

EFFECTIVE POLLINATION OF *ERYTHRINA FUSCA* BY THE ORCHARD ORIOLE (*ICTERUS SPURIUS*): COEVOLVED BEHAVIORAL MANIPULATION?¹

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ABSTRACT

Based on observations in Panama, the male orchard oriole is shown to be the most effective pollinator of *Erythrina fusca*. It is hypothesized that the identical color of the male oriole's body plumage and the floral parts surrounding the nectar indicates a coevolved relationship.

Erythrina fusca Loureiro is a large and abundant tree in the Panama Canal Zone and occurs pantropically (Krukoff & Barneby, 1974). I observed nectar-feeding birds visiting a pure stand of *E. fusca* growing in swampy ground near the Pedro Miguel locks of the canal (Table 1). The avian activity in 4 tree crowns was observed for a total of 16 hours during January and March 1974 and March 1975. The orchard oriole (*Icterus spurius*) vastly outnumbered all other species combined both in numbers present and in total time spent nectar-feeding. This species's outstanding importance to the effective pollination of *Erythrina fusca* here is underlined by four facts that form the basis for the hypothesis that *E. fusca* and this oriole may have coevolved.

1. Of the 13 bird species observed feeding on *Erythrina fusca* nectar, only the male orchard oriole correctly opened the flowers (see below) to obtain nectar and to receive pollen for transfer to other flowers. The others either robbed nectar by piercing the calyx or standard base, by using only extrafloral nectaries, or by visiting only flowers previously opened by the orchard oriole.

2. The orchard oriole, a migrant that breeds in North America, occurs in large flocks of up to several hundred, far exceeding the numbers of other potential avian pollinators. This species robs nectar from other species of trees, such as *Tabebuia guayacan* (Seem.) Hemsley, easily piercing the corolla with its long sharp bill, but not from *Erythrina fusca* flowers.

3. Only adult male orchard orioles were observed to open *Erythrina fusca* flowers. Females and immature males, which have greenish olive plumage, were excluded by the black and burnt orange adult males. The burnt orange color of the adult male oriole is exactly matched by a portion of the *E. fusca* flower that becomes visible only after the standard has been pushed back.

4. *Erythrina fusca* flowers during a period when the orchard oriole is most abundant.

These facts will be discussed together with corollary information on the bird and the plant to support the hypothesis that the plant is manipulating the behavior of the male oriole to most effectively affect pollination, particularly outcrossing.

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PHENOLOGY OF *ERYTHRINA FUSCA*

Erythrina fusca begins to show mature inflorescences nearly synchronously on both Pacific and Atlantic slopes of the Canal Zone at the beginning of the dry season. On 29 December 1974, trees at both the Pedro Miguel locks site, which is about 10 km from the Pacific coast, and trees near Gatun, 4 km from the Atlantic coast, had an estimated 1% mature flowers. Flowering lasted from then until 4 March 1975 (66 days), when the smaller trees still had unopened flowers. Figure 1 shows the manner in which flowers are arranged. The flowers are arranged radially around the thick stem which provides a strong perch for the oriole. There are from 2 to 12 inflorescences in each cluster, a flower measuring about 50 mm from the calyx to the tip of the standard.

Leaves are shed before flowers mature as is typical for many *Erythrina* (Standley, 1922). The flowers are highly visible and appear uniform dull yellow-orange until opened when the rich burnt-orange color of the wing petals is uncovered.

Shortly after the flowering period ends, leaves appear coincident with the onset of the rains in late April. The next season's flower buds form at this time but remain in an immature stage throughout the rainy season. The calyx attains a mature size early and its tough texture no doubt protects the immature parts within. Significantly, an extrafloral nectary located at the tip of the calyx (see Fig. 1), secretes nectar during this 8 to 9 month period between bud formation and flower maturation. Probably these nectaries function to nourish ants (species undetermined) which live in the tree's hollow twigs (pers. obs.; see also Feinsinger et al., this symposium). However, several bird species were observed to use this extrafloral nectar source (Table 1). Some pods attained mature size even while flowers were maturing, but they dried and opened when flowering stopped in the late dry season (April).

ORCHARD ORIOLE BEHAVIOR

GENERAL BEHAVIOR

This oriole, wintering from southern Mexico to southern and central eastern Colombia and northwestern Venezuela (Anonymous, 1957), becomes abundant in Panama during late September and remains in large numbers until late March. During fall their center of abundance is the drier Pacific slope where they concentrate on the flowers of trees such as *Luehea* sp. Large night roosts of several thousand birds form from the congregation of smaller flocks streaming in from all directions. With the advent of the dry season orchard orioles begin foraging for nectar in synchronously flowering trees such as *Tabebuia* sp. and then *Erythrina fusca*. Orchard oriole flocks nectar-feeding in all species of trees except *Erythrina fusca* are composed of all sex and age classes; only adult males (rarely first year males) are found in *E. fusca* trees. This observation is so common among ornithologists familiar with the species that it is mentioned in a field guide to bird identification (Ridgely, 1976)! This is not due to choice on the female's part. The females are largely excluded because adult males are

TABLE 1. Species of birds and their characteristics while nectar-feeding on *Erythrina fusca*.

Species	Floral Parts Searched ^a	Ave. Peak Numbers/Tree
Orange-chinned parakeet (<i>Brotogeris jugularis</i>)	NR, eats pollen too	6
White-necked jacobin (<i>Florisuga mellivora</i>)	FAO	1
Rufous-tailed hummingbird (<i>Amazilia tzacatl</i>)	FAO	1
Red-crowned woodpecker (<i>Melanerpes rubricapillus</i>)	NR, FAO	2
Red-legged honeycreeper (<i>Cyanerpes cyaneus</i>)	FAO, EFN	10
Tennessee warbler (<i>Vermivora peregrina</i>)	FAO, EFN	5
Yellow-backed oriole (<i>Icterus chrysater</i>)	FAO, NR	3
Orchard oriole (<i>Icterus spurius</i>)	OF, FAO	128
Northern oriole (<i>Icterus galbula</i>)	FAO	5
Blue-gray tanager (<i>Thraupis episcopus</i>)	FAO, NR, EFN	4
Palm tanager (<i>Thraupis palmarum</i>)	NR, FAO	4
Crimson-backed tanager (<i>Rhamphocelus dimidiatus</i>)	NR, FAO	6
Streaked saltator (<i>Saltator albicollis</i>)	NR	2

^a Abbreviations. FAO = flowers already opened; NR = nectar robber; OF = open flowers; EFN = extra-floral nectary.

able to dominate them in aggressive encounters. It is possible that females can locate *E. fusca* trees without aggressive males and obtain nectar from them.

ORCHARD ORIOLE BEHAVIOR WHILE IN *ERYTHRINA FUSCA* TREES

Aggressive Behavior.—The occurrence of birds in flowering *Erythrina fusca* trees is dynamic. At one moment there are no birds in the crown, the next moment the crown is filled with 30 or more orchard oriole males chasing each other, females, and the smaller honeycreepers while continuously uttering a harsh aggressive chatter. After the initial sorting out of feeding positions the chattering subsides but is resumed whenever a straggler flies into the tree. It is impossible to document the amount and direction of aggressive chases and displacements by the inhabitants of an entire tree crown so I watched three orchard oriole males from 1200 to 1300 hrs that were typical of the rest. Each averaged 9 chases directed against other male orchard orioles, 12 against female and immature male

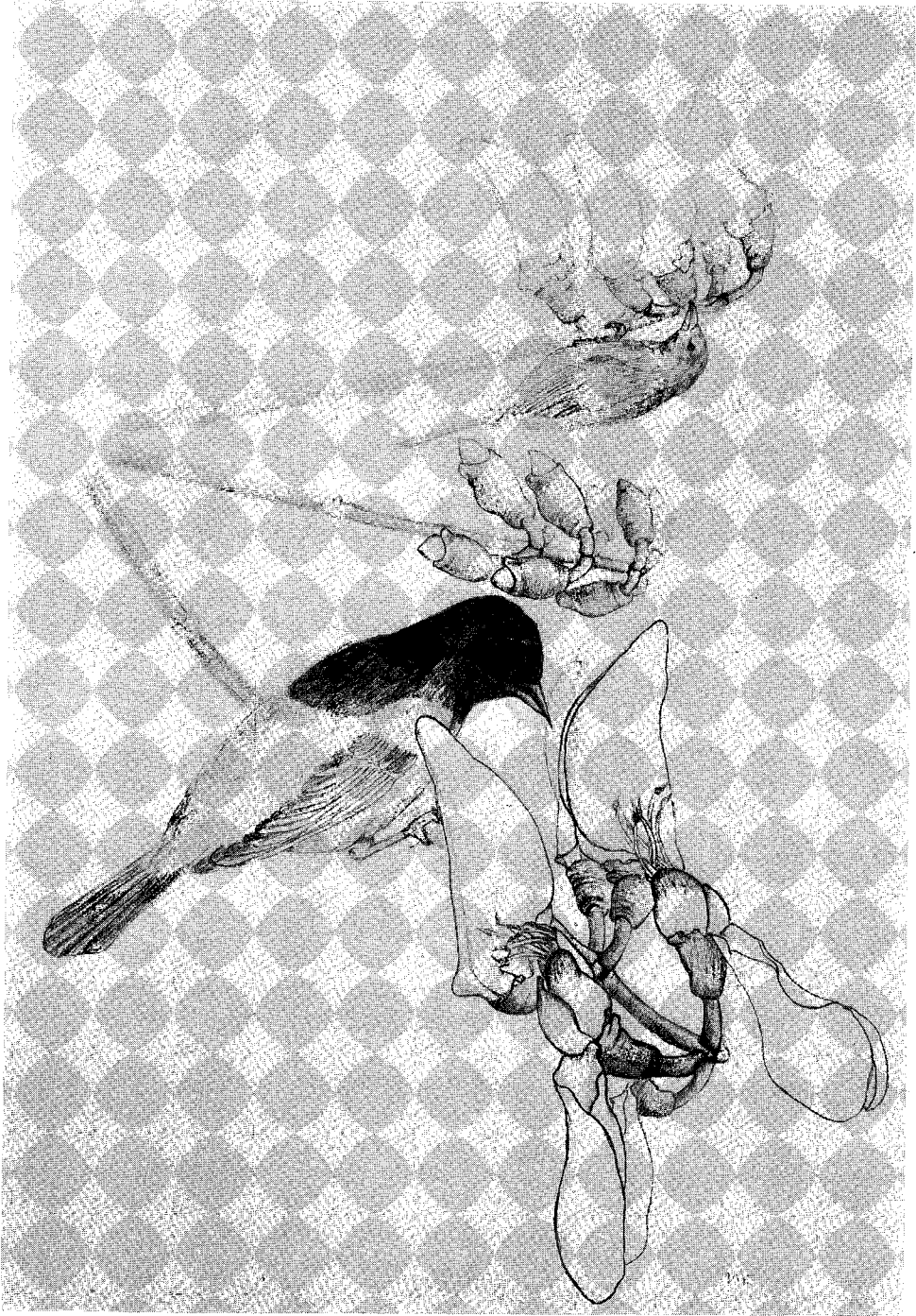
orchard orioles, 20 chases against red-legged honeycreepers (*Cyanerpes cyaneus*), one against a Tennessee warbler (*Vermivora peregrina*). With each male oriole chasing about once each 1.4 minutes a tree with 30–40 males presents an active scene.

Both male and female northern orioles (*Icterus galbula*), a less common migrant, fed upon already opened *Erythrina fusca* flowers and were dominant over orchard orioles. The red-crowned woodpecker (*Melanerpes rubricapillus*) occurred as a single pair within one tree crown, each pair excluding other woodpeckers, and displacing orchard orioles infrequently but at will. Orchard orioles ignored and were ignored by the similarly sized palm and blue-gray tanagers (*Thraupis palmarum* and *T. episcopus*). I also saw no interaction between orchard and the three resident yellow-backed orioles (*Icterus chrysater*), but the resident orioles did chase off conspecifics once. Orange-chinned parakeets (*Brotogeris jugularis*) occasionally chased conspecifics, but they were ignored by the other bird species. Crimson-backed tanagers (*Ramphocelus dimidiatus*) were also ignored by orchard orioles.

Orchard orioles exhibit a lower “social tolerance” in the presence of *Erythrina fusca* nectar than when feeding on other tree nectars. This is likely due to the relatively rich nectar source provided by *E. fusca* (see below). Social tolerance is often a highly flexible aspect of avian behavior and is known to be influenced by the economics of food exploitation strategies (Leck, 1972). The high caloric content of nectar also permits, in a proximal sense, the high rate of costly high energy chases that permit access to nectar. As an ultimate factor, nectar feeding reduces the need for effort expended hunting insects that are high in protein but low in calories (Ford & Paton, 1976).

Nectar-Feeding Behavior.—The time orchard orioles remain in their defended area in an *Erythrina fusca* crown is important to the coevolutionary hypothesis. During the 16 observation hours the orioles were actively opening flowers for only about 5 hours. Most of the time was spent off the *E. fusca* trees in trees retaining their leaves. Here these were predominantly *Guazuma ulmifolia* Lam. Male and female orioles were in flocks and showed little aggression. Some insect foraging was observed, primarily by females, but preening and “loafing” occupied most time. A few males could be found in *E. fusca* crowns during lulls in nectar feeding, but the vast majority alternated between rushing into the *E. fusca en masse*, spending 20–30 minutes nectar feeding then retiring to densely leaved trees for insect foraging and resting. No individual birds were banded so it is not known if a male returns to the same place in an *E. fusca* crown. The observations suggest that a tree crown is a “grab bag” and that individual birds do not retain the same foraging dominance area every time they return to the trees.

As shown in Table 1, the male orchard oriole was the only bird to correctly open the *Erythrina fusca* flowers. *Erythrina fusca* flowers are erect on the parent rachis even though radially arranged on it (Fig. 1). The commissure formed by the lateral margins of the standard faces inward towards the rachis such that a bird approaching the flowers along the rachis would confront the commissure. The rhombic-ovate blade of the standard completely encloses the other floral



parts in the unopened mature flower. To obtain nectar, the orchard oriole sidles down the rachis, places its bill into the commissure while facing downward, opens the bill when it is fully inserted³ and at the same time pushes with its head. In a mature flower this will cause the standard to fall backwards, its constricted base acting as a hinge. When this happens, the stamens and style are released against the bird's throat and upper breast. This action by the bird seems to take some effort and some, probably immature flowers, are not opened even though probed. It is doubtful that even the largest bees (e.g., *Eulaema* sp.) can gain access to the nectar. An opened flower contains such quantities of nectar that an oriole will sip from four or five flowers and quit.

Except for the orchard oriole, other species robbed the flowers by clinging to the rachis from beneath and puncturing the standard or calyx (Fig. 1), or they visited flowers already opened by the oriole. They did not align themselves in any consistent manner to receive pollen and probably contribute relatively little to the pollination of *Erythrina fusca* in Panama.

Nectar Constituents.—Herbert and Irene Baker kindly sent an analysis of a nectar sample taken from the trees I observed (Table 2). The histidine scale score of 7, an index to amino acid concentrations, is extremely high for a bird-pollinated flower (ave. of 21 species was 3.31) (Baker & Baker, 1975). This concentration might diminish the need for insect food for male orchard orioles relative to females. This would concur with the observation that females, excluded from *Erythrina fusca* trees, spend more time insect hunting than males when *E. fusca* nectar is available.

DISCUSSION

The data presented show that the orchard oriole is the most effective pollinator of *Erythrina fusca* flowers among the bird species observed. But it is the color of the floral parts surrounding the nectar, identical to the male oriole's body plumage, that indicates a coevolved relationship. I suggest that this color is both attention-getting and aversive to a male orchard oriole. Furthermore, it only shows in a flower that has been opened and drained of nectar. Thus the more flowers an oriole has opened in the small foraging area to which the bird is restricted because of the aggressive conspecifics surrounding it, the more "signals"

³ Of the birds visiting *E. fusca*, only orioles use this bill scissoring technique in foraging. They often hunt insects in dead twig tips by inserting the bill, opening it, and then looking down the open bill commissure for exposed prey. This may have preadapted them for correctly opening *E. fusca* flowers.

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FIGURE 1. In the foreground, a male orchard oriole (*Icterus spurius*) is about to open a flower of *Erythrina fusca*. The two opened flowers at the rachis tip show the bright oriole-matching color of the wing petal tips. In the center, a rachis with immature flowers shows the prominent extrafloral nectary located on the calyx tip. In the background, a palm tanager (*Thraupis palmarum*) is shown in the hanging position taken by several nectar-robbing species as they prepare to pierce the calyx or standard from below.

TABLE 2. Nectar constituents from *Erythrina fusca* in Panama.

Reagents	Results		
Ninhydrin	7 on histidine scale = 3.125 μ moles/ml		
Osmic acid	No saturated lipids		
Dichlorophenol-indophenol	Some organic acids		
Dragendorff's	No alkaloids		
p-Nitraniline	No phenols		
Brom-phenol Blue	No proteins		
Amino-acid Analysis			
Alanine	++	Methionine	+
Arginine	+	Phenylalanine	+ -
Glutamic	+ -	Proline	++
Glycine	+	Serine	+ -
Histidine	+	Threonine + Glutamine	++
Isoleucine	+	Tyrosine	+ -
Leucine	+	Valine	+
Lysine	+	plus two non-protein amino acids	
Sugar concentration of 20% (w/w) sucrose equivalents; fructose 30%, glucose 42%, sucrose 28%. Ratio of sucrose to glucose plus fructose = 0.40.			

it receives to move on to another tree. The value to the *E. fusca* tree in incorporating the oriole's color in this manner is therefore to increase outcrossing. In addition to the color, the rhombic-ovate blade of the standard is designed to conceal this color until it is needed to, in essence, repel the oriole, i.e., after the individual is covered with pollen to be carried elsewhere.

Obviously, this is only a hypothesis, but one that has an inherent test yet to be made. If there is a coevolved relationship between orchard oriole and *Erythrina fusca* in Panama, then one would predict that *E. fusca* populations should have different flower coloration where the orchard oriole does not occur. Snow & Snow (1972) list the color of *E. glauca* (= *fusca*) in Trinidad as red. However, Feinsinger (pers. comm.) reports the flower color the same as the Panamanian population. From a color slide sent to me by Feinsinger, it appears that the Trinidadian flowers do differ: the calyx is wine or reddish color in flowers from Trinidad, dull brown in Panama. The wing petals and standard look the same from both areas. Trinidad is the same latitude as my study site (9° N) but orchard orioles do not occur on Trinidad (French, 1973). The question remains if flowers still more remote from the wintering range of orchard orioles will lose the burnt orange color. In Malaya, the color is "purple" (Corner, 1940).

Since the orchard oriole is confined in winter primarily to Middle America and *Erythrina fusca* occurs pantropically, the opportunity exists for a comparative study of pollinator-*E. fusca* coevolution. Does species-specific coevolution involve a threshold in pollinator abundance with some *E. fusca* floral parts assuming the generalist bird attracting color of red in regions where an abundant migrant species is not found?

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