SHORT COMMUNICATIONS

A SHIFT IN THE MORPH RATIO CLINE IN THE BANANAQUIT ON GRENADA, WEST INDIES

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The two Bananaquit (*Coereba flaveola*) color morphs and the morph ratio cline on Grenada have been described in detail by Wunderle (1981a). The yellow morph is restricted to the dry northeastern and southwestern portions of the island. The melanic, or black morph, occurs throughout the island, but in lesser numbers in the northeast and southwest. Steep clines in the ratio of the two morphs exist in these areas and may be of recent origin. The observations of avian collectors in the late 1800s and early 1900s suggest that the yellow morph was exceedingly rare in Grenada. Subsequent range expansion in the southwest by the yellow morph established the morph ratio cline in its present position, perhaps by March 1929 (J. Bond, pers. comm.). Recent samples of this cline over a five-year period (1974–1978) showed no movement (Wunderle 1980).

Clines can be divided into two categories: equilibrium and dynamic. In an equilibrium cline there is a balance between gene flow and selection and thus no directional movement of the cline (Endler 1977). Those situations in which the cline is moving, such as a traveling wave of new alleles through a population, are designated as dynamic clines (Fisher 1937). To discriminate between these two categories of clines it is necessary to have good historical information. Unfortunately, if the cline is moving very slowly it is often difficult, if not impossible, to detect unless sampling has occurred over an extremely long period of time. This note uses recent observations in conjunction with earlier censuses (Wunderle 1980) to document movement of the morph ratio cline in the Bananaquit on Grenada, West Indies. Such movement might suggest a shift in the selective gradient, a fitness change in one of the morphs, or the appearance of a barrier to gene flow; conversely, lack of movement (equilibrium) indicates a balance between gene flow and selection.

I censused different areas by walking slowly and observing Bananaquits along trails and roads as shown in Wunderle (1980), and in Figure 1 for southwestern Grenada. Only those sites where 10 or more Bananaquits were observed are included in my analysis. I surveyed south-western and northeastern Grenada every August and September in 1974 through 1978 and again in September 1981. Estimates of morph ratio obtained by observation did not differ significantly from those obtained by mist-netting and banding (Wunderle 1981a). I mist-netted and banded Bananaquits at Pinquin (location B, Fig. 1) during August and September 1976, 1977, 1978, and 1981. Nets were set from 06:30 to 17:30 over a four- or five-day period with ten 12-m and four 6-m nets each year.

I found no evidence of movement in the cline in northeastern Grenada in 1981 as shown in Table 1. Of the eight northeastern sites censused in 1981, six were within the 1974–1978 ranges. Only at two sites did the percentages fall outside the range.

The results of my surveys of the cline in southwestern Grenada are summarized in Figure 1. The percentage of black morphs observed at each 1981 census site fell below the lowest points of the 1974–1978 ranges at 13 of 15 sites (sign test, $P = .0037$). Only at sites N and O, at the far end of the cline where blacks predominated, were observations within the 1974–1978 ranges. The percentage of black morphs observed at each census site in 1981 fell below the 1974–1978 means in all of the 15 sites (sign test $P < .005$). In 1981, the percentage of black morphs decreased by an average of 14.1 from the 1974–1978 means for the first five sites (A–E), decreased by an average of 17.4 from the 1974–1978 means in the next five sites (F–J) and decreased by an average of 9.9 from the 1974–1978 means in the last five sites (K–O).

Because of the small samples of the observational data I could not detect changes in the percentage of the black morphs within any one sampling site. However, large mist-netting samples from Pinquin showed a significant decrease in the percentage of black morphs in 1981. In 1978, 24.5% of the captured Bananaquits ($n = 66$) were black while only 4.0% of the total captured ($n = 76$) in 1981 were black ($G = 7.542$, $P < .01$). The three-year mean (1976–1978) from netting at Pinquin ($n = 180$) was 15.6% black morph and was also significantly different ($G = 8.104$, $P < .005$) from the 1981 results. This is the first instance of a significant change in morph ratios at any of my netting sites despite yearly sampling at nine sites during 1976 through 1978 (Wunderle 1981b).

The 1978 widths of the cline (as defined by May et al. 1975) in southwestern Grenada were 2.5 km, 4.5 km, and 4.8 km for the north, central, and south transects, respectively, as shown in Wunderle (1981a). Despite the recent movement of this cline, the 1981 widths were similar with values of 3.0 km, 4.3 km, and 4.1 km for the three respective transects.

The cline in southwestern Grenada has shifted approx-

TABLE 1. Summary of the 1974–1978 mean percent black morph, range, and the 1981 percent black morph and sample size for eight sites in northeastern Grenada.

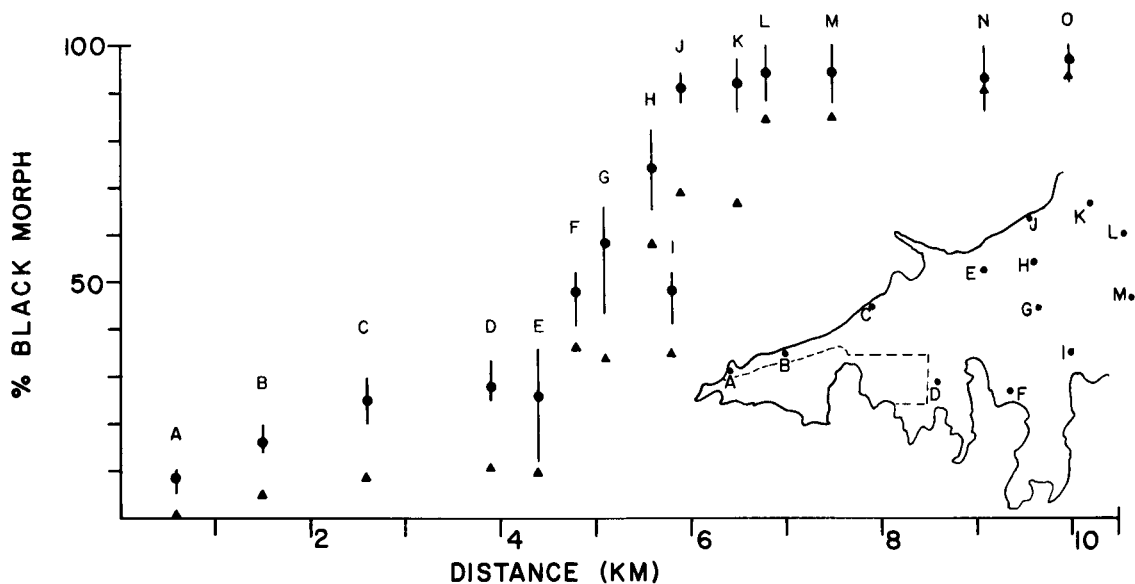| Locality	Percent black morph					Direction change
	1974–1978			1981		
	%	*n*	Range	%	*n*	
Mt. Rose	98.8	70	(93.8–100%)	100	17	+
River Sallee	87.6	57	(80.0–91.7%)	94.7	19	+
Chambord Estate	66.0	66	(60–77.0%)	69.2	13	+
Levera Hill One	63.9	71	(50.0–76.5%)	42.3	14	−
Levera Hill Two	62.2	65	(58.3–65.0%)	61.1	18	−
Levera Pond	64.9	76	(54.0–84.6%)	80.0	15	+
Bedford Point	56.3	61	(35.7–70.0%)	40.0	10	−
Rose Hill	98.1	79	(94.4–100%)	100	12	+

FIGURE 1. The percentage of black morph Bananaquits and sampling sites in southwestern Grenada. The means and ranges of percentage black morph for 1974–1978 and the 1981 sample means (triangles) are graphed against distance from the westernmost point (Point Saline). In the lower right corner is shown a map of all sampling sites[1] except N and O, which are shown in Wunderle (1980). The dashed line within the map encloses an area of suitable habitat destroyed by recent airport construction.

imately 1.3 km to the northeast of Point Saline since my August–September 1978 census. This shift over a three-year period occurred at a minimum velocity of 433 m per year. This rate can be used to estimate the selective coefficient necessary to drive a new allele through a population with Fisher's (1937) equation for the velocity of a traveling wave of alleles as discussed in Wunderle (1981a). For example, a wave of yellow alleles traveling at 433 m per year would require a selective coefficient of .172. Both the recent cline velocity and its estimated selective coefficient are considerably larger than the velocities of 94–300 m per year and selective coefficients of .008–.082 estimated for the movement of the yellow allele in the early 1900s.

From the observations of early avian collectors, I predicted (Wunderle 1981a) that if the 1974 southwestern cline were still moving at 94 m/year it would be statistically undetectable until 1986. The present movement of the cline is much too large to be explained only by such movement. In addition, the lack of any detectable movement in the cline in northeastern Grenada suggests that major climatic changes are not responsible for the shift in the southwestern cline.

Since 1978, the construction of a new airport has destroyed approximately 1.7 km² of habitat suitable for Bananaquits from Point Saline to True Blue (Fig. 1). This disturbance may have forced the resident Bananaquits (predominantly yellow morphs) to move to other areas of the southwestern cline, thus changing local morph ratios and resulting in a shift in the cline. I examined this possibility by estimating the population and morph ratios of the displaced Bananaquits using previous population counts (Wunderle 1980). I assumed that their dispersal showed either a negative exponential or negative arithmetic de-

cline with distance from the disturbed site. Isoclines were drawn every 0.5 km from the airport construction site and the total Bananaquit population estimated within the boundaries of each isocline. A fraction of the displaced Bananaquit population was added to each of these populations, the actual number depending upon whether an arithmetic or exponential decay was used. When I assumed that the displaced population consisted of 1,700 individuals (a high estimate) with 9% black morphs, the resultant shift in the cline (with either arithmetic or exponential dispersal) was significantly smaller than the observed 1981 shift. Thus, it seems unlikely that population flooding by displaced yellow Bananaquits could account for all of the movement in this cline.

If the new airport acts as a barrier to gene flow it could shift the midpoint of the cline (e.g., Endler 1977, Barton 1979). This shift might account for the observed movement. However, habitat change associated with the airport parallels the southern edge of the cline (see Fig. 1), rather than running across the cline where it might serve as a more effective barrier. It is not certain how the airport's geographic position might impede gene flow.

Another possible explanation for the cline shift is that there has been no change in the selective gradient, but rather a shift in some aspect of fitness of one of the morphs that is independent of locality. Endler (1977) suggested that this would uniformly shift the position of the cline because it results in a change in the position of the net selective gradients of the two morphs while the actual selective gradients may remain in the same place. Unfortunately, no evidence for this explanation exists.

The field evidence provided here suggests that there has been a shift in the morph ratio cline and major habitat change since 1978. The clinal shift may have been associated with the habitat disturbance, although I was unable to determine how this occurred. Habitat change (e.g., changes in sugar cane cultivation) may explain the cline's movement in the late 1800s on Grenada and similar fluctuations on St. Vincent (Wunderle 1981c). Unfortunately no conclusions can be made for several more years about whether or not the cline is still moving.

[1] Listed below are the site codes, site names, percentage black morphs and number of Bananaquits observed (in parentheses) in southwestern Grenada in 1981: A. Point Saline, 0.0% (14); B. Pinquin, 4.5% (22); C. Parc à Boeuf, 8.0% (25); D. True Blue, 13.0% (23); E. Blue Horizons Hotel, 11.1% (18); F. Lance aux Epines, 36.7% (49); G. Grand Anse Estate, 30.4% (23); H. Grand Anse Hillside, 86.4% (22); I. Mt. Hartman Estate, 35.0% (20); J. Grand Anse Beach, 69.2% (26); K. Golf Course, 66.7% (21); L. Woodlands Estate, 84.4% (32); M. Woburn, 85.2% (27); N. Calivigny Estate, 95.5% (22); O. Westerhall, 93.5% (31).

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OBSERVATIONS OF EMPEROR GEESE FEEDING AT NELSON LAGOON, ALASKA

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Estuaries along the north side of the Alaska Peninsula provide essential habitat for most of the American population of Emperor Geese (*Chen canagica*) during migration (Petersen and Gill 1982). Most of the population passes through Nelson Lagoon in spring and fall, with over 40,000 birds recorded there (Gill et al. 1981). Little is known about the feeding activity of Emperor Geese while they are in estuaries, and the importance of estuaries as staging areas during spring and fall migration is poorly understood. Here I report observations on the feeding activity of Emperor Geese at one estuary (Nelson Lagoon).

Nelson Lagoon (56°00′N, 161°10′W) is a large (141 km²), shallow estuary with extensive flats (47% of the lagoon) exposed at mean low tide. There is a wide diversity of habitats in and around the lagoon, but geese use only the intertidal zone, beaches, and dunes (Gill et al. 1981). Intertidal substrates vary from mud to a mixture of sand and gravel. The daily tidal regime is two lows and two highs with a mean diurnal range of 5.4 m (Gill and Sanger 1979). Bivalves, including blue mussels (*Mytilus edulis*) and balthica macoma (*Macoma balthica*), and polychaete worms (primarily *Eteone longa*), dominate the benthic and epibenthic fauna; aquatic plants are rare in the intertidal zone.

The intertidal zone has been described in detail by Gill and Jorgensen (1979) and Petersen (1980, 1981). A peninsula and a series of long narrow islands separate Nelson Lagoon from the Bering Sea. Beaches above mean high tide zone are generally open sand cobble merging to sand dunes. The vegetation above the mean high tide zone is a dune elymus association (Viereck and Dyrness 1980) dominated by lyme grass (*Elymus arenarius*).

I systematically observed an average of 377 Emperor Geese (SE = 28.6, range 10–1, 995), in a 252-ha portion of the lagoon, feeding in the intertidal zone and roosting on the adjacent beach. Observations were made with a spotting scope at about three-day intervals from 20 April to 26 June and 25 August to 11 October 1977, and from 19 August to 30 September 1979. I counted the number of birds that were feeding and roosting every 2 h from 08:00 to sunset in 1977 (*n* = 32 days), and from 06:00 to sunset in 1979 (*n* = 10 days). Observations of geese in the dune areas and at night were made at irregular intervals.

I converted the percentage of geese feeding at each hour of the tide to angular transformations and tested them by using one-way analysis of variance tests (Sokal and Rohlf 1969).

RESULTS

Emperor Geese fed in the intertidal zone either by dipping their heads in water as deep as about 30 cm, or by walking in shallow water and feeding with only their bills in the water. Adult-plumaged and hatching-year birds appeared to use the same method of feeding, as geese of all age groups fed as family groups and in flocks with non-breeding or failed breeding individuals. After feeding, geese walked to the adjacent beach to roost. In fall, some geese left the intertidal zone and adjacent beaches at high tide and went to the dunes.

The height and stage of the tide influenced feeding activity in the intertidal zone during the two daily tide cycles. The percent of geese feeding differed significantly among the various tide stages ($F_{11, 182} = 12.31$, $P < 0.001$); most geese fed at low tide (Fig. 1). Geese began feeding by 3 h before low tide and continued feeding through 3 h after low tide. Geese fed the same amount of time at each stage of the tide in spring and fall in both years.

DISCUSSION

Geese fed in intertidal areas when invertebrates were accessible. This feeding pattern left about half of each day for geese to roost on the beach (spring and fall), or feed or roost in the dunes (fall). This general pattern of feeding in the intertidal zone has been noted (Turner 1886, Murie 1959, Kenyon 1961); however, geese primarily ate aquatic vegetation exposed at low tide (Palmer 1976). At Nelson Lagoon, geese appeared to eat invertebrates.

My observations suggest that the intertidal zone may be an important feeding area for geese staging at Nelson Lagoon in spring and fall. Emperor Geese arrive on breeding areas with heavy accumulations of fat (Portenko 1972) and, like other geese nesting in the arctic (for a review see