

# MOVEMENTS OF ADULT AND JUVENILE BANANAQUITS WITHIN A MORPH-RATIO CLINE

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**ABSTRACT.**—Adult and juvenile Bananaquits (*Coereba flaveola*) were captured and banded at nine different sites in southern Grenada in August–October 1976, 1977, and 1978. The proportion of black morphs decreased to seaward on Point Saline. The morph-ratio cline was steeper for adults than for juveniles, because juveniles move greater distances than postbreeding adults. Home-range sizes of adults are larger during the dry season than in the wet season, which under some circumstances can bring about temporal changes in the steepness of a cline. Received 22 September 1980, accepted 26 January 1981.

DESPITE the substantial theoretical literature on clines (for a review see Endler 1977), few empirical studies of avian clines needed to test this theory have been reported (i.e. O'Donald and Davis 1959, Southern 1962, Cooch 1963, Gill 1973, Cooke et al. 1975). To understand the interacting forces producing a cline, it is often necessary to have a thorough knowledge of the organism's biology. For example, information concerning dispersal distances is essential for obtaining estimates of gene flow. In addition, it may be valuable to determine the distances over which an organism forages within a cline, as well as its general foraging behavior. For instance, this may help us to understand whether the organism interacts with the critical environmental variables in a coarse-grained or fine-grained fashion. Changes in foraging distances (i.e. home-range sizes) might change the steepness of some clines. The purpose of this paper is to describe the movements of adult and juvenile Bananaquits (*Coereba flaveola*) and their effects upon a morph-ratio cline on the island of Grenada, West Indies.

The two Bananaquit color morphs in the morph-ratio cline on Grenada have been described in detail by Wunderle (1981). The yellow-breasted morph (designated as the yellow morph) is restricted to the dry southwest and the northeast portions of the island. The melanic (designated as the black morph) is found throughout the island with reduced numbers in the southwest and the northeast regions of Grenada. This paper first describes the postbreeding season movements of adults and juveniles of the two morphs within the cline and then examines the seasonal trends in foraging movements.

## STUDY SITE AND METHODS

Grenada, with an area of 310 km<sup>2</sup>, is located at the southern end of the Lesser Antilles. The annual pattern of rainfall is seasonal, with a distinct dry season from January through May. This study was conducted in the driest, southwest section of the island (Fig. 1). The severe dry season of this area is correlated with a deciduous thorn scrub vegetation (Beard 1949), although much of this area has now been extensively disturbed by man for resort or agricultural purposes.

At the end of the local Bananaquit breeding season in late August through October 1976, 1977, and 1978, I mist-netted foraging Bananaquits at nine different locations (Fig. 1). These particular sites were chosen because Bananaquits were abundant, the morph ratios were different, and the locations were

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protected from livestock damage to the nets. Nets were set from 0630 to 1730 over a 4- or 5-day period with 10 12-m and 4 6-m nets at each site. All captured Bananaquits were aged by the extent of skull ossification (adult or juvenile) and then given a unique combination of color-bands.

The mist-netting program was not started until the end of the breeding season, when less than 3% of the population was still breeding at study sites at Point Saline, True Blue, and Grand Anse (see Wunderle 1980). To control for seasonal changes in the proportions of adults and juveniles over the 40-day netting period, one netting site was designated as a control. At the control site, nets were run for 4 days at the beginning of the netting period and again at the end of the netting period. No significant differences in adult and juvenile ratios were found between the first netting run at a control site and the last netting run at the same control site. Copies of the control data are available from the author on request.

The sequence in which the sites were sampled varied from year to year. In 1976 nets were run in the following order: Blue Horizons Hotel (control), Grand Anse Estate, Parc à Boeuf, Lance aux Epines, Pinquin, Grand Anse Beach, Golf Course, Point Saline, True Blue, and Blue Horizons Hotel. In 1977, Lance aux Epines served as the control, followed by Blue Horizons Hotel, Parc à Boeuf, Pinquin, Grand Anse Estate, Grand Anse Beach, True Blue, Point Saline, Golf Course, and Lance aux Epines. In 1978, Pinquin was used for the control, followed by Parc à Boeuf, Golf Course, Grand Anse Beach, Lance aux Epines, Grand Anse Estate, Blue Horizons Hotel, Point Saline, True Blue, Golf Course, and Pinquin.

I color-banded Bananaquits in late August 1978 at Pinquin and the Golf Course and then returned to both sites and netted in late September 1978, to compare the recapture rates of adults and juveniles. All recaptured birds that had been banded previously that August were recorded.

To determine the distances traveled by foraging Bananaquits from their roosting nests in the wet and dry season, I ran 10 12-m and 4 6-m nets at Pinquin (21–24 March 1975), Parc à Boeuf (18–20 March 1975, 13–19 May 1975, 8–12 April 1976), Lance aux Epines (29 May–3 June 1975), and Grand Anse Estate (22 April–2 May 1975, 28–30 April 1976) in order to band foraging birds. Following these dry season and my 1976 and 1978 wet season netting sessions, I systematically searched 900 ha of southern Grenada to relocate color-banded individuals at their roosting nests.

To determine whether or not visitation rates to *Hibiscus* declined in the wet season, I ran 6 12-m nets for 5 days in a *Hibiscus* garden in Lance aux Epines in the late dry season (29 May–3 June 1975) and again in the wet season (21–25 July 1975). To control for possible seasonal changes in the number of flowers in the garden, I counted all flowers within a 3-m section of the hedge in both the wet and dry season.

## RESULTS

*Postbreeding season movements.*—The percentage of blacks increased with distance from Point Saline (Fig. 1), as was described by Wunderle (1981). The cline in percentage of black morphs was steeper for adults than for juveniles in late August and September 1976, 1977, and 1978 (Fig. 2). From Point Saline through True Blue, the percentage of black morphs was higher within the juveniles than within the adults, while the percentage of black morphs was higher within adults from Blue Horizons through the Golf Course. This sequence of a higher percentage of black morphs within juveniles captured at the four southwestern-most sites followed by five sites with a higher percentage of black morphs within adults was significant in all 3 yr (runs test,  $P = 0.05$ ).

To examine the possible recruitment of juveniles of the two morphs at each location, I calculated the percentage of juveniles in each of the morphs captured at each netting site (Fig. 3). Among the captured black morphs there was a higher percentage of juveniles than among yellow morphs from Point Saline through True Blue, but a lower percentage of juveniles from Blue Horizons Hotel through the Golf Course. This sequence was significant in all 3 yr (runs test,  $P = 0.05$ ). Thus, there is a higher proportion of black juveniles in locations where the yellow morph predominates (except location E) and a higher proportion of yellow juveniles in areas where the black morph predominates. These results are consistent with the expectation of juvenile dispersal from areas with high black and high yellow morph frequencies, respectively, if population densities do not differ.

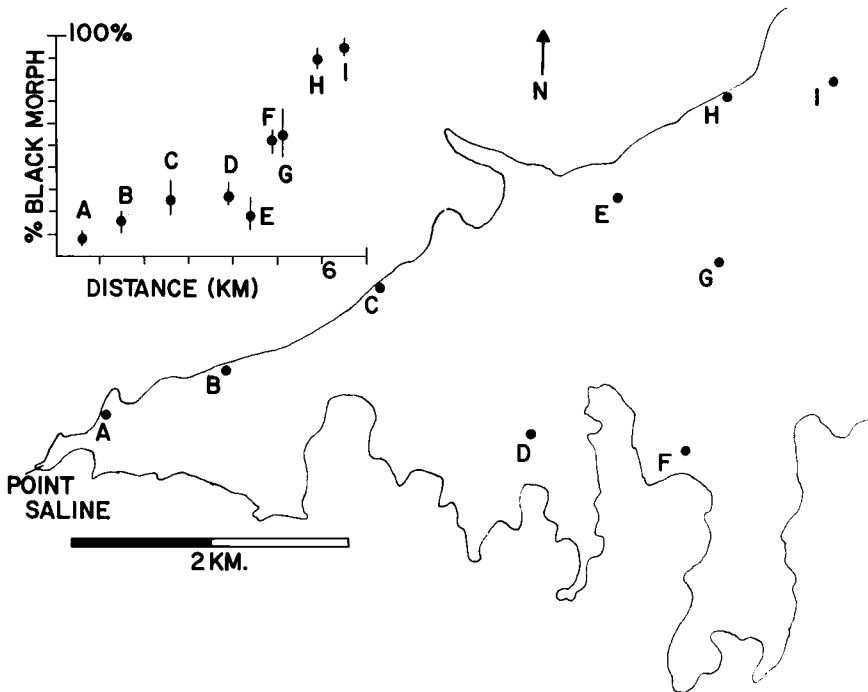


Fig. 1. Location of nine netting sites in southern Grenada (A. Point Saline, B. Pinquin, C. Parc à Boeuf, D. True Blue, E. Blue Horizons Hotel, F. Lance aux Epines, G. Grand Anse Estate, H. Grand Anse Beach, I. Golf Course). In the left corner are shown the mean and range (for 1976–1978) of the percentage of black morphs at each of nine netting sites graphed against the distance from the Point Saline Lighthouse.

Of the Bananaquits recaptured at a site other than the original banding site ( $n = 16$ ), 93.8% were juveniles; only 64.9% of all banded individuals ( $n = 1,109$ ), however, were juveniles. The significant difference (a test of percentages, Sokal and Rohlf 1969: 608;  $t = 3.037$ ,  $P < 0.01$ ) between these two percentages suggests that juveniles are moving greater distances than postbreeding adults. In addition, I compared the recapture rates of adults and juveniles at the site of initial banding after approximately 1 month. Data were pooled for both Pinquin and the Golf Course for 1978. Of the color-banded adults ( $n = 37$ ), 27.6% were recaptured a month later at the site of initial capture, compared to only 7.9% of the 105 color-banded juveniles ( $t = 4.843$ ,  $P < 0.001$ ). These last results could be explained by either differential mortality or dispersal.

*Seasonal trends in foraging movements.*—The distance traveled by foraging adults from netting sites to roosting sites is shown in Fig. 4. During the dry season the distances traveled by adults [ $667.6 \text{ m} \pm 646.4 \text{ m}$  (SD)] were significantly greater (Mann-Whitney  $U = 1,916$ ,  $P < 0.01$ ) than the wet season distances ( $201.9 \text{ m} \pm 240.1 \text{ m}$ ).

In conjunction with my studies of wet and dry season movements of adults, I compared my mist-net capture rates of individuals feeding on an artificial food source, *Hibiscus* flowers, in both seasons. The Bananaquit capture rate declined over a 5-day netting period in a *Hibiscus* garden in Lance aux Epines during the dry season (29 May–3 June 1976). This effect was probably due to birds becoming

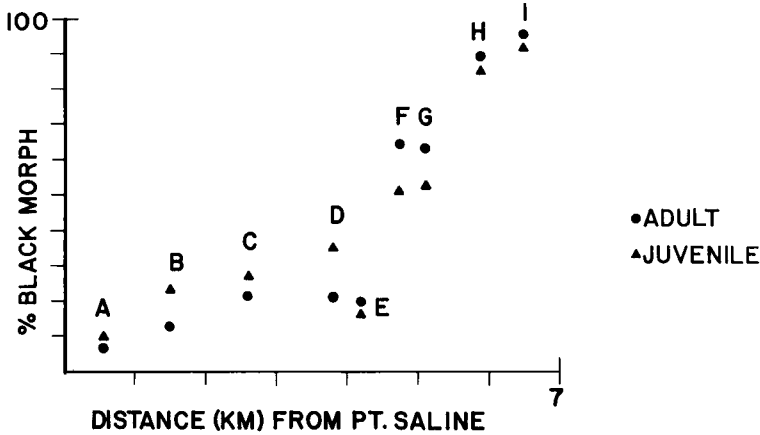


Fig. 2. Percentage of black morphs among adults and among juveniles captured at nine sites within the cline (data pooled for 1976-1978). The names and locations of the nine sites are shown in Fig. 1.

familiar with the nets, and can be characterized by the regression  $Y = 3.28 - 0.047X$  where  $X =$  net days and  $Y =$  capture rate. I returned to the site again for 5 days in the wet season (21-25 July 1976), using the same nets (6 12-m nets) in the same locations, and found that the capture rate also decreased with time ( $Y = 3.38 - 0.109X$ ). The wet season capture rate, however, decreased at a significantly [ $F_{(1,6)} = 162.8, P < 0.001$ ] faster rate than that of the dry season (Fig. 5), because Bananaquits were less dependent upon *Hibiscus* nectar. A count of flowers in a 3-m section of the *Hibiscus* hedge in both the dry and wet season (24 flowers dry; 27 flowers wet) showed no seasonal change in the number of *Hibiscus* flowers.

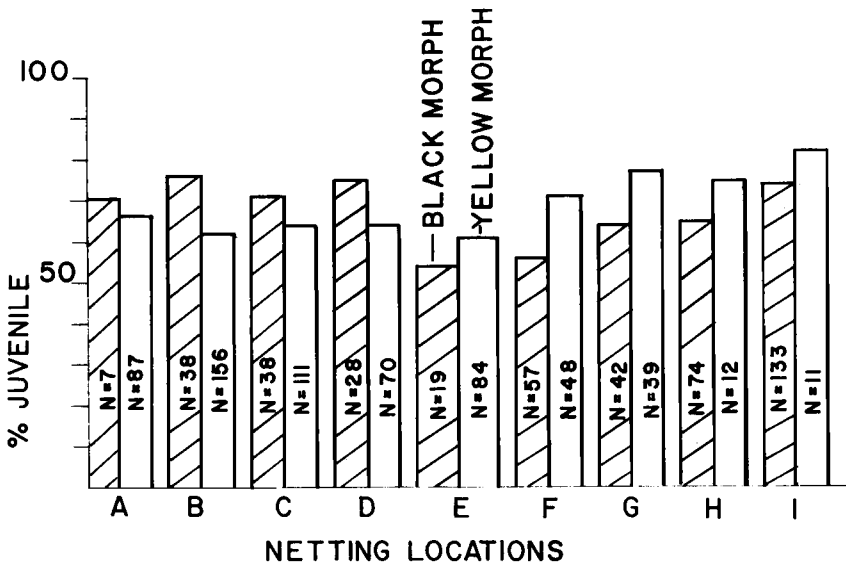


Fig. 3. The percentage of juveniles of each of the two color morphs at nine sites from Point Saline through the Golf Course (pooled for 1976-1978). The sites are arranged in geographic order from the closest to farthest from Point Saline. N refers to the total sample size (juveniles + adults) of each morph.

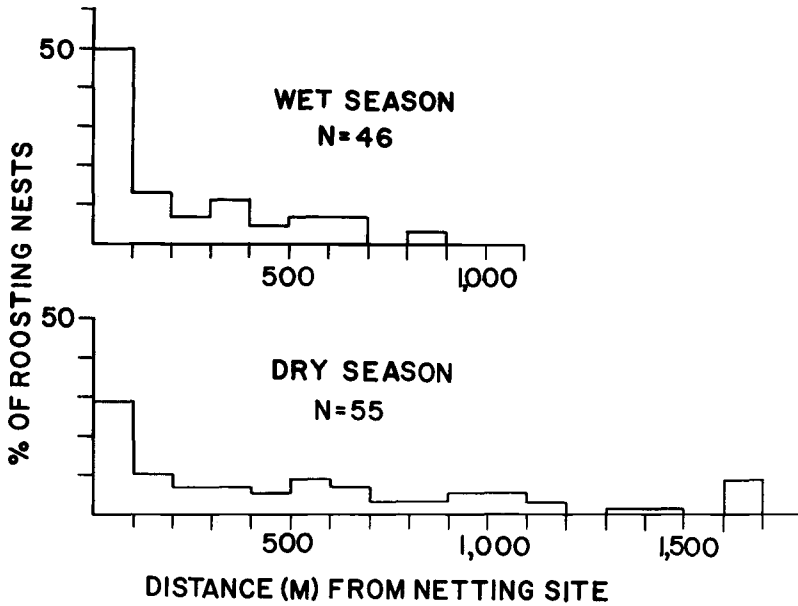


Fig. 4. Wet and dry season movements of adults from roosting nests to mist-net capture sites.

#### DISCUSSION

Bananaquits are food and habitat generalists and, possibly as a result, are the most abundant bird species on Grenada (Wunderle pers. obs.). Adults were found in all major habitats feeding upon nectar, fruit, insects, and spiders. My recaptures of individuals at 1 km or more away from their original banding site as well as my observations of marked individuals as far as 1.5 km from their roosting nests suggest that Bananaquits forage over large areas at some times of the year. During the dry season they forage on the nectar of various flowers (i.e. *Tecoma stans*, *Tabebuia serratifolia*, *Bignonia unguis-cacti*, *Hibiscus* sp., and *Erithrina micropteryx*) and over a wide area. During the wet season, however, their reliance upon nectar declines with a decrease in the number of native flowers, and they concentrate upon insects and spiders. The increasing abundance of insects during the wet season rains (Tanaka pers. comm.) may account for the shorter wet season foraging distances from their roosting nests.

If the Bananaquit populations are in Hardy-Wienberg equilibrium, the proportion of black morphs at any one site should be equivalent within the captured adults and juveniles. Such an equilibrium was found in the morph ratios of adults and nestlings at three sites in the cline (Wunderle 1981). My comparison of morph ratios within the adults and within juveniles, however, demonstrated a slight but consistent disparity at nine sites within the cline. In regions where the yellow morph predominated, there was a higher percentage of juveniles among the black morphs than among the yellow morphs. An exception occurred at Blue Horizons Hotel (site E, Fig. 1), where a 100-m open field and housing tract probably served as a barrier to dispersal or movement from an area with a high proportion of black morphs at Grand Anse Beach. In other areas of the cline where the black morph predominated,

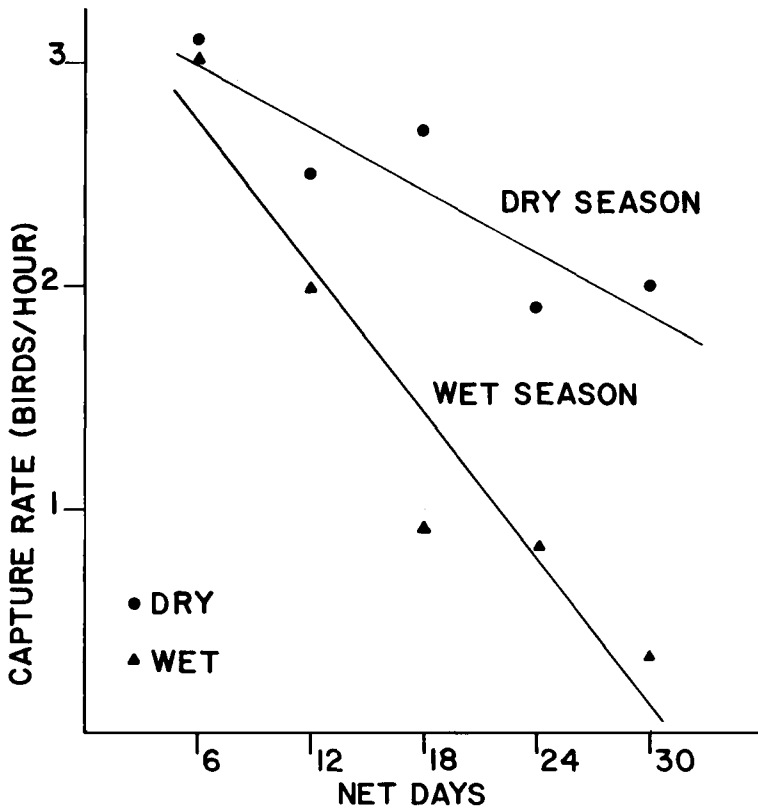


Fig. 5. Decrease in capture rates of Bananaquits in a *Hibiscus* garden over 30 net days in both the wet and dry season.

there was a higher percentage of juveniles among the yellow morphs than among the black morphs.

The more gradual morph-ratio cline found within juvenile Bananaquits, as compared to the steeper cline within adults, is consistent with the greater distances moved by juveniles than by post-breeding adults. In September, adults are foraging from a fixed site (their sleeping dormitory) to which they show considerable philopatry (Wunderle 1980). At this time, however, most juveniles have not yet started to use sleeping dormitories and thus are not restricted to a particular location until their first breeding season (Wunderle pers. obs.). As suggested by my recapture data, juveniles are wandering over greater distances than adults and thus are less likely to be recaptured again at the same netting location. Such juvenile movements probably consist of a dispersal component as well as foraging movements. Thus, differences in movements of adults and juveniles alone can explain why the cline in September was steeper for adults than juveniles.

Two different effects were studied here, an increase in the home-range size of all Bananaquits during the dry season and the greater wandering of juveniles than adults at the end of the breeding season. Both these effects would result in a more gradual cline. The greater wandering of juveniles could result in indefinitely increasing the cline width. Over a 5-year period in which I monitored this cline

(Wunderle 1981), however, I found no evidence to suggest a reduction in the cline's slope. Thus, it is likely that juveniles that wander too far from their birthplace have a higher mortality or that, after a period of wandering following fledging, juveniles tend to return to the vicinity of their birthplace to breed. The distance dispersed by nestlings to their first breeding site was moderately large (root-mean-square dispersal distance = 738.6 m, Wunderle 1981), suggesting that juveniles do leave their immediate birthplace. Juveniles do wander more widely than adults and may incur higher mortality before establishing a fixed home range. Unfortunately, I was unable to obtain the data necessary to substantiate this explanation.

Numerous factors that influence the steepness (width) of clines have been suggested (Endler 1977). This may be the first study, however, to suggest that changes in home-range size might bring about changes in the steepness of some clines. As suggested in this study, if all morphs within a nonlinear cline were to increase or decrease their home-range sizes (assuming overlapping home ranges), a change in a nonlinear cline width could occur. Such simultaneous changes in home-range size (either all increase or all decrease) are not unlikely in nonlinear clines within seasonal environments. For example, the greater dry season home ranges of Bananaquits could result in a more gradual cline than that produced by the reduced wet season home ranges. It is likely, however, that changes in home-range sizes have only minor effects upon cline widths, particularly when compared with the effects of gene flow, selection, barriers, habitat selection, heterozygosity, and so on.

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#### LITERATURE CITED

- BEARD, J. S. 1949. The natural vegetation of the windward and leeward islands. Oxford, Clarendon Press.
- COOCHE, F. G. 1963. Recent changes in distribution of color phases of *Chen c. caerulescens*. Proc. 13th Intern. Ornithol. Congr. 1962: 1182-1194.
- COOKE, F., C. D. MACINNES, & J. P. PREVETT. 1975. Gene flow between breeding populations of Lesser Snow Geese. Auk 92: 493-510.
- ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton, New Jersey, Princeton Univ. Press.
- GILL, F. B. 1973. Intra-island variation in the Mascarene White-eye, *Zosterops borbonica*. Ornithol. Monogr. 12: 1-66.
- O'DONALD, P., & P. E. DAVIS. 1959. The genetics of the colour phases of the Arctic Skua. Heredity 13: 481-486.
- SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman and Co.
- SOUTHERN, H. N. 1962. Survey of Bridled Guillemots, 1959-60. Proc. Zool. Soc. London 138: 455-472.
- WUNDERLE, J. M. 1980. Breeding ecology of the Bananaquit (*Coereba flaveola*) on Grenada. Unpublished Ph.D. dissertation. Minneapolis, Minnesota, Univ. Minnesota.
- . 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, W.I. Evolution 35: 333-344.