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A Bill Color Polymorphism in Young Darwin's Finches

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Knowledge of bill color variation in Darwin's finches is summarized in a statement by Swarth (1929): "Color of bill varies seasonally and with age, being black or dusky in adults of both sexes during the breeding season, yellowish or otherwise light colored in adults at other seasons and in the young". This applies to all members of the sub-family Geospizinae, although R. I. Bowman (pers. comm.) has pointed out to us that, in addition, captive *Geospiza difficilis* from Islas Wolf and Darwin may breed when their bills are still partly yellow.

We report here another type of variation. We studied the breeding of ground finches (*Geospiza* spp.) on Islas Genovesa, Pinta, Wolf, and Daphne in 1978 and found that nestling bill color was polymorphic. All nestling bills could be assigned to one of two categories: pink and yellow. The color is present in both mandibles and is recognizable at hatching. During nestling growth the upper mandible becomes pigmented with melanin (brown-black) and the original color is masked or lost, but it is retained in the lower mandible for several weeks or months after fledging. We recorded the lower mandible color in nestlings and in immatures captured in mist nets. We also confirmed that, on Isla Wolf only, some breeding adults (*difficilis*) had partly yellow bills.

The polymorphism exists in all seven species studied in 1978 (Table 1), i.e. all six species of the ground finch, genus *Geospiza*, and the Warbler Finch, *Certhidea olivacea*. In addition, our notes on birds captured in a previous study (Grant et al. 1975) show that the polymorphism occurs in the tree-finch (*Camarhynchus parvulus*) at Bahía Borrero, I. Santa Cruz. R. I. Bowman (pers. comm.) has observed the polymorphism in captive *Geospiza* species. The polymorphism occurs on more islands than those shown in Table 1. Polymorphism was found in small samples of immature G. fortis, G. fuliginosa, and G. scandens netted on I. Santa Cruz and nestlings of G. scandens and G. fortis on I. Plaza Sur and G. fuliginosa on I. Plaza Sur (n = 12) and G. conirostris (n = 14) and Certhidea olivacea (n = 4) on I. Española.

Pink and yellow morphs often occur in the same clutch. Furthermore, the presence of both morphs, or just one, tends to be repeated in successive clutches of the same parents. Thus on Genovesa, 12 out of 15 pairs of G. magnirostris repeatedly produced both morphs or just the pink morph in their 2-4 clutches, and 9 out of 15 pairs of G. conirostris were similarly consistent in their 2-4 clutches.

Species	Island	Age of birds	Num- ber of clutches	Number of nestlings of particular bill color			Frequency of both morphs in some
				Pink	Yel- low	% Yellow	clutch (%)
Geospiza magnirostris	Genovesa Genovesa	Nestling Immature	48	138 23	29 12	17.8 34.3	35.4
Geospiza conirostris	Genovesa Genovesa	Nestling Immature	45	104 27	36 15	25.7 35.7	52.4
Geospiza difficilis	Genovesa Genovesa	Nestling Immature	55	160 320	3 0	1.8 0.0	1.8
Geospiza difficilis	Pinta Pinta	Nestling Immature	24	68 39	0 0	0.0 0.0	0.0
Geospiza difficilis	Wolf Wolf	Nestling Immature	18	0 0	40 39	100-0 100.0	0.0
Geospiza fuliginosa	Pinta Pinta	Nestling Immature	46	129 111	7 2	$5.1 \\ 1.8$	6.5
Geospiza fortis	Daphne Daphne	Nestling Immature	47	141 111	22 60	$\begin{array}{c} 13.5\\ 35.1 \end{array}$	34.0
Geospiza scandens	Daphne Daphne	Nestling Immature	40	96 51	30 35	23.8 40.7	35.0
Certhidea olivacea	Genovesa Genovesa	Nestling Immature	8	$\frac{11}{2}$	0 3	0.0 60.0	0.0

TABLE 1. Morph frequencies in Darwin's finches.

Morph frequencies differ among species on the same island. On Genovesa, the yellow morph is much rarer among *difficilis* nestlings than among *conirostris* ($\chi_1^2 = 38.28$, P < 0.001) and *magnirostris* nestlings ($\chi_1^2 = 22.70$, P < 0.001). On Daphne it is appreciably rarer among *fortis* nestlings than among *scandens* nestlings ($\chi_1^2 = 4.56$, P < 0.05). Differences between species on the same island are not universal, however. On Genovesa for example, there is no detectable difference in frequencies between *conirostris* and *magnirostris* nestlings ($\chi_1^2 = 3.18$, P > 0.05).

Morph frequencies also differ among populations of the same species. The yellow morph was not recorded among *difficilis* nestlings on Pinta, yet constituted 100% of the *difficilis* nestling sample on Wolf. Wolf was the only island where the yellow morph was in the majority. Nestling *difficilis* on Wolf were also unusual in having a pink tip to a yellow upper mandible and variable intensity of yellow in the lower mandible. These birds had a noticeable yellow tinge to the skin in general and to the legs in particular.

In several populations the frequency of the yellow morph was higher in the sample of netted immatures than in the sample of nestlings (Table 1). Two factors are responsible. On Daphne, bill color was found to change in some individuals from pink to yellow (but not the reserve) during the first 3 months out of the nest. This was established with birds banded as nestlings and captured as immatures. The yellow of previously pink bills was not as intense as the yellow of originally yellow bills, but the difference was only apparent with birds in the hand. Postfledging color change limits the period of usefulness of the color dimorphism to a few weeks after fledging. The other factor is postfledging survival, dispersal, or both. On Genovesa there was no color change in the first 2 months of life, yet morph frequencies differed significantly between nestling and immature samples of magnirostris (χ_3 ² = 5.12, P < 0.05). Preliminary analysis of data suggests that yellow morphs disperse from territories earlier than pink morphs in this species and that there was a net influx of yellow morph immatures into our study area.

The gape color of nestlings also varied. Three variants were recognized: dark yellow on upper and lower surfaces of the rictal flanges and tomia, pale yellow on both surfaces, and pale yellow upper and dark yellow lower surfaces. The first was associated with yellow bills, the second with pink bills, and the third with both. Like the bill color polymorphism, frequencies differ between species on the same island; e.g. between *conirostris* and *magnirostris* on Genovesa, $\chi_3^2 = 18.74$, P < 0.001.

Gape-color polymorphisms have been noted in some parasitic species of birds (e.g. Fraga 1979, Nicolai 1964, Rothstein 1978), but we know of none in nonparasitic species, and we do not know of any cases of bill color polymorphism similar to the one in Darwin's finches. We do not know the significance of the color variation. From studies of domestic fowl, it is known that all skin colors are based on melanin, which is manufactured in dermal cells, and xanthophyll, which is ingested and stored in body tissues including all layers of the skin; pink skin lacks both. The genetic control of melanin production and xanthophyll deposition can be complicated, although the appearance of yellow color in bill and legs due to xanthophyll may be controlled by recessive alleles at a single autosomal locus (Hutt 1949).

The color variation we have observed may simply be an associated effect of variation in other morphological and physiological traits and therefore of no particular significance. On the other hand, bill color may have an individual recognition signal value in communication between parents and offspring, in which case variation in color reflects variation in signals (e.g. see Rothstein 1978). Either way, we offer the hypothesis that the color variation is a visible expression of underlying genetic variation for two reasons: Both morphs are present in some clutches and are recognizable at hatching, i.e. before the nestlings have been fed; and species living in the same environment and known to feed on similar foods in the breeding season have different morph frequencies (e.g. magnirostris and difficilis), while others, which differ in diet (e.g. Certhidea and G. conirostris), have the polymorphism (Grant and Grant MS). Likewise, gape-color variation may be genetically determined in Darwin's finches, as in other species (e.g. Hutt 1949, Nicolai 1964). Breeding data are now needed to investigate the hypothesis of genetic control.

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Effects of Vegetation on Nesting Success of Vesper Sparrows

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Avian reproductive success is influenced by many factors, some of which have been quantified (e.g. Best 1978, Miller and Burger 1978). One factor, the structural characteristics of the vegetation directly surrounding the nest, has not been quantitatively linked with nesting success. Do subtle vegetational differences exist that may affect the success of nesting attempts? Here we ask if the success of a Vesper Sparrow (*Pooecetes gramineus*) nest is affected by the surrounding vegetation. We studied Vesper Sparrows breeding in West Virginia on reclaimed surface mine habitat, where the vegetation is structurally heterogeneous and variable.

Four reclaimed surface mines, located within a 3.3-km radius of Valley Point, Preston County, West Virginia $(39^\circ 37'N, 79^\circ 35'W)$, were used. The sites ranged in size from 16.4 to 41.5 ha, varied in age from 3 to 6 yr, and averaged 579 m in elevation. Mining and reclamation procedures were similar on all