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COLOR VARIATION AND HYBRIDIZATION AMONG *NESOSPIZA* BUNTINGS ON INACCESSIBLE ISLAND, TRISTAN DA CUNHA

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ABSTRACT.—*Nesospiza* buntings have speciated at the Tristan da Cunha archipelago in the central South Atlantic Ocean. Two species, the Tristan Bunting (*N. acunhae*) and Wilkins' Bunting (*N. wilkinsi*), differ markedly in size and co-occur without interbreeding on Nightingale Island. Nearby Inaccessible Island supports two altitudinally segregated color morphs of *N. acunhae*, as well as a hybrid complex involving *acunhae* and *wilkinsi*. Plumage variation was evaluated for 581 buntings, most of which were caught on Inaccessible Island. *Nesospiza* plumages vary with age and sex; immature plumage is retained for at least two years. Despite age and sex differences, there is no overlap in coloration between the upland and lowland morphs of *N. acunhae* on Inaccessible Island. The two morphs are distinct from the time of hatching; chicks of lowland *acunhae* are pinkish, whereas upland *acunhae* are yellow. Color differences between *acunhae* morphs were quantitative rather than qualitative; their feathers contain the same suite of carotenoid pigments, but at three times greater concentration in upland birds. Dispersion of different bunting populations on Inaccessible Island is closely related to vegetation types. Individually marked individuals were largely sedentary; only immature birds moved more than 400 m. The parapatric dispersion of *acunhae* morphs probably results from habitat-specific dietary differences. *Nertera* fruits are likely sources of carotenoid pigments in the diets of buntings, but feeding experiments on captive birds are needed to elucidate fully the basis of color variation between morphs. Whatever the proximate cause, plumage-color variation may allow population differentiation if birds mate assortatively on the basis of color. A review of previous visits to the islands suggests that the diversity of forms on Inaccessible Island could have been overlooked. *Received 3 August 1992, accepted 22 November 1992.*

MUCH OF OUR CURRENT understanding of the evolution of natural populations has come from studies of small, isolated populations that have the potential for relatively rapid evolutionary change. Among birds, study of the radiation of Darwin's finches led to the formulation of the allopatric model of speciation (Lack 1947) and provided some of the best evidence for the importance of ecological interactions during speciation, including character displacement and release (Grant 1975, Boag and Grant 1984, Schluter et al. 1985), as well as the influence of competition on community structure (Schluter and Grant 1984). However, the interpretations underpinning some of these theories are not without their opponents (e.g. Gould and Lewontin 1979, Connell 1980, Strong et al. 1984, Zink and Remsen 1986). Comparative studies of radiations similar to that undergone by Darwin's finches allow independent tests of current theories, and may provide novel insights into the evolution of natural populations.

There have been relatively few passerine radiations arising from a single ancestral group that arrived at an oceanic archipelago (Lack 1947, 1971). Lack (1947) contrasted the extensive radiations among Darwin's finches and the Hawaiian honeycreepers with the initial stages of radiation found among *Nesospiza*, a genus of buntings restricted to the Tristan da Cunha archipelago in the South Atlantic Ocean. Based on limited observations, *Nesospiza* has become entrenched in the literature as a simple, two-species radiation, with the large-billed Wilkins' Bunting (*N. wilkinsi*) specializing on seeds of the tree *Phylica arborea* that are unavailable to the small-billed Tristan Bunting (*N. acunhae*; e.g.

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Lack 1947. Abbott 1978, Williamson 1981). However, this apparent simplicity is misleading. During the 1982-1983 Denstone Expedition to Inaccessible Island (Swales et al. 1985), M. W. Fraser found differences in the coloration of Tristan Buntings. The lower slopes of the island were characterized by drably plumaged "lowland" birds, whereas the plateau supported brightly plumaged "upland" birds (Fraser 1983, Collar and Stuart 1985, Fraser and Briggs 1992). Fraser detected no other morphological differences between these two color morphs, but suggested that there were differences in their calls (Collar and Stuart 1985, Fraser and Briggs 1992). The two morphs were described on the basis of few individuals, with little regard to variation between individuals and between localities (Fraser and Briggs 1992).

In this paper, we address these omissions and examine the possible basis of color variation among Tristan Buntings on Inaccessible Island. We also report the occurrence of widespread interspecific hybridization between Wilkins' and Tristan buntings on the eastern plateau of Inaccessible Island, and give an account of the dispersion of buntings of various taxa in relation to vegetation types. This paper describes the diversity of *Nesospiza* populations on the basis of plumage variation, and reports their dispersion and movements on Inaccessible Island; details of their morphology, ecology and evolution are presented elsewhere.

METHODS

The Tristan da Cunha group of islands lies near 37°S, 12°W in the South Atlantic, roughly midway between the southern tip of Africa and South America, and more than 3,000 km from the nearest continental landmass. The group consists of three main islands—Tristan (96 km^2, 2,060 m high), Inaccessible (13 km^2, 511 m) and Nightingale (4 km^2, ca. 350 m)—within 40 km of each other. The islands are of volcanic origin, lying 500 km east of the mid-Atlantic Ridge, and range in age from 0.2 m.y.b.p. (Tristan) to 18 m.y.b.p. (Nightingale). Wace and Holdgate (1976) provide a detailed account of the islands' natural history. Extant *Nesospiza* populations are restricted to Nightingale and Inaccessible, with distinct morphological subspecies of both species found on each island: *N. a. questi* and *N. w. wilkinsi* on Nightingale; and *N. a. acunhae* and *N. w. dunnei* on Inaccessible. Both islands are uninhabited and seldom visited by man (e.g. Hagen 1952, Richardson 1984).

P.G.R. and C.L.M. visited Inaccessible Island during the spring of 1987, 1988, and 1989, and during the summer of 1989-1990. Brief visits were made to Nightingale Island during 1988 and 1989. We caught 581 buntings, some 5% of the population, using hand nets or mist nets. We described plumages and related these to bird age and sex based on field observations (breeding status, song, etc.). Subjective estimates of color were made by comparison with color swatches (Smithe 1974, 1975, 1981); colors used in this paper are followed, parenthetically, by their Smithe reference number. Buntings were marked with unique combinations of one metal and two color bands; resightings of banded birds were used to estimate movements.

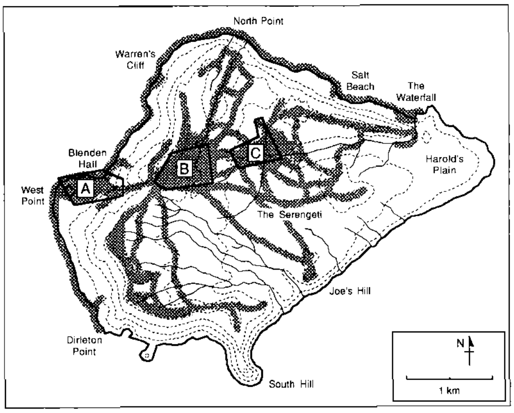

Fig. 1. Areas where buntings were examined (shaded) and the three main study areas on Inaccessible Island: (A) Blenden Hall; (B) Ringeye Valley; (C) Denstone Hill. Contour interval is 100 m.

Buntings were caught on Inaccessible Island in all three major habitat types: *Spartina arundinacea* tussock grassland on the coastal lowlands and seaward cliffs; *Blechnum palmiforme* wet heath on the western plateau; and *Phylica arborea* woodland on the eastern plateau (Roux et al. 1992). Although sampling occurred over most of the island, most birds were caught in three study areas, one in each vegetation type (Fig. 1). On Nightingale Island, buntings were caught along the path from the huts (at sea level) to The Ponds (altitude 200 m) in tussock grassland with some *Phylica* trees, similar to habitat found at Blenden Hall.

A permit was issued to collect six Tristan Buntings and one Wilkins' Bunting from each taxon, including the two color morphs of Tristan Bunting on Inaccessible Island. In addition, a few buntings were killed accidentally. Flat skins prepared from all collected birds are housed in the Durban Natural Science Museum (DM 36356-DM 36379). These skins were used to assess objectively color differences between bunting plumages. The gross distribution of pigment types in feathers was examined using both dissecting and compound microscopes. A crude index of contour-feather length was obtained by measuring the length (flattened, to nearest 0.5 mm) of feathers plucked from the belly and central back. Five feathers were sampled from each region of 12 Tristan Buntings, 6 of each color morph. A nested ANOVA was used to compare differences in contour-feather length within and between morphs (Zar 1984).

We used a Spectraflash 500 (ICS Texicon 1990) reflectance spectrophotometer to compare plumage color, following the protocol of Johnson and Brush (1972) and Johnson (1980). Reflectance spectra of uniformly colored, unruffled areas of lower belly and back plumage were measured using an 11-mm sample aperture with an illumination source equivalent to 6,500 K daylight, and a measurement sensor angle of 2°. Measurements were restricted to birds in adult plumage, because the extensive streaking typical of immature plumage precluded the selection of uniformly colored areas. This limited the sample size to 10 Tristan Buntings from Inaccessible Island (five of each color morph) and one from Nightingale Island, as well as one Wilkins' Bunting (*N. w. dunnei*).

Reflectance spectra were recorded between 400 and 700 nm, and colors were classified by the segment classification method (Endler 1990). This involves calculating the total reflected energy in each of four equal wavelength intervals: *B*, 400–475 nm; *G*, 476–550 nm; *Y*, 551–625 nm; and *R*, 626–700 nm (roughly corresponding to blue, green, yellow and red). Results are plotted on a two-dimensional color space with axes LM ($= R - G$) and MS ($= Y - B$). Chroma is expressed as the Euclidean distance to the origin, and hue as the angle (clockwise) from the origin (relative to the abscissa, *R*). This procedure allows color classification independent of specific properties of any given visual system (Endler 1990). Total reflectance is the proportion of reflected energy summed over the entire range of the visible spectrum (400–700 nm).

J.H. analyzed carotenoid types and concentrations in feathers from the two Tristan Bunting color morphs. Tail and belly feathers were removed from more than 20 birds of each morph. Pigments were extracted from feathers under dim light in warm, acidified (HCl) pyridine (Hudon and Brush 1992). All hydrophobic compounds were transferred to hexane in a separatory funnel. Organic epiphases were washed repeatedly with tap water and stored over anhydrous sodium sulfate in the dark and cold. Extracts in hexane were concentrated under a stream of air.

Fruits eaten by the buntings were examined as likely sources of carotenoids. There are few potential sources given the depauperate angiosperm flora on the islands (Roux et al. 1992). *Empetrum rubrum* and three species of *Nertera* produce fleshy fruits that are eaten by Tristan Buntings (Ryan 1992). Only two of the three *Nertera* species were sampled; *N. holmboei* is scarce on Inaccessible Island and is much less frequent in the diet of buntings compared with the other two *Nertera* species. Bunting diets on Inaccessible Island were determined during summer 1989–1990 by direct observation (Ryan 1992). Fresh ripe fruits were collected and dried prior to sampling. Pigments were extracted in ethanol, acetone and hexane, successively, after grinding with a mortar and pestle. The plant pigments were not elucidated structurally.

We recorded total absorbance and individual absorption spectra of pigments in hexane with a Bausch and Lomb Spectronics 2000 spectrophotometer. Pigment concentration was determined from the absorbtion at 435 nm, using an extinction coefficient $E^{1\%}_{1cm}$ of 2,500 (Britton 1985). Thin-layer chromatography (TLC) was performed on each extract. Because all feather extracts contained the same pigments, they were pooled for pigment identification (with the exception of lowland belly feathers, which contained insufficient pigments and several contaminants). Individual pigments were isolated by preparative TLC on precoated plates of silica gel (Anasil G, Analabs, New Haven, Connecticut). The pigments were resolved with a solvent mixture of hexane : acetone (2:1), eluted from the gel with acetone, and transferred back to hexane after filtration (Cameo 13N syringe filters, nylon, 0.45 micron; Micron Separations Inc., Westboro, Massachusetts).

We chromatographed the extracts and individual pigments on silica gel (Chromagram sheets, Eastman Kodak Co., Rochester, New York) in the hexane : acetone solvent system. Pigments were identified on the basis of relative mobility (R_f) on the Chromagram plates, and comparison with known standards (canthaxanthin, lutein and zeaxanthin; Hoffman la Roche, Basel). The presence of carbonyl groups in individual pigments was tested with sodium borohydride in methanol (Hudon and Brush 1992).

RESULTS

All *Nesospiza* buntings are green-brown above and pale yellow beneath; often they are washed green on the flanks. The coverts and contour feathers on the upperparts have dark grayish-brown (20) centers, with paler fringes in various shades of green and brown. Adults have a poorly defined yellow supercilium, and the lores and cheek around the eye are faintly washed gray, giving a slightly masked appearance. The throat typically is yellow, but in some birds there is a small grayish "bib" extending down from the chin. Hagen (1952) and Fraser and Briggs (1992) gave detailed descriptions of the plumages of adults and juveniles for both subspecies of Tristan and Wilkins' buntings, from which we highlight the major features. There are no substantive plumage differences between the species, and the following account applies equally to Tristan and Wilkins' buntings. The two species differ primarily in size

(Abbott 1978), with Wilkins' Buntings weighing 50 to 90% more than Tristan Buntings (Ryan 1992).

Plumage variation within taxa.—Plumage varies both with age and sex. Breeding takes place in early to midsummer (austral), and is followed by a complete postbreeding molt. At least some nonbreeding birds begin molt earlier than do breeding birds. There is no evidence of a prebreeding body molt (although this may occur before our earliest arrival at the islands in mid-September; there are no observations or specimens collected during winter). The plumage of fledglings (juveniles) is characterized by extensive streaking produced by dark grayish-brown (20) feather centers. This streaking is retained after the postjuvenile molt of contour feathers, which occurs six to eight weeks after hatching. In addition to the dark feather centers on all contour feathers, immature plumage is characterized by narrower pale fringes to the wing and tail feathers than adult birds. The color of the pale fringes on the upperpart feathers tends to be more buffy and less green than those of adults. The only region lacking streaks is the central belly.

When approximately one year old, immature birds undergo a complete molt, but retain the streaky, immature plumage. The second-year plumage is less heavily streaked on the breast and flanks than the first-year plumage, but is heavily streaked on the back, and more closely resembles the plumage of juveniles than that of adults. Hagen (1952) inferred the existence of a second-year plumage from a specimen in molt collected on Nightingale Island, and this was confirmed when one-year-old birds banded on Inaccessible Island in October 1988 were retrapped in immature plumage a year later. It is possible that some one-year-old birds fail to molt, because small numbers of immatures with extremely worn feathers (i.e. outer remiges and rectrices faded almost white and virtually lacking barbs and barbules) were captured during the spring.

Adult plumage is characterized by reduced streaking, but there is considerable variation among individuals. The loss of streaking may be a gradual process related to age. There is no evidence to indicate whether all immatures assume adult plumage after two years. Some immatures may molt into adult plumage after one year, whereas others may take three years or longer.

Adult males are less streaked than adult females. The underparts and rump are completely uniform in some adult males, but traces of darker feather centers (reduced both in extent and contrast) remain on the back, crown and wing coverts. Some females also have virtually unstreaked rumps, but typically are more heavily streaked on the back than are males. The plumage of adult females also tends to be more subdued than that of males in the intensity of the yellow and green component, although there is individual variation in this character (see below).

Plumage variation between taxa.—Just as interspecific plumage differences are limited, there are few plumage differences between *Nesospiza* subspecies. Previous reports of differences between island populations based on small numbers of skins (e.g. Lowe 1923, Broekhuysen and Macnae 1949, Voous 1962) are confounded by the extensive age- and sex-related plumage variation. Hagen (1952), who had the most extensive field experience prior to Fraser (Fraser and Briggs 1992), reported no differences between island populations (contra Rand 1955). In our experience, adult *N. w. wilkinsi* appear brighter green/yellow than *N. w. dunnei*, but the difference is small. Differences between island populations of Tristan Buntings are negligible compared with the variation within the Inaccessible Island population (see below).

Field observations and examination of collected birds confirmed that Tristan Buntings on the plateau of Inaccessible Island (elevation 300–500 m) are markedly "brighter" than those on the coastal lowlands, where brightness refers to the intensity of yellow/green coloration in the plumage (Table 1). This difference is consistent across all age groups and applies to all parts of the plumage. Only immatures with very worn plumage, that appear to have skipped the first complete molt, cannot readily be placed in one or other category (but see below for some problem areas). Matching with Smithe's color swatches fails to emphasize the large differences observed in the intensity of the yellow/green coloration. Lowland birds look washed out and drab compared with the rich colors of upland buntings. In a series of adult skins, differences between morphs are greater than those between sexes, with male uplands brighter than female uplands, which are in turn brighter than both male and female lowlands.

Quantitative analysis of back and belly plum-

TABLE 1. Subjective estimates of green/yellow plumage color[a] for different age and sex classes of two morphs of Tristan Bunting on Inaccessible Island.

Body region	Lowland morph	Upland morph
	Adult males	
Back and crown	Auxiliary olive-green (47)	Basic olive-green (46)
Nape and rump	Washed smoke gray (44)	Washed grayish-olive (43)
Wing coverts	Auxiliary olive-green (47)	Basic olive-green (46)
Throat and supercilium	Pale spectrum yellow (55)	Spectrum yellow (55)
Breast and belly	Straw yellow (56)	Spectrum yellow (55)
Vent	Buff-yellow (53)	Spectrum yellow (55)
	Adult females	
Back and crown	Grayish-olive (43)	Auxiliary olive-green (47)
Nape and rump	Washed olive gray (42)	Citrine (51)
Wing coverts	Grayish-olive (43)	Auxiliary olive-green (47)
Throat and supercilium	Pale spectrum yellow (55)	Spectrum yellow (55)
Breast and belly	Straw yellow (56)	Pale spectrum yellow (55)
Vent	Buff-yellow (53)	Spectrum yellow (55)
	Juveniles	
Back and crown	Pale buff (124)	Sulphur yellow (57)
Nape and rump	Buff (124)	Sulphur yellow (57)
Wing coverts	Buff-yellow (53)	Olive-yellow (52)
Throat and supercilium	Buff (124)	Straw yellow (56)
Breast and belly	Pale cream (54)	Straw yellow (56)
Vent	Cream (54)	Buff-yellow (53)

[a] Nomenclature and numbers (in parentheses) refer to color standards (Smithe 1974, 1975, 1981), but qualifiers such as "pale" are used to emphasize differences in color intensity rather than hue. Immature plumage is roughly intermediate in color between juvenile and adult plumage.

age color confirmed that upland birds have more intense yellow coloration than lowland birds. Color scores of the two morphs did not overlap (Fig. 2). Upland birds had consistently greater scores for both *LM* (red-green) and *MS* (yellow-blue), irrespective of sex, resulting in the color of both the back and belly plumage having a significantly greater chroma (color "saturation") than lowland birds (Table 2). There was little difference in the hue of the colors between the two morphs, but lowland birds had a greater total reflectance (Table 2). Females tended to have less intense coloration than males, but this was less evident than the difference between morphs.

The coloration of other *Nesospiza* taxa tends

TABLE 2. Mean coloration of *Nesospiza* plumages determined from reflectance spectra.

Taxon (*n*)	Chroma	Hue	Total reflectance	*LM*	*MS*
		Back plumage			
Male upland (3)	0.270	0.972	0.066	0.156	0.221
Male lowland (3)	0.168	0.930	0.104	0.100	0.135
N. a. questi (1 male)	0.218	0.940	0.078	0.132	0.166
Female upland (2)	0.220	0.943	0.080	0.147	0.203
Female lowland (2)	0.175	0.897	0.099	0.109	0.136
N. w. wilkinsi (1 female)	0.221	0.915	0.081	0.147	0.191
Upland vs. lowland[a]	**	ns	**	**	**
		Belly plumage			
Male upland (3)	0.351	0.974	0.302	0.197	0.290
Male lowland (3)	0.254	0.987	0.343	0.139	0.213
N. a. questi (1 male)	0.306	0.995	0.307	0.176	0.257
Female upland (2)	0.315	0.948	0.304	0.184	0.255
Female lowland (2)	0.212	0.940	0.349	0.149	0.203
N. w. wilkinsi (1 female)	0.264	0.951	0.337	0.144	0.222
Upland vs. lowland[a]	**	ns	**	**	**

[a] Mann-Whitney *U*-test, males and females combined. **, $P < 0.01$; ns, not significant ($P > 0.05$).

to be intermediate between the two Tristan Bunting morphs from Inaccessible Island. Only one skin of an adult Tristan Bunting from Nightingale Island was available for comparison. The color of its back and belly feathers was intermediate between the two morphs from Inaccessible Island (Table 2). The back color of a single Wilkins' Bunting from Inaccessible Island fell within the lower end of the range of upland Tristan Buntings, whereas its belly color was similar to that of lowland birds (Table 2). This agrees with the subjective impression that "pure" Wilkins' Buntings on Inaccessible Island were fairly drab beneath, resembling lowland Tristan Buntings more than upland buntings in coloration.

The brighter yellow/green coloration of upland bunting plumage emphasizes the contrast with the dark feather centers, making upland birds appear more streaked than lowland birds. It also makes the dark feather centers appear darker than those of lowland birds. Among upland adults, the streaks on the crown are particularly prominent because they retain a high degree of contrast with the green feather edges. The bright yellow underparts of upland birds also contrast more strongly with the blackish neutral gray (82) underdown when the plumage is ruffled than do the underparts of lowland birds. In addition to the effects of reduced contrast, streaking on the upperparts of lowland birds (back, nape and crown in particular) is less marked than that of upland birds because of reduced definition of the green feather edges (i.e. the transition from dark to pale coloration within each feather is less clear-cut among lowland birds).

The color differences between the two Tristan Bunting morphs exist from hatching. Both have grayish down, but the skin of newly hatched lowland buntings is pink (7), whereas that of upland buntings is chrome orange (16). Similarly, the bill and legs of lowland chicks are pink and the gape is pale straw yellow (56), whereas the bill of upland birds is tinged yellow, and the legs and gape are bright spectrum yellow (55). Older chicks differ in the color of the base of the bill: pale straw yellow in lowland birds, and orange-yellow (18) in upland birds. Wilkins' Bunting chicks on Inaccessible Island are similar to lowland chicks in coloration (but see below for hybrids). Differences between the juvenal plumages of the two Tristan Bunting morphs are listed in Table 1.

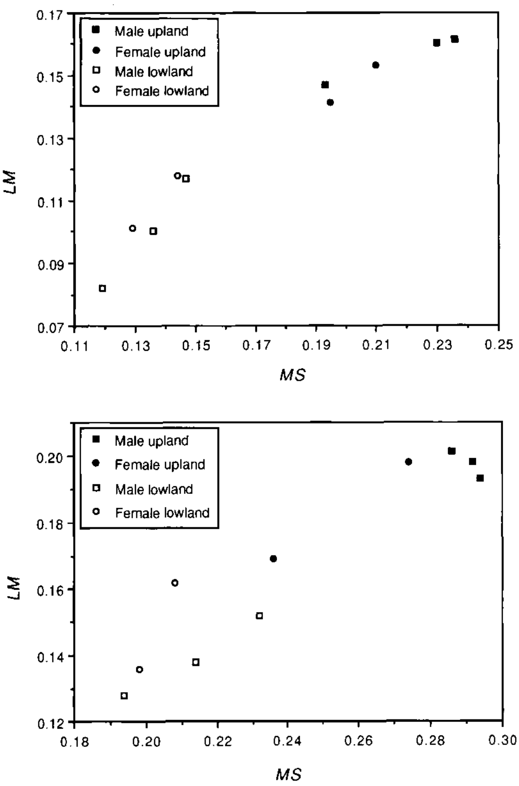

Fig. 2. Color of back (upper panel) and belly (lower panel) plumage of upland and lowland morph Tristan Buntings on Inaccessible Island. Color scores derived by segment classification (Endler 1990; see methods) from reflectance spectra between 400 and 700 nm. Color intensity (chroma) denoted by distance from origin, and hue by angle from origin.

Feather structure and pigmentation.—We found no structural differences between the feathers of the two Tristan Bunting morphs, or among other *Nesospiza* taxa. The only difference between morphs was for longer contour feathers among upland birds ($F_{1,9} = 8.357$ and 8.570 for back and belly contour feathers, respectively, $P < 0.05$). This difference resulted in upland birds having somewhat thicker, denser body plumage than lowland birds.

Feather coloration in *Nesospiza* results from the interaction of two pigment types: dark brown melanins and yellow carotenoids. Yellow feathers such as those found on the underparts have only carotenoids, whereas dark feather centers have only melanins. Greenish coloration is formed by a combination of the two pigment groups, with melanins in the barbules and carotenoids in the barbs. In some back,

TABLE 3. Concentrations of carotenoid pigments in the feathers of Tristan Bunting color morphs on Inaccessible Island.

Sample	Pigment concentration (mg carotenoid·g^{-1}) Lowland	Upland
Belly feathers	0.016[a]	0.051
Tail feathers	0.009	0.026

[a] Including a contaminant.

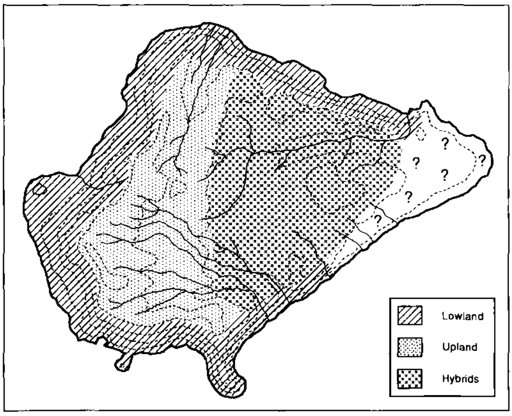

Fig. 3. Distribution of Tristan Bunting morphs and interspecific hybrids on Inaccessible Island. Question marks indicate areas not searched.

wing and tail feathers, all three combinations were found together. Near the rachis, both the barbs and barbules contain melanins, giving a dark brown feather center. Farther from the rachis, the barbs become yellow, but the barbules remain brown, giving a green appearance to the feather. Finally, at the edge of the feather, the barbules lose their melanins and contain only carotenoids, resulting in a yellow fringe. Plumulaceous feathers differ from pennaceous feathers in having blacker melanins in discrete nodules at intervals along the barbules; they lack carotenoids and appear grayish.

There were no differences between Tristan Bunting morphs in the distribution or types of pigments within feathers. The main difference between color morphs was that upland birds had approximately three times greater concentrations of carotenoids in their feathers than lowland birds (Table 3). All feather extracts had identical absorption spectra and contained at least three pigments (R_f = 0.38, 0.24 and 0.19). The main pigment co-migrated with lutein and zeaxanthin on TLC (R_f = 0.19), which suggests a dihydroxycarotenoid. Its absorption spectrum, with maxima at 416, 439 and 468 nm, indicative of one less double bond in conjugation than lutein (λ_{max} at 418, 443 and 472 nm), suggests tunaxanthins (ε,ε-carotene-3,3′-diols) in the extracts. A second pigment (R_f = 0.24; λ_{max} at 437 and 467 nm) produced a dihydroxycarotenoid on reduction; based on its spectrum and mobility, it probably is a canary-xanthophyll, 3′-hydroxy-ε,ε-caroten-3-one (Hudon 1991). Another canary-xanthophyll, ε,ε-carotene-3,3′-dione, α-cryptoxanthin or both, made up the third pigment band (R_f = 0.38; λ_{max} at 414, 439 and 468 nm); α-cryptoxanthin is suspected because the pigment band was only partly reduced by sodium borohydride. A rapidly migrating yellow pigment (R_f = 0.50; no spectrum) was present in very low concentrations; its nature remains uninvestigated.

TABLE 4. Concentrations of carotenoid pigments in fleshy fruits eaten by Tristan Bunting on Inaccessible Island, and frequency of fruits in bunting diets during summer.

Sample	Pigment concentration (mg carotenoid·g^{-1})[a]	Percent in Tristan Bunting diet[b]	
		Lowland	Upland
Empetrum rubrum	0.007	9.1	2.1
Nertera depressa	1.7	1.8	4.1
N. assurgens	3.1	0.0	5.4
N. holmboei	No data	0.0	0.3

[a] Based on fruit dry mass.

[b] From Ryan (1992).

Nertera fruits are the most likely sources of carotenoids in the buntings' diets; both species sampled contain large concentrations of carotenoids (Table 4). The main pigment in both species sampled migrated rapidly on TLC (R_f = 0.75) and is presumed to be a carotene. Other, less common and slower-migrating pigments also were present (R_f = 0.51, 0.34 and 0.22 for *N. assurgens* and R_f = 0.34 for *N. depressa*). The pigment extracts of *Nertera* fruits had absorption maxima at relatively long wavelengths (λ_{max} at 456 nm for *N. assurgens* and 442, 467 and 497 nm for *N. depressa*; cf. 425, 449 and 476 nm for β-carotene; Britton 1985). The main pigment in the *Nertera* fruit probably is an acyclic carotene like lycopene (λ_{max} at 444, 470 and 502 nm; Britton 1985). *Empetrum rubrum* fruits contained relatively few pigments, which migrated closely on TLC, in the vicinity of dihydroxycarotenoids (R_f values of 0.26, 0.21 and 0.15).

Distribution of color morphs on Inaccessible Island.—Knowledge of the distribution of buntings is best for the northwestern part of Inaccessible Island, although at least brief visits were made to most parts of the island (Fig. 1). The two morphs of Tristan Bunting have largely parapatric distributions, each found in different vegetation types (Fig. 3; for vegetation map, see Roux et al. 1992). Upland buntings occur primarily in *Blechnum palmiforme* and wet heath on the plateau, whereas lowland buntings are largely restricted to *Spartina arundinacea* tussock grassland on the coastal slopes of the island. In the spring (October), small numbers of immature upland buntings were captured near sea level at Blenden Hall, but none was recorded after breeding commenced in December. Only one lowland bunting was captured on the western plateau near North Point, where there is a large patch of *Spartina* tussock on the plateau edge.

Despite the small size of Inaccessible Island (13 km^2), the rugged topography and dense vegetation preclude continuous sampling over the entire island. In particular, the steep seaward cliffs limit the possibilities for examining the interface between upland and lowland Tristan Bunting populations. The only accessible area of contact is the slope above Blenden Hall, where the cliffs are 450 m high, and unbroken tussock grassland extends up to 300 m. The upper 150 m is characterized by *Blechnum penna-marina* heath, grading into wet heath. Tristan Bunting morphs remain closely associated with different vegetation types, with only lowlands in the tussock grassland, and only uplands in the wet heath. However, two "mixed" pairs (both with upland male and lowland female) were found in *Blechnum penna-marina* heath at 300 to 350 m altitude. These were the only mixed pairs found, and constituted less than 1% of Tristan Bunting pairs. Their offspring were intermediate in color between those typical of upland and lowland birds.

The situation on the eastern plateau is confused by the widespread occurrence of hybrids between Wilkins' and Tristan buntings in the *Phylica arborea* woodland (Fig. 3). The hybrids are characterized by a complete range of intermediate sizes between the large Wilkins' and small Tristan buntings. The morphology of these hybrids is dealt with in detail elsewhere (Ryan 1992), but their plumage is most closely allied to upland buntings. Although two apparent lowland females were caught at the Denstone Hill study area, all other adult birds and fledglings exhibited the bright yellow coloration typical of upland birds. This character, together with the male song and the small size of the offspring, distinguished the only pair of apparent "Wilkins' " Buntings found breeding in the hybrid area from Wilkins' Buntings found breeding on the coastal lowlands. The plumage of interspecific hybrids resembled upland Tristan Buntings, except for a tendency for some morphologically intermediate hybrids to have a clearly defined dark bib. In some birds, notably adult males, this was almost black, and resembled that found in adult Gough Buntings (*Rowettia goughensis*), a related species restricted to Gough Island, 350 km south of the Tristan group.

Denstone Hill is fairly close to the plateau edge. No lowland-type birds were observed elsewhere in the central part of the eastern plateau, where "Tristan" Buntings (i.e. those falling within the size range typical of Tristan Buntings elsewhere on the island) are very richly colored (subjectively assessed as being even brighter yellow than typical upland birds). It remains unclear whether they constitute part of the hybrid complex or are upland Tristan Buntings (although their calls suggest they are associated with the hybrid complex; Ryan 1992). Some lowland birds were encountered along the plateau edge, where *Phylica* woodland grades directly into *Spartina* tussock grassland. This was also the only area where typical Wilkins' Buntings were observed (defined by song as well as plumage characteristics).

The size range of hybrids appeared to vary in different parts of the eastern plateau. Few birds were caught outside the Denstone Hill study area, but observations suggested that the densely wooded valley above The Waterfall contained almost exclusively large hybrids (no small-billed birds were seen), whereas smaller hybrids and "Tristan" Buntings predominated on The Serengeti, an area of relatively open woodland in the central eastern plateau. This trend appeared to be related to tree size, with large hybrids found in areas with large trees (a trend evident even within the Denstone Hill study area). The ecotone between the *Blechnum palmiforme* heath of the western plateau and *Phylica* woodland of the eastern plateau is occupied by Tristan Buntings with a few small hybrids. These Tristan Buntings tend to be less bright than typical upland buntings, but we have treated them as upland birds because they are located between bright populations, and because they do not differ morphologically from other upland buntings.

"Pure" Wilkins' Buntings, defined in terms of plumage, song and behavior, are restricted largely to the coastal slopes of Inaccessible Island, where there are scattered *Phylica* trees in *Spartina* tussock grassland (Fig. 3). Small numbers of Wilkins' Buntings occur along the edge of the plateau, with several birds seemingly always present in tussock grassland on the plateau edge near Molly Bog, at the western end of the island. There are no *Phylica* trees near this site, but all the birds observed there have been immatures. The only breeding pair found on the plateau was within 50 m of the plateau edge in Ringeye Valley, and the male bird regularly flew off the plateau to feed in *Phylica* trees on the coastal cliffs. Unlike the hybrid chicks, the offspring of this pair was pink skinned and had drab plumage, as is typical of Wilkins' Buntings.

Movements.—Adult buntings exhibited strong site fidelity. No marked birds were sighted more than 400 m away from the area of initial capture either within or between years ($n = 64$ bunting-years). Immature birds dispersed farther than adults, with movements of up to 1.6 km recorded for birds foraging along the beach. However, only one movement between habitat types was recorded. An immature hybrid banded on the plateau at Denstone Hill (altitude 250 m) was retrapped 62 days later at Wilkins' Copse, Blenden Hall (altitude 20 m), having moved more than 2.5 km, or slightly less than half the longest axis of the island (5.4 km). The occurrence of immature upland birds on the coast in spring suggests that there may be seasonal altitudinal movements, but this was not confirmed by resightings of banded birds.

DISCUSSION

Many avian color morphs result from variable deposition of carotenoids in the plumage (Brush 1990). Several bird species have morphs or closely related taxa varying in the amount of yellow pigmentation in the plumage (e.g. Johnson and Brush 1972, Brush and Johnson 1976, Brush 1990). However, the occurrence of color variation within the Tristan Bunting population on Inaccessible Island is remarkable, given the ability of individuals to disperse over virtually the entire island. The known examples of plumage polymorphisms among populations of terrestrial island birds (Gill 1973, Wunderle 1981) occur on islands more than an order of magnitude larger than Inaccessible Island. Only the subdivision of the population of male Large Cactus-Finches (*Geospiza conirostris*) on Isla Genovesa into two discrete song types (Grant and Grant 1989) occurs on an island as small as Inaccessible. The color morphs of Tristan Bunting also are unusual in having virtually no overlap in breeding ranges, with a stepped cline along habitat boundaries.

Our results confirm that two color morphs of Tristan Bunting on Inaccessible Island occupy largely discrete ranges and associate with different habitats. In addition, there is frequent interspecific hybridization in one part of the island. It seems unlikely that this remarkable variation within populations has arisen within the last few decades, but is it plausible that the variation could have been overlooked by earlier researchers?

Summary of Nesospiza *field studies.*—There have been fewer than 50 visits by naturalists to the Tristan islands (Wace and Holdgate 1976, Fraser et al. 1988). *Nesospiza* buntings were first reported and later collected on the main island of Tristan (Dupetit Thouars 1811, Carmichael 1818, Brierly 1842 *in* Wace and Holdgate 1976, Cabanis 1873, Stresemann 1953). By 1873 the Tristan population was on the verge of extinction, if not actually extinct (Willemöes-Suhm 1876, Moseley 1892); there have been no subsequent sightings. The first collections on the uninhabited islands were made during the visit of the *Challenger* Expedition in 1873 (Moseley 1892). Since then there have been some 18 visits to Inaccessible Island by naturalists (Table 5). Most of these visits lasted only a few days, and many visitors failed to reach the plateau, which is accessible only from the exposed, western side of the island. Even the scientists who visited the island for longer periods (viz. Hagen, Rowan and Elliott; see Table 5) failed to collect buntings on the island plateau. The paucity of field experience and collected specimens, especially on the island's plateau, coupled with the considerable age- and sex-related plumage variability within taxa, presumably accounts for the two Tristan Bunting color morphs being

TABLE 5. Scientific expeditions visiting Tristan islands, and other observers of Tristan landbirds, with resultant publications mentioning *Nesospiza*.

		Duration of visit (days)[a]			
Expedition/observer	Date	T[b]	N	I	Publications on *Nesospiza*
A. Dupetit Thouars	Jan 1793	?	—	—	Dupetit Thouars 1811
D. Carmichael	Nov–May 1816/1817	ca. 160	—	—	Carmichael 1818, Cabanis 1873, Stresemann 1853
B. Boyd	Mar 1842	3	—	—	Brierly, in Wace and Holdgate 1976, Bourne and David 1981
J. MacGillvray	Nov 1852	1	—	—	Bourne and David 1981
Challenger Expedition	Oct 1873	1	1	1	Willemöes-Suhm 1876, Sclater 1881, Moseley 1892
P. C. Keytel	1907–1909	—	—	?	Winterbottom 1976
Quest Expedition	Jun 1922	—	1	1	Wilkins 1923, Lowe 1923
H. M. Rogers	1922–1926	—	?	?	Lowe 1927, Mathews and Gordon 1932
P. Lindsay	1927–1928	—	?	?	
Norwegian Expedition	Dec–Mar 1937/1938	—	16	17	Hagen 1952
J. Kirby	1945–1946	—	?	?	Roberts and Kirby 1948
Fishing Co. investigations	Feb–Mar 1948	—	?	?	Broekhuysen and Macnae 1949
(M. K. Rowan)	Jan–Nov 1949/1950	—	26	ca. 20	—
R. Upton	1950–1951	—	?	?	Rand 1955
H. F. I. Elliott	1950–1952	—	?	?	Elliott 1953, 1954, 1957
N. Scheer	1958–1960	—	?	?	Voous 1962
Royal Society Expedition	Jan–Mar 1962	—	3	2	Holdgate 1965
M. E. Richardson	1972–1974	—	10	4	Richardson 1984
Denstone Expedition	Oct–Feb 1982/1983	—	—	88	Fraser 1983, 1984, Collar and Stuart 1985, Fraser and Briggs in press
FitzPatrick Institute	Sep–Oct 1987	—	—	16	—
	Oct–Nov 1988	—	1	23	Ryan and Moloney 1991a, b
	Oct–Mar 1989/1990	—	4	125	This study

[a] T = Tristan, N = Nightingale, I = Inaccessible. ? is used for visits of unrecorded duration. Most such visits likely to have been brief (less than a week), but Elliott made several such trips to the islands.

[b] Visits to main island of Tristan only are reported prior to 1900, by which time *Nesospiza* was extinct on the island.

overlooked until the 1982–1983 Denstone Expedition. Prior to the Denstone Expedition, the only possible allusion to an upland bird is a single specimen described as being brighter yellow beneath than three *N. a. questi* from Nightingale Island (Voous 1962; collection locality on Inaccessible unrecorded, but the collector, N. Scheer, did visit the plateau).

Interspecific hybridization is even more likely to have been overlooked on Inaccessible Island than is the existence of color morphs, because hybrids are difficult to distinguish in the field and because they are largely restricted to the most inaccessible part of the island. Among naturalists, only Elliott and Fraser are known to have visited the eastern plateau. Fraser seldom visited the area, and caught no buntings there (M. W. Fraser pers. comm.), but did record a bird seemingly intermediate between a Tristan and Wilkins' bunting near North Point (M. W. Fraser *in* Collar and Stuart 1985). The first morphologically intermediate hybrids were caught in 1988, but the extent of hybridization was only realized in 1989, when mist netting commenced on the eastern plateau area. However, it is likely that hybrids have occurred on Inaccessible Island for some time; based on observations in Waterfall Gulch, an area with many large-billed hybrids, Elliott (1957) reported *N. w. dunnei* to be "much yellower" than *N. w. wilkinsi*, which concurs with hybrid plumage rather than "pure" *N. w. dunnei.*

Basis of color variation.—Both genetic and environmental factors could, singly or in concert, result in the observed color variation among Tristan Buntings on Inaccessible Island. The variation in soft-part coloration of *Nesospiza* chicks mirrors that found among Darwin's finches (Grant et al. 1979), which has been shown to be under fairly simple (Mendelian) genetic control (Grant and Grant 1989). There are few examples of polymorphisms among young birds (Buckley 1987), and the distinction between upland- and lowland-morph chicks is more marked than that in *Geospiza conirostris* (Grant and Grant 1989: plate 1). The apparent invariance with which upland birds produce yellow chicks and lowland birds pink chicks suggests that if this trait is under genetic control, then the controlling genes must be almost fixed in the two populations. A similar situation occurs among Sharp-beaked Ground-Finch (*G. difficilis*) populations, with pink and yellow morphs being fixed on different islands (Grant et al. 1979).

Strictly, polymorphism refers to discontinuous variation in a phenotypic trait (e.g. Mayr 1963, 1970). The two color morphs of Tristan Bunting on Inaccessible Island are largely discrete, but the difference between them is quantitative rather than qualitative. Also, the offspring of mixed pairs are intermediate in coloration, and there is some local variation in coloration within morphs. These observations suggest that, if plumage coloration is genetically determined, there is either incomplete dominance or it is a polygenic trait.

A simpler explanation is that plumage color differences are ecophenotypic, induced by dietary differences between habitats. All carotenoid feather pigments ultimately are derived from a bird's diet (Brush and Power 1976, Brush 1978, 1990), and the yellow coloration of Great Tits (*Parus major*) breeding in different habitats has been shown to vary as a result of differences in the amount of carotenoid in the diet (Slagsvold and Lifjeld 1985, Partali et al. 1987). This offers a parsimonious explanation for the close relationship between bunting color-morph distribution and vegetation types, and is supported by the different amounts of carotenoid-rich *Nertera* fruits in the diets of the two morphs. *Nertera* fruits comprise almost 10% of prey items of upland Tristan Buntings, compared with less than 2% of lowland Tristan Bunting diet (Ryan 1992). The differential intake of carotenoids from *Nertera* fruit is increased still further by two results. First, the concentration of carotenoids is much greater in *N. assurgens* fruit; this species is restricted to the plateau of Inaccessible Island (Roux et al. 1992) and is frequent in the diet of upland birds (Table 4). Second, the main pigments in *Nertera* fruits are acyclic carotenoids, which generally are not assimilated by birds (Fox and McBeth 1970. Fox et al. 1970); thus, the other, less abundant pigments are the likely precursors of feather carotenoids in Tristan Buntings, and these pigments are found primarily in *N. assurgens.*

Hill (1992) suggested that plumage brightness of male House Finches (*Carpodacus mexicanus*) is determined by the carotenoid content of the diet immediately prior to and during molt (but see Hudon 1994). If this mechanism applies to *Nesospiza* buntings, habitat-specific differences in carotenoid availability could account for the color difference observed between upland and lowland Tristan Buntings morphs, given that birds remain on the breeding territory throughout the molt period. *Nertera* fruit are available throughout the premolt and molt period (January-March). However, feeding experiments on captive birds are required to elucidate fully the basis of the color variation in Tristan Buntings (cf. Brush and Power 1976, Hill 1992).

Whatever the proximate cause of the color variation, it may have evolutionary significance (cf. Hill 1990, 1991). Coloration is important in avian displays, and is under strong selective pressures (e.g. Brush and Power 1976, Brush and Johnson 1976, Burtt 1986, Butcher and Rohwer 1989, Hill 1990). If Tristan Bunting morphs on Inaccessible Island mate assortatively on the basis of plumage color, genetic differences between the two color morphs could accumulate, allowing adaptation to local conditions to occur. This is consistent with the initial stages required for parapatric speciation (Endler 1977).

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