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THE OCHRE-BELLIED FLYCATCHER AND THE EVOLUTION OF LEK BEHAVIOR

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The Ochre-bellied Flycatcher (*Pipromorpha oleaginea*) is an inconspicuous, small forest tyrant-flycatcher, olive green above and ochre-colored below; it lacks the brightly colored crown feathers of many flycatchers. It is, however, of particular interest because of its unusual lek mating system (Skutch 1960). The social organization of McConnell's Flycatcher (*P. macconnelli*) appears to be similar, as is probably also that of the third member of the genus, the Grey-hooded Flycatcher (*P. rufiventris*) (Willis et al. 1978).

While resident from 1957 to 1961 in the Arima Valley of Trinidad, we found 60 occupied nests of Ochre-bellied Flycatchers and we trapped, examined and banded individuals near our house. We also observed the fruit-eating habits of this flycatcher (hereafter, for brevity, referred to as "pipromorpha"), and B.K.S. studied males at their lek perches. The data on breeding and molting seasons have been summarized previously (Snow and Snow 1964). The rest of the data, while not extensive, supplements the information presented by Skutch for Costa Rica. Knowledge of the natural history of this species may throw light on the evolution of lek systems in tropical forest birds.

AGE AND SEX DIFFERENCES

In his revision of the genus *Pipromorpha* Todd (1921) noted that the outer primaries of some individuals were emarginated. He suggested that emargination might be a peculiarity of older birds but stated that it was not related to sex. Our evidence, however, indicates that emargination of the four outer primaries (7th to 10th) is typical of the adult male and that lack of emargination is characteristic of young males before their first wing molt and of females.

From mid-January 1959 to September 1961 each individual trapped was examined for emargination and categorized into "male-type" (emarginate) wing, "female-type" (nonemarginate) wing, or intermediate wing (Table 1). Most of the 55 birds with male-type wings had wing lengths of 64–66 mm, with a peak about 65 mm. The wing lengths of the 52 birds with female-type wings were more varied, presumably due to the presence of young birds in the sample, but were mostly shorter than the male-type wings, with a peak at 60 mm. The 18 birds with intermediate wing emargination had intermediate wing lengths. Four birds when first trapped had female-type wings with lengths of 60–64 mm but when retrapped after the next molt had male-type wings, two of which were now longer. (These birds are not included in Table 1.) There were no other changes of wing type in retrapped birds. Two color-marked males that sang and displayed from their lek perches near the netting area had very distinctly emarginate wings with lengths of 65 and 67 mm. The wing length and emargination of one that was trapped 11 times between June 1958 and August 1961 remained constant.

The wing lengths of pipromorphas trapped elsewhere in Trinidad and sexed by dissection were as follows: 6 females 57–61 mm, average 58.7 mm; 16 males 62–68 mm, average 64.8 (Snow and Snow 1963). Of these 16 males all had male-type wings except for one August juvenile with a female-type wing of 62 mm and another with an intermediate-type wing of 63 mm. Five of the sexed females had a female-type wing and one had an intermediate-type wing.

We were unable to assign any function to the male's emarginate outer primaries. The most conspicuous visual display of males at the lek is alternate wing-raising (see below). We could not detect any sound from this action, but our distance and the high level of insect noise would have made slight sounds inaudible.

Many of the adult male pipromorphas that Skutch (1960) heard singing at leks in Costa Rica had yellow gape flanges, a feature he did not see in adult females. In the Belém area the gape is yellowish in *P. oleaginea* and dark in the sympatric *P. macconnelli* (see T. Lovejoy, *in* Willis et al. 1978). We did not notice yellow gapes in either sex among the birds that we handled or

watched in Trinidad. Geographical variation is quite marked in the species. We have not studied the emargination of the outer primaries in detail, but inspection of museum specimens suggests that it is more pronounced in the Trinidad race (*pallidiventris*) than in other races.

ABUNDANCE

From June 1958 to the end of September 1961 we caught a total of 135 different pipromorphas in mist nets along 400 m of St. Patrick's Stream, a tributary of the Arima River. Of these, 42 were trapped two or more times, giving a total of 210 trappings. Nets were set in secondary forest approximately 25 years old, previously planted with citrus, coffee and nutmeg trees, and still containing some large primary forest trees. Over the same period of time in the same nets the trapping figures for the two other common forest flycatchers of similar size were: Slaty-capped Flycatcher (*Leptopogon superciliaris*), total 20, 9 individuals, 4 of them retrapped at least twice; Euler's Flycatcher (*Empidonax euleri*), total 16, 8 individuals, 4 of them retrapped. All three species frequently fed low in the forest, and the likelihood of capture was probably sufficiently similar for these figures to be a real indication of their relative abundance.

An independent measure of pipromorpha abundance was derived from the number of nests found along sections of forest stream which were regularly searched. Along approximately 720 m of Tripp Stream, a tributary of the Arima River running through primary forest, we found eight nests in the breeding season of 1959, four being the largest number occupied at any one time. In 1960 along the same stream the numbers were five and three respectively. The highest density of nests was recorded along the Jumbie Stream, another tributary of the Arima River running through primary forest, where in 1959 four nests were simultaneously occupied along about 300 m of stream.

That pipromorphas are exceptionally abundant in Trinidad is indicated by comparison of trapping figures from elsewhere: during a trapping program in the Kanuku Mountains of southern Guyana where 100 ft of net were set just inside the forest near a stream, 5 *P. oleaginea* were trapped in 124 h of trapping between 21 January and 21 March 1970 (dry season). In Trinidad between 21 January and 21 March 1959 (also dry season), in 95 h of trapping with 80 ft of net, 25 pipromorphas were trapped, 19 new birds and 6 retraps. Although the numbers seem low in Guyana, the pipromorpha was the fourth most abundant bird trapped.

TABLE 1. Wing lengths of Ochre-bellied Flycatchers with different wing types.

Wing length (mm)	Number with male-type wing	Number with intermediate wing	Number with female-type wing
68	1		
67	1		
66	15		
65	15	2	1
64	13	1	
63	4	4	6
62	2	1	5
61	3	5	7
60		2	13
59		3	7
58			7
57			2
56			2
55			1

Lovejoy's (1974) extensive trapping program at Belém showed *P. oleaginea* as the third to sixth most abundant species, excluding hummingbirds, in the forests sampled. The figures indicate, however, that the density must be considerably lower than in Trinidad. For instance in Trinidad in one year (May 1958 to May 1959) and 11 months (Nov. 1959 to the end of Sept. 1960) 102 pipromorpha individuals were trapped in three or four 20-ft nets set for 742 h. At Belém, taking only Lovejoy's captures at the Station A terra firme and second growth forests as ecologically most like Trinidad, 70 different *P. oleaginea* were trapped in 2,000 ft of nets set in groups, in 726 h over a period of 23 months.

FOOD

Skutch (1960) gave a general account of the pipromorpha's feeding habits in Costa Rica. In addition to insects and small spiders snatched from foliage and twigs, he mentioned that they regularly take fruit, including mistletoe berries and the fruits of *Xanthoxylum, Alchornea* and *Siparuna*. We did not pay special attention to their insect-eating, but our observations confirmed that fruit is an important part of their diet. While we were studying the feeding behavior of tanagers and honeycreepers from January 1960 to September 1961 (Snow and Snow 1971), we extended our records to include all instances of avian fruit-eating. We assigned to each individual bird one feeding record while it took fruit from one plant and a further record if it then flew to another plant, whether of the same or a different

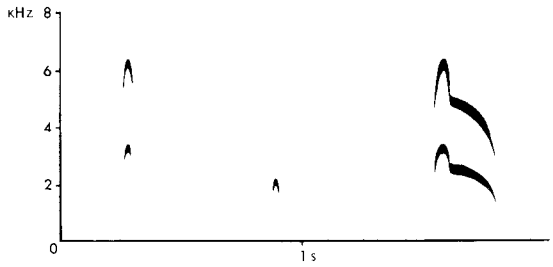

FIGURE 1. Vocalizations of male Ochre-bellied Flycatcher at the lek: the *"chup"* (first note), *"up"* (second note), and *"char"* (third note). The *char* has a moderately strong second harmonic which is not shown. Intervals between the notes are adjusted to fit into the figure (see text). Recorded by D. W. Snow, Arima Valley, Trinidad.

TABLE 2. Breeding and molting seasons of *Pipromorpha oleaginea* in Trinidad.[1]

	Number of clutches started	Percentage of trapped adults in molt
March	2	0
April	7	0
May	18	8
June	22	3
July	9	15
August	2	43
September	1	26
October	—	28

[1] No clutches were started and no adults in molt were trapped between November and February.

species. We recorded 37 instances of pipromorphas taking fruit from the ten trees and shrubs listed below in order of frequency of use: *Alchornea glandulosa* (Euphorbiaceae), *Trema micrantha* (Ulmaceae), *Miconia myriantha* (Melastomaceae), *Clusia* sp. (Guttiferae), *Protium heptaphyllum* (Burseraceae), *Sloanea stipitata* (Tiliaceae), *Sapium aucuparium, Maprounea guianensis, Hieronyma caribaea* (Euphorbiaceae), *Cordia curassavica* (Boraginaceae). Eighty percent of the recorded fruit-eating was between 11 and 50 feet above the ground.

Tanagers dependent on an insect diet were far less plentiful than those that are frugivorous or partly frugivorous. Likewise, the two small manakins, which are mainly frugivorous, were more abundant than any other forest birds of similar size. It seems probable, therefore, that the considerable quantity of fruit in the pipromorpha's diet is one of the reasons why it is more abundant than the other forest flycatchers of comparable size. We recorded no fruit-eating by *Leptopogon superciliaris* or *Empidonax euleri*, whose combined abundance, as shown earlier, was only about one-eighth that of the pipromorpha, if all trapped individuals are counted, or about one-fifth, if only the retrapped (i.e. locally resident) individuals are counted.

BEHAVIOR OF MALES AT THE LEK

Song is the chief form of advertisement employed by male Ochre-bellied Flycatchers. In Trinidad males sing at their leks from the end of March to the first week of August, but some marked individuals did not sing for more than four months, usually April to July inclusive. This is also the main breeding season (Table 2).

The song consists of a continuous *chup, up* repeated about every two seconds, interspersed with occasional louder elements which we transcribed as *char, char* (Fig. 1). The *chup* is delivered with the beak open; the *up*, which follows after an interval of 0.8–0.9 s, is given with the beak closed and is audible only at close range. The *char* may be uttered singly or twice or thrice in succession, typically with intervals of about 0.9–1.0 s. When male A's song was fully monitored for 20 min, on 27 April 1961, there were, on average, 2.7 *char* sequences per minute, of which 17% were single, 70% were double, and 13% were triple. The only other vocalization heard, but not recorded, was a harsh churring uttered by a male when chasing another male out of his lek area.

As recorded by Skutch, pipromorphas have a habit of flicking first one wing and then the other above the back. When the left wing is raised the bird pivots to the right, and vice versa. Males at their leks regularly flick their wings, but so also do birds, including females, engaged in other activities.

Six males sang along 800 m of St. Patrick's Stream, the same area of old secondary forest where the trapping took place. The lek areas of these birds were within 10 to 200 m of the stream in thick vegetation, especially tangles of vines. One group of three, two of which were color-banded, were mutually audible to each other, as were two other males 800 m away. In between was a solitary male out of earshot of the others. Persistent observations were made on only one marked male, male A, one of the group of three. In 1960 and 1961 he occupied, and mainly sang within, an area of approximately 15 × 15 m on top of a small knoll about 30 m from the stream. The vegetation was

dense in this area and included a tangle of vines. When he was alone in his lek area he usually sang at a height of 2–3 m, spending one to three minutes at a perch before flitting to another perch a few feet away. Often when he moved he caught a resting insect from the back of a leaf or, occasionally, an airborne insect. Periodically he increased the tempo of his song and the number of *char* elements when he came down to a very low perch 0.3–1.0 m above ground in a dense vine tangle. Here, perched with the breast lowered, he made frequent wing-flicks. Twice he descended to the low perch on the arrival of a conspecific in the lek area. Other times he did so when we saw no other bird, but spotting such inconspicuous birds in dense vegetation is extremely difficult. Once he was watched for nearly a minute hovering and fluttering 0.6–1.0 m above the ground in dense cover in the vicinity of his low perch. Possibly this was a courtship display, but no other bird was seen. Willis et al. (1978) mentioned that *P. macconnelli* also has a hovering display.

During watches on male A between 07:00 and 09:00 h, totalling 7.5 h, he was present and singing for 66–96% of the time, with an overall attendance of 84%. His absences were usually of two or three minutes duration unless he was chasing other pipromorphas from the lek area, when his absences were longer. Skutch (1960) noted that in Costa Rica male pipromorphas sing throughout the day, which was also our impression although we did not confirm it by day-long observation.

During any one watch it was usual for male A to fly off in the same direction for each absence. It was not possible to follow him to where he fed, but once just before departing, he was seen spitting out the seed of *Doliocarpus dentatus*, a vine known to be fruiting in the direction in which he left.

In 1961 the second half of April and most of May were exceptionally dry and all six of the pipromorphas along St. Patrick's Stream stopped singing from 15 to 23 May; neither was any singing heard in the surrounding forest during this week. The drought broke on 22 May and singing resumed on the 24th. Breeding activities of the White-bearded (Black and White) Manakin (*Manacus manacus*) also decreased during the dry spell. A study of this species (Snow 1962) showed marked correlations between lack of fruit and decrease in lek and breeding activity; a decrease in fruit abundance resulting from the drought may have caused the pipromorphas to desert their leks.

BREEDING

THE NEST

By regular searches along streams in the Arima Valley we found many nests (65% of the total), either while they were being built or when building was finished but no eggs had been laid. The pendent nest, described in detail by Skutch (1960), is a pear-shaped mass of moss inside which is the nest chamber with a porched side entrance. It is suspended from a dangling root or vine not far above the ground or water. Of the 60 nests with contents which we found, 50 were beside streams and half of these dangled over the water, 15–244 cm above it, with an average height above water of 82 cm. The others were hanging from steep banks carved by the water. The ten nests not beside streams were either attached beneath the overhangs of steep roadside banks or to the small cliffs of dry gullies, except for two which hung over shafts, one a mine shaft and one the natural shaft of a cave system.

The time taken to build a nest varies greatly. A nest started at the beginning of March at a site used the previous year was not completed until the end of April; another started at the beginning of April took 25 days to complete. Two nests started in May took 13 and 14 days to build. One, found as a pear-shaped loop of moss (an early stage of building) in the third week of June, contained the first egg six days later. This reduction in building time as the season advances has been noted by Skutch (1960) in other flycatchers. The interval between nest completion and the laying of the first egg is also reduced as the season advances. Thus six nests with eggs laid in April and May remained empty for an average of 11.8 days (range 5–22 days), while nine nests with eggs laid in June and July remained empty for an average of 3.8 days (range 2–7 days).

THE CLUTCH

Our observations on egg-laying agree with Skutch's (1960), who found that eggs are laid on alternate days. Of 32 clutches from nests found at the building or egg stage, 26 had three eggs, three had two eggs, two had four eggs and one had five eggs. The apparent clutch of five may have been laid by more than one female, because nine days after the first egg was laid the nest was found on the ground with five eggs in it, three of them slightly developed and two completely fresh. Genuine clutches of five

TABLE 3. Calculation of nesting success of Ochre-bellied Flycatchers in Trinidad by the method of Mayfield (1961).

Period	Exposure days	Number of nests	Number surviving	Survival rate per day	Overall survival rate
Laying	130	39	28	0.9154	0.7022
Incubation	391	36	13	0.9412	0.2976
Fledging	181	14	9	0.9724	0.6042

eggs may, however, be laid, for we found a nest containing five small young all of about the same size which were subsequently reared. Omitting the doubtful clutch of five, the mean size of 31 clutches was 2.97. Our figures suggest that clutches may be slightly larger in Trinidad than in Costa Rica as Skutch found no clutch of more than three eggs.

BREEDING SUCCESS

In order to calculate nest success we used only nests found during building or when the first egg of the clutch had been laid. We followed every nest until it either succeeded or failed, except for a few periods when we were away from the area. Nests from which the young would have fledged while we were away are omitted from consideration, whatever their state at the time when last seen. Using these criteria, which eliminate most sources of observer bias, we have 33 nests available for the analysis of success. Of these, 11 (33%) failed during laying, 17 (52%) failed during incubation (including 3 nests with infertile eggs incubated for the full period), one (3%) failed during fledging, and 4 (12%) survived. From the 33 nests 8 young fledged, giving a success rate of 0.23 young per nesting attempt.

We have also analyzed nesting success using the Mayfield (1961) method, which allows us to use 48 nests. As pipromorphas lay on alternate days, we have taken four days as the egg-laying period for a three-egg clutch, and have considered the day when the last egg was laid to be the first day of incubation. We have taken the incubation period to be 20 days and the fledging period 18 days (Skutch 1960). Results are in Table 3. The total survival rate over the nesting period is calculated by multiplying the survival rates for the three periods: $0.702 \times 0.298 \times 0.604 = 0.126$. This is very close to the 12.1% survival rate calculated by our first method.

A similarly high rate of loss was found in other small forest birds in the same area. In the White-bearded Manakin only 19% of 227 nests produced fledglings, each nesting attempt producing on average 0.33 young (Snow 1962). In the Hairy Hermit hummingbird (*Glaucis hirsuta*) 17% of 185 nests produced fledglings, each nesting attempt producing on average 0.28 young (Snow and Snow 1973).

The causes of failure of the 29 unsuccessful nests were as follows: predation, 10 (nest intact or only slightly disarranged, eggs gone); eggs infertile, 3 (eggs were considered infertile if they were incubated to full term but did not hatch); eggs or young lost due to collapse or flooding of the nest, 4; eggs deserted, 3; eggs in or below nest, cracked or intact, 9.

All failures in the last category occurred either during laying or near the beginning of incubation. Egg predators were not responsible, as the egg contents were not eaten. Usually the nests were slightly disarranged, as if the material was being taken by other birds. Female pipromorphas were seen on two occasions dismantling one nest to build another elsewhere, and once one was seen taking material from the nest of a Yellow-olive Flycatcher (*Tolmomyias sulphurescens*). Thus, we think it likely that failures in the last category were mostly caused by interference by conspecifics.

The incidence of infertility (as defined above) was rather high. We have records from 13 nests which were under observation during the hatching period and were not preyed upon in this period (six of these have not been used in the breeding success analysis either because they were found after the clutch was complete or because the final outcome was not known). Thirty-six eggs were laid in these nests, from which 26 young (72%) hatched and survived to at least six days old. The 10 eggs that failed to hatch were from five nests, three with total infertility and two with partial infertility.

We know of no data adequate for a comparison of the nesting success of *P. oleaginea* in Trinidad and on the continent. Nine nests of the closely related *P. macconnelli* (Willis et al. 1978), found in forest near Belém and Manaus, were considerably more successful, with a survival rate of 55% calculated by the method of Mayfield (1961). Our data for 48 nests, analyzed by Mayfield's method, gave a survival rate of 12.6%. For the Wood Pigeon (*Columba palumbus*), Murton (1965) showed that the proportion of nests preyed on increases with increasing nest density. If the same is true for the pipromorpha, the high rate of nest predation

may be attributable to the high population density.

Three of the five nests of *Leptopogon superciliaris* found in the pipromorpha study area were successful. These pendent nests, hung a few feet from the ground under overhanging dry banks, were all found while being built. They were beside the same streams as the pipromorpha nests and thus likely to be subject to similar predation pressures, but not to interference from conspecifics as none were found close together.

REPLACEMENT NESTS

Although we did not watch pipromorphas at the nest it seems safe to assume that when a nest was repaired and re-used, or when a new nest was built a few yards away from an old one that had recently been used, it usually indicated another breeding attempt by the same female. In two cases the first egg of the presumed replacement clutch was laid 8–10 days after the failure of the previous attempt. The clutches of these females were laid, respectively, in May and June, and June and July. In another case, also following a failure, where the old nest was repaired and re-used, the interval was 18–19 days (clutches laid in June and July). At a site that was used three times in the same breeding season, a clutch of probably infertile eggs, abandoned in early July, was replaced by another 24–26 days later. The second nest was plundered when it contained young. The third nest almost certainly belonged to another female, as the first egg was laid in it only three days after the nest with young was torn down. This observation suggested, as did the losses apparently caused by conspecific interference, that there was a shortage of preferred nest-sites overhanging streams.

DISCUSSION

Keast (1972) has shown that the Tyrannidae have radiated into many different feeding niches and have evolved different bills and proportions of wing and tarsus to fit these niches. His comparisons indicate that the pipromorpha is intermediate and unspecialized in its proportions. In its reproductive behavior, however, this species has diverged from the usually monogamous tyrannid pattern towards the polygamous lek mating systems of many manakins and cotingas. Striking sexual dimorphism in plumage is usual in lek birds, or if there is no sexual dimorphism males may have loud advertising calls, as in *Lipaugus* and *Perissocephalus* (Snow 1961, 1972). The lack of both sexual dimorphism and loud advertising calls in the pipromorpha, and the fact that it is a fairly unspecialized member of a family in which monogamy is the rule, suggest that its lek behavior may be a relatively recent development, or possibly a primitive holdover of a successful early stage in the evolution of lek behavior. It is therefore interesting to see whether the pipromorpha shows any ecological or behavioral characteristics that may have favored the evolution of a lek system.

We tentatively suggest that feeding habits and nest type may both have played a part. Our observations agree with Skutch's (1960), indicating that fruit is an important part of the pipromorpha's diet. Apparently it is more frugivorous than other forest flycatchers of its size, and we have suggested that this may account for the fact that it is the most abundant of the smaller forest flycatchers in Trinidad and elsewhere. Frugivory is one of the factors favoring the evolution of lek behavior in altricial birds (Snow 1971), as it allows adult birds to feed themselves in a small fraction of the daylight hours. This in turn enables females to tend a nest alone, and males to devote most of their time to competing with other males for mates.

Emancipation of the male from the nest also depends, however, on the kind of nest that is built and on other aspects of a bird's breeding behavior. For example, lek behavior has not developed in hole-nesting birds, in which both parents are needed to defend the nest-hole against usurpers, nor has it developed in pigeons, in which both secrete crop milk to the young. In addition to the pipromorpha, Skutch (1960) reported four genera of tyrant-flycatchers in which there is apparently no pair formation, and males never go near the nest: *Myiobius, Terenotriccus, Oncostoma* and *Rhynchocyclus*. In *Oncostoma* solitary males restrict themselves to isolated display areas where they advertise themselves with a harsh song. In all of these genera the nest is a hanging roofed structure. The Helmeted Pygmy-Tyrant (*Colopteryx galeatus*), a forest flycatcher of Amazonia and Guiana, should probably be added to this group; males call persistently in isolated display areas, and the nest is a roofed structure attached to the underside of a palm frond (pers. observ.). Little is known of the feeding ecology of these flycatcher genera, but they appear to be entirely or mainly insectivorous. The combination of factors that has led to their present social organization is

therefore unknown, but it is a reasonable hypothesis that, in them as in the pipromorpha, a roofed nest in which the young can remain dry while the female forages may have been an essential prerequisite for the emancipation of the male from the nest.

The method of bringing food to the nest may also be important. Female manakins (Snow 1962, Skutch 1969) and female bellbirds (Snow 1970) carry fruit to the nest in the throat or stomach and regurgitate it for their young. Female pipromorphas also feed their young by regurgitation, and as far as known are the only tyrant-flycatchers to do so (Skutch 1960). Female manakins, bellbirds and pipromorphas bring food to the nestlings at relatively long intervals, presumably because a large amount of food can be brought at each visit. These facts suggest that the female's ability to regurgitate food for nestlings may be one of the factors involved in male "emancipation."

It seems unlikely that the male would become emancipated from the nest if family size were limited by the amount of food that could be supplied to the young. We suggest that the type of nest is often the limiting factor (Snow 1970, 1976). Especially in the case of pendent nests the materials and the method of attachment and construction may limit the weight of young birds that can safely be contained. The pipromorpha's solid nest can hold up to five young, while the smaller and flimsier roofed nests of the other genera mentioned above may not be able to hold more than the two young that apparently constitute their normal family (Skutch 1960).

SUMMARY

Ochre-bellied Flycatchers (*Pipromorpha oleaginea*) were studied in Trinidad over a four-year period, 1957–1961. Sixty occupied nests were found, and 135 individuals were examined. The sexes were distinguished by wing-length and degree of emargination of the outer primaries. This species is the most abundant forest flycatcher in Trinidad, and its abundance is tentatively attributed to the fact that it is to a large extent frugivorous. Males sing and display within a loosely defined lek area, in which individuals are usually within earshot but not visual range of one another. Breeding success in the study area was very low (12% of nests started), failures being attributed to predation and also to interference from conspecifics. This species appears to illustrate an early stage in the evolution of lek behavior. Important predisposing factors for this habit include frugivory, nest type, and probably also the female's ability to regurgitate relatively large amounts of food for the young at each visit to the nest.

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