

Characterization of an Orange Variant of the Bananaquit (*Coereba flaveola*) on La Désirade, Guadeloupe, French West Indies

JOCELYN HUDON,^{1,5} HENRI OUELLET,² ÉDOUARD BÉNITO-ESPINAL,³
AND ALAN H. BRUSH⁴

¹ Provincial Museum of Alberta, 12845-102 Avenue, Edmonton, Alberta T5N 0M6, Canada;

² Département de sciences biologiques, Université de Montréal, Case postale 6128,
Succursale "Centre-Ville," Montréal, Québec H3C 3J7, Canada;

³ B.P. 795, 97173 Pointe-à-Pitre, Cedex, Guadeloupe, Antilles françaises; and

⁴ Department of Physiology and Neurobiology, U-156, University of Connecticut, Storrs, Connecticut 06269, USA

The Bananaquit (*Coereba flaveola*) is a phenotypically variable species of the American tropics that varies markedly in the extent and intensity of both its carotenoid and melanin pigmentation. Paynter (1968) recognized 41 subspecies of Bananaquits, and plumage color polymorphism has been reported on some Caribbean islands (Wunderle 1981a, b, c). Despite this variability, until now, no orange Bananaquit has been described.

On La Désirade, a small island of the Guadeloupe Archipelago in the Lesser Antilles where Bananaquits are common (Bénito-Espinal 1990), small numbers of individuals have a pronounced orange wash on their underparts. This unusual coloration occurs as orange blotches of variable size and location on the predominantly yellow plumage of the breast and upper abdomen. In a few individuals, orange almost entirely replaces the yellow color. Orange birds were first recorded on La Désirade on 26 March 1988 as part of a banding program.

Both genetic and environmental factors could account for the color variation of La Désirade Bananaquits. The Bananaquit has a bright red mouth lining and gape and thus appears to have the capability to manufacture red pigments endogenously from yellow dietary pigments. The variants may express this capability ectopically, as in the liver or the feather follicles, so as to present red pigments to the growing feathers. Variation in the position and extent of the orange coloration could arise from the necessarily poor spatial and temporal control of either pigment production or follicular uptake in a new color morph. A regulated increase in the concentration of yellow pigments in the plumage of Bananaquits also might produce an orange phenotype.

Alternatively, the introduction of a new food source (flower, fruit, or invertebrate), or greater access to a preexisting one, could have supplied previously unavailable red pigments to the Bananaquits on La Désirade. Under this scenario, variation in the timing of pigment uptake in relation to feather replacement

could explain variation in the distribution of the orange color. In the Cedar Waxwing (*Bombycilla cedrorum*), a causal relationship of this sort was demonstrated recently between a red carotenoid pigment (rhodoxanthin) present in introduced food sources (Morrow's and Tartarian honeysuckles; *Lonicera morrowii* and *L. tatarica*) and a variant (orange) tail-band color (Hudon and Brush 1989, Brush 1990, Mulvihill et al. 1992). Orange variants of the Yellow-breasted Chat (*Icteria virens*) and the Kentucky Warbler (*Oporornis formosus*) appear to deposit extraneous pigment in the same fashion (Mulvihill et al. 1992). As in all of these species, the color variation in the Bananaquit appears to be of recent origin, is variable in expression, and is limited geographically.

To discriminate between an endogenous and an exogenous origin of variant color in Bananaquits, we characterized the pigments in feathers of both common yellow and variant orange individuals. We predicted that, if the color change were endogenous, the pigments would be identical to pigments commonly observed in birds. If dietary-based, the pigment combination seen in the variants would match the carotenoid make-up of an external pigment source.

Methods.—La Désirade (2 × 11 km) lies about 8 km east of Grande-Terre, one of the two main islands of Guadeloupe. La Désirade consists of a low-lying plateau (278 m maximum elevation) dissected by numerous ravines and surrounded by a narrow shoreline. Three banding stations were established about 3 km NE of Grande-Anse, the island's administrative center.

One male and two female Bananaquits with orange in their plumage (Orange Yellow [18], almost Spectrum Orange [17]; following Smithe 1975) and three typical yellow individuals (one male, two females; Spectrum Yellow [55]; Smithe 1975) were collected on La Désirade on 27 November 1988. Two additional birds, one of each color, were collected on 25 November 1989. We examined the plumages for the presence and extent of orange coloration. No obvious differences were detected between the sexes. The colored portions of individual feathers were of uniform color, so the orange and yellow feathers of variant birds were extracted separately.

⁵ E-mail: jhudon@mcd.gov.ab.ca

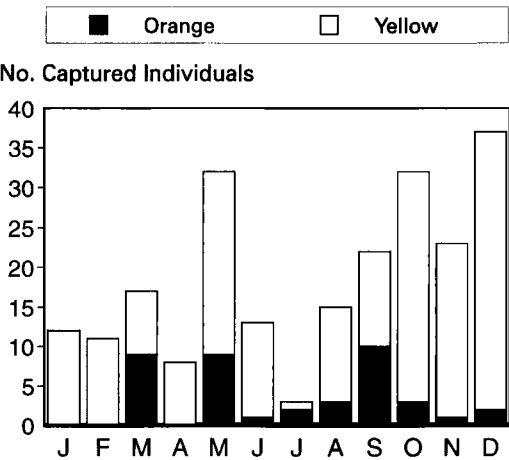


Fig. 1. Numbers and breast color of Bananaquits captured on Plateau de la Désirade, Guadeloupe, in 1988.

The feather carotenoids were extracted in warm, acidified (HCl) pyridine and transferred to hexane with tap water in a separatory funnel (Hudon and Brush 1992). We performed preliminary analytical thin-layer chromatography (TLC, Kodak Chromagram plates, Rochester, New York) and high-performance liquid chromatography (HPLC) on all pigment extracts (Hudon 1991). Individual carotenoids were isolated by preparative TLC on pre-coated silica gel plates (Anasil G, Analabs, New Haven, Connecticut) (Ryan et al. 1994). Absorption spectra of individual pigments in hexane were recorded with a Beckman DU-65 spectrophotometer.

We determined R_f values (i.e. ratio of pigment migration to solvent-front migration) of pigments in a typical run on the Chromagram plates. Standards of echinenone, canthaxanthin, lutein and zeaxanthin (from Hoffman La Roche, Basel), astaxanthin (from a lobster shell; Hudon 1991), and canary-xanthophylls (from the yellow feathers of an American Goldfinch

[*Carduelis tristis*]) were available for comparison. We tested chemically for the presence of carbonyl groups in individual pigments with sodium borohydride in methanol (Hudon and Brush 1992) and for the presence of allylic OH groups with acidified methanol (Curl 1956).

Results.—Close to 20% of Bananaquits captured in 1988 showed some orange color on the breast (Fig. 1). Orange variants were captured throughout 1988 beginning 26 March (Fig. 1). Five color variants were captured more than once (Table 1). Two individuals (nos. 707 and 784) maintained the original breast color throughout the banding period until 30 September, when they were last captured. Three other variants changed color during the banding period: bird 718 changed from orange to yellow, whereas birds 024 and 919 changed from yellow to orange. The change in color of bird 024 occurred earlier than in bird 718. The timing of the color change in bird 919 cannot be determined from the capture data.

The yellow feathers of all Bananaquits contained at least seven yellow pigments, one of which ($R_f = 0.18$; $\lambda_{max} = 417, 439, 466$ nm; strongest peak in italics) accounted for over one-half of the absorption at 450 nm on HPLC tracings. This pigment contained two hydroxyl groups, at least one of which was allylic, and no carbonyl group, which matched the chemical structure of lutein. The presence of lutein was confirmed on HPLC. The absorption of this pigment at shorter wavelengths than published values for lutein (421, 445, 474 in petroleum ether; Britton 1985) suggests that carotenoids may be isomerized by the Anasil matrix, during or following pigment separation (this probably also applies to Ryan et al. 1994). Two other faster, yellow pigments—with R_f values of 0.39 ($\lambda_{max} = 415, 439, 466$ nm; no allylic OH or carbonyl group) and 0.26 ($\lambda_{max} = 404, 422, 466$ nm; this was probably a mixture, with evidence of allylic OH and carbonyl groups as with 3'-hydroxy- ϵ,ϵ -caroten-3-one, a canary-xanthophyll)—also were abundant. There were additional yellow pigments with R_f values of 0.86 (probably a carotene), 0.58, and 0.47. An orange pigment ($R_f = 0.30$) also was present in trace amounts.

TABLE 1. Coloration of the breast feathers of variant banded Bananaquits captured on more than one occasion on La Désirade, Guadeloupe, in 1988.

Date of capture	Bird no.				
	707 (male)	784 (female)	718 (male)	024 (male)	919 (sex unknown)
26 Mar	Orange	Orange	Orange		
23 Apr				Yellow	
27 May	Orange			Orange	Yellow
25 Jun			Orange		
23 Jul			Orange		
27 Aug		Orange			
30 Sep	Orange	Orange	Yellow		
1 Nov			Yellow		
27 Dec			Yellow		Orange

The last four pigments were present in amounts too small to be chemically characterized.

The orange feathers contained three red pigments in addition to the yellow pigments. The main red pigment had a R_f value of 0.51 ($\lambda_{\max}$ = 462, 492, 528 nm). There was also a faster-migrating pigment band (R_f = 0.68; $\lambda_{\max}$ = 437, 465, 495 nm) and a slower-migrating band (R_f = 0.30). The quality of the absorption spectra of these red pigments generally was poor. The mobility of the red pigments on TLC and HPLC differed from that of red carotenoids commonly encountered in birds: canthaxanthin (R_f = 0.42), astaxanthin (R_f = 0.13), and echinenone (R_f = 0.60). Although one of the red pigments co-migrated with rhodoxanthin on TLC (R_f = 0.30), it did not separate in three bands as rhodoxanthin typically does. The low concentration of the red pigments precluded their further characterization.

Discussion.—The feathers of orange Bananaquits contained three red pigments in addition to the yellow pigments typically found in this species. The red pigments were unlike the common avian 4-keto-carotenoids, canthaxanthin, astaxanthin, and echinenone, or other red pigments previously reported in birds, such as rhodoxanthin.

4-keto-carotenoids are the only red pigments that birds have been demonstrated to synthesize endogenously (Völker 1962, Davies 1985). The red pigments might be 4-keto-carotenoids not considered in this study, e.g., 3-hydroxy-echinenone has a similar mobility on TLC to that of the main red pigment in the variants, but the pigments have markedly different spectra ($\lambda_{\max}$ of 457 nm for 3-hydroxy-echinenone [Britton 1985]; compared with the three peaks of the main red pigment at 462, 492 and 528 nm). Based on its spectrum and high mobility on TLC, the main red pigment in the variant birds more likely is a 3,4,(3',4')-di(tetra)dehydro- ψ,ψ -carotene, such as 3,4-dehydrolycopene or spirilloxanthin, or an esterified 4-keto-nor-carotenoid like actinioerythrin (Britton 1985). Spirilloxanthin, unfortunately, is known only from photosynthetic purple bacteria, and actinioerythrin from sea anemones, both questionable sources of pigments for Bananaquits. In contrast, dihydrolycopene has been reported in a few groups of insects (Goodwin 1984). As this and related pigments occur in certain types of fungi, they are believed to originate from fungal endosymbionts living in these insects (Goodwin 1984). We can offer no candidate (known or hypothetical) 4-keto-carotenoid for the fastest red pigment. The unusual character of the red pigments in the variant Bananaquits does not support an endogenous origin for the color variation. The biochemical evidence suggests instead that the Bananaquits on La Désirade have access to a source of unusual red pigments that can be deposited alongside the yellow pigments in the plumage.

Bananaquits are food generalists that feed primarily on nectar, fruits, insects, and spiders, depending on seasonal availability (Wunderle 1981c). They would,

therefore, be likely to encounter new sources of carotenoids that became available on the island. Although uncommon in nature, red carotenoids have been reported in a wide variety of organisms (Goodwin 1980, 1984). Moreover, sources of red pigments are still incompletely known. For example, few terrestrial invertebrates have been examined in detail (see Goodwin 1984). Because we are unable to precisely identify the red pigments in the variant Bananaquits, we cannot suggest any candidate source for these pigments.

An exogenous origin for the red pigments in the feathers of variant Bananaquits is also supported by changes in plumage color of individuals captured on more than one occasion. In two of the birds (nos. 718 and 919), the color change was recorded in association with the postbreeding (i.e. prebasic) molt, which typically occurs from July to December (Bénito-Espinal and Ouellet pers. obs.). The third individual apparently acquired its orange coloration during the molt from the juvenal to first basic plumage. These instances highlight the labile character of the orange color and the lack of specific rules for color change. The lability of the variant color is also underscored by the apparent scarcity of orange birds recently noted on La Désirade (É. Bénito-Espinal pers. obs.).

Persistence of the orange coloration in some variants could indicate site fidelity, some degree of food specialization, or repeated chance encounters with an exogenous source of red pigments. Individual Bananaquits appeared to be moderately site faithful because several banded birds not observed at banding sites for several weeks were subsequently retrapped at the original sites.

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Is Singing Costly?

ABBOT S. GAUNT,¹ THERESA L. BUCHER,² SANDRA L. L. GAUNT,^{1,4}
AND LUIS F. BAPTISTA³

¹ Borror Laboratory of Bioacoustics, Department of Zoology, Ohio State University, Columbus, Ohio 43210, USA;

² Department of Biology, University of California, Los Angeles, California 90024, USA; and

³ California Academy of Sciences, Department of Birds and Mammals, Golden Gate Park, San Francisco, California 94188, USA

In an interesting paper testing for the energetic cost of singing in a passerine bird (Carolina Wren, *Thryothorus ludovicianus*), Eberhardt (1994) concluded that singing in passerines is a costly activity that "accounts for 9.4 to 24.7% of the total energy budget." She attributed this cost to sexual selection for expensive displays. We find this paper disturbing at several levels. In order of increasing specificity, these are: (1) the author's interpretations exceed the limits of her data and are linked to questionable theoretical considerations; (2) the data, even if correct, are subject to alternative interpretations; and (3) the method used to obtain and analyze the physiological data is questionable.

Theoretical problems.—Eberhardt (1994:124) stated, "Theories of sexual selection predict that mate choice

will lead to the evolution of costly displays that indicate the health or condition of displayers." True, some theories do make such predictions (Zahavi 1987), and some elaborate signals may reasonably be attributed to such tactics (e.g. long tails in weaver finches; Andersson 1992). However, theories of sexual selection predict only that costly displays are one means of advertising fitness, if this is in fact truly an issue. That sexual selection does appear to employ costly displays in some species does not suggest that this condition is universal. Further, reliable signals need not be costly (Maynard Smith 1994), and "liars" may be penalized by various means. When and where might we expect costliness to be appropriate?

It is generally supposed that organisms expend considerable energy to enhance reproductive success and that energy so expended may be parceled to various activities, each of which contributes to total success (Cody 1966). If the energy available for reproduction is limited, then parceling approaches a zero-sum game.

⁴ Address correspondence to this author. E-mail: sgaunt@magnus.acs.ohio-state.edu