of the annual cycles of Jamaican forest birds under the direction of D. Lack, supported by a grant from the Natural Environment Research Council. My wife and P. Lack helped with the field work. Permission to use the Field Station of the Institute of Jamaica at Green Hills, and the hospitality of the Zoology Department of the University of the West Indies at Mona, are gratefully acknowledged. I also thank D. Amadon for the loan of specimens from the American Museum of Natural History, and D. W. Snow for measurements of Trinidad Bananaquits and for access to specimens in the British Museum (Natural History) at Tring. Earlier drafts of this paper were improved by criticisms from P. R. Grant, M. P. Harris, C. Kepler, D. Lack, C. M. Perrins, and D. W. Snow. R. J. O'Connor gave valuable assistance with computer facilities.

SUMMARY

Wing length, bill length, and weight of adult Bananaquits in Jamaica are positively correlated with altitude and mean annual rainfall. Adult male Bananaquits throughout the range of the species in continental South and Central America show similar variation in wing and bill length. This variation, and that on Jamaica, is interpreted in terms of Bergmann's ecogeographic rule.

Black-and-White Warblers of both sexes show altitudinal variation in wing length on Jamaica; this may be due either to selection of different altitudes by birds of different ages, or to hitherto unrecognized variation in relation to climate in the species' breeding quarters.

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