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ON BEHAVIOR AND NESTING OF McCONNELL'S FLYCATCHER (*PIPROMORPHA MACCONNELLI*): DOES FEMALE REJECTION LEAD TO MALE PROMISCUITY?

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ABSTRACT.—Near Manaus, Brazil, McConnell's Flycatcher (*Pipromorpha macconnelli*), a small Amazonian tyrant-flycatcher very like the sympatric Ochre-bellied Flycatcher (*P. oleaginea*), tends to be a bird of forest and *oleaginea* a bird of second-growth. Calls of male *macconnelli* at singing areas near forest creeks are more like those of the southern Brazilian *P. rufiventris* than calls of *oleaginea*; in contrast to both, *macconnelli* displays close to the ground. Nests of *macconnelli* are oven-shaped and hang over forest creeks. Three small white eggs are laid on alternate days. Incubation and nestling periods are about 19 days each. Incubation and brooding constancy are low, and young grow very slowly. There is considerable brood reduction or loss of nestlings (one out of every three), although loss of nests is only 1.4% per day (45% loss in 43 days). One case of brood reduction was associated with rainy weather, but the species is nesting January–March, at the height of the rainy season. Possibly females care for nests alone because males would raise predation or lower uncertain food supplies near nests, especially in rainy or difficult periods. Promiscuity of males in this and other lek species may thus arise because of female rejection of male help, not because of male dominance of good sites as in polygamous species. *Received 22 June 1976, accepted 10 April 1977.*

McCONNELL'S Flycatcher (*Pipromorpha macconnelli*, Tyrannidae) is a sibling Amazonian relative of the widely-distributed neotropical Ochre-bellied Flycatcher (*P. oleaginea*). Small greenish birds with ochraceous underparts, they differ mainly in the presence of faint buffy wing edges in Ochre-bellied Flycatchers. T. Lovejoy (pers. comm.) has found that the gape is darkish in *macconnelli* and yellowish in *oleaginea*. Chubb (1919) originally described *macconnelli* from Guyana as a subspecies of *oleaginea*, and not until Todd (1921) was it realized that the two species are widely sympatric in northeastern Amazonia and from eastern Perú south to eastern Bolivia (range of *macconnelli* courtesy of J. Haffer).

The behavior of Ochre-bellied Flycatchers involves vocal and wing-flashing displays by semi-isolated males, while females alone care for eggs and young in distant ball-shaped nests pendent on vines between tree buttresses or over water (Skutch 1960:561–570). In 1973–74, we studied McConnell's Flycatcher during research on other species at Reserva Ducke, near Manaus, Brazil. Here we report on its behavior, and suggest a possible route of evolution for lek behavior in it and related tyranniform birds.

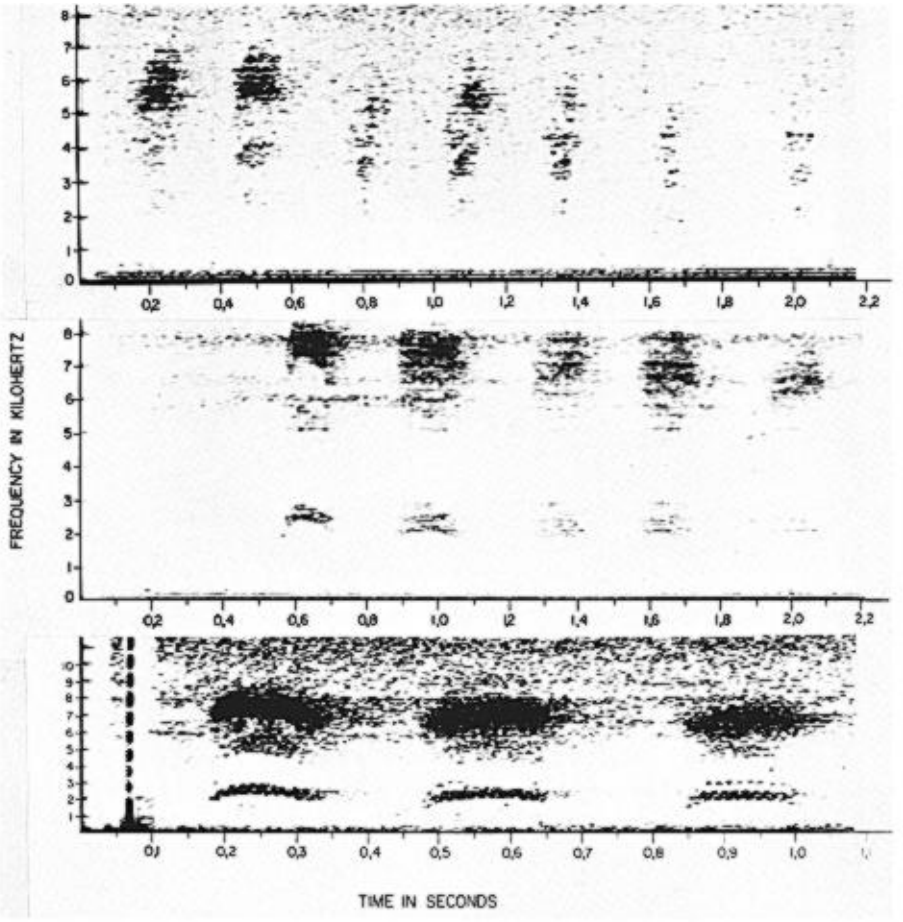

Fig. 1. Sonograms of "thrush-like" calls of Pipromorphas. *Above*: *Pipromorpha rufiventris* at Fazenda Barreiro Rico, Anhembí, São Paulo state; *Center*: *P. macconnelli* at Reserva Ducke; *Below*: first three notes of same series of calls of *macconnelli*.

SPECIES DIFFERENCES

Habitat.—Near Reserva Ducke, *macconnelli* is fairly common in forest and forest plantations while *oleaginea* is confined to second-growth, forest edge, and orchards. We have only one record for *oleaginea* in the Reserva itself, from a low woodlot at the entrance, but it displays commonly (at least October to January) in an orchard of marí (*Poraqueiba sericea*, Icacinaceae) trees in second-growth at Km 25 of the Manaus-Itacoatiara highway, only 1 km W of the Reserva entrance. It is fairly common in second-growth and patchy woodlands on the outskirts of Manaus, where we did not find *macconnelli*.

In and near the forest reserves (Área de Pesquisas Ecológicas do Guamá) of the Instituto de Pesquisa Agropecuária do Norte (IPEAN) at Belém, Pará, we and others (Pinto 1953, Oniki 1972, T. Lovejoy, pers. comm.) have found both species in interdigitating forest, second-growth, and tidally flooded forest (várzea), but *macconnelli* is becoming uncommon with the decrease in area of upland forests. There, as in Central America, *oleaginea* is most abundant in second growth or at forest edges, but occurs inside forest as well.

Fig. 2. Nests of McConnell's Flycatcher at Reserva Ducke. *Left*: distant view of a nest that was unsuccessful; *Right*: another nest with two young nearly ready to fly.

In southeastern Brazil, *P. oleaginea* is restricted to the eastern tropical-forested lowlands, and is replaced by a plain-winged and gray-headed species, *Pipromorpha rufiventris*, in forests and woodlands from southern Espirito Santo across to northern Argentina and Paraguay.

Foraging.—At Reserva Ducke and Belém, *P. macconnelli* regularly follows the interspecific flocks of small insectivores of the forest interior. It forages distant from forest creeks or near them, without obvious microhabitat restrictions. Foraging 1–25 m up, it peers with slow but exaggerated sweeps of the lowered head and sallies short distances to foliage for small insects or fruit. Periodically it flashes out one wing or the other. Both *P. oleaginea* and *P. rufiventris* have similar behavior, but less often follow mixed flocks and seldom forage over 10 m above the ground.

Display.—Only presumed male *Pipromorpha* on display grounds are noisy. Skutch (1960) and Slud (1964) describe the display of *P. oleaginea*, which sounds to us the same at Manaus as in Panamá or British Honduras: a variable series of spaced chirps and twitters alternating with measured series of several rapid "choo" or "pitchoo" sneezes. The singer is usually 2–6 m up on a slender horizontal perch, flashing one wing or the other alternately or repeatedly, and looking about with crest raised. *Pipromorpha rufiventris* sits stolidly and sings a slow antbird-like (Bertoni 1901 compares it to songs of *Thamnophilus*) or nuthatch-like tinny series of "rin rin rin rin rin rin rin" notes with long pauses between, from perches 2–6 m up, and gives descending series of rough thrush-like (*Turdus*-like) "wiib" notes now and then (Fig. 1, above).

P. macconnelli, however, sings and displays near the ground, often near the base of a buttressed tree, giving series of rough thrush-like "wiib" notes (Fig. 1) varied now and then with an odd and rapid nuthatch-like "rin-tin-tin-tin-tin-tin-tin-tin-tin-tin." At times the thrush-like notes and nuthatch-like ones are given from a perch 1–2 m up, or while foraging with a bird flock near the display grounds, but displays with fluttering and dancing were near the ground. The voice is not at all like *P. oleaginea*, and somewhat resembles *P. rufiventris*. Compared with *macconnelli*, the thrush-like notes of *rufiventris* are slightly shorter, lower in overtone (above) but not fundamental (below) pitches, descend more between notes, and are uttered at up to 3.5 notes/sec rather than 3 notes/sec (Fig. 1; the quavering fundamentals, between 2 and 3 kHz, are almost lost in the faint recording of *rufiventris*). In view of the unmarked wings of *P. macconnelli* and *P. rufiventris*, the two may be closely related.

Displays of *macconnelli* involve fluttering short flights and hovering, and at times involved two birds. We did not observe displays closely, as the birds disappeared for other places just out of sight when we tried to get unobstructed views. General locations of displays were much the same from day to day, zones up to 50 m across in slight swales on gentle slopes near forest creeks. Sites of different callers are separated by 50–100 m or more, but at times group loosely. Such a lek follows a creek on the Reserva boundary some 500 m south of Km 26.2, and is thus only about a kilometer from the loose *P. oleaginea* lek in the marí orchard at Km 25.

NESTING

At Manaus, we found eight occupied nests of *macconnelli* over forest creeks, and saw many other abandoned nests in similar locations. Occupied nests were commonly 100–200 m apart along the creeks, as were unoccupied nests in a census taken by Wechsler along other creeks on 4 March 1974.

Nests were leafy or strand (rhizomorph) balls with side entrances, pendent on vines or at the tips of twigs 1.0–1.5 m above pools or other wide stretches of water. The nests differed greatly in material and appearance, but as far as we could tell from brief views of adults none were of *oleaginea*. Moss, common in nests of *oleaginea* in Central America (Skutch 1960), was generally absent. A short entrance tunnel inclines up to a central nest cup of soft material, so that only when young became large and the lip of the cup worn down were contents visible through the entrance (Fig. 2). A nest pictured by Pinto (1953, plate 13) seems to have the entrance torn open. Skutch (1960) pictures the rather similar nest of *P. oleaginea*.

Three eggs were laid 2 January, 4 January, and 6 January 1974 in our first nest, discovered by Wechsler. The last nest was one that young left 21 February and that had a second egg of a late brood 12 March and a third egg 14 March. Skutch (1960) found *P. oleaginea* laying eggs 2 days apart. All eight nests, plus the second brood of the last nest, had either three eggs or young. Eggs were white, thin-shelled, and pointed at the small ends. Three in the first nest measured 13 or 13.5 mm × 19 mm, and weighed 1.6–1.8 g each.

The adult flushed off a nest only once in six visits before clutch completion. Usually eggs are cold, and the fact that young of a brood hatch at most a day apart suggests that there is normally little incubation before clutch completion. The adult flushed on 55 of 85 visits to nests with three eggs, suggesting incubation constancy of 65%. Skutch (1960) found similarly low constancy for several small tyrannids. At one

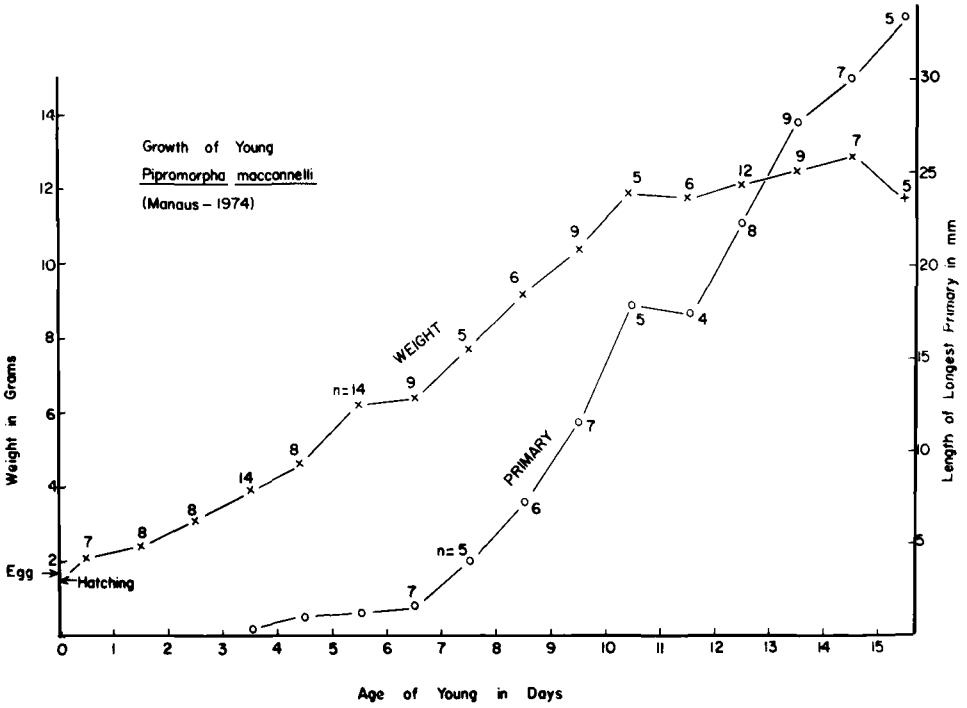

Fig. 3. Growth of young McConnell's Flycatchers, in weight and in length of fifth primary.

nest, an adult flushed on all 15 visits, suggesting the possibility of aid by the male (Pinto, 1953, reports one male of *oleaginea* collected "incubating"; direct observations are needed, however, since no male tyrannid is known to incubate). Ordinarily the adult flushes when the observer is a few meters away, stops briefly 10–15 m from the nest and looks back, then flees silently. There is no attempt to protect the nest. Incubation (from last egg to last young) was about 19 days in two cases.

In the 30 visits we made during the first 6 days of nestling life at 5 nests, adults flushed only 8 times; thereafter the adult was rarely on the nest when we passed.

Very slow growth of young is characteristic of this species, the weight gain from 1.5 g at hatching to 12–13 g taking 10 days (Fig. 3). R. Ricklefs (pers. comm.) fitted a logistic growth equation to the data in Fig. 3 with the following results: asymptote, 14.5 g; growth rate (k) = 0.288; t_{10-90} = 15.3 days; age at the inflection point = 7.5 days. Ricklefs (1976) found tropical flycatchers have rates of 0.28–0.46, so *P. macconnelli* growth is slow for the family. Small young have pink skins, gray down, and whitish bills with dark tips. The claws cling unusually well to the nest lining within a day or two of hatching; the adaptation probably prevents falling from shallow nests on mobile vines over water. Young squeak when removed only during the first few days. Growth of the fifth primary is shown in Fig. 3. The tips of dorsal feathers are beginning to open 10 days or so after hatching; buff tips open on the ventral feathers 2 days earlier. By 2 weeks in the nest the young are well-feathered, and have yellowish gapes and black bill tips; thereafter they were not examined, to avoid premature departure. They look out from the nest entrance, but are visible only from opposite or somewhat below it. Fledging was at 17 (flushed; flew well), 18 (once), 19 (once), or 20 (three times) days after hatching of the last young.

Only 2 nests had 3 young until nest-leaving; 2 other broods of 3 were reduced to 2 and 1 of 3 was reduced to 1; in 1 nest 2 young hatched and 1 survived; in another nest 1 young hatched but the nest was later robbed; and 2 young died on hatching day in the second brood of the final nest of the study, leaving 1 egg unhatched. One nest with 3 eggs was torn open and robbed. The case of brood reduction from three to one was associated with 2 days of almost constant rain, suggesting starvation or cooling; it occurred in the nest with possible help by the male. Therefore, 12 of 18 eggs in successful nests produced young that survived to fledging. Six of 9 nests produced 1 or more fledglings. Loss of nests (method of Mayfield 1975) was 1.4% per day, or nest success of about 55% for 43 days from first egg to last young.

DISCUSSION

A pattern in which one species is geographically widespread and at forest edges or in second-growth, while another is in forest in Amazonia, occurs also in *Piaya cayana* and *P. melanogaster*. Presumably this type of separation by habitat is necessary when foraging niches are very close, as is the case with *Pipromorpha oleaginea* and *P. macconnelli*. Origins of *P. macconnelli* remain obscure; possibly it originated from *P. rufiventris* or the reverse, and it may have converged on *P. oleaginea* in color for habitat reasons or for competitive mimicry (Cody 1969).

This study of *Pipromorpha macconnelli* raises anew the perennial question: why do females care for nests alone and males display on leks in some tyranniform birds (including most manakins and some cotingas) but not others? Fruit use is often correlated with loss of male care of young. The suggestion is often that local superabundances of fruit or other resources allow "supermales" to exclude young males from good sites and turn to polygamous spreading of their genes among the local females, who have little choice but to accept. This theory seems to apply in many cases of polygamy (Verner 1964), but does not apply to most lek or promiscuous species: the females often do not nest or feed anywhere near a lek, and hence cannot be restricted in their choice of males by any male dominance of good areas. Snow (1963) suggested instead that female manakins need not have male help because they eat easily located fruit; but if food is abundant for females, the male could stay and help a female raise more young. Snow does not suggest how or why females keep males from helping, thus accepting the general attitude that such females are deserted by selfish males.

Smith (1968) indicated that females can control matters rather than males: a female may keep out the male if he uses too much of a poor, undependable, or localized food supply and cannot help enough to rear young. In several small neotropical forest flycatchers, the vine-tangled habitats used are small areas and might not support a male together with a female and offspring. Males would be especially dispensable if an increased rate of territorial or other activity near the nest led to high predation that counterbalanced the increased number of young that males could feed.

In the case of *P. macconnelli*, nesting is confined to linear creeks. Male attendance at nests might force each nesting female to have a longer territory, since males consume food too. If food is easily found but slowly renewed, as is perhaps the case for fruit, the female might raise more young by excluding or avoiding the male and feeding young slowly herself. There were several cases of brood reduction—once in rainy weather—suggesting limited or unpredictable food for young. The genus is in a habitat, the forest interior, that is extreme for the family Tyrannidae. Nesting in the

rainy season probably is necessary because of high creek levels for sustained protection of nests, or because food supplies are higher on the average, but occasional long rains must cause problems with foraging. Under these circumstances, local reduction of fruit supplies by the male might force the female to eat insects she could otherwise give to the young.

Safe nests probably help females to do rather well alone, by permitting slow feeding rates and growth. The average clutch size in *macconnelli* (3.0) was the highest Oniki found at Reserva Ducke, except in *Odontophorus gujanensis* (with precocial young) and *Crotophaga ani* (with communally fed young). Thus, it seems possible that female pipromorphas actively exclude or avoid males, which then use peripheral areas and sing for females, because females can normally raise larger broods without male help than with them. Insectivorous males could offset what they eat by finding hidden insects for young, but frugivorous or partly frugivorous males might often reduce local food supplies unduly.

Female dominance of males is known to be associated with female care of nests alone in *Dendrocincla fuliginosa* (Willis 1972), a species in which food supplies are undependable because it is low in interspecific peck orders. Females divorce males quickly and leave them feeding young in *Pithys albifrons*, another species with undependable food supplies because it is low in the interspecific peck order (Willis MS). These transitional situations differ from that suggested for *P. macconnelli* mainly in the reason postulated for occasionally low food supplies. In Charadriiformes (Graul 1974) and probably others, such as Tinamiformes, females leave the males caring for nests alone in similar cases of low or uncertain food supplies. This degree of female success was perhaps not attainable for females in other families, in which males never incubate eggs: Tetraonidae (with precocial young), Trochilidae (with safe nests and nectar for food), and neotropical tyranniform birds. Presumably the best road open for these females to produce more young was to expel or avoid males and care for nests alone.

Once females of a group or species start expelling or avoiding males, the males are likely to start displaying and competing for females. Group displays of males can easily evolve, because certain sites are better located and more dependable over time for females than others, leading to various types of leks. Lek formation thus is one way to separate foraging areas of males and females, and can reduce intraspecific competition in birds for which reproductive rates are not lowered too.

Lill (1974) suggests that heavy nest predation leads to small nests, which hold only small and easily-fed broods, and that chauvinistic males leave females and start leks because they are no longer needed. It is true that some lek-forming birds do have small nests, but so do doves and potoos in which males help. It seems more likely that low clutch size permits a small nest than that small nests force low clutch sizes. Moreover, McConnell's Flycatchers and some other lek-forming tyrannids have large nests, large clutches, and high nest success. Even manakins should be able to put a third young in a barely larger nest were it possible for the male to stay and help feed the young. The idea of food superabundance for fruit-eating birds comes mainly from watching males and other birds that are more free to move about in periods of food shortage than are birds feeding young. Reports on studies of growth and losses of young manakins are needed to see if starvation occurs occasionally.

To understand the evolution of lek behavior, we think that future workers should look also at species less showy and evolved than manakins, grouse, and ruffs. Further studies of McConnell's Flycatcher should be relatively easy, for its nests are

easily found along creeks; these studies could show if females dominate males and exclude them from nest areas. If so, the generic name *Pipromorpha* ("of the form of *Pipra*," type genus of the manakins or Pipridae) could prove prophetic of the route of evolution of behavior in the lek-forming tyranniform birds.

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