GEOGRAPHIC VARIATION IN BODY MASS OF THE BANANAQUIT (*COEREBA FLAVEOLA*) IN THE TRINIDAD AND TOBAGO ARCHIPELAGO

FLOYD E. HAYES[1], STEWART A. WHITE[2], RICHARD P. FFRENCH[3], AND STEFAN BODNAR[4]

[1]*Department of Life Sciences, University of the West Indies, St. Augustine, Trinidad and Tobago*; Current address: *Department of Biology, Pacific Union College, Angwin, CA 94508,* USA; [2]*Department of Environmental and Evolutionary Biology, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ,UK*; [3]*Toftingal, Laurieston Road, Gatehouse of Fleet, Dumfries and Galloway DG7 2BE, UK*; and [4]*995 Chester Road, Birmingham B24 0HG, UK*

Abstract.—An analysis of body mass data from 1571 individual Bananaquits (*Coereba flaveola*) within the Trinidad and Tobago archipelago revealed significant differences among six geographic regions. Multiple comparison tests indicated two geographic trends in body mass variation. First, body mass was higher in the mountains, where temperature is cooler and humidity higher, than in the lowlands of both Trinidad and Tobago. Second, there was a west-east trend toward higher body mass from the Bocas Islands and Trinidad in the west to Tobago and Little Tobago in the east. An inverse correlation between temperature and body mass was consistent with Bergmann's rule. The relationship between body mass and humidity was less clear. An assessment of published data on the foraging ecology, interspecific competition, genetic drift, and predation of Bananaquits in the archipelago failed to find any other satisfactory explanation for geographic variation in body mass.

Key words: *Bananaquit*, *body mass*, Coereba flaveola, *geographic variation*, *Trinidad and Tobago archipelago*

*Resumen.—*VARIACIÓN EN MASA CORPORAL DEL MIELERO FLAVO (*COEREBA FLAVEOLA*) EN EL ARCHIPIÉLAGO DE TRINIDAD Y TOBAGO. Un análisis de datos de masa corporal de 1541 individuos del Mielero Flavo (*Coereba flaveola*) en el archipiélago de Trinidad y Tobago demostró diferencias significativas entre seis regiones geográficas. Pruebas de comparaciones múltiples indicaron dos patrones geográficos en la variación de masa corporal. Primero, la masa corporal fue mayor en las montañas, donde la temperatura es más fría y la humedad es más alta, que en las tierras bajas de Trinidad y Tobago. Segundo, hubo un patrón ascendente de masa corporal de oeste a este, de las islas Bocas y Trinidad en el oeste hasta Tobago y Little Tobago en el este. Una correlación inversa entre la temperatura y masa corporal concordó con la regla de Bergmann. La relación entre masa corporal y humedad fue menos clara. Una evaluación de datos publicados sobre la ecología de forrajeo, la competencia interespecífica, la deriva genética y la depredación sobre el Mielero Flavo en el archipiélago no encontró otra explicación adecuada para la variación geográfica en masa corporal.

Palabras clave: archipiélago de Trinidad y Tobago, Coereba flaveola, *masa corporal*, *Mielero Flavo*, *variación geográfica*

Résumé.—VARIATION DE LA MASSE CORPORELLE DU SUCRIER À VENTRE JAUNE (*COEREBA FLAVEOLA*) DANS L'ARCHIPEL DE TRINITÉ ET TOBAGO. L'analyse de la masse corporelle de 1571 sucriers à ventre jaune provenant de l'archipel de Trinité et Tobago a révélé des différences significatives parmi les 6 régions géographiques. Des tests de comparaison multiple ont montré deux tendances géographiques dans la variation de poids. Premièrement, cette masse corporelle est supérieure dans les montagnes où la température est plus fraîche et l'humidité plus élevée par rapport aux zones de basse altitude de Trinité et de Tobago. Deuxièmement, il existe un gradient croissant depuis les îles terme et Trinité à l'ouest vers Tobago et Little Tobago à l'est. La corrélation inverse entre masse corporelle et température est encore avec la loi de Bergmann. La relation entre masse corporelle et humidité est moins claire. Une étude des données publiées sur l'écologie de l'alimentation, la compétition interspécifique, la dérive génétique et la prédation des sucriers n'a pas permis de trouver d'explication satisfaisante pour cette variation géographique de la masse corporelle.

Mots-clés: Sucrier à ventre jaune, masse corporelle, Coereba flaveola*, variation géographique, archipel de Trinité et Tobago*

THE IMPORTANCE OF documenting geographic variation in organisms has long been recognized by evolutionary biologists who seek to understand the underlying causes of such variation (e.g., Mayr 1970, Gould and Johnston 1972). In birds, geographic variation in body size is typically attributed to natural selection, environmental induction, or stochasticity (Zink and Remsen 1986). The strong correlation of intraspecific variation in body size in birds with climatic and topographical variables, coupled with a high degree of concordance among species, suggests that such variation is the result of natural selection for polygenic traits representing adaptation to local conditions (e.g., James 1970, Zink and Remsen 1986). However, experimental transplants of Red-winged Blackbird (*Agelaius* *phoeniceus*) eggs between distant regions demonstrated that a significant proportion of regional differences in body size was attributable to non-genetic environmental induction (James 1983). Because a plethora of ecological variables (e.g., annual productivity, degree of seasonality, habitat quality, food availability, prey size, competition, and predation) potentially affect body size and presumably covary with climate and topography (e.g., James 1970, Cody 1974, Case 1978, Zink and Remsen 1986), seeking the causes of geographic variation in body size is exceedingly difficult, requiring considerable study.

The Bananaquit (*Coereba flaveola*) is a widely distributed passerine exhibiting considerable geographic variation in plumage within the Caribbean region (see Seutin *et al.* 1994 and references therein) and elsewhere in the Neotropics (e.g., Ridgely and Gwynne 1989, Ridgely and Tudor 1989, Howell and Webb 1996). Diamond (1973) demonstrated that body mass, bill length, and wing length of the Bananaquit were significantly correlated with elevation in Jamaica, and that bill length and wing length (insufficient data for body mass) were similarly correlated with elevation in Central America and South America. In the Trinidad and Tobago archipelago, which is inhabited by the black-backed, yellow-bellied subspecies *C. f. luteola* of northern South America, Snow and Snow (1963) and ffrench (1973, 1991) reported that the body mass of populations inhabiting the relatively dry Bocas Islands off northwestern Trinidad averaged lower than the populations on Trinidad and Tobago. Feinsinger *et al.* (1985) reported no significant differences in body mass of Bananaquits between Trinidad and Tobago. However, these studies did not compare body mass of montane and lowland populations on Trinidad or Tobago, or on Little Tobago at the eastern end of the archipelago. In this paper we provide a more thorough comparison of geographic variation in body mass of the Bananaquit throughout the Trinidad and Tobago archipelago, and discuss the potential causes of such variation.

METHODS

We obtained body mass data from 1571 Bananaquits during routine mist-netting operations conducted intermittently by ourselves and others throughout the Trinidad and Tobago archipelago from 1958 to 2002. Each captured individual was weighed with a spring scale to the nearest 0.1 or 0.5 g. Because of the difficulty of sexing and aging captured individuals, the data for sex and age classes, as well as during all seasons of the year, were combined for analysis. We did not attempt to analyze other body size measurements because of variation by investigators in the measurements obtained.

Table 1. Geographic variation in body mass (g) of the Bananaquit (*Coereba flaveola*) in six regions of the Trinidad and Tobago archipelago.

Region	Mean	SD	Min	Max	*n*
Bocas Islands	9.4	0.97	7.0	11.5	127
Trinidad, Northern Range	10.5	0.91	6.0	13.8	967
Trinidad, Lowlands	10.2	0.90	6.5	12.5	254
Tobago, Main Ridge	11.0	0.82	9.5	13.6	77
Tobago, Lowlands	10.5	0.79	9.0	13.0	95
Little Tobago	10.5	0.97	8.6	13.0	67

For the purposes of analysis, we combined data within six regions. These include: (1) Bocas Islands (elevation <100 m): Chacachacare and Monos (D. Snow and B. Snow, 17 October 1958 to 13 April 1960, n = 55; ffrench, 19 February 1961 to 22 June 1975, n = 61; Bodnar, 30 September to 7 October 1999, n = 10); (2) Northern Range of Trinidad (elevation 240–900 m): El Tucuche, Paria Springs, Morne Bleu, Las Lapas, and Arima Valley (ffrench, 23 April 1962 to 24 April 1982, n = 140; White, 11 July 1994 to 19 August 2001, n = 797; Hayes, C. Ramjohn, and Bodnar, 3 October 1999 to 10 March 2002, n = 30); (3) Lowlands of Trinidad (elevation <100 m): Arena Forest Reserve, Rio Claro, Victoria-Mayaro Forest Reserve, and Guayaguayare (T. Lovejoy, 24 June to 24 July 1973, n = 63; White, 29 August 1994 to 8 August 2001, n = 191); (4) Main Ridge of Tobago (elevation 300–550 m): Centre Hill, Gilpin Trace, and Argyle River Trail (Hayes, 30 June 1996 to 8 August 2001, n = 77); (5) Lowlands of Tobago (elevation <100 m): Grafton Estate (ffrench, 18 May 1974 to 13 April 1975, n = 79); and (6) Little Tobago (elevation <100 m; Bodnar, 12 October 1999 to 30 June 2000, n = 67).

Because the distributions tended to be bimodal rather than normal, presumably due to sexual dimorphism, the assumptions of parametric tests were not met. We therefore used a non-parametric Kruskal-Wallis test (H statistic) to test for differences among the six regions, and non-parametric multiple comparison tests between pairs of regions (Zar 1984). The statistical tests were computed with Statistix 7.0 software (Anonymous 2000), with two-tailed probabilities and $\alpha = 0.05$.

Table 2. Matrix of non-parametric multiple comparisons of body mass (g) of the Bananaquit (*Coereba flaveola*) among six regions of the Trinidad and Tobago archipelago. S = significant; NS = non-significant.

		Trinidad		Tobago	
Region	Bocas Islands	N. Range	Lowlands	M. Ridge	Lowlands
Trinidad, Northern Range	S				
Trinidad, Lowlands	S	S			
Tobago, Main Ridge	S	S	S		
Tobago, Lowlands		S	NS	NS	S
Little Tobago	S	NS	NS	S	NS

RESULTS

The body mass of Bananaquits varied significantly among the six regions ($H = 165.2$, $P < 0.0001$; Table 1). Multiple comparison tests (Table 2) revealed that body mass was significantly lower in the Bocas Islands and significantly higher in the Main Ridge of Tobago than in any other region. Body mass was significantly higher in the Northern Range than in the Lowlands of Trinidad, and significantly higher in the Main Ridge of Tobago than in the Lowlands of Tobago. Body mass was significantly higher in the Main Ridge of Tobago than in the Northern Range of Trinidad, but was not significantly higher for the Lowlands of Tobago than in the Lowlands of Trinidad. Body mass in Little Tobago was significantly lower than in the Main Ridge of Tobago and significantly higher than in the Bocas Islands.

DISCUSSION

A variety of univariate and multivariate metrics have been used to assess body size in birds; of the univariate metrics, body mass and tarsus length appear to be the most accurate (Rising and Somers 1989, Freeman and Jackson 1990). Although body mass is more readily available and widely used than tarsus length, individual variation in body mass may be considerable due to variability in nutrition, time of day, season, migration, age, sex, and reproductive status (Clark 1979). Thus, our data should be viewed with caution. However, the large sample sizes for most of our regions would tend to minimize the effects of individual variation.

Our data revealed two clear trends. First, body mass was higher in the mountains, where temperature is cooler and humidity is lower (Berridge 1983), than in the lowlands of both Trinidad and Tobago. The same trend has been documented in Jamaica, Central America, and South America (Diamond 1973). Second, there was a west-east trend toward higher body mass from the Bocas Islands and Trinidad in the west to Tobago and Little Tobago in the east. Temperatures in the more oceanic, windward islands of Tobago and Little Tobago probably average cooler, with less seasonal variation, than at corresponding elevations in Trinidad and the Bocas Islands (Berridge 1983). The relationship between body mass and temperature in this study appears to be consistent with Bergmann's "rule," which predicts that body size is inversely correlated with temperature (James 1970, Zink and Remsen 1986).

Bergmann's rule has also been modified to predict that body size is inversely correlated with humidity (James 1970). However, our data contradicted this prediction in that body mass was lowest in the relatively dry Bocas Islands, situated in the rain shadow of Trinidad (Berridge 1983, Hayes and Samad 2002), and highest in the humid mountains of Trinidad and Tobago. Because body mass was significantly higher in Little Tobago, at the east end of the archipelago, than in the similarly dry Bocas Islands at the west end (Berridge 1983), humidity alone cannot explain geographic variation in body size. Bananaquit densities are sensitive to the severity of drought, which is greater in lowlands than in mountains (Faaborg *et al.* 1984), and may affect body mass as well. But this hypothesis is apparently falsified by the significant differences in body mass between the Bocas Islands and Little Tobago, which are probably subject to similar periods of drought.

In a comparative study of nectar-feeding bird guilds in Trinidad and Tobago, Feinsinger *et al.* (1985) provided crucial data for several ecological variables potentially affecting body size in Bananaquits, which forage chiefly on nectar (Snow and Snow 1971). Seasonal variation in the nectar supply was a hundredfold on both islands, with alternating periods of surplus and shortages in supply. The guild-wide ratio of demand to supply for nectar was no more variable on either island, and the median monthly ratio of demand to supply did not differ significantly between the two islands. Neither the median monthly diet breadth of the guild nor the diet breadth of Bananaquits differed significantly between the two islands. Diamond (1973) suggested that heat stress limiting foraging at midday may explain the lower body mass of Bananaquits at lower elevations in Jamaica, Central America, and South America, but no data are available on the foraging rates of Bananaquits within the archipelago. These results suggest that variation in seasonality, productivity, food availability, and diet may not provide an adequate explanation for geographic variation in body size of Bananaquits. Further studies, however, are warranted.

Reduced interspecific competition in Tobago and Little Tobago, which have fewer species of birds than Trinidad (ffrench 1973, 1991), might explain the trend for larger body mass on these islands, but Feinsinger *et al.* (1985) found no significant differences in the intensity of exploitative competition with other species on the two islands, and reported that Bananaquits won a significantly higher proportion of interspecific aggressive encounters in Trinidad than in Tobago. Furthermore, body mass was significantly smaller in the Bocas Islands, which have fewer species and presumably less interspecific competition than Tobago (Hayes and Samad 2002).

Feinsinger *et al.* (1985) suggested that the larger body size of several hummingbird species in Tobago might be explained by genetic drift (stochasticity). Because the correlation of body mass with elevation in Bananaquits occurs in other parts of its range (Diamond 1973) and numerous other species of birds average larger body size in Tobago than in Trinidad, including a handful of endemic subspecies in Tobago recognized solely on the basis of larger size (ffrench 1973, 1991), such concordance is unlikely to be explained by stochasticity alone. Feinsinger *et al.* (1985) also suggested that larger body size in Tobago may be due to the founder effect (a form of genetic drift), in which the most likely colonists from Trinidad populations might be those phenotypes having the longest wings or largest fat reserves. However, Tobago was almost certainly connected with Trinidad during the most recent glacial periods (Comeau 1991), when considerable gene flow must have taken place.

Predation may also account for geographic variation in body size, but no data are available on annual survivorship or predation rates of Bananaquits in the archipelago. However, all six regions are inhabited by bird-eating snakes (Murphy 1997) and raptors (ffrench 1991).

Finally, in a review of this paper, J. M. Wunderle (pers. comm.) suggested that the impact of hurricanes presumably increases competition for nectar and might put a premium on large body mass for competitive interactions during post-hurricane food shortages. In Jamaica, Bananaquits declined sharply and apparently moved from montane to lowland habitats following Hurricane Gilbert in 1988 (Wunderle *et al.* 1992). Although Tobago may experience a higher hurricane strike frequency than Trinidad, both islands are south of the normal western Atlantic hurricane paths and are only rarely subjected to hurricanes; the most recent strikes were in Tobago in 1963 and Trinidad in 1933 (ffrench 1973, 1991, Berridge 1983).

In conclusion, temperature appears to be the only factor correlated with geographic variation in the body mass of Bananaquits in this study, but because of the complexity of ecological interactions, seeking a single explanation may be elusive. Furthermore, it remains uncertain whether such variation is heritable or induced by the environment. Egg transplantation experiments such as those conducted by James (1983) would be useful to assess the roles of environment and heritability in the ontogeny of body mass in Bananaquits.

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