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NESTING BIOLOGY OF THE YELLOW-THROATED EUPHONIA: LARGE CLUTCH SIZE IN A NEOTROPICAL FRUGIVORE

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ABSTRACT.—I studied the nesting biology of Yellow-throated Euphonias (Thraupinae: *Euphonia hirundinacea*) in Monteverde, Costa Rica, in 1987–1990. Most nesting occurred from April to July (N = 69 nests) in covered nests in road banks. Modal clutch size was five eggs ($\bar{x} = 4.4$), an unusually large number for a tropical passerine. Only females incubated eggs, but both parents fed nestlings. Parents regurgitated food for nestlings, and examination of nestling fecal samples indicated that fruit made up most of the diet starting from the day of hatching. Morphological specializations of the digestive tract may enable, or even require, them to use fruit in the nestling diet more extensively than other birds. Parents visited the nest infrequently, arrived at the nest together, and accompanied one another to the nest entrance in what may be a distraction display to confuse potential nest predators. The covered nests, the infrequent visits to the nest, and the behavior at the nest may all contribute to reducing nest predation in this species. The combination of large clutch size, extreme nestling frugivory, and coordinated parental behavior is unique, and the inclusion of euphonias in comparative studies addressing the evolution of these traits should prove valuable.

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The twenty-five species in the genus *Euphonia* share several unusual features setting them apart from other members of the Thraupinae. They completely lack a gizzard (Forbes 1880, Wetmore 1914), apparently a specialization of the digestive tract for a diet of fruit. Available data also suggest that euphonias have an unusual breeding biology (see Isler and Isler 1987 for compilation): they build covered nests, they lay larger clutches than the typical two eggs of most tropical passerines (Ricklefs 1970, Skutch 1985), and they feed fruit to nestlings to a greater extent than other frugivorous birds (Morton 1973). However, detailed information is lacking, and many species remain completely unstudied. Understanding the breeding biology of euphonias in greater detail may help shed light on several longstanding questions in ornithology, such as constraints on the use of fruit in the nestling diet and factors influencing clutch size determination.

Yellow-throated Euphonias (*Euphonia hirundinacea*) occur from southern Mexico to Costa Rica (Isler and Isler 1987) and are common in disturbed habitats. They are typical members of the genus: male plumage is yellow below and blue above, female plumage is dull green, they have short tails and stocky bodies, and they eat fruit. They occur in pairs

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throughout the year but do not defend territories. Scattered reports in the literature provide an outline of their basic nesting habits (Eaton and Edwards 1948; Sutton et al. 1950; Skutch 1954, 1985; Isler and Isler 1987). The pair builds the covered nest together, and the clutch size is five (based on three clutches). Only the female incubates, but both sexes feed the nestlings; when arriving at the nest the parents "race" to the entrance. The only information on incubation and nestling periods comes from one nest described by Skutch (1954), and these were 16 and 17 days, respectively.

I present information from 69 nests from a single mid-elevation site in Costa Rica. I describe: (1) variation in clutch size, (2) degree of frugivory of the nestling diet, (3) parental behavior at the nest, and (4) frequency of nest predation.

STUDY SITE AND METHODS

The study was conducted in Monteverde, Costa Rica, during 1987–1990. Monteverde (10°18′N, 84°48′W) is in the mountains of northwestern Costa Rica, at the top of the Pacific-facing slope. Nests were located at 1340–1490 m elevation, along roadsides and in pastures. The vegetation and bird community are described in Wheelwright et al. (1984). At this site, the rainy season begins in early to mid-May and continues through mid-December, and precipitation averages 2519 mm per year.

A total of 69 nests was found by searching road banks and watching adult birds. In 1987, a 3-km stretch of road was walked almost daily, but in other years nests were found more opportunistically. In 1988, I did not arrive in Monteverde until 1 June, but in other years I was at the site before nesting activity started. In all years, I left the site before the breeding season was completely over. In 1989, I returned in the first week of September and stayed through the next season. I estimated the date of clutch initiation for nests found later in the nesting cycle by using average incubation time and average growth rates of nestlings.

In 1987 and 1988, I weighed chicks using a Pesola spring scale at the same time ± 1 h each day (1987) or every two days (1988). Most were weighed between 07:00 and 12:00 h CST. Individual chicks were given color bands at age 8–10 days, but prior to this the brood as a whole was weighed together and mean chick mass calculated by dividing group mass by number of chicks. I measured the lengths of tarsi, remiges and rectrices using dial calipers. I collected fecal samples in vials when chicks were weighed. Fecal material was preserved in 75% ethanol and later examined with a dissecting microscope. I identified seeds by comparing them to those in fruits collected in the area during the breeding season.

Nest observations were made by sitting along roadbanks 5 m or more away from the nest. Observations lasted 1.25 to 3.4 h and ended with an event (pair visit to nest, female leaving nest), rather than having a fixed duration. Most observations were made in the morning, but some were made after noon.

A relatively small proportion of the population was color-banded, a total of 17 adults in different years. Thus, most data were from unmarked birds, and in only a few cases was I able to determine whether individuals or pairs made repeated nesting attempts within seasons or between years. Statistical tests were performed using StatView II (Feldman et al. 1987).

RESULTS

Nest sites and nest description.—Sixty-eight of 69 nests found during the study were in dirt road banks, approximately 1–3.5 m above the road surface. Nests were constructed in a slight recess in the bank, often near the top and associated with clumps of short vegetation. Another nest was on the side of a tree trunk in a pasture near forest edge. The nest itself was 1.3 m from the ground at the base of a clump of epiphytes. The birds may round out the recess in which the nest is built, but they do not excavate dirt. Although Cherrie (1892) reported that they nest in holes one foot deep, and that twigs were used in nest construction, I never observed this. I suspect that the nest he described may have belonged to a House Wren (*Troglodytes aedon*). They commonly nest in the same road banks as euphonias, and frequently use twigs. Skutch (1954) describes two nests from Guatemala in the tops of rotting fenceposts, but in spite of the many rotting fenceposts in my area, I never found a nest in one.

The nests were constructed of narrow leaves, rootlets, moss, and lichen in a globular form (ca 8–9 cm diameter). The round side entrance (ca 35 mm high by 40 mm wide, 20–30 mm above the floor of the nest) typically had an overhanging "awning." The outer part of the nest, especially the awning, was usually well camouflaged with lichen and moss. The lip of the entrance, where the birds alight, was the sturdiest part of the nest. Roots in the bank were sometimes incorporated into the structure, tying the nest into the bank. A layer of lanceolate, bamboo-type leaves usually lined the interior part of the roof and floor, with a nest cup lining of fine black rootlets (see also Isler and Isler 1987, Stiles and Skutch 1989).

Males and females built the nest together, as described by Skutch (1954). During the earliest phase, when the pair was choosing a suitable location, the male appeared to spend more time than the female along road banks, investigating potential nest sites. The female perched nearby, joining the male occasionally. During construction, the pair arrived near the nest together, each carrying material. One waited while the first (usually the male) went to the nest and added the material. The first one then waited nearby while the second one (usually the female) added and arranged material, then left the area together. The female spent longer in the nest toward completion. Pairs waited one to 14 days between nest completion and clutch initiation ($N = 15$), with the longest waiting periods occurring at the beginning of the breeding season.

Pairs built new nests for each nesting attempt. In only one case did a pair begin to reline a previously used nest from which they had successfully fledged young two weeks before, but this nest was destroyed before the new clutch was laid. In successive years, two marked females nested 8 m and 50 m, respectively, from where they had nested in the previous year.

Nesting phenology.—Most clutches were initiated in May (27 of 52 nests, Fig. 1) near the onset of the rainy season (13–17 May 1987–1990). Later nesting attempts continued into early August. This pattern of nesting phenology is typical of many bird species at Monteverde (pers. obs.) and

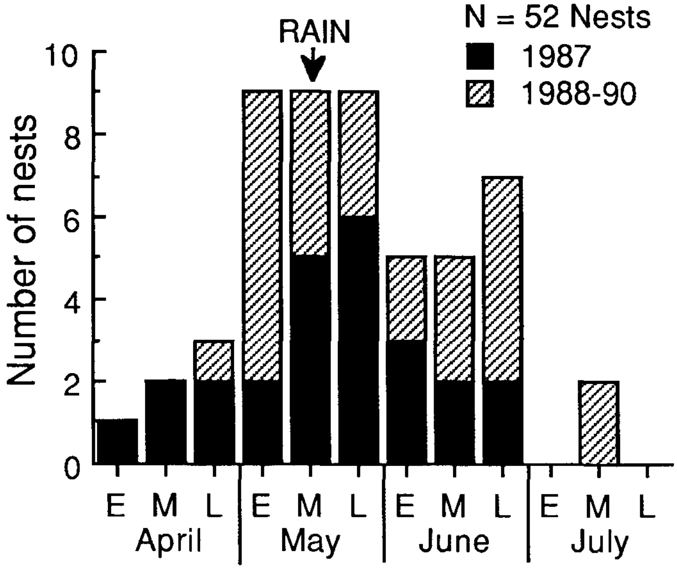

FIG. 1. Number of clutches initiated during 10-day periods of April through July, 1987–1990. E = early (1st–10th), M = middle (11th–20th), L = late (21st–30th or 31st). The arrow indicates the onset of the rainy season. Initiation date was estimated by chick mass and verage incubation period in cases where the nest was found later.

throughout Costa Rica and Central America (Skutch 1950, Stiles and Skutch 1989). In the absence of a marked population, I was unable to determine how many nesting attempts were made by each pair in each year, but none of the marked birds raised more than one brood in a season. Also, the young appeared to stay with the parents for at least several weeks after fledging, reducing the possibility of multiple broods in one season.

Clutch size and incubation behavior.—Females laid eggs at one-day intervals until clutch completion. Eggs were as described elsewhere (Cherrie 1892, Skutch 1954, Isler and Isler 1987). Average egg mass was 1.4 ± 0.22 g (N = 4 clutch means [total mass/number of eggs]), which was 8.2% of female body mass (16.97 g ± 1.09, N = 9). Clutch sizes ranged from three to five, with most consisting of five eggs (Fig. 2, $\bar{x}$ = 4.44 ± 0.65, N = 36). Incubation lasted 15 days (range = 14–16 days, N = 17), starting the day the last egg was laid. Twelve of 109 eggs in 24 nests failed to hatch (11.0%). One possible case of intraspecific brood parasitism occurred; in one nest four eggs appeared in three days.

Only the female incubated the eggs, but the male almost always accompanied her to the nest, as described by Skutch (1954) and Sutton et al.

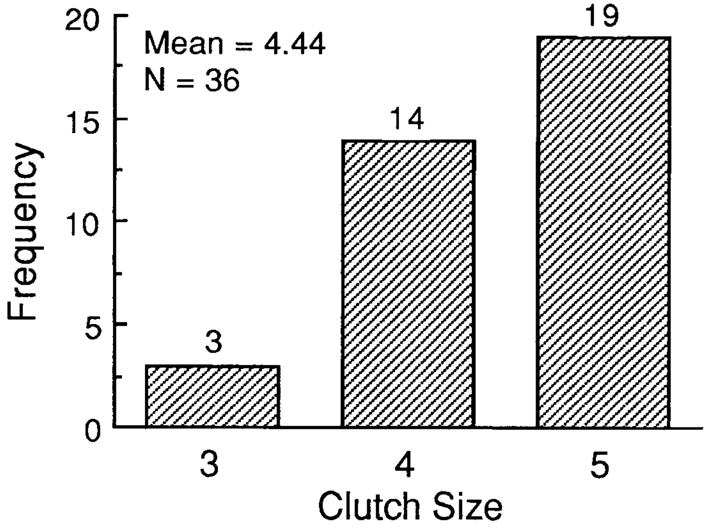

FIG. 2. Clutch sizes, 1987–1990.

(1950). Females spent 71.4 ± 6.8% of observation time incubating eggs (N = 5 nests, 10 h observed). They stayed on the eggs a mean of 42.9 ± 15.4 min (N = 5 observations at 5 nests, ranging from day 4–11 of incubation). The mean duration of intervals away from the nest was 17.2 ± 3.1 minutes. On several occasions the male examined the eggs just before the female returned to sit on them. On one occasion the male appeared to feed the female on the nest by regurgitation; this was during the longest observed incubation bout (65 min). Generally, the male remained nearby some of the time that the female was on the nest and gave alarm calls when pedestrians, etc., approached along the road. Often the male called to the female just before she left the nest, or she would call from nearby just after leaving, and they would leave the vicinity of the nest together.

Nestling feeding rate and pair-visiting behavior.—Parents visited the nest in pairs, arriving at the nest together every 25–66 min. The mean visit rate for pairs was 1.41 ± 0.49 visits/hour (Fig. 3), or every 44 ± 12 min (N = 20 observation periods at 10 nests, totalling 38 hours). The visit rate showed a slight, non-significant increase with chick age (r = 0.39, P = 0.093), and no relationship with brood size (r = 0.21, P = 0.369). Only one of 45 observed visits to nests was made by a single parent alone; this solo visit was made by a female on the third day after hatching, while she was still brooding the young. I never observed a male to visit a nest alone.

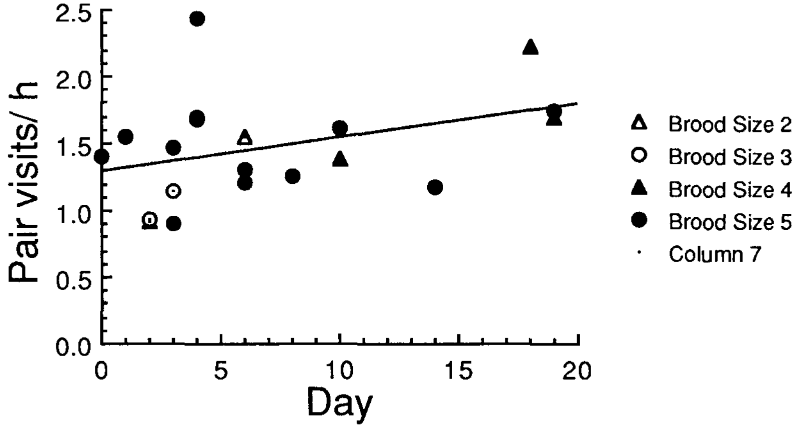

FIG. 3. Feeding rate of nestlings during the 19-day nestling period. Symbols represent different brood sizes. Line represents regression of feeding rate on nestling age ($r = 0.39$, $P = 0.09$).

Females continued to brood the young through day 6 or 7 after hatching. During this time, the female was on the nest 39.3 ± 13.8% of the time (N = 11 observation periods at seven nests, 25.5 hours). The pair were away from the nest 58.8 ± 12.9% of the time. The interval away from the nest was 27 ± 13 min, significantly longer than the interval away from the nest during incubation, but shorter than the interval away from the nest after brooding ceased (39 ± 8 min, N = 8 observation periods; $F = 13.47$, $P = 0.0001$, 2 df). During this period the male sometimes did not enter the nest to feed chicks, but nonetheless accompanied the female to the nest entrance as described below.

All pair visits that I observed followed a set pattern. The pair would arrive at a perch near (ca 3–6 m) the nest, often a low branch on a tree opposite the nest. Pairs typically used one or two favorite perches when approaching the nest. They were sometimes silent, but often called to each other as they arrived at a perch. The first bird to visit the nest (usually the male) would initiate the flight to the nest and the second (the female) followed, flying very close (0.5 m) behind the first. The first bird landed at the entrance to the nest while the second bird continued flying up past the nest entrance and returned to the original perch, or to another perch nearby. When the first one finished at the nest, it returned to the perch and the two changed roles. This first parent would then accompany the second one to the nest, flying behind it, passing by the nest, and returning to the perch. The closeness of following varied, as did the timing. It sometimes took the parents several false starts to get to the nest, but this might have been related to disturbance along the road. The second bird sometimes waited several minutes before taking its turn to visit the nest, or it would start its flight the instant the first one left the nest, causing the first one to double back in mid-flight to perform its accompanying duty.

Males spent an average of 1.33 ± 0.74 min (N = 18 observation periods at eight nests, over entire nestling period) at the nest feeding chicks, while females spent 1.49 ± 0.36 min (N = 8 observation periods at five nests, after brooding ends on day 7), not a significant difference ($T = 0.58$, $P = 0.57$). All chicks were fed during each visit, but I was unable to observe whether each parent fed each chick or whether each parent fed only some of the chicks.

Parents swallowed fecal material from chicks. I observed no fecal sacs. Chicks turned around and presented the cloaca to the parent after being fed. On two occasions I observed parents regurgitating chick feces after leaving the nest. When the chicks were older, especially in a large brood, fecal material was sometimes voided by chicks directly out of the nest, creating a splattering of seeds on the bank below the nest.

Parents gave alarm calls from near the nest, increasing in intensity if the cause of disturbance approached the nest. One call was reminiscent of the alarm call of the Clay-colored Robin (*Turdus grayi*), but in general the calls did not resemble those of other species.

Diet of nestlings.—Parents fed nestlings by regurgitation. After feeding, chicks had large bulges on each side of the neck, the color of the food material showing through the skin (most often green, occasionally blue or purple). Examination of fecal material revealed that the majority of each sample consisted of fruit pulp and seeds, with only a few, if any, insect parts (Table 1). Seeds most commonly encountered were from *Cecropia* spp. (Moraceae) and *Conostegia bernoulliana* (Melastomataceae). In addition to occasional seeds, consumption of *Ficus* sp. fruits was indicated by the presence of other fruit parts, including anthers, scales that enclose individual seeds, and in one case a male fig wasp (Agaeonidae). Only two of ten fecal samples with insect parts contained large numbers of parts; these two had many large pieces of homopteran nymphs. In the rest, the insect component consisted of a very small amount of material (e.g., a single leg) which may have been ingested accidentally.

Just over half of the samples contained small translucent white or yellow flakes of material that appeared to be from very small snail shells (Table 1). I found one whole miniature shell and several of the central spirals of the same translucent material. Several samples contained the whole opercula of snails (5–6 mm long, red).

Nestling development.—Nestlings gained approximately 1 g per day

TABLE 1
NESTLING FECAL SAMPLE CONTENTS

Item	Percent of samples
Seeds	100
Moraceae	
Cecropia spp.	62
Ficus spp. (seeds or other fruit parts)	69
Melastomataceae	
Conostegia bernoulliana	79
Sp. 2	3
Sp. 3	3
Viscaceae	
Phoradendron flavens	21
P. sp. 2	3
Ericaceae	
Macleania sp.	14
Unidentified seeds	7
Insects	41
Snails	52

[a] Numbers represent percent of samples in which each item was present (N = 29 samples, from nine nests on 1–6 different days.)

until day 11 after hatching (Fig. 4). Their mass stabilized after day 12, at about 13.5 g. Eyes were open by about day five. Remex pins started to form at day six, and the remiges started to emerge from pins at day 12. At fledging, the rectrices were not completely emerged from the shafts. I measured tarsi on chicks in only two nests, but it appeared that tarsus growth continued through day 15, the oldest chicks I measured. Chicks fledged at 19 days (18–20, N = 4 nests where both hatching date and fledging date were known and fledging was apparently spontaneous).

I observed brood reduction in five nests, involving a total of six chicks, out of 18 nests in which nestlings lived for at least 10 days. One case occurred between days 1–3 after hatching, one sometime between days 1–12, and the others between days 6–9. I found a dead chick in a nest once, but in the other cases the chick was simply missing.

Nest outcomes.—Forty-one nests had known outcomes (Table 2); 16 of these (39%) successfully fledged young. Three were abandoned by the parents during laying or the first days of incubation. Twenty-two others (53.7%) succumbed to predation during laying (N = 3), incubation (N = 6), or nestling (N = 13) stages. Predation was defined as a nest suddenly empty of eggs, a nest destroyed, e.g., on the ground with no sign of eggs or young, or the lining pulled out of the nest entrance indicating that the

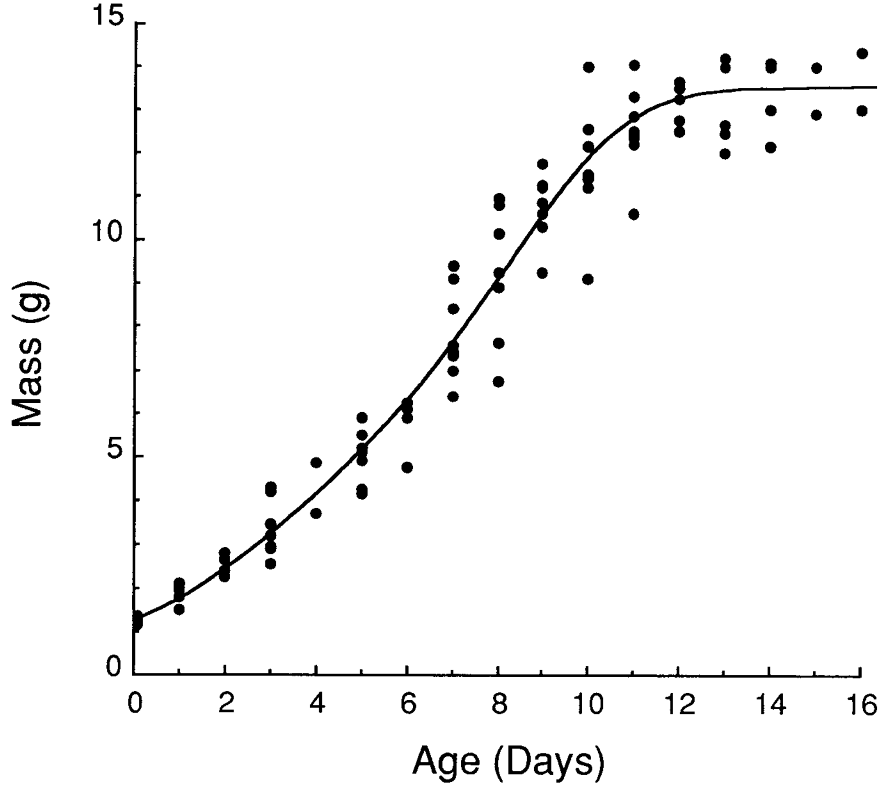

FIG. 4. Mean mass for nestlings. Points represent means per nest, N = 16 nests. Day 0 = day of hatching. The curve was fitted by eye.

young were taken while clinging to the lining (cf Skutch 1985). Calculated on a per egg basis, nesting success was 35.5% (59 out of 166 eggs) and predation was 44.4%.

Mayfield survival estimators (Mayfield 1975) were calculated using information from 52 nests over the four years; this method is used to adjust for the higher probability of encountering nests that have already survived earlier stages. The overall nest survival probability was 0.336, the product of 0.846 probability of survival of the laying period, 0.793 probability of surviving the incubation period (15 days), and 0.501 probability of surviving the nestling period (19 days). The daily survival probabilities were 0.959, 0.985, and 0.964, respectively, for these three periods. The weighted average daily survival probability was 0.972 for the entire nest period.

Fifteen of the 16 successful nests fledged 59 chicks ($\bar{x}$ = 3.93 ± 1.03).

TABLE 2

NEST OUTCOMES, BY NESTING STAGE, 1987–1990

	Laying	Incubation	Nestling	Total
Depredated	3	6	13	22 (53.7%)
Abandoned[a]	2	1		3 (7.3%)
Successful				16 (39%)
Total				41
Nest survival probability[b]	0.846	0.793	0.501	0.336

[a] Not including a female that abandoned because of capture.

[b] Per stage probabilities calculated by the Mayfield method (Mayfield 1975) using data from 52 nests.

The sixteenth "successful" nest fledged prematurely as a result of partial predation, with an uncertain number of chicks (but at least two) fledging.

DISCUSSION

Yellow-throated Euphonias exhibit several remarkable features in their breeding biology. First, the modal clutch size of five is unusually large for a tropical passerine. Second, nestlings are fed fruit regurgitate starting on the day of hatching. Third, parents visit infrequently and virtually always accompany one another to the nest entrance. Fourth, frequency of nest predation may be relatively low. I discuss these subjects separately below.

Clutch size. —The clutch size of the Yellow-throated Euphonia is among the highest reported for neotropical passerines. Skutch (1985) reports clutch sizes of 136 species, and only two others commonly have clutches of five eggs (Rough-winged Swallow [*Stelgidopteryx serripennis*], and Band-backed Wren [*Campylorhynchus zonatus*]). Only three other species occasionally or rarely lay this many eggs (Ochre-bellied Flycatcher [*Mionectes oleagineus*], Gray-breasted Martin [*Progne chalybea*], House Wren [*Troglodytes aedon*]). Other species of euphonias typically lay three or four eggs (Isler and Isler 1987); these too are larger than the average clutch size for monogamous, tropical land birds (2.4 eggs, Ricklefs 1980). Four other euphonia species are reported to lay up to five eggs occasionally, but no information on clutch size is available for 10 of the 25 euphonia species (Isler and Isler 1987).

Fruit diet of nestlings. —Perhaps the most significant finding in this study is the high degree of frugivory by nestlings in this species, supporting Morton's (1973) classification of euphonias as "total" frugivores. Nestling fecal samples contained seeds on the day of hatching, indicating that their first meals consist of essentially the same regurgitated fruit slurry that they receive throughout the nestling period. Also, there was no indication of change from more to less animal food as nestlings grew. Most birds that are frugivores as adults nevertheless feed nestlings substantial quantities of insects or other sources of animal protein, especially during the early nestling period (Morton 1973, Ricklefs 1976, Skutch 1976, Wheelwright 1983). Various authors have attributed this reliance on animal protein to the low protein levels in fruit pulp (Morton 1973), the low protein-to-calorie ratio of fruit pulp (Ricklefs 1976, Foster 1978), or the size limitation of feeding whole fruits to nestlings (Foster 1978, Wheelwright 1983).

It is not surprising that euphonias show a high degree of frugivory even during the nestling stage; they possess unusually clear morphological adaptations of the digestive tract to a frugivorous diet (Walsberg 1975, Moermond and Denslow 1985). They have no gizzard, or pyloric or cardiac sphincters (Forbes 1880, Wetmore 1914). This presumably makes insect digestion difficult or inefficient, because they are unable to grind insect exoskeletons, a function normally served by the gizzard. Those insects I found in fecal samples were often whole (fig wasp, fruit fly) or in large pieces (homopteran nymphs).

The behavioral trait of mandibulating food items and selectively swallowing soft matter while excluding hard parts ("mashing", Levey 1987) has accompanied the morphological specialization of the gut so that mechanical work is done by the bill rather than the gizzard. This behavior may create problems in using fecal remains to characterize the diet. The birds appeared to avoid ingesting hard parts of some food items, such as fig seeds. More fecal samples contained soft fig parts than contained hard fig seeds. Nonetheless, it is unlikely that the birds could be feeding extensively on insects, for example, without incidental ingestion of hard parts, and identifiable pieces should appear in the feces. The fragments of small snail shells in the samples suggest that these molluscs may be an important source of protein, and perhaps minerals, and one food source that is more amenable than insects to handling and digestion by these birds. Spider consumption during breeding has been observed in other species of euphonias (pers. obs., Isler and Isler 1987). Given the frequency of miniature snail shells in the feces, observers noting "gleaning" by euphonias and other birds should not assume that the birds are searching for insects.

Physiological adaptations to a fruit diet may also be expected in these birds. There are advantages to feeding fruit to nestlings, because it is abundant and easy to obtain (Snow 1971, Morton 1973). However, protein may be the limiting nutrient for nestlings, and it has long been thought that fruits contain too little total protein, or too small a protein-to-calorie ratio, to provide good nutrition for growing chicks (Ricklefs 1976, Foster 1978). Other highly frugivorous bird species use lipid-rich, high-calorie fruits (bellbirds, Snow 1970; quetzals, Wheelwright 1983) which have higher protein content as well (but not those used by oilbirds, see Bosque and de Parra 1992). Euphonias may increase the effective ratio of protein to sugar in their diet by incompletely assimilating sugars. Recent work indicates that some frugivorous birds, such as Cedar Waxwings (*Bombycilla cedrorum*), have low digestive efficiencies of sugars, largely as a result of rapid gut passage times (Levey and Karasov 1989, Martinez del Rio et al. 1989, Karosov 1990). Euphonias certainly fit this pattern; they have short digestive tracts with no sphincters and short retention times (pers. obs.), so they may have relatively low sugar assimilation rates. The actual protein content of the nestling diet is not clear. Regurgitation potentially allows the manipulation of the nutrient balance of the regurgitate to a more favorable protein-to-calorie ratio for nestling growth (Foster 1978). Exploiting fruits for nestlings may lead to larger clutch sizes if birds experience less constraint in resources available for raising young (Lack 1954, 1968). However the cases of brood reduction observed in this study do suggest that food quality or quantity is inadequate in some cases.

Pair-visiting behavior.—Why do breeding euphonias visit the nest together and follow each other to the nest entrance? The accompaniment behavior exhibited by pairs has been described by others and is common to all euphonias and chlorophonias that have been observed at their nests (Sutton et al. 1950, Skutch 1954, Isler and Isler 1987). Visiting in pairs may reduce the frequency (although not the total duration) of activity at the nest, decreasing the likelihood that predators will be attracted to the nest by the parents. If a predator did observe the birds at the nest, it might be confused by the accompaniment behavior, its eyes following the bird that keeps moving rather than the bird that disappears into the nest. On the other hand, the distinctive behavior of pairs at the nest is certainly easy for humans to learn to recognize. If this behavior serves an antipredator function, it could be effective only against visually oriented diurnal predators.

A possible alternative explanation for the accompaniment behavior is that of mate guarding. Evidence in favor of a mate guarding explanation includes several observations made during this study. On two occasions, a female returning to the nest during incubation was followed by more than one male. In both instances, chasing and emphatic calling between the males ensued after the female entered the nest. In one case, the interaction concluded with bill-to-bill contact in mid air, with the males tumbling to the ground. Sutton et al. (1950) observed several similar encounters at a nest in Mexico. In the absence of resource-based breeding territories, males may have to accompany their mates everywhere and be ready to defend them. However, several facts are inconsistent with mate guarding as the sole explanation for the accompanying behavior. First, males accompany females throughout the nesting cycle, not just during the fertile period. Also, the female accompanies the male to the nest entrance just as regularly as he accompanies her.

Nest predation.—The frequency of nest predation was slightly lower in this study than in comparable studies in the literature. Calculated in the simplest way (no. of successful nests/total nests), the nest success for this study (39%) is higher than values reported by Skutch (33.3%, 1985) for 42 species of open cup nesting birds in the wet tropics, but less than the 60.6% he reports for hole nesting birds of the wet tropics, although the absence of variance estimates prevents statistical tests from being performed. On a per egg basis (no. of successful eggs/total eggs), Skutch reports 29.5% for open cup nesters, while I found 35.5% success. Predation on a per egg basis was comparable to temperate zone birds that build covered nests (Kulesza 1990). The Mayfield estimate of nest predation (0.664) is comparable to open-cup nesters in shrubs in Iowa (Martin 1988a). The daily predation rate during the incubation stage (0.015) is lower than those reported by Martin (1988b) for Arizona nests on the ground (0.027) and in several tree species (0.047–0.081). Thus, the birds in this study may have experienced somewhat less nest predation than would be expected for a tropical or temperate open-cup nester, in spite of nesting in disturbed habitat (Gibb 1991). Although Gibb suggests that the high nest predation often reported from tropical studies may be a consequence of these studies being conducted in human disturbed habitats with altered predator populations, it is possible that roadsides are a relatively safe nesting habitat if the roads themselves cause high predator mortality or sufficient human disturbance to interrupt hunting by predators. Another factor may be elevation. Skutch (1985) has noted lower predation rates at higher elevations, so perhaps the predation experienced by birds at this site is low for the species as a whole.

A large clutch size and a nestling diet of fruit have both been proposed to cause higher rates of nest predation. Skutch (1949) originally proposed that high rates of nest predation might have selected for the typically small clutch sizes of tropical birds. Larger clutch size may lead to increased nest predation for a variety of reasons (Slagsvold 1982). Smaller clutches permit fewer feeding visits by parents, reducing the likelihood of a predator finding the nest by observing parental behavior. Smaller clutches also mean less lost effort when a nest is depredated. In addition, a nestling diet of fruit should lead to higher nest predation if nestlings grow slowly as a result of protein deficiency and take longer to fledge. Morton (1973) described a tradeoff between the advantages of feeding fruit to nestlings (availability, ease of capture) and the greater exposure of nestlings to predators resulting from slower growth and more time spent in the nest.

Paradoxically, Yellow-throated Euphonias in this study did not appear to experience the predicted high rates of nest predation. Yellow-throated Euphonias may have succeeded in ameliorating potentially high levels of nest predation in several ways. First, euphonias build covered nests, and these, in general, are associated with larger clutches and greater nest success (Lack 1968; Ricklefs 1970; Skutch 1976, 1985; Kulesza 1990). Second, they visit the nest infrequently. They feed nestlings by regurgitation, which permits them to deliver relatively more food per visit and, therefore, visit the nest less frequently than if they carried individual food items in the bill (Skutch 1976). Third, both parents visit at the same time, further reducing the frequency of activity near the nest. Fourth, the distinctive accompaniment behavior that the birds exhibit when visiting the nest may confuse or distract potential predators that do see parents visiting the nest. Each of these steps may aid in reducing nest predation. Without knowledge of the sensory capabilities and searching behaviors of predators that destroy these nests, the relative contributions of each step cannot be assessed.

The Yellow-throated Euphonias in this study had a shorter time to fledging than the Thick-billed Euphonias (*E. laniirostris*) studied by Morton (1973), but additional work needs to be done on these species to understand nestling growth rates, nutrition, and the extent of protein limitation. Either Yellow-throated Euphonias are unusually efficient at extracting protein from fruit pulp, or their nestling diet actually has a higher protein content than suggested by the large volume of fruit material and minute volume of animal material in nestling feces. Protein analysis of regurgitate fed to nestlings, as well as work on the digestive capabilities of euphonia nestlings, could answer this question. It is possible that they have low protein requirements as found in oilbird nestlings (Bosque and de Parra 1992).

Yellow-throated Euphonias present an unusual constellation of traits relating to their nesting biology. The basic pattern appears to be shared with the other species of euphonias for which this information is available: White-vented Euphonia (*E. minuta*), Blue-hooded Euphonia (*E. elegantissima*), Spot-crowned Euphonia (*E. imitans*) (Skutch 1954, 1972, based on 3–14 nests per species), and Thick-billed Euphonia (*E. laniirostris*) (Barnard 1954, Morton 1973). However, even the nests of eight species of euphonia remain undescribed (Isler and Isler 1987). Comparative studies of Yellow-throated and other euphonias could further elucidate the tradeoffs between resource availability, clutch size, nest predation, and parental care. Further studies of euphonias would be especially valuable in understanding their adaptations to a frugivorous diet, especially in nestlings.

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