

## COLORS OF FRUIT DISPLAYS OF BIRD-DISPERSED PLANTS IN TWO TROPICAL FORESTS

NATHANIEL T. WHEELWRIGHT AND CHARLES H. JANSON\*

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853;  
Department of Zoology, University of Washington, Seattle, Washington 98195

*Submitted August 24, 1984; Revised March 18, 1985; Accepted May 13, 1985*

Fruit-eating birds are the primary seed dispersers for many plant species in various habitats (Ridley 1930; van der Pijl 1969). Because seed dispersal is important for plants (Howe and Smallwood 1982), the criteria that birds use in choosing fruits should directly affect the reproductive success of plants that depend on avian seed dispersal. Any fruit trait that enhances the likelihood that an appropriate seed disperser will consume the fruit should be favored (Jenkins 1969; Snow 1971). Traits such as nutritional value, seed-to-fruit ratios (Howe and Vande Kerckhove 1980), taste (Sorensen 1983), time of ripening (Wheelwright 1983), and spatial display (Denslow and Moermond 1982) have been demonstrated to influence birds' selection of fruits. Until recently (Stiles 1982; Willson and Thompson 1982) there has been little research on fruit colors and their significance for seed dispersal.

With their excellent visual acuity and well-developed color vision (Jacobs 1981), birds probably use color to find and recognize fruits. If birds do notice and choose among fruits on the basis of color, existing differences in fruit colors between plant species may be the evolutionary result of differential selection by birds for increased fruit conspicuousness or attractiveness.

The conspicuousness of a plant's fruit display is likely to be a compromise between conflicting selection pressures. If plants benefit from the rapid removal of the greatest number of their fruits by appropriate seed dispersers (McKey 1975), natural selection should favor prominent fruit displays. Such displays may have associated costs, however (Snow 1971). Energy is invested in producing the display; frequently, accessory structures are enlarged and contrastingly colored, as in the bracts of *Heisteria* species (Olacaceae). Moreover, prominent fruit displays may attract seed predators and inappropriate dispersers as well as appropriate dispersers. Birds probably differ in their visual sensitivity and the way in which they find individual fruit trees; many bird species may encounter fruiting trees opportunistically, locating bright displays more readily than cryptic dis-

\* Present address: Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794.

plays. If such opportunists are poor dispersers (McKey 1975; but see Wheelwright and Orians 1982), excessively prominent displays could result in the effective dissemination of low numbers of seeds (Howe and Smallwood 1982).

Darwin (1859) noted that fruits eaten by birds (hereafter, "bird fruits") tend to be brightly colored, at least to human perception. Like Darwin, Ridley (1930) interpreted bright colors as serving three functions: to draw the attention of potential seed dispersers to a fruiting plant, to reveal the location of individual fruits, and to signal ripeness. Ridley considered red to be the most common color of bird fruits. Later data from European plants corroborated Ridley's impression (Turcek 1963) and cemented the idea that bird fruits are typically red (Raven et al. 1976), a perception echoed by researchers in the Neotropics (McKey 1975; Janzen 1983*a*) and supported by data on fruits eaten by birds of paradise (Beehler 1983).

Introducing an evolutionary approach, Willson and Thompson (1982) found that fruit displays of two or more colors occurred with greater frequency in seasons or regions with few fruit-eating birds. They argued that multicolored fruits have evolved because of the advantage of being conspicuous in conditions under which the probability of seed dispersal would otherwise be low. Their hypothesis gained support from the experiments of Morden-Moore and Willson (1982) and Willson and Melampy (1983), who showed that birds remove fruits more rapidly from isolated multicolored displays than from single-color displays. Stiles (1982) proposed that fruits exhibiting dual color changes are more common among summer-fruiting species, when only resident birds are available to disperse seeds.

In presenting the results of a comparative study of tropical bird fruits, we have two main aims. First, we present a detailed analysis of the frequency and associated traits of bird fruits of different colors in two species-rich tropical habitats. These data are contrasted with fruit-color frequencies in two temperate-zone regions and one subtropical one. Second, we attempt to interpret observed distributions of color patterns by considering some of the selective forces on the evolution of fruit displays. Using our data from northwestern Costa Rica and eastern Peru, we evaluate hypotheses relating fruit colors to habitat, relative abundance of fruit-eating birds, fruit morphology, and fruit nutritional value.

#### FUNCTIONS OF FRUIT COLORS

The colors displayed by fruits may be important in a plant's physiology (Willson and Thompson 1982), although physiological roles for fruit colors remain to be demonstrated. Green, of course, is an exception: developing fruits may contribute a major proportion of their own photosynthate (Bazzaz et al. 1979). Dark colors (blue, black, and brown in our classification) may absorb more radiation in the visible spectrum than pale colors (white, yellow, orange, red), thereby raising fruit temperatures, increasing metabolic and developmental rates (Janzen 1983*b*), and shortening the time a fruit remains on a plant exposed to predators and pathogens (Thompson and Willson 1978; Herrera 1982). This benefit of dark coloration would apply only to fruits regularly exposed to direct sunlight, but most of the species we discuss occur in the forest understory (61% in Costa Rica; 73% in Peru). In addition, dark mature fruits usually acquire their dark color only after

most of their development has been completed and their seeds are ready to be dispersed (Ridley 1930). Fruits of *Ocotea bernouliana* (Lauraceae), for example, turn from green to black within 48 h. None of these physiological roles alone is likely to explain either the diversity of bird-fruit colors or the divergence in the color of fruits of related plants that rely on different classes of seed dispersers (van der Pijl 1969; Willson and Thompson 1982; Janson 1983a).

Fruit color displays may have two other functions, to be conspicuous and to attract. The function most often ascribed to bird-fruit colors (Darwin 1859; Ridley 1930; van der Pijl 1969) is the former, their enhanced visibility to potential seed dispersers. Bright colors are the "flag" (Ridley 1930; Stiles 1982) that catches birds' attention. If conspicuousness were the sole reason for color displays in bird fruits, we would expect similar fruit displays under similar visibility conditions.

In addition to signaling location, a fruit's color may convey information about its quality that would influence a bird's choosing the fruit. Obvious examples of such information are the changes in nutritional value and digestibility that a bird can anticipate with the change in fruit color during ripening (Biale 1975). The bird's interpretation of spectral information depends on context, however: a red raspberry is nutritious, a red blackberry is unpalatable, a red beetle is probably poisonous. Nothing inherent in the color red signals edibility or ripeness. Color may allow birds to identify a fruit, thereby indirectly giving information about nutritional quality. (Color may also lead birds to misidentify a fruit, as in the case of mimetic fruits or seeds providing no nutritious pulp [Ridley 1930; van der Pijl 1969].) Fruits may conceivably be detected and eaten more readily if they produce colors that are important in other aspects of the lives of their seed dispersers (e.g., colors also used by birds in social signaling, or characteristic of other preferred food items). Color itself may be a resource (Janzen 1983b): carotenoids produced by the plant ultimately supply vitamin A, essential for the vertebrate visual system, and the precursors for many pigments required for feather coloration in birds (Rothschild 1975).

#### STUDY SITES AND METHODS

##### *Study Areas*

Fruits were collected in two habitats approximately equally distant from the equator, the lower montane wet and rain forests (Holdridge 1967) of Monteverde, Costa Rica (10°18'N, 84°48'W), and the tropical moist forest of Cocha Cashu in the Manu National Park, Peru (11°52'S, 71°22'W). We studied fruit-eating birds and their food plants in Costa Rica between June 1979 and February 1984 (N.T.W.) and bird fruits in Peru from September 1980 until December 1981 (C.H.J.). The Monteverde site (MV) straddles the continental divide at an elevation of 1350–1550 m. Steady northeastern trade winds deposit precipitation along a steep moisture gradient, creating a diversity of habitats on the plateau in the 15-km<sup>2</sup> study area. The Cocha Cashu Biological Station lies at an elevation of 400 m, where silt deposited by the meandering Manu River creates a variety of successional habitats within the 2-km<sup>2</sup> site (CC).

The Peruvian site differs from the Costa Rican site primarily in having a richer flora (ca. 1200 known species of higher plants [R. Foster, pers. comm.] vs. ca. 800 species at MV [W. Haber, pers. comm.]). Fruit-eating birds constitute a smaller proportion of the total bird community at CC, and they appear to be generally less abundant there than at MV (Janson, pers. obs.), although MV has considerably fewer species of fruit-eating birds (ca. 85 vs. 105 at CC). Mammals, especially monkeys, are more notable as seed dispersers at CC than at MV. Rainfall is equally seasonal at the two sites, falling mainly from May to December in Costa Rica and from December to May in eastern Peru (annual precipitation: 2529 mm at MV, ca. 2100 mm at CC).

### *Bird Fruits*

Bird fruits were defined as (1) those fleshy fruits known to be eaten by birds (ca. 50% of the species analyzed), or (2) those fruits having traits that correspond to van der Pijl's (1969) characterization of fruits of bird-dispersed plants: persistent fruits often borne terminally and usually less than 25 mm in diameter, with soft pulps or arils surrounding the seed and no husk covering the pulp when ripe (see Janson 1983a). Color was not a criterion used in determining whether or not a fruit was considered a bird fruit. At MV, fruits known to be eaten by birds did not differ significantly from the rest of the fruits classified as bird fruits in mean weight (Mann-Whitney  $U$  test,  $P > .26$ ), diameter ( $P > .39$ ), net pulp ( $P > .07$ ), or color (with the omission of white fruits;  $\chi^2$  two-sample test,  $P > .05$ ). The former group, however, had significantly larger seed-to-pulp ratios than the latter (Mann-Whitney  $U$  test,  $P < .05$ ). Mechanically dispersed or wind-dispersed fruits (e.g., *Croton* spp.) consumed by avian seed predators (such as parrots), but not by seed dispersers, were not included as bird fruits in this study.

Many of the fruits that we call bird fruits are eaten by mammals as well (chiefly monkeys and bats), but for the vast majority of those included here, our observations, as well as those of other researchers (E. Dinerstein, G. Murray, pers. comm.), suggest that birds are important seed dispersers (Wheelwright et al. 1984). Of course, the mere fact that birds are observed removing fruits of a particular species does not necessarily mean that they are also responsible for effective seed dispersal (Wheelwright and Orians 1982). The question of what animal is a plant's primary seed disperser has been studied in only a handful of species (Hutchins and Lanner 1982). Nonetheless, as long as birds have a net positive effect on seed dissemination, they could be important selective agents on the evolution of fruit color, even if other animals are major seed dispersers of these plants. For instance, *Muntingia calabura* (Elaeocarpaceae) is chiefly dispersed by bats (T. Fleming, pers. comm.), which are color-blind and nocturnal, but it produces conspicuous red fruits. Because the fruits of bat-dispersed plants are not usually red (van der Pijl 1969), the bright color of *Muntingia* fruits has probably been selected for by the additional benefits plants gain from occasional dispersal by birds.

### *Sampling Procedures and Fruit Measurements*

Fruits were collected throughout the study periods by following fruit-eating birds or by searching at regular intervals along established transects. We mea-

sured fruits of 254 plant species at MV and fruits of 129 plant species at CC. Sampling procedures are described in detail in Wheelwright et al. (1984) and Wheelwright (1985). It is unlikely that our sampling procedure biased the results in any systematic way because we used the same procedure for fruits of each color category. We may have failed to notice some dull-colored fruits because they tend to be less visible to humans. We probably missed only a small number of such species, however, because we systematically searched for fruits looking for form and position on the plants, in addition to color. Moreover, fewer than 0.1% of the seeds collected in seed traps beneath display perches of various MV bird species were from fruits that we did not measure ( $N > 2000$ ; Wheelwright et al. 1984).

For each species, we calculated the mean values of the following characteristics: mass of entire fresh fruit; wet mass of its seeds; and solute concentration of the crushed pulp measured in grams of solute per hundred grams of solution (Bolten et al. 1979) with Bausch and Lomb pocket refractometers. Solute concentration was chosen as a rough determinant of caloric density principally because of its ease of measurement in the field (crushed fruit pulp from watery fruits was spread over the glass of the refractometer) relative to more accurate but difficult and costly procedures, such as the analysis of total nonstructural carbohydrates (TNC). Solute concentration determined by refractometry is correlated with TNC in the 15 MV species for which we have complete nutritional data (Spearman rank correlation:  $r_s = .47$ ;  $P < .05$ ) and in 33 CC species ( $r = .68$ ;  $P < .001$ ). In a larger sample of temperate-zone fruit species, solute concentration determined by refractometry is also correlated with concentrations of carbohydrates, carbohydrates plus protein, total solutes, and especially lipid-free solutes (White and Stiles 1985).

Ideally, one would like to have complete nutritional information for each fruit species: concentrations of amino acids, fat, carbohydrates, and minerals, presence of toxins, proportion of indigestible structural carbohydrates, and so on. However, solute concentration and percent water were the only nutritional indexes readily obtained in the field. We were unable to analyze nutritional values of the fruits of all the 380+ species included in this study.

From our measurements of fruits we derived specific parameters thought to influence fruit choice by birds (see Herrera 1982): total fruit mass; net pulp mass (total fruit mass minus seed mass); seed-to-fruit ratio (seed mass divided by fruit mass); solute concentration (as measured by refractometer); percent water ( $1 - [\text{dry pulp mass}/\text{fresh pulp mass}]$ ); and an estimate of the total energetic value per fruit (net pulp mass  $\times$  % solute concentration  $\times$  16.7 kJ/g). The latter formula provides only an approximate measure of available energy in a fruit because, in part, it overestimates the energetic value by including the weight of the fruit skin (exocarp), which is often indigestible. It underestimates the energetic value, however, by not measuring other sources of energy, such as proteins and lipids. Nonetheless, the omission of proteins and lipids as energy sources is probably not important for most species (excluding the Lauraceae and Palmae) because their contribution to the energetic value of the pulps of bird fruits tends to be low (Herrera 1982). For example, a sample of the fruits of 16 nonlauraceous species at MV had median dry-weight values of only 0.79% nitrogen and 1.8% lipid, compared to 19.1% TNC (Wheelwright et al. 1984).

*Classification of Fruit Colors*

Ripe- and unripe-fruit colors were categorized in the field against their natural background. We assigned fruits to one of eight broad color categories commonly employed by other researchers (Turcek 1963; Willson and Thompson 1982): black (which included dark-bluish and reddish black; e.g., black cherry, *Prunus serotina*); blue (including violet and purple; e.g., wild blueberry, *Vaccinium corymbosum*); brown (including dull dark red; e.g., many figs, *Ficus* spp.); red (including scarlet and pink; e.g., tomato, *Lycopersicon*); green (e.g., avocado, *Persea americana*); yellow (e.g., banana, *Musa*); orange (e.g., orange, *Citrus aurantium*); and white (e.g., white mulberry, *Morus alba*). Except for a small number of species whose fruits were intermediate between categories, fruits could be unambiguously classified. Note that our classification incorporated only one of the three components of contrast, hue. We did not quantify saturation or brightness.

Studies of fruit colors should measure spectral irradiance of ambient illumination and spectral reflectance of fruit and background surfaces (J. Hailman, pers. comm.), or fruit colors should be assigned according to common standards, such as the Munsell color system (D. Levey, unpubl. data). Unfortunately, we were not able to take reflectance measurements, and we note that they are often missing in other studies (e.g., Turcek 1963; Willson and Thompson 1982) and in published species descriptions (Long 1971; Croat 1978). We present our results with the aim of raising new questions about the evolution of fruit colors that can be tested more quantitatively in future studies.

Although we did not have standards in the field, we were able to assess directly the agreement between the authors in choosing color names. Under identical lighting conditions, each of us independently classified into the color categories used in this study 100 randomly selected Munsell color chips and Kodachrome slides of 47 fruits (21 from MV and 26 from CC). Of the 147 objects, there were only 13 discrepancies in our classifications, most of which were the assignment of chips to adjacent color categories (yellow/orange, dark blue/black, purple/red). The results strongly support the null hypothesis that there is no difference between our criteria for naming fruit colors ( $G$ -test, with Williams' correction,  $P > .995$ ). The actual effect of this small discrepancy rate on our community comparisons of fruit color is even less than the 8.8% observed in our test because many of the disagreements occurred in colors that are scarce among bird-dispersed fruits. Using color- and observer-specific discrepancy rates from our test comparison, we calculated that, had each of us evaluated the fruits in the other's community, about 3.2% of the species would have changed categories, and none of the comparative conclusions presented below would have changed.

Ripe fruits typically occur in displays with contrastingly colored bracts, pedicels, persistent sepals, capsules, arils, or unripe fruits. Fruits in a display involving two or more different colors were termed multicolored fruits (cf. "bicolored fruits," Willson and Thompson 1982). If ancillary colors were green or brown (colors we considered cryptic against a background of leaves or branches),

the fruit was considered simple and was categorized according to the color of the ripe fruit (e.g., many fruits classified as "black" may occur with green unripe fruits). Because of the commonness of multicolored fruits, we subdivided them into "black and red," "black and other" (i.e., black ripe fruits associated with ancillary colors other than green, brown, or red), and "mixed" (all multicolored combinations not involving black). In the absence of detailed information about avian color perception (see below), we refer to the colors red, orange, yellow, and white as "bright," and black, blue, brown, and green as "dull." We recorded the season of fruit ripening and the mean height at which fruits of each species are presented (<1 m, 1–10 m, >10 m at MV and, in the taller forest of CC, <1 m, 1–15 m, >15 m). For season, the year was divided into four quarters that correspond to the seasons of changing precipitation (early dry, late dry, early rainy, and late rainy). For plant species that produced ripe fruits in more than one season the median fruiting date was used.

Many of the original fruit measurements, nutritional values, and color classifications for MV plant species are given in Wheelwright et al. (1984). Except where noted otherwise, all statistical tests are nonparametric (Siegel 1956).

#### *Avian Color Perception*

No primarily frugivorous bird species has been measured for color perception. The color vision of both pigeons and Japanese quail is based on at least three visual pigments with probable absorption maxima at 500, 540, and 600 nm (Jacobs 1981). Peak spectral sensitivities are in the blue, green, and yellow regions (Bowmaker 1977), with optimum wavelength discrimination in the green (500 and 540 nm) and orange-red (600 nm) regions (Wright 1972). The color vision of nonavian seed dispersers (Neotropical monkeys, bats) and insects (which eat fruit pulp but do not disperse the seeds of the species in this study) is either insensitive to red or marked by poor wavelength discrimination between hues near red (Chapman 1971; Jacobs 1981). Thus, red is a color associated with bird-dispersed or bird-pollinated plants.

Stable preferences for particular colors of food have not been unequivocally demonstrated among birds (Bene 1945; Davison 1962; Grant 1966; Collias and Collias 1968; Miller and Miller 1971; but see also Hailman 1967; Snodderly 1978; Kovach 1980; Mason and Reidinger 1983). Some species in the wild are known to avoid food items colored green, orange, or yellow (Kalmbach and Welch 1946; Thompson 1953).

Certain color combinations that are conspicuous to humans may not be so to birds. For example, because red and green are complementary colors to humans, red is often considered the most conspicuous color for birds, particularly against a background of green leaves (Ridley 1930; van der Pijl 1969; for hummingbird flowers, see Grant 1966; Stiles 1976; Diamond 1982). There is, however, no straightforward connection between the mathematical notion of complementary colors and conspicuousness. Moreover, even if there were a connection, there is no empirical evidence that red and green are complementary colors for birds.

Some birds are sensitive to ultraviolet (UV; Kreithen and Eisner 1978;

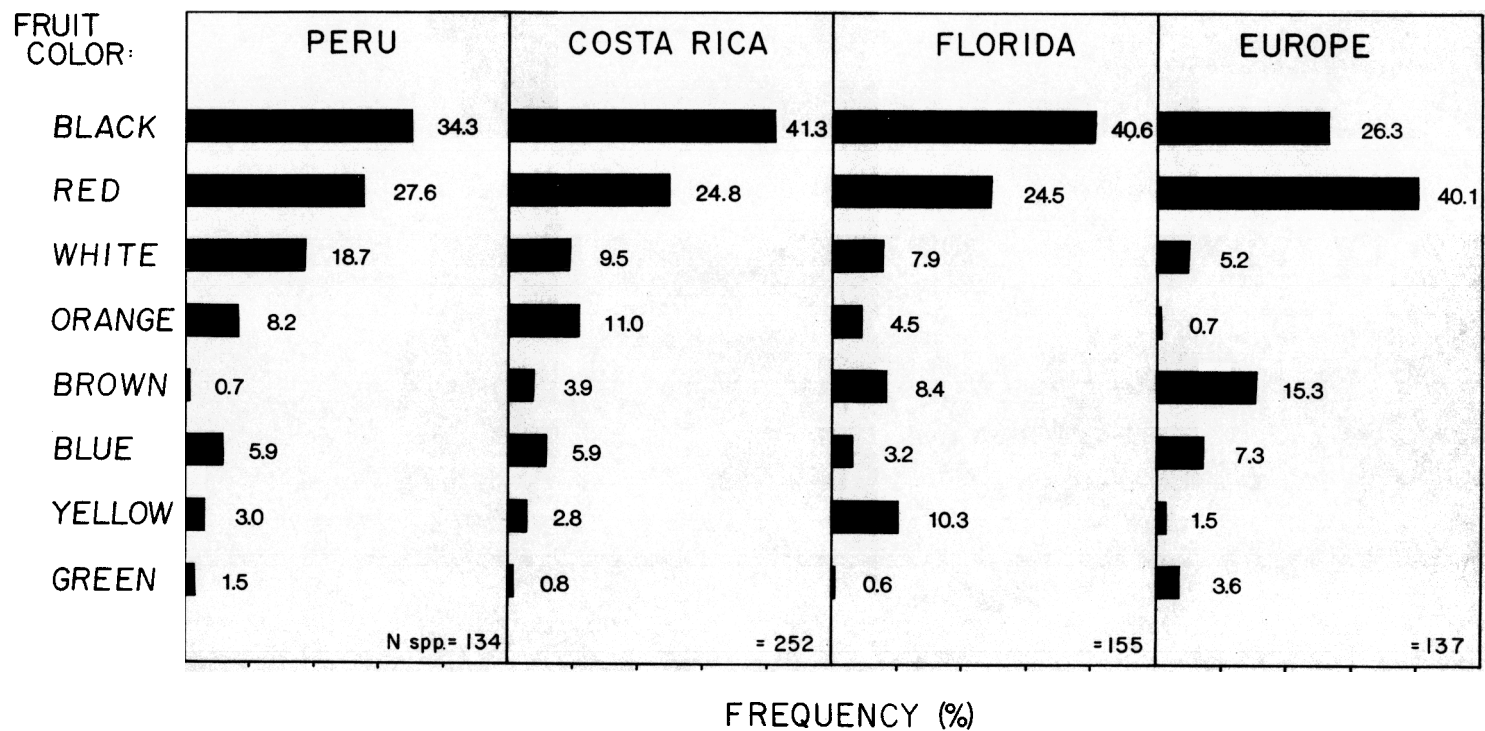


FIG. 1.—Frequencies of bird-dispersed plant species producing ripe fruits of various colors in four habitats. Numbers refer to the percentage of species in each color class. Florida data from Long (1971); European data from Turcek (1963).



Goldsmith and Goldsmith 1979), and the cutin coat of some fruits reflects UV (Burkhardt 1982). The lenses of most vertebrates apparently absorb short wavelengths, however, and may fluoresce when exposed to UV light (D. Varner, pers. comm.); moreover, birds have their best wavelength discrimination in regions of longer wavelength (Jacobs 1981). For this reason, and because we were unable to measure UV reflectance in the field, we limit our analysis to fruit colors in the spectrum visible to humans.

## RESULTS

### *General Color Patterns*

The proportion of plant species producing bird fruits of different colors is broadly similar in our study sites, in subtropical Florida (Long 1971), and to a lesser extent in Europe (Turcek 1963). To make the data comparable, only ripe-fruit colors are considered in figure 1, and the colors of associated structures or unripe fruits are temporarily ignored.

Black is the most frequent color of ripe bird fruits in MV, CC, and Florida. In Europe, red is the most common color, although it is unclear whether Turcek (1963) used criteria similar to ours in classifying colors and distinguishing bird fruits. The frequencies of ripe-fruit colors do not differ significantly between MV and CC ( $\chi^2$  two-sample test:  $P > .5$ ). Moreover, neither Neotropical site differs with respect to fruit-color frequencies from the New World subtropical site, Florida ( $P > .05$ ). Although their data are not strictly comparable, Willson and Thompson (1982) found "blue-to-black" fruits predominant in Illinois (50% of 154 bird-dispersed plant species), as in our Neotropical sites, whereas red fruits accounted for only 36% of the species. All these New World sites differ from Turcek's (1963) European sites in the frequencies of bird-fruit colors ( $P < .01$ ). A review of the flora of Britain (Martin 1965) gave independent support for the distinctions between fruit color patterns in the New World and in Europe: almost 60% of 96 British plant species apparently dispersed by birds bear red fruits; only about 30% have black fruits. In all four regions in figure 1, the colors black and red predominate in fruit displays, making up 61.9%–66.4% of all bird-dispersed species.

Green is a rare color for ripe bird fruits, being the least common color category everywhere except Europe. Orange (and perhaps white) appears to be more common in tropical habitats, whereas brown is less common there.

If the colors of unripe fruits and associated structures are considered along with ripe-fruit color (table 1), 44.2% of MV and 58.9% of CC bird-fruit displays involve red; 46.4% of MV displays and 41.1% of CC displays involve black. The single most frequent color display consists of some combination of black plus red, accounting for 18.4% of MV plant species and 17.8% of CC species. Black plus green follows in frequency at MV (12.4% of species), followed by red plus green (8.3%). At CC, red plus green is the second most common color combination (14.0%), followed by black plus green (7.8%). Thus, the exact answer to the question "Are bird fruits red?" depends on location, and whether associated

TABLE 1  
PLANT SPECIES PRODUCING FRUIT DISPLAYS OF DIFFERENT COLOR COMBINATIONS (IN PERCENT)

RIPE-FRUIT COLOR	COLOR OF UNRIPE FRUITS OR ASSOCIATED STRUCTURES																		TOTAL
	BLACK		BLUE		BROWN		GREEN		RED		ORANGE		YELLOW		WHITE		MULTICOLORED		
	uf	s	uf	s	uf	s	uf	s	uf	s	uf	s	uf	s	uf	s	uf	s	
Black			<b>5.1</b>		1.8	0.5	<b>12.4</b>		<b>9.2</b>	<b>7.8</b>	0.9	1.8	0.9		3.2				43.8
			1.6	.6			<b>7.8</b>		<b>9.3</b>	<b>8.5</b>	0.8	3.1	0.8					0.8	34.1
Blue			<b>0.9</b>				1.4			0.9			0.5		0.9				4.6
	<b>0.8</b>						3.9			1.6									6.2
Brown					0.9	0.5	1.4		.8						0.5				5.1
					0.8														0.8
Green							0.5			0.5									0.9
					0.8		0.8												1.6
Red		1.4			0.9	1.4	<b>7.8</b>	0.5	2.8	0.5	<b>5.1</b>		1.4		0.9		0.8		24.0
						3.1	<b>7.0</b>	<b>7.0</b>		0.8	2.3	1.6	2.3		2.3		0.8	0.8	27.1
Orange		1.4				0.5	<b>6.9</b>	0.5				0.9			0.5	0.5	0.9		12.0
		1.6		0.8	0.8	0.8	3.1						0.8						7.8
Yellow							2.3								0.5				2.8
							2.3						0.8						3.1
White						0.5	<b>5.5</b>								0.5		0.5		6.9
				1.6			3.1	0.8		7.0		1.6		1.6				3.9	19.4
TOTALS	0	2.8	6.0	0	3.6	3.4	38.2	1.0	13.8	9.7	6.0	2.7	2.8	0	7.0	0.5	2.2	0	
	0.8	1.6	1.6	4.0	2.4	3.9	28.0	7.8	9.3	17.9	3.1	6.3	4.7	1.6	0	2.3	0.8	4.7	

NOTE.—uf, unripe fruits; s, structures (bracts, pedicels, capsules, arils, sepals). Data from 218 plant species at Monteverde, Costa Rica, and 129 plant species at Cocha Cashu, Peru; Monteverde frequencies are listed above Cocha Cashu frequencies. Species that have green or brown unripe fruits but contrastingly colored structures are listed under structure color. Species with unripe fruits or structures colored other than green or brown (multicolored fruits) are classified in the text as "black and red," "black and other," or "mixed." Color combinations representing more than 5% of all fruiting species are in boldface type.

colors are considered. Nonetheless, in none of the four habitats described in figure 1, nor in Illinois (Willson and Thompson 1982), do the majority of bird-dispersed species have red fruits. This result is not caused by our separating orange and red fruit colors; black remains the most common fruit color in the New World even when red and orange are combined.

Ripe-fruit colors may be ranked by the frequency with which they occur with plant parts (unripe fruits, bracts, etc.) of contrasting colors other than green or brown. Using only ripe color categories for which we have a sample of 10 or more species, and averaging the results for MV and CC, 71.8% of species with black ripe fruits have associated contrasting colors. For other categories of ripe-fruit color, the proportion of species having contrasting associated colors is as follows (table 1): blue (50.0%), brown (45.1%), white (42.8%), red (38.0%), and orange (33.2%). (White was the only color to have markedly different associations in the two habitats: MV, 13.0%; and CC, 78.1%.)

There are many combinations of colors that either do not occur or are scarce. Of 72 possible combinations, only 38 at MV and 32 at CC are represented at all. In both sites we rejected the null hypothesis of independent association of ripe with unripe or accessory colors ( $\chi^2$  two-sample test: MV,  $P < .01$ ; CC,  $P < .02$ ). Some color combinations occur much more commonly than expected: black ripe with red unripe (or accessory); red ripe with orange unripe; red, orange, or yellow ripe with green unripe. The combination of black and red occurs in at least 21 families at MV and 19 at CC (total: 26 families in 6 subclasses).

#### *Fruit Colors and Nutritional Traits*

Fruit nutritional characters were not correlated with color pattern at either study site (table 2). We estimated the fruits' nutritional value for birds by assuming that, all other things being equal, fruits with a greater net mass of pulp, smaller seed mass for a given fruit mass (lower seed-to-fruit ratio), higher sugar concentrations in the pulp, and higher estimated energetic value per fruit were better-quality fruits (see Herrera 1981). Water content of the pulp, known for only 37 species at MV, showed no significant relationship to fruit color and is not discussed further.

At CC there were no significant differences between fruit colors in any of our indexes of fruit quality, whether all indexes were taken singly (Kruskal-Wallis one-way ANOVA,  $P > .05$  in all tests) or independent indexes were considered together (Friedman two-way ANOVA,  $P > .5$ ). When color patterns were combined into what we termed bright versus dull displays (multicolored, red, orange, yellow, or white displays vs. simple black, brown, blue, or green displays), most tests still showed no significant differences between color groups. Total fruit mass had a strong tendency to vary between dull, simple bright, and multicolored classes (Kruskal-Wallis one-way ANOVA,  $P = .06$ ): fruits in bright displays tended to be larger than dull-colored fruits.

At MV there were no significant differences between fruit colors for sugar concentration, estimated energetic content, or seed-to-fruit ratio (Kruskal-Wallis one-way ANOVA,  $P > .40$ ), but there were significant differences between fruit colors for total fruit mass and net pulp mass, with black-and-red fruits being more

TABLE 2  
RIPE-FRUIT COLORS AND FRUIT QUALITY FOR TROPICAL PLANT SPECIES

Ripe-Fruit Color	Fruit Mass (g)	Seed Mass/ Fruit Mass	Fruit Mass - Seed Mass (g)	Estimated Kilojoules/Fruit	Pulp Solute Concentration (determined by refractometer)
Black	2.05 (3.95, 32)	.26 (.22, 31)	1.21 (1.89, 30)	0.97 (1.29, 21)	8.00 (3.73, 22)
	0.50 (.28, 12)	.32 (.16, 12)	0.38 (.22, 13)	0.97 (.68, 13)	13.30 (5.0, 14)
Blue	1.01 (1.45, 11)	.28 (.26, 10)	0.66 (.87, 10)	1.55 (3.06, 8)	6.63 (5.32, 8)
	0.49 (.32, 5)	.35 (.16, 5)	0.45 (.49, 5)	0.92 (1.20, 5)	12.8 (11.2, 5)
Brown	0.06 (.01, 3)	.17 (.03, 3)	0.05 (.01, 3)	0.08 (—, 1)	12.00 (—, 1)
	0.35 (—, 1)	.28 (—, 1)	0.25 (—, 1)	0.36 (—, 1)	8.7 (—, 1)
Green	9.20 (—, 1)	.23 (—, 1)	7.10 (—, 1)	—	—
	19.92 (23.74, 2)*	.22 (.14, 2)	16.80 (22.1, 2)*	30.91 (41.16, 2)*	11.7 (3.8, 2)
Red	0.51 (.60, 28)	.33 (.28, 28)	0.38 (.51, 26)	0.54 (.73, 22)	7.44 (4.39, 25)
	0.97 (1.11, 24)*	.41 (.23, 21)	0.61 (.71, 21)	1.23 (1.35, 23)	13.65 (5.9, 25)
Orange	0.61 (.56, 19)	.19 (.14, 18)	0.44 (.32, 18)	0.59 (.61, 17)	8.22 (3.64, 18)
	1.66 (3.02, 6)	.33 (.15, 6)	1.38 (2.70, 6)	2.34 (4.58, 6)	9.8 (1.6, 6)
Yellow	0.57 (.61, 5)	.26 (.15, 5)	0.46 (.49, 5)	1.26 (1.10, 3)	11.00 (1.00, 3)
	0.46 (.49, 4)	.15 (.20, 2)	0.54 (.44, 2)	0.83 (.71, 2)	9.4 (1.7, 4)
White	0.35 (.30, 17)*	.18 (.21, 17)*	0.29 (.24, 17)	0.32 (.36, 13)*	6.64 (5.61, 14)
	1.11 (1.21, 4)	.32 (.19, 5)	0.51 (.39, 5)	1.02 (1.04, 5)	11.12 (5.2, 5)
Mixed	0.96 (1.44, 38)	.28 (.24, 38)	0.59 (.62, 38)*	0.89 (1.29, 32)	8.50 (6.19, 32)
	0.67 (1.18, 31)	.48 (.23, 34)	0.56 (1.02, 35)	1.35 (2.33, 28)	12.32 (5.6, 32)
Black & red	2.26 (2.49, 36)***	.38 (.21, 36)***	1.22 (1.12, 35)***	1.45 (1.54, 23)	7.74 (4.00, 23)
	0.58 (.55, 24)	.36 (.21, 22)	0.43 (.39, 23)	1.02 (1.44, 23)	12.35 (6.6, 23)
Black & other	0.52 (.65, 32)	.31 (.26, 31)	0.41 (.58, 33)	0.63 (.70, 26)	13.58 (9.14, 26)
	0.63 (.70, 9)	.44 (.26, 9)	0.47 (.41, 9)	0.88 (.83, 8)	13.58 (8.5, 9)
All colors (mean)	1.15 (2.14, 222)	.29 (.23, 218)	0.72 (1.10, 213)	0.85 (1.25, 166)	8.74 (5.94, 172)
	0.76 (1.11, 124)	.39 (.23, 119)	0.56 (.90, 121)	1.19 (1.81, 115)	12.51 (5.98, 126)

NOTE.—Following the mean for each index of fruit quality are the standard deviations and the number of plant species sampled. The samples were from Monteverde, Costa Rica (upper values), and Cocha Cashu, Peru (lower values). In each group unripe fruits are green (or rarely brown) and there are no contrastingly colored structures, except for those fruits categorized as "black and red," "black and other," and "mixed" (definitions in text). Indexes that differ significantly from the values of all the other species sampled are designated \*,  $P < .05$ , and \*\*\*,  $P < .001$  (Mann-Whitney  $U$ -test).

massive and white fruits being less massive than fruits of other colors ( $P < .01$ ). If the Lauraceae (23 species, almost all of which produce large fruits) are excluded, however, none of our indexes of fruit quality differed between fruit colors. The same results were obtained when color patterns were combined into dull versus bright displays, except that there were significant differences for total fruit mass and net pulp mass even with the exclusion of the Lauraceae. As at CC, when independent food-quality indexes (sugar concentration, seed-to-fruit ratio, and net pulp mass) were analyzed together, there were no significant differences between color categories, with or without the Lauraceae (Friedman two-way ANOVA,  $P > .50$ ).

#### *Fruit Colors and Growth Form*

At MV, bright color combinations (red, orange, white, or yellow fruits, or multicolored displays involving black) were significantly more common in the understory ( $\chi^2$  two-sample test,  $P < .02$ ). Dull colors and multicolored displays not involving black (i.e., mixed) were more common in the overstory. Black-and-red fruits were represented more among trees than shrubs, mostly because of 13 species of Lauraceae that are canopy trees. At CC there was no significant association between growth form and color; any possible trends appeared to contradict those at MV.

#### *Fruit Colors and Phenology*

Fruit-color frequencies did not vary significantly with respect to season or relative abundance of potential seed dispersers at either MV or CC ( $\chi^2$  two-sample test,  $P > .10$ ). Bird fruits are abundant at MV from March to July and relatively scarce from October through December or January (W. Haber, G. Frankie, pers. comm.; pers. obs.). During the latter period some species (three-wattled bellbirds, *Procnias tricarunculata*; resplendent quetzals, *Pharomachrus mocinno* [Wheelwright 1983]) migrate to different habitats.

Although not statistically significant, there was a suggestion of a seasonal effect at MV, where four of the seven bright color categories were more frequent, on the average, during the period of relative fruit shortage (rainy season) than during the rest of the year; a fifth, orange, was about equally common in the dry and rainy seasons. Only one bright color category ("black and other") was less frequent in both quarters of fruit scarcity. At CC there was no significant heterogeneity in color frequency over the seasons. Unlike at MV, dull colors at CC were relatively scarce in the early dry season when competition for dispersers is least.

#### *Preferred Fruit Colors and Social Signals*

We examined the distribution of fruit colors among fruit species eaten by the five species of birds at MV whose diets were best known and consisted principally of fruits. Each species eats a minimum of 30 species of fruits (Wheelwright et al. 1984). Emerald toucanets (*Aulacorhynchus prasinus*) and long-tailed manakins (*Chiroxiphia linearis*) appeared to select fruit species without regard to the color of the display per se (figs. 2A,B;  $\chi^2$  two-sample test,  $P > .10$ ; for a similar result with preferences of *Saltator* species, see Jenkins 1969). Observed frequencies

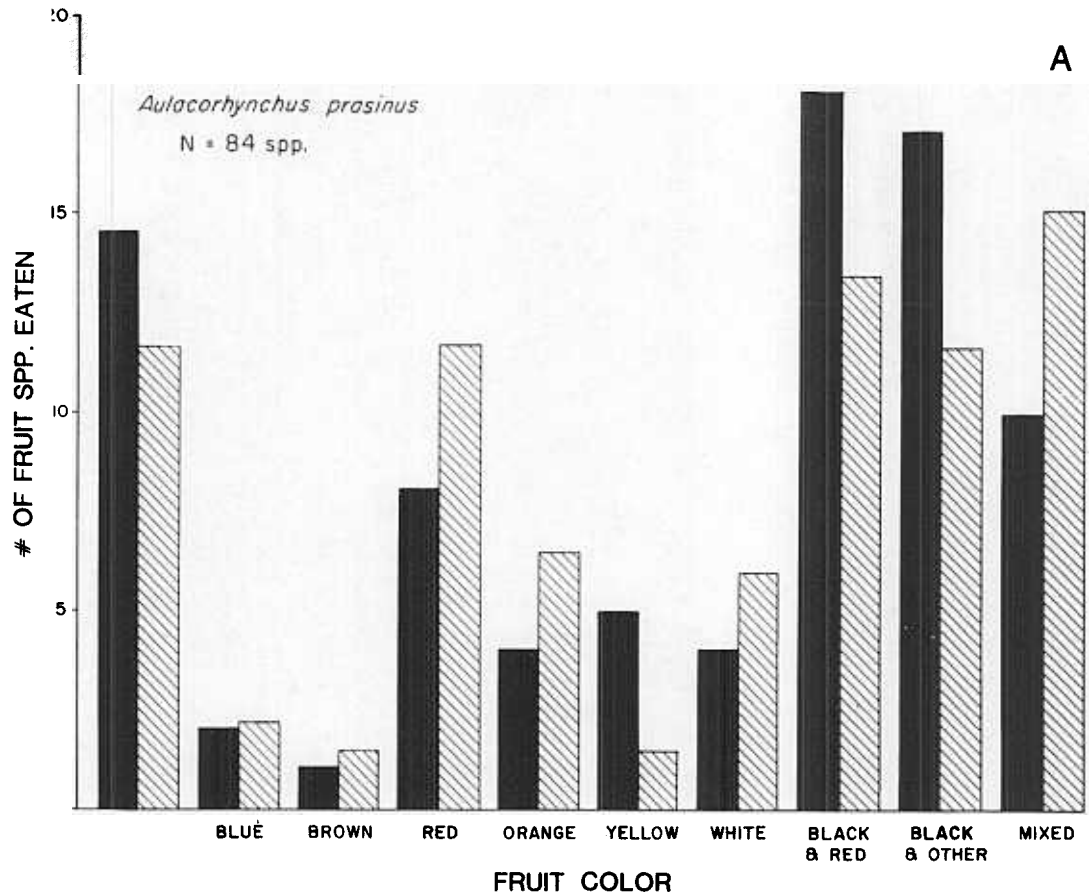
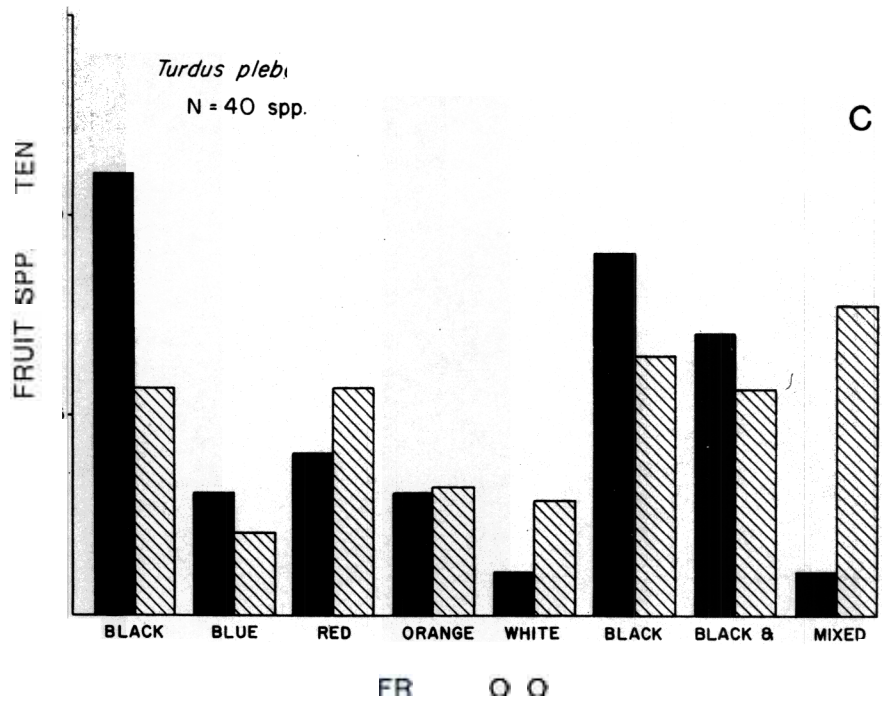
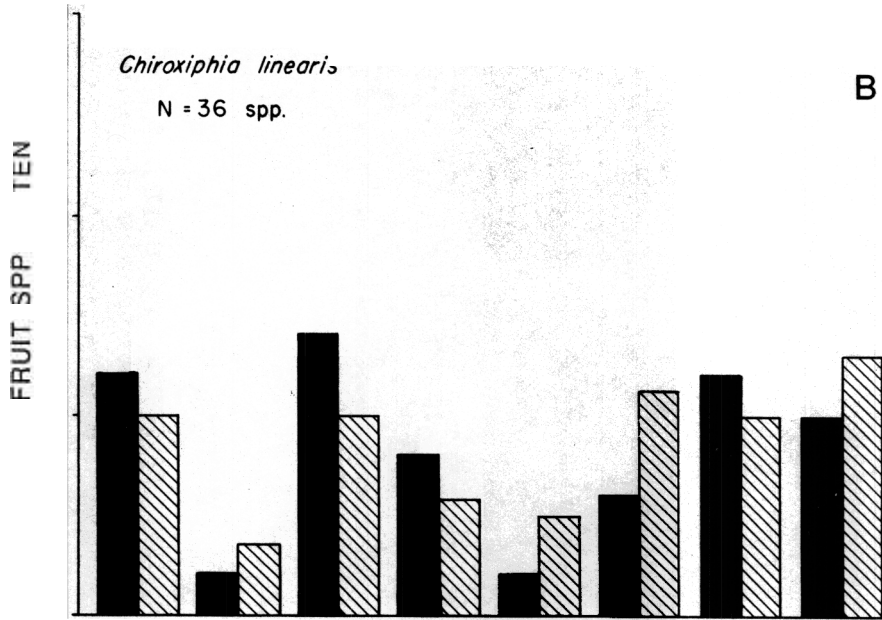
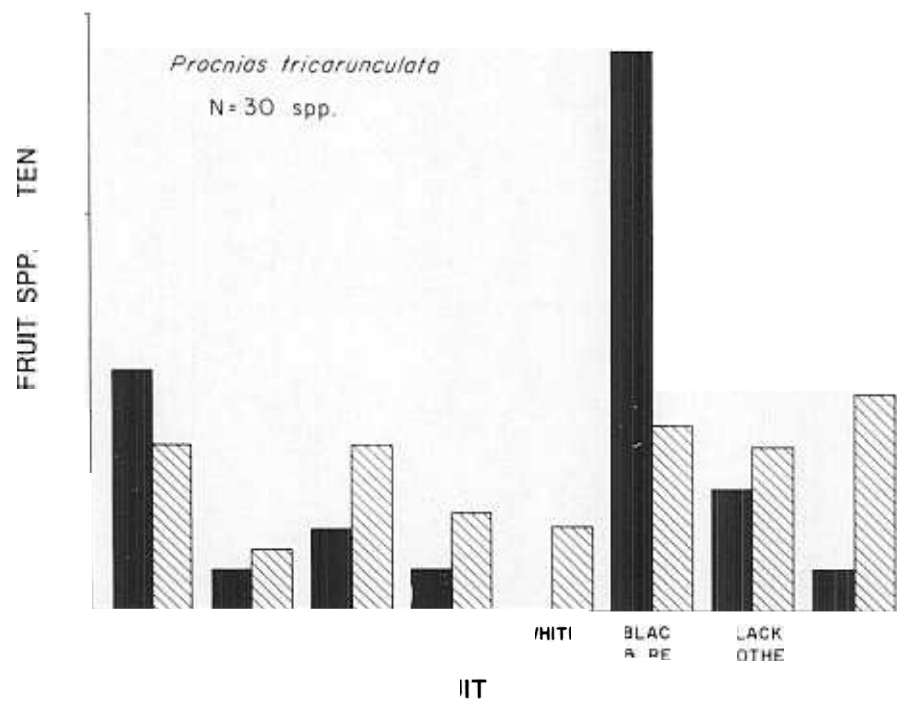
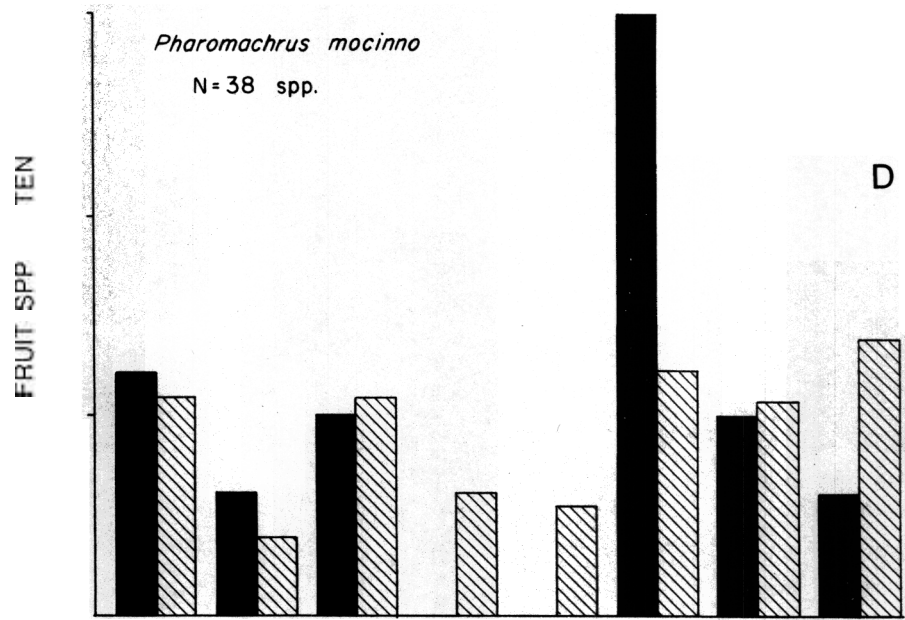


FIG. 2.—Observed colors of fruits eaten by five primarily fruit-eating bird species at Monteverde, Costa Rica (solid bars). Expected frequencies of colors (hatched bars) are based on the proportion of plant species with fruits of a given color in the same area. A, Emerald toucanet (*Aulacorhynchus prasinus*). Facing page: B, long-tailed manakin (*Chiroxiphia linearis*); C, mountain robin (*Turdus plebejus*). (Continued)

were compared with those expected if the birds did not choose fruit species with respect to color; expected frequencies were derived from the frequencies of fruit species of different colors in the habitat as a whole. Fruit color in the diet of mountain robins (*Turdus plebejus*) was nearly nonrandom (fig. 2C;  $P = .05$ ) mainly because of their preference for black fruits and their apparent disinterest in mixed fruits. Resplendent quetzals and three-wattled bellbirds showed a significantly nonrandom selection of fruit species according to color (figs. 2D,E;  $P < .01$  and  $P < .001$ , respectively) because of their preference for black-and-red fruits. Neither species chose a random sample of black-and-red fruits, however; most of the black-and-red fruits that they ate were species in the Lauraceae.

For all five bird species, black fruits were consistently represented in the diet at frequencies greater than expected, and in each case white and mixed fruits were underrepresented (fig. 2). Red and orange fruits—"classic" bird-fruit colors—tended to be underrepresented in all diets except that of manakins.





bel Proci ed). plendei uet 'har 'hr



## DISCUSSION

Our data on the patterns of color association in fruit displays may provide clues about the relative conspicuousness of various colors to birds. What we considered to be dull ripe-fruit colors (black, brown, blue, and green) were associated with contrasting colors in 45%–72% of all species. It may be inferred that these colors are inherently less conspicuous to dispersers than colors usually displayed solitarily or with only green or brown (i.e., red, orange, yellow, and white). Against a background of leaves or branches, in the faint light of a tropical forest understory, dark fruits may not be readily noticed by birds unless they have associated contrasting colors.

An unexpected finding of this study was that dull or dark colors are common among ripe fruits, contrary to popular conceptions about bird fruits. Just as a small proportion of eye-catching birds gave rise to the inaccurate generalization that tropical birds are more brightly colored than temperate-zone birds (Bailey 1978), certain flashy fruits have prompted the notion that bird fruits are highly conspicuous, particularly in the tropics. Not only are many bird fruits not brightly colored, but tropical bird fruits also appear no more brightly colored than those of Europe, Illinois, or Florida. One of the most common bird fruits, accounting for about 1 in 10 species at MV and CC, is a drab black berry, or drupe, that is green when unripe and lacks contrastingly colored accessory structures. Indeed, black occurs in the fruit displays of more species than does red, and black is the most common color of ripe bird fruits in three distinct New World sites. Unless it can be shown that birds perceive black as more conspicuous than red under natural conditions, our results show that bird fruits are not always selected to be conspicuous.

Colors of fruit displays are far from randomly distributed, however. One's first impression in a tropical forest is that bird fruits occur in an overwhelming variety of hues, but equally striking is the apparent convergence of unrelated plant species on a limited number of color patterns. Fruit displays involving both black and red probably evolved independently in the 26 different plant families in which they occur in the Neotropics: different structures (unripe fruits, bracts, persistent calyces, swollen receptacles, or peduncles) typically contribute to the display. More than 50 bird-dispersed species at MV (20% of the species measured) and 28 species at CC (21.8%) produce fruit displays involving only black or only red (table 1). Green and blue are unimportant colors for ripe bird fruits in all habitats. Brown and yellow are also uncommon, and orange may occur frequently only in the tropics.

Given such an array of fruits, how can birds best make choices among them? Are there predictable associations between the colors of fruit displays and quality, growth form, plant life history traits, and fruiting phenology? This study suggests that fruit color conveys little information about quality. Since green, yellow, and orange are particularly common colors for unripe (table 1) or bulky, monkey-dispersed fruits (Janson 1983a), birds may tend to associate those colors with unpalatable fruits (Kalmbach and Welch 1946). The data on observed versus expected frequencies of fruit colors represented in some birds' diets support this

idea: white, orange, and mixed fruits are underrepresented, even though these fruits are otherwise suitable for birds (fig. 2). Because red is such a common color of unripe, unpalatable fruits, whereas black rarely is (table 1), birds experiencing novel fruits may be more inclined to sample ones that are black or black and red, giving plants with fruits of those colors an advantage, in spite of their reduced visibility, and possibly explaining the prevalence of black-and-red fruits in so many different habitats. When captive American robins (*Turdus migratorius*) are presented a choice of different ripe cultivars of commercial cherries (*Prunus*), they overwhelmingly prefer black to red, and tend to ignore gold (Brown 1976; Wheelwright, unpubl. data). Purple grapes (*Vitis*) are favored over green (Wheelwright, unpubl. data).

At MV, at least, black fruits are more common in overstory species than would be expected if colors were distributed randomly with respect to plant growth form. Against a background of sun-glossed leaves, black may actually be a more conspicuous color than red (see Endler 1978). Red, orange, yellow, and white are more common fruit colors among understory species (shrubs, vines, and lianas) at MV, but not at CC. In their survey of Illinois bird fruits Willson and Thompson (1982) found that 48% of bird-dispersed herbs bear red fruits and 28% produce blue-to-black fruits; among trees, 46% bear red fruits and 54% black fruits. Although these figures lend weak support to the notion of brightly colored fruits in the understory, Willson and Thompson (1982) found that a smaller proportion (30%) of shrubs as compared with canopy plants had red fruits. Different forest structures and incident light levels may make comparisons between regions less meaningful. For instance, large naturally occurring open habitats are rare except in landslides at MV, but are common at CC, where 18 of the 20 species with dull-colored fruits occur. Shrubs or herbs in open habitats may correspond to trees in closed habitats in terms of light levels, height relative to the canopy, and visits by canopy-foraging birds.

Some color patterns are noticeably absent in bird fruits. For example, there are almost no transparent fruits (the temperate-zone species *Lonicera quinquelocularis* [Caprifoliaceae] is a rare exception). Spotted fruits are practically absent (outside of mammal-dispersed species and a few species in the Liliaceae, Rubiaceae, and Araliaceae), and we know of no bird-consumed fruits exhibiting stripes or checkerboard patterns even though such displays might be highly conspicuous to potential seed dispersers. Fruiting displays that emphasize or exaggerate particular features of fruits (such as size, roundness, or other measures of quality) are not apparent, despite some intriguing hypotheses about the design and adaptive significance of color signals proposed by Zahavi (1978). Birds' ability to learn through experience may select against false fruit signals.

Few other generalizations about bird-fruit colors emerge from our data. Fruits do not seem to be more conspicuous at times of greater competition for seed dispersers, in contrast to the results of Willson and Thompson (1982) or Stiles (1982). We found little support for the hypothesis that brightly colored fruits are less nutritious than inconspicuous fruits. Although our results suggest that the nutritional traits of differently colored fruits are similar and that the few significant differences result from random sampling, specific selection pressures may explain

several color patterns. For example, mixed-color fruits tend to be capsules, which often have dry or oily arils, perhaps to avoid desiccation after the capsule opens. Because of their high nutritional content per weight, such pulps can be smaller for a given seed size than watery pulps (Snow 1971) and still be equally attractive to birds, which may explain why mixed-color fruits have significantly low net pulp weights at MV and high seed-to-fruit ratios at CC. In addition, differences in fruit quality between color patterns may be learned by birds. Birds at MV avoided white fruits (shown as low quality in table 2) and preferred black-and-red ones (high quality), at least in terms of the number of species of different color classes eaten.

The lack of correlation between fruit conspicuousness and nutritional traits, habitat, or phenology could exist for several reasons. One problem may lie in our definition of "conspicuousness" in bird fruits and our lack of knowledge about what birds see. Fruits (e.g., red and yellow) that appear conspicuous to humans with normal color vision may not be equally conspicuous to birds. It is even more likely that birds' detection of "dull" fruits is far better than our own. Nonetheless, a glance at any bird guide suggests that red and yellow are key colors in social signaling among birds (see also Hailman 1977; Baker and Parker 1979). From that, and from our results on fruit color associations, one may infer that these colors are particularly conspicuous to birds.

Our classification of fruit displays according to brightness or conspicuousness did not include the presentation of fruits (but see Denslow and Moermond 1982). Aggregated plants or plants with clustered fruits borne terminally are probably more noticeable at a distance than solitary plants or plants with isolated, axially held fruits, irrespective of fruit color. Moreover, birds undoubtedly use other cues besides color to find fruits. They may discover likely locations of fruit by recognizing plant forms or leaf characteristics (Stiles 1982). At MV, mountain robins and emerald toucanets move directly between fruiting trees of *Hampea appendiculata* (Malvaceae), which are identifiable at a distance by their brownish leaf undersides. In the case of several species of Lauraceae that produce relatively small crops of inconspicuous fruits, birds seem to find fruiting trees by keying in on the activity of other birds. Thereafter, birds may remember the location of individual trees, since they revisit them even after fruit crops have been depleted.

Phylogenetic conservatism may explain much of the uniformity of fruit color patterns among closely related plants of different life form or phenology (Janson 1983b). Most Solanaceae, whether vines, shrubs, or trees, tend to have red or orange berries that are green when unripe. Even within solanaceous genera that produce dark fruits (e.g., *Cestrum*), most species produce the same kinds of fruits, irrespective of height or time of the year. The Ericaceae and Lauraceae are also remarkably homogeneous families in terms of their fruit displays.

By contrast, the Flacourtiaceae and Rubiaceae, and even such genera as *Xylosma* and *Psychotria*, may produce a broad array of fruit color patterns. Thus, while convergence on a small number of color patterns is notable, diversity within taxa must also be explained. Jenkins (1969) hypothesized that if plants competing for the same seed dispersers are unable to provide nutritionally complete fruits, they may be selected to specialize nutritionally. If that is the case, fruits low in

overall quality but high in particular trace elements, amino acids, or vitamins would benefit by signaling their uniqueness and by diverging in color pattern from their competitors. The next step, then, is to investigate subtle nutritional differences between fruit color classes.

We have only briefly considered one problem faced by bird-dispersed plants: in the process of appearing conspicuous to one set of animals (appropriate seed dispersers), it is difficult to remain cryptic to others (inappropriate seed dispersers, seed predators, and fruit parasites). Raven (1972) hypothesized that the color red might be prevalent in bird-pollinated flowers because insects (which Raven presumed to be inadequate pollinators for these plants) have limited vision in the longer wavelength region of the visible spectrum (Chapman 1971) and would be less likely to detect red flowers. Fruits may be red or black for the same reason, to be less visible to insect predators. If so, it is not obvious why black fruits should be so common, yet black flowers so rare. Red may also be less conspicuous than other colors to red-insensitive mammals (including all Neotropical primates tested; Jacobs 1981); but since many fruits eaten by Neotropical mammals are red (Terborgh 1984; Fleming, pers. comm.), color cannot be an absolute barrier to visibility by animals that may be inappropriate dispersers. It should be noted, however, that fruits need not be invisible to predators or inferior seed dispersers as long as they are unattractive to them (see Herrera 1982). Thus, if sufficiently protected against predators or poor dispersers by chemical or morphological defenses, fruits can be brightly colored without negative consequences.

Our results suggest that future studies on the significance of fruit colors should focus on one species-rich taxonomic group with variation in fruit colors—a genus like *Psychotria* or a family like the Flacourtiaceae—to control for phylogenetic constraints. Rather than classifying fruits by color, which is a subjective variable, the spectral reflectance of fruits should be measured in situ along with associated structures and against their natural background (see Endler 1978; Snodderly 1979). Color standards should be used, and data analyzed at both the species and genus levels to minimize the problem of independence of samples (Janson 1983*b*). Detailed knowledge of the plants' life histories, phenologies, growth forms, fruit presentations, seed dispersers, and seedling requirements may be essential for a more meaningful interpretation of the colorimetric information. The predictions and questions raised here will also be refined as more is learned about foraging theory and avian visual physiology.

#### SUMMARY

Color is a key characteristic of fruits because it affects the probability that they will be noticed or selected and, consequently, that their seeds will be dispersed. This paper examines the colors of fruit displays of 383 bird-dispersed plant species in two diverse tropical forests in Costa Rica and Peru. We detail the frequency of ripe-fruit color displays and try to explain these patterns by considering a general model of selection on fruit colors.

The generalization that "bird fruits tend to be red" is shown not to apply to the Neotropics—most ripe bird fruits in our sample are black, with red being the

second most common color. The proportion of plant species bearing either black or red fruits is remarkably similar in Costa Rica, Peru, Europe, and Florida (62%–66%).

Certain color combinations in fruit displays, formed by ripe fruits plus contrasting unripe fruits or accessory structures (bracts, peduncles, persistent calyces), are especially common. The colors black and red, for example, co-occur in about 18% of all fruit displays in both Peru and Costa Rica, including species from 26 plant families. Some ripe-fruit colors (black, brown, blue, green) tend to be associated with unripe fruits or accessory structures of contrasting color; other colors (red, orange, white, yellow) tend to occur alone.

We propose a model of fruit color suggesting that there is a cost of bearing conspicuous color patterns, either in attracting inappropriate consumers to the fruit or in manufacturing pigments or associated structures. Plants should be selected for increased conspicuousness of fruit display if the benefits of attracting more dispersers outweigh the costs of incidentally attracting lower-quality dispersers or of being limited in the number of fruits that can be produced. Plant species especially likely to benefit by attracting many dispersers include colonists of patchy habitats, plants with generalized seed and seedling requirements, and plants whose fruits are unlikely to be discovered or eaten because they are nutritionally poor, they occur in small crop sizes, or they grow under poor visibility conditions or at times when dispersers are scarce.

#### ACKNOWLEDGMENTS

M. Lawton, D. Varner, and Organization for Tropical Studies course 80.3 deserve thanks for provocative discussions on color patterns in bird fruits. We would also like to thank W. Haber and R. Foster for plant identification, the Monteverde community for gracious hospitality, and the Peruvian Ministry of Agriculture, Forestry Institute, and ORDEMAD for support and permission to work at Manu. H. Howe and M. Willson kindly shared unpublished manuscripts, and P. D. Boersma, G. Butcher, J. Endler, J. Hailman, D. Janzen, G. Orians, and M. Snodderly offered helpful criticisms of previous versions of this paper. A. Thornton, G. Russell, and W. Adams aided in the preparation of the manuscript. The study was funded by grants from the National Science Foundation, Sigma Xi, New York Zoological Society, the Frank M. Chapman Fund, and a Carr Postdoctoral Fellowship to N.T.W.

#### LITERATURE CITED

- Bailey, S. 1978. Latitudinal gradient in colors and patterns of passerine birds. *Condor* 80:372–381.
- Baker, R. R., and G. A. Parker. 1979. The evolution of bird coloration. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* 287:63–130.
- Bazzaz, F. A., R. W. Carlson, and J. L. Harper. 1979. Contribution to reproductive effort by photosynthesis of flowers and fruits. *Nature (Lond.)* 279:554–555.
- Beehler, B. 1983. Frugivory and polygamy in birds of paradise. *Auk* 100:1–12.
- Bene, F. 1945. The role of learning in the feeding behavior of black-chinned hummingbirds. *Condor* 47:3–22.

- Biale, J. B. 1975. Synthetic and degradative processes in fruit ripening. Pages 5–18 in N. F. Haard and D. K. Salunkhe, eds. Postharvest biology and handling of fruits and vegetables. AVI, Westport, Conn.
- Bolten, A. B., P. Feinsinger, H. G. Baker, and I. Baker. 1979. On the calculation of sugar concentration in flower nectar. *Oecologia (Berl.)* 41:301–304.
- Bowmaker, J. K. 1977. The visual pigments, oil droplets and spectral sensitivity of the pigeon. *Vision Res.* 17:1129–1138.
- Brown, R. G. B. 1976. Bird damage to fruit crops in the Niagara Peninsula. *Can. Wildl. Serv. Rep. Ser.* 27:1–57.
- Burkhardt, D. 1982. Birds, berries and UV. *Naturwissenschaften* 69:153–157.
- Chapman, R. F. 1971. The insects. Elsevier, New York.
- Collias, N. E., and E. C. Collias. 1968. Anna's hummingbirds trained to select different colors in feeding. *Condor* 70:273–274.
- Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif.
- Darwin, C. 1859. On the origin of species. Murray, London.
- Davison, V. E. 1962. Taste, not color, draws birds to berries and seeds. *Audubon* 64:346–350.
- Denslow, J. S., and T. C. Moermond. 1982. The effect of accessibility on rates of fruit removal from tropical shrubs: an experimental study. *Oecologia (Berl.)* 52:170–176.
- Diamond, J. 1982. Rediscovery of the yellow-fronted gardener bowerbird. *Science (Wash., D.C.)* 216:431–434.
- Endler, J. A. 1978. A predator's view of animal color patterns. *Evol. Biol.* 2:319–364.
- Goldsmith, T. H., and K. M. Goldsmith. 1979. Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri*. *J. Comp. Physiol. A, Sens. Neural Behav. Physiol.*, 130:209–220.
- Grant, K. A. 1966. A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. *Am. Nat.* 100:85–97.
- Hailman, J. P. 1967. Mirror-image color-preferences for background and stimulus-object in the gull chick (*Larus atricilla*). *Experientia* 22:257–258.
- . 1977. Optical signals. Indiana University Press, Bloomington.
- Herrera, C. M. 1981. Are tropical fruits more rewarding to dispersers than temperate ones? *Am. Nat.* 118:896–907.
- . 1982. Defense of ripe fruits from pests: its significance in relation to plant-disperser interactions. *Am. Nat.* 120:218–241.
- Holdridge, L. 1967. Life zone ecology. Tropical Science Center Publication, San José, Costa Rica.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13:201–228.
- Howe, H. F., and G. A. Vande Kerckhove. 1980. Nutmeg dispersal by birds. *Science (Wash., D.C.)* 210:925–927.
- Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia (Berl.)* 55:192–201.
- Jacobs, G. H. 1981. Comparative color vision. Academic Press, New York.
- Janson, C. H. 1983a. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science (Wash., D.C.)* 219:187–189.
- . 1983b. Adaptation and phylogenetic inertia in the taxonomic distribution of neotropical fruit characters. *Bull. Ecol. Soc. Am.* 64:52–53.
- Janzen, D. H. 1983a. Dispersal of seeds by vertebrate guts. Pages 232–262 in D. J. Futuyma and M. Slatkin, eds. *Coevolution*. Sinauer, Sunderland, Mass.
- . 1983b. Physiological ecology of fruits and their seeds: physiological plant ecology. Pages 625–655 in O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds. *Encyclopedia of plant physiology*. Springer-Verlag, Berlin.
- Jenkins, R. 1969. Ecology of three species of saltators with special reference to their frugivorous diet. Ph.D. diss. Harvard University, Cambridge, Mass.
- Kalmbach, E. R., and J. F. Welch. 1946. Colored baits and their value in safeguarding birds. *J. Wildl. Manage.* 10:353–360.
- Kovach, J. K. 1980. Mendelian units of inheritance control color preferences in quail chicks (*Coturnix coturnix japonica*). *Science (Wash., D.C.)* 207:549–551.

- Kreithen, M. L., and T. H. Eisner. 1978. Ultraviolet light detection by the homing pigeon. *Nature (Lond.)* 272:347-348.
- Long, R. W. 1971. A flora of tropical Florida. University of Miami Press, Coral Gables, Fla.
- Martin, W. K. 1965. The concise British flora in colour. Ebury Press and M. Joseph, London.
- Mason, J. R., and R. R. Reidinger, Jr. 1983. Generalization of and effects of pre-exposure on color-avoidance learning by red-winged blackbirds (*Agelaius phoeniceus*). *Auk* 100:461-468.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pages 159-191 in L. E. Gilbert and P. H. Raven, eds. *Coevolution of animals and plants*. University of Texas Press, Austin.
- Miller, R. S., and R. E. Miller. 1971. Feeding activity and color preference of ruby-throated hummingbirds. *Condor* 73:309-313.
- Morden-Moore, A. L., and M. F. Willson. 1982. On the ecological significance of fruit color in *Prunus* and *Rubus*: field experiments. *Can. J. Bot.* 60:1554-1560.
- Raven, P. H. 1972. Why are bird-visited flowers predominantly red? *Evolution* 26:674.
- Raven, P. H., R. F. Evert, and H. Curtis. 1976. *Biology of plants*. Worth, New York.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. Reeve, Ashford, England.
- Rothschild, M. 1975. Remarks on carotenoids in the coevolution of signals. Pages 20-52 in L. E. Gilbert and P. H. Raven, eds. *Coevolution of animals and plants*. University of Texas Press, Austin.
- Siegel, S. 1956. *Nonparametric statistics*. McGraw-Hill, New York.
- Snodderly, D. M. 1978. Eggshell removal by the laughing gull (*Larus atricilla*): normative data and visual preference behaviour. *Anim. Behav.* 26:487-506.
- . 1979. Visual discriminations encountered in food foraging by a neotropical primate: implications for the evolution of color vision. Pages 237-279 in E. H. Burt, Jr., ed. *The behavioral significance of color*. Garland, New York.
- Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113:194-202.
- Sorensen, A. E. 1983. Taste aversion and frugivore preference. *Oecologia (Berl.)* 56:117-120.
- Stiles, E. W. 1982. Fruit flags: two hypotheses. *Am. Nat.* 120:500-509.
- Stiles, F. G. 1976. On taste preferences, color preferences, and flower choice in hummingbirds. *Condor* 78:10-26.
- Terborgh, J. 1984. *Five New World primates*. Princeton University Press, Princeton, N.J.
- Thompson, H. V. 1953. The use of repellents for preventing mammal and bird damage to trees and seed. *For. Abstr.* 14:129-136.
- Thompson, J. N., and M. F. Willson. 1978. Disturbance and the dispersal of fleshy fruits. *Science (Wash., D.C.)* 200:1161-1163.
- Turcek, F. J. 1963. Color preferences in fruit- and seed-eating birds. *Proc. Int. Ornithol. Congr.* 13:285-292.
- van der Pijl, L. 1969. *Principles of dispersal in higher plants*. Springer-Verlag, New York.
- Wheelwright, N. T. 1983. Fruits and the ecology of resplendent quetzals. *Auk* 100:286-301.
- . 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66:808-818.
- Wheelwright, N. T., and G. H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* 119:402-413.
- Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16:173-192.
- White, D. W., and E. W. Stiles. 1985. The use of refractometry to estimate nutrient rewards in vertebrate-dispersed fruits. *Ecology* 66:303-307.
- Willson, M. F., and M. N. Melampy. 1983. The effect of bicolored fruit displays on fruit removal by avian frugivores. *Oikos* 41:27-31.
- Willson, M. F., and J. N. Thompson. 1982. Phenology and ecology of color in bird-dispersed fruits. *Can. J. Bot.* 60:701-713.
- Wright, A. A. 1972. Psychometric and psychophysical hue discrimination functions for the pigeon. *Vision Res.* 12:1447-1464.
- Zahavi, A. 1978. Decorative patterns and the evolution of art. *New Sci.* (19 October):182-184.